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# *Moraxella, Acinetobacter,* and the *Mimeae*

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## INTRODUCTION

The literature about *Moraxella, Acinetobacter, and the Mimeae* is very extensive and, at least to the uninitiated, highly confusing. The same organisms have been known under a variety of names, and different organisms often have received the same label. In many of the papers the organisms which are being dealt with are very poorly identified, and their identity is uncertain. It is the purpose of this review to survey the literature on these organisms, in particular the organisms now considered to belong to the genera *Moraxella* and *Acinetobacter*, and to try to dispel some of the confusion. Main emphasis will be on taxonomy, nomenclature, and on the relationship of these organisms between themselves and to certain other taxa, such as the "true" and "false" neisseriae (i.e., *Neisseria* and *Branhamella* according to the proposal of Catlin [110]). The role of these organisms in human and veterinary medicine, both as commensals and as pathogens, will also be discussed.

## HISTORICAL SURVEY

In 1896 Morax (387) reported the isolation of a gram-negative diplobacillus, which he considered as the cause of a, apparently very common, subacute angular conjunctivitis in man. Axenfeld (18, 19) made the same discovery, independently of Morax, only a short time later. The organisms depended upon the presence of serum or other biological fluid in the media for growth and liquefied heat-coagulated serum. In the following years numerous reports confirmed these discoveries and showed that the organism and the disease that it was believed to cause were of world-wide distribution.

In 1899 and 1900 Petit (426, 427) reported the isolation from cases of corneal ulcers of a diplobacillus, "*diplobacille liquefiant*," which resembled the Morax-Axenfeld diplobacillus, but differed from it in growing in media without serum and in liquefying gelatin. This organism was believed by some authors to be a variety of the Morax-Axenfeld diplobacillus, whereas others believed it to be a separate species.

In 1916 Scarlett (490) described two new kinds of diplobacillus that were isolated from corneal ulcers. One of these resembled the diplobacilli of Morax and Petit, but failed to liquefy serum or gelatin. For this reason Scarlett called it *bacillus duplex non liquefaciens*. The second kind was named *diplobacillus Josefi*, because it had been isolated from a patient

named Joseph; it resembled the other diplobacilli morphologically, but was gram-positive. The latter organism has never been isolated again, the original culture does not exist, and the description is insufficient to recognize it. The name is, therefore, to be considered as a nomen dubium.

Oliver and Wherry (404) in 1921 were the next authors to mention the nonliquefying organism of Scarlett. They found it "not infrequently" in the sputum in cases of bronchitis. They modified the name to *Bacillus duplex-nonliquefaciens*. Then the species appears to have been forgotten for three decades.

In 1923 Jones and Little (285) described a diplobacillus isolated from infectious keratoconjunctivitis in cattle. It was able to grow on plain media, hemolyzed blood agar, and liquefied gelatin and serum.

Flamm in 1956 (163) described a strain isolated from meningitis and named *Moraxella saccharolytica*. This strain has recently been shown by Lautrop (324) to be identical with *Flavobacterium meningosepticum* King 1959, and thus does not belong to *Moraxella*.

In 1957 (175) he described another strain, isolated from spinal fluid, which he named *Moraxella polymorpha*. This strain was later studied by Bøvre and Henriksen (69) and was found to belong to the same species as a group of strains studied by them. For reasons to be given later they found the name *M. polymorpha* unsuitable and proposed a new name, *M. phenylpyrouvica*, based on the production of phenylalanine deaminase. This new name has been conserved by the Judicial Commission (JC) of the International Committee on Systematic Bacteriology (ICSB) (292).

Bøvre studied a collection of strains believed to represent Scarlett's species, now known as *Moraxella nonliquefaciens* (53), and found that it could be divided into three groups, one of which later became the species *M. phenylpyrouvica*. Another group which could be separated from *M. nonliquefaciens* was named *M. osloensis* by Bøvre and Henriksen (68). Later the same authors (244) described still another species, *M. kingii*, which produced acid from certain sugars and hemolyzed blood agar.

Lautrop, Bøvre, and Frederiksen (325) studied a number of *Moraxella*-like strains, mostly isolated from the genitourinary tract. They did not formally name this new species, but suggested that, if its relationship to *Moraxella* were confirmed, *M. urethralis* would be a suitable name.

Pande and Sekariah (411) in 1960 published a preliminary report on the isolation of a new species, *Moraxella caprae*, from eye infections in goats. Nothing more seems to have been published about this species, and an attempt to obtain a culture failed. The existence of this species, therefore, remains to be confirmed.

Recently van Bijsterveld (43) described a strain isolated from an infected eye, which he considered a new species, but did not name. Finally Sutton et al. (526) described a strain isolated from a corneal abscess and considered to be a representative of a new species. The taxonomic position of these two, closely similar strains remains to be decided.

All of the species and strains described so far are oxidase positive.

In 1911 Beijerinck (31) studied an organism isolated from soil. He named it *Micrococcus calco-aceticus*, but did not describe it. His report, therefore, has been overlooked until very recently, when one of his strains, which had been maintained, was reexamined and found to be related to organisms which had been described in the meantime under various names: *Bacterium anitratum*, *Moraxella glucidolytica*, and *Neisseria winogradskyi*. A similar, very strongly hemolytic organism was described by Henriksen in 1937 (232) under the name *Alcaligenes haemolysans*. It differed from the organisms just mentioned in failing to produce acid from sugars. The original strains have been lost, and the name has only been used by very few authors (180, 398, 399).

In 1939 DeBord (125) published a preliminary report on a group of gram-negative, *Neisseria*-like bacteria, actually rods, which he considered as a new tribe named *Mimeae* because the strains "mimicked" *Neisseria*. The type species, which was asaccharolytic, was named *Mima polymorpha*. He felt that these organisms represented a source of error in the microscopical diagnosis of gonorrhoea. His report was extremely short. In 1942 (126) he published a somewhat more detailed description of the tribe and its three genera, with the species *M. polymorpha* with a var. *oxidans*, *Herellea vaginicola*, and *Colloides anoxydana*. The latter species had all the biochemical characters of *Citrobacter*, and the name is consequently superfluous and illegitimate. *H. vaginicola* has been confused with *Bacterium anitratum* (correct name *Acinetobacter calcoaceticus*), but DeBord's description makes it clear that it must have been a different, now unknown species. The name *Herellea vaginicola* has recently been rejected by the JC (290). As for *Mima polymorpha*, the description from 1939 (125) was very incomplete and could hardly be considered to be sufficient to meet the requirement of the Code of Nomenclature for valid publication of a name. The description from 1942 (126) was

somewhat more detailed, although still lacking in detail, but in the meantime Audureau (16) in 1940 had described a similar organism, probably the same, under the name *Moraxella lwoffi*. DeBord's strains do not exist, and their exact identity can not be established. In view of the fact that Audureau was the first (Henriksen's description being left out of consideration) to give a reasonably complete description of this species, the JC, after a request by Henriksen, conserved the epithet *lwoffi* instead of *polymorpha* (290).

In 1948 Schaub and Hauber (491) described an organism, which they named *Bacterium anitratum*, characterized by coccal and coccobacillary shape, by failure to reduce nitrate to nitrite, and by oxidation of certain aldoses. The same organism was studied by Stuart, Formal, and McGann (524) and by Ferguson and Roberts (160).

An organism described by D. and M. Piéchaud and Second (438) under the name *Moraxella lwoffi* var. *glucidolytica* and later (439) raised to the rank of a species, *M. glucidolytica*, has been shown (79) to be the same organism. This organism has also been described by Lemoigne, Girard, and Jacobelli (336) under the name *Neisseria winogradskyi*. It is quite clear that this is a later synonym and that the organism is no *Neisseria*.

In 1954 Brisou (75) proposed to include *B. anitratum* in the genus *Achromobacter*, and in 1957 Brisou and Prévot (81) created the new genus *Acinetobacter* for the nonmotile species of *Achromobacter*. Mannheim and Stenzel (370) studied a number of strains and found that they could be divided into several groups based on variations in hemolysis and in certain biochemical reactions, and in 1963 Stenzel and Mannheim (521) formally proposed that they should be divided into five species and two subspecies: *Achromobacter mucosus*, *A. conjunctivae*, *A. haemolyticus* (with the two subspecies *haemolyticus* and *alcaligenes*), *A. metalcaligenes*, and *A. citroalcaligenes*.

The indiscriminate use of all the names cited above as well as of unorthodox recombinations of generic names and specific epithets caused a great deal of confusion, with marked tendencies to different usage in different countries and even by different scientists in the same country.

In order to clarify this confusion an Ad Hoc Committee was set up by the ICSB to study *Moraxella* and related organisms at the International Congress in Montreal in 1962. In 1966 at the International Congress in Moscow the Ad Hoc Committee was established as a Subcommittee of the ICSB. The work of this Subcommittee as well as of many scientists outside the Subcommittee has led to a considerable clarification of these matters, which it is hoped to make clear in this review.

## TAXONOMY

All recognized species of *Moraxella* share a number of characters, suggesting relationship. This impression is strengthened, with some exceptions, by studies of their genetic compatibilities as demonstrated by transformation studies (47–57, 109, 111), by nucleic acid hybridization (58, 59), and by studies of the deoxyribonucleic acid (DNA) base composition (56, 57, 62). Studies of the metabolism of the organisms (29, 186, 419, 432, 433) and gas chromatography studies (71, 173, 282) also support this impression. A summary of the results of transformation studies is presented in Table 1. Table 2 shows the results of nucleic acid hybridization and of analyses of DNA base composition.

The results show that the organisms belonging to *Moraxella* can be divided into several homogeneous groups, within each of which there are extensive genetic homologies between the strains. Between the groups varying degrees of homology or lack of homology can be demonstrated.

One group consists of strains believed to represent the Morax-Axenfeld diplobacillus, Petit's diplobacillus, and some gelatin liquefying strains isolated from guinea pig eyes by Ryan (482). Transformation studies, DNA composition, and nucleic acid hybridization (51, 56, 58, 62) indicate a very close relationship between all of these strains, with ratios of interstrain to intrastrain transformant numbers from 0.1 to 0.96. These high ratios appear to correspond to a relationship at the level of a uniform species, according to conventional criteria. Within the group three clusters can be distinguished, the Morax-Axenfeld strains, the Petit strains, and the Ryan strains. Within each cluster interstrain to intrastrain transformant ratios were very close to 1, whereas ratios between clusters were lower, but above 0.1. This suggests that these clusters might be of the same phylogenetic origin, but have deviated slightly, perhaps as a consequence of isolation. The strains all have DNA base compositions in a narrow range, 41.5 to 43 mol% guanine plus cytosine (G+C). The only difference in conventional characters is the need of one of the clusters, and not of the others, for serum or ascites fluid. Lwoff (356) showed that this apparent requirement actually is due to sensitivity to some compound contained in certain

TABLE 1. *Genetic relationships of the Neisseriaceae as demonstrated by transformation*[a]

| Recipients | Donors of DNA | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *M. lacunata* | *M. nonliquefaciens* | *M. bovis* | *M. osloensis* | *M. phenylpyrouvica* | *M. kingii* | *N. catarrhalis* | *N. ovis* | *N. caviae* | "True" *Neisseria* | *M. urethralis* | *Acinetobacter* |
| *M. lacunata* | 0.1: 0.96 | 0.0045: 0.0048 | 0.0012 | 0 | 0 | 0 | 0 | + | | | | 0 |
| *M. nonliquefaciens* | 0.001: 0.0052 | 0.34: 0.99 | 0.0015: 0.0075 | 0 | 0 | 0 | + | | | 0 | 0 | 0 |
| *M. bovis* | 0.0087: 0.018 | 0.0017: 0.0026 | 0.53 1.1 | 0 | 0 | 0 | + | + | (+) | | | 0 |
| *M. osloensis* | | + | 0 | 0.32: 1.0 | (+) | 0 | (+) | (+) | | 0 | 0 | ((+)) |
| *M. kingii* | 0 | 0 | 0 | 0 | 0 | 0.46: 0.92 | | | | | | |
| *N. catarrhalis* | | + | | (+) | (+) | | 0.3: 0.94 | (+) | (+) | 0 | 0 | ((+)) |
| *N. ovis* | + | + | + | (+) | (+) | 0 | + | 0.91: 0.95 | (+) | | 0 | ((+)) |
| "True" *Neisseria* | | | | | | 0 | | 0 | | 0.01[b]: 4.68 | 0 | |

[a] Figures represent ratios between interstrain or interspecies to intrastrain transformant numbers. +, Low frequency of transformants in quantitative experiments (interrupted by deoxyribonuclease); (+), transformants only detected in semiquantitative experiments with continuous exposure to DNA; ((+)), only very few transformants in semiquantitative experiments. The strains of *M. phenylpyrouvica*, *N. caviae*, *M. urethralis*, and *Acinetobacter* were incompetent in transformation.

[b] Data from Catlin, various interspecific combinations.

brands of peptone. The function of biological fluids, cholesterol, oleic acid, or simple dilution of the media with water is to neutralize or to reduce the effect of the toxic component.

Henriksen and Bøvre (242) concluded that the difference between *Moraxella lacunata* and *M. liquefaciens* can only be considered to be on the infrasubspecific level and that they should be united in the single species *M. lacunata*. This conclusion seems to be supported by the studies of nutritional and biochemical characters by Baumann, Doudoroff, and Stanier (29), which only showed a slight difference between the two former species. Opinions seem to be divided, and some specialists wish to maintain *M. liquefaciens* as a species or as a subspecies of *M. lacunata*.

A study of a number of strains isolated from various human sources and believed to be *M. nonliquefaciens* (49, 53) showed the group to be unhomogeneous and to be divisible into three homogeneous subgroups, both by conventional and genetic criteria. Confusion was about to arise when different authors (49, 109, 111) used members of different subgroups as representatives of *M. nonliquefaciens*. Therefore, Bøvre and Henriksen (68) proposed the retention of the most fastidious subgroup in *M. nonliquefaciens*, whereas the two other groups represented new species, *M. osloensis* (68) and *M. phenylpyrouvica* (69). One of the reasons for this was that the fastidious strains are the most common in the respiratory tract and therefore are probably the same as the strains studied by Scarlett (490) and by Oliver and Wherry (404). Another reason was that these strains, by genetic criteria, appear to be most closely related to the "classical" species *M. lacunata* and *M. liquefaciens*, and therefore are most likely to remain in the genus, whereas the other species

TABLE 2. *DNA compositions and nucleic acid homologies, determined by pulse RNA-DNA hybridization of representatives of the family Neisseriaceae*[a]

| Source of DNA | DNA base composition (mol% G+C) | Source of pulse RNA[b] | | |
|---|---|---|---|---|
| | | *M. nonliquefaciens* | *N. catarrhalis* | *N. ovis* |
| *M. nonliquefaciens* | 40–42 | 100 | 8.4 | 4.9 |
| *M. lacunata* | 41.5–43 | 34.2, 32.2 | 4.5, 4.6 | 7.5, 8.7 |
| *M. bovis* | 42.5–43 | 13.1 | 2.4 | 9.7 |
| *M. osloensis* | 43–43.5 | 2 | | |
| *M. phenylpyrouvica* | 43.1–43.5 | 1.2 | | |
| *N. catarrhalis* | 41–42.5 | 6.5 | 100 | 2.4 |
| *N. ovis* | 44.5–45 | 7.1 | 2.9 | 100 |
| *N. caviae* | 44.5 | 4.5 | 2.5 | 5.5 |
| *M. kingii* | 44.5 | 0.4 | | |
| *Acinetobacter* | 38–45 | 0.6 | | |
| *N. flavescens* | 46.5–47.5 | 0.3 | 0.6 | 0.7 |
| *N. cinerea* | 49 | 0.6 | 0.7 | 0.6 |
| *N. flava* | 47.5 | 0.8 | 0.5 | 0.5 |
| *N. elongata* | 53 | 0.5 | 0 | 0.2 |
| *E. coli* | 50 | 0 | 0.01 | 0.14 |

[a] Data from K. Bøvre, ref. 49–58.
[b] Figures are percentages of homologous hybridization.

appear to be much less closely related to these species.

The strains of *M. nonliquefaciens*, thus defined, showed very high mutual compatibility in transformation and had DNA base compositions within a very narrow range.

The strains of *Moraxella bovis* also show very high mutual genetic compatibility (59) with interstrain to intrastrain transformant ratios between 0.53 and 1.1. The DNA base composition varied from 42.5 to 43 mol% G+C. The strains also are very uniform in cultural and biochemical characters (29). There are fairly high mutual compatibilities between the species *M. lacunata*, *M. nonliquefaciens*, and *M. bovis*, with transformant ratios from 0.001 to 0.018 (Table 1). Also the three species have DNA base compositions in the same range.

Henriksen and Bøvre (242) discussed whether these three taxa should be considered as separate species or as subspecies of the same species. They concluded that it was preferable to keep them as separate species. They can be differentiated by simple tests, and it would be no obvious advantage to change their rank. Also, although they show marked genetic homologies, the degree of mutual compatibility between the taxa is of a lower order than within each taxon.

One of the groups which Bøvre (53) separated from *M. nonliquefaciens*, the "provisional 19116/51 group," differed from this species in being less fastidious, in utilizing citrate as sole source of carbon, in growing on plain media, in accumulating poly-β-hydroxybutyrate, and in being somewhat less sensitive to penicillin (29). It also is much more versatile nutritionally.

Bøvre and Henriksen (68) described the species and named it *M. osloensis*. It showed very low degrees of compatibility with the other *Moraxella* species and with the "false neisseriae" (interspecific to intrastrain transformant ratios from about $6 \times 10^{-6}$ to $4 \times 10^{-5}$). The G+C content of the DNA was 43.5 mol%.

The second group which could be distinguished from *M. nonliquefaciens* (53, 69), the "provisional 752/52 group," differed from the other species in very small colony size, production of urease, and deamination of phenylalanine and tryptophan. The strains were incompetent in transformation, but showed a very slight affinity with *M. osloensis*, *Neisseria catarrhalis*, and *N. ovis* as donors of transforming DNA. No compatibility with *M. nonliquefaciens* was demonstrated. The DNA base composition was 43 to 43.5 mol% G+C.

The strain described by Flamm (165) under the name *M. polymorpha* was found to have the same characters with the exception of urease production. For reasons given in the chapter on nomenclature, Bøvre and Henriksen (69) proposed to change the name to *M. phenylpyrouvica*.

King (unpublished data) had collected some strains which showed some resemblance to *Moraxella* morphologically, in being oxidase-positive and sensitive to antibiotics, but which differed from the known species in acidifying glucose and maltose. It was hemolytic. Hen-

riksen and Bøvre (244) studied some of her strains and an isolate of their own and named the new species *M. kingii* (in memory of the late E. O. King). Later (239), additional strains were discovered, which differed from previously described strains in growing with colonies of the "spreading-corroding" type. The strains of *M. kingii* which were studied showed high mutual compatibility with one another in transformation, as high as between strains of the other *Moraxella* species, but no compatibility at all could be demonstrated with any other *Moraxella* species or with "true" or "false" *Neisseria*. The DNA contained 44.5 mol% G+C.

In view of the marked deviations from other *Moraxella* species in conventional characters and the complete lack of detectable compatibility with other species, doubt has been raised that *M. kingii* actually belongs in *Moraxella*. But no better alternative has been suggested. The apparent lack of genetic compatibility with other species is not a sufficiently strong argument against its inclusion in *Moraxella*, because no rule has been laid down, or can be, as to the degrees of genetic affinity to be required of members of a genus.

*M. urethralis*, the organism described by Lautrop, Bøvre, and Frederiksen (325), resembles *Moraxella* in some respects: morphology, oxidase reaction, and penicillin sensitivity. It differs from them in manner of growth on agar media and in DNA base composition (46 mol% G+C). Like *M. osloensis* and unlike the other species it accumulates poly-$\beta$-hydroxybutyrate. The strains studied were incompetent in transformation and showed no sign of compatibility with the other *Moraxella* species or with *Neisseria ovis* or *N. meningitidis* when used as donors of transforming DNA. The authors were uncertain about the classification and only mentioned *Moraxella* as a possibility. Thus the taxonomy of this species is undecided.

Bøvre (50) and Catlin (109, 111) demonstrated by transformation experiments that certain *Neisseria* species showed marked affinity to certain *Moraxella* species. Further studies (54, 57) indicated that *N. catarrhalis*, *N. ovis*, and *N. caviae* had marked affinities to *M. lacunata*, *M. bovis*, and *M. nonliquefaciens* with interspecies to intrastrain transformant ratios varying from $7.5 \times 10^{-5}$ to $1.1 \times 10^{-3}$. *M. osloensis* also showed somewhat lower affinities to these *Neisseria* species. On the other hand *N. flavescens* and *N. cinerea* showed no homologies with either the *Moraxella* species or with *N. catarrhalis-N. ovis*. These findings were corroborated by nucleic acid hybridization (58) and by results of gas chromatography of methanolysates of bacterial cells (71).

These results suggest a relationship between the three "classical" *Moraxella* species (*M. lacunata*, *M. bovis*, *M. nonliquefaciens*) and the "false neisseriae" (*N. catarrhalis*, *N. ovis*, *N. caviae*). They also suggest some more remote relationship of *M. osloensis* to these species. On the other hand "true" *Neisseria* showed no indication of relationship to any of these species, either by transformation, by DNA hybridization, or by gas chromatography.

These and other results led Henriksen and Bøvre (243) to the conclusion that *N. catarrhalis*, *N. ovis*, and *N. caviae* are more closely related to *Moraxella* than to the rest of *Neisseria* and that they should be transferred to *Moraxella*. As an acceptable, although less favored, alternative they suggested the creation of a new genus in the *Neisseriaceae* for these three coccal species. Shortly afterwards, Catlin (110) proposed that *N. catarrhalis* should be transferred to the new genus *Branhamella*. Because this is a matter of taxonomy and not of nomenclature, whether one wishes to follow Henriksen and Bøvre or Catlin would seem to be optional.

In this connection it may be mentioned that a similar situation now exists in the genus *Neisseria* because Bøvre and Holten (79) described a rod-shaped organism with similar genetic affinities to *Neisseria* as *N. catarrhalis* to *Moraxella*. The new organism was named *N. elongata*. Several additional strains of this species have recently been isolated and found to show homologies with one another and with the type strain at levels suggesting a very close relationship (Bøvre, Fuglesang, and Henriksen, to be published).

This brings us to the oxidase-negative organisms which are called *Acinetobacter calcoaceticus* in this review. These bacteria share some characters with *Moraxella*. They usually have rather plump cells, often coccoid or coccobacillary, but also with distinct rods, varying with medium, growth conditions, and age, and they usually have a marked tendency to diplo-arrangement. But the differences from *Moraxella* are also quite marked: higher growth energy, much higher metabolic and nutritional versatility, negative oxidase reaction, different habitat (soil), and often low sensitivity to penicillin and other antibiotics. They have DNA base compositions reasonably close to those of the *Moraxella* species, about 38 to 45 mol% G+C.

In transformation experiments (55) DNA

from streptomycin-resistant strains produced some very rare transformants of *N. ovis*., *N. catarrhalis*, and *M. osloensis*, but not of other species. The significance of these findings is questionable, but they may possibly be indications of remote relationship. Juni and Juni and Janik (293–296), by using a transformable strain of *Acinetobacter calcoaceticus* as recipient, found that this strain could be transformed by DNA from a variety of oxidase-negative organisms labeled *Acinetobacter*, *Achromobacter*, *Alcaligenes*, *Bacterium*, *Diplococcus*, *Herellea*, *Micrococcus*, *Mima*, *Moraxella*, and *Neisseria*, i.e., a complete series of synonyms, indicating that a variety of biotypes were represented. DNA from oxidase-positive *Moraxella* and *Neisseria*, as well as from a variety of other, obviously unrelated, organisms failed to transform the recipient. These results suggest: (i) that in spite of rather marked heterogeneity in biochemical reactions, the oxidase-negative group under discussion may be close relations, and (ii) that no relationship to oxidase-positive *Moraxella* and *Neisseria* was demonstrated in this transformation system.

It has also been demonstrated by the use of conventional methods that organisms labeled *M. glucidolytica*, *B. anitratum*, *Micrococcus calcoaceticus*, and *N. winogradskyi* are closely similar and should be placed in the same taxon (30, 79, 80, 184–186, 261, 431, 432, 434).

The taxonomy of these organisms and their relationship to *Moraxella* have been controversial for many years. When Lwoff (354) in 1939 created the genus *Moraxella* it contained only (with the exception of *M. josefi*) organisms which are recognized by everybody today as genuine members of the genus, all of which were later found to be oxidase-positive and inhabitants of eyes or the respiratory tract of man and animals. The problems arose when Audureau in 1940 (16) added the species *M. lwoffi*, which differed from the other species in growing in simple mineral media with ethanol as the sole source of carbon and, as was found later, in being oxidase-negative. In 1951 D. and M. Piéchaud and Second (438) added a new variety, var. *glucidolytica*, which differed from *M. lwoffi* in producing acid from certain sugars. In 1953 (439) this variety was raised to the rank of species, *M. glucidolytica*, and proteolytic and nonproteolytic varieties were described.

In 1952 Henriksen (234) studied some *Moraxella* strains, including one of Audureau's strains of *M. lwoffi*. He divided the strains into two groups, one oxidase-positive group, including strains of *M. lacunata* and *M. nonliquefaciens*, and an oxidase-negative group comprising the strain of *M. lwoffi* and another oxidase-negative strain. The oxidase-positive strains, in contrast to the negative ones, had a low or moderate growth energy and were highly sensitive to penicillin. He suggested that only the oxidase-positive group should remain in *Moraxella*. He pointed out certain similarities between *Moraxella* and *Neisseria* and suggested that *Neisseriaceae* might be a suitable family for *Moraxella*.

In 1953 Brisou (75) proposed the inclusion of the organisms in question in the genus *Achromobacter*, and in 1957 Brisou and Prevot (81) proposed the creation of the genus *Acinetobacter* for the nonmotile species of *Achromobacter*. In the same year Brisou (76) selected *A. anitratus* as type species of the new genus.

The fact that many authors have been using the names *Mimeae*, *Mima*, and *Herellea*, introduced by DeBord (125, 127), on the same organisms has increased the confusion. These problems are dealt with in the following section on nomenclature.

Seeliger, Schubert, and Schleiber (501), based on the assumption (499, 500) that *A. calcoaceticus* was the same organism as *Diplococcus mucosus* von Lingelsheim (341), proposed the transfer of this species to still another new genus, *Lingelsheimia*. For reasons given in the following section, this proposal does not seem to be acceptable.

The extensive research that has been carried out in recent years, both on *Moraxella* and *Acinetobacter*, has provided a much better basis for forming a sound opinion on these taxonomic problems. It has become increasingly clear that the *Acinetobacter* species differ from *Moraxella* on too many points to be placed in the same genus. On the other hand, it has also become clear that the *Acinetobacter* strains are a group of closely interrelated organisms, which deserve to have a genus of their own. About the relationship of *Moraxella* to *Acinetobacter*, however, opinions remain divided, some feeling that these two genera are related, whereas others are doubtful. These matters were discussed by the *Moraxella* Subcommittee during the International Congress in Mexico in 1970, and in spite of differences of opinion, a compromise solution was reached on the following recommendations. (i) The genera *Moraxella* and *Acinetobacter* are to be included in *Neisseriaceae*. (ii) *N. catarrhalis*, *N. ovis*, and *N. caviae* are to be transferred from *Neisseria* to *Branhamella* as suggested by Catlin (110) or to *Moraxella* as suggested by Henriksen and Bøvre (248, 249).

Like all proposals and recommendations on taxonomic matters, these do not have the force of law and can be modified as knowledge increases.

As for the subdivision of *Acinetobacter* into species, several alternatives are possible. One alternative, which appears to be winning support, is to recognize only one species, *A. calcoaceticus*, for the time being. A second alternative is to follow the customary practice of recognizing two species, *A. calcoaceticus* for the strains which produce acid from sugars in customary fermentation media and *A. lwoffi* for those which do not. A subdivision in proteolytic and nonproteolytic subspecies or varieties has also been proposed (439). The establishment of species or subspecies on the basis of differences in a single character is contrary to modern trends in taxonomy.

A third alternative is represented by the proposal of Stenzel and Mannheim (521) to create five different species, one of them with two subspecies, based upon differences in hemolysis, alkalinization of citrate medium, acid production from sugars, and gelatin liquefaction.

It seems questionable, particularly in view of the mutual genetic compatibilities of these biotypes, that any of these differences are of such significance as to justify subdivision into different species. Thus the difference in acid production from sugars may be quantitative rather than qualitative, because strains which fail to produce acid in ordinary media may do so in diluted media or in mineral salt solutions (4). Hemolysis, in those strains that show it, is an extremely striking character, but in order to evaluate its significance, it would be useful to know something about its genetic basis. Differences in gelatin liquefaction, a character that is not even quite constant in the species proposed by Stenzel and Mannheim, or alkalinization of citrate medium also appear to be weak grounds for separating species.

More significant, however, than these arguments are the findings of Juni and Juni and Janek (293–297) that a competent strain could be transformed by DNA from a variety of biotypes. These results indicate that all of these biotypes are genetically related and that, until more knowledge has been gathered, it would be better to recognize only one species.

The taxonomy of the organisms under discussion is summarized in Table 3.

## NOMENCLATURE

The nomenclature of *Moraxella* has been discussed by Henriksen. References to the early literature cited below can be found in his papers (236, 237). The early authors, Morax, Axenfeld, and Petit, did not give formal names to the organisms which they described. The diplobacillus of Morax and Axenfeld (18, 19, 387) was placed in *Bacterium* by Chester (237) and in *Bacillus* by Lehmann and Neumann (237). The generic name *Bacterium* has been rejected, and the name *Bacillus* has been reserved for sporulating rods. MacNab (362) used the name *Diplobacillus liquefaciens* for Petit's organism, but he did not make it clear that he proposed a generic name. For the diplobacillus of Morax and Axenfeld he used several different designations, and the most nearly acceptable name was *Diplobacillus* Morax-Axenfeld. It is doubtful that this actually constitutes valid publication of a name, and there is reason to think that *D. liquefaciens* was only a translation of Petit's "diplobacille liquefiant." A second objection to the name is that Weichselbaum (237) used the name *Diplobacillus brevis endocarditidis*. Although this name was illegitimate according to the present rules of nomenclature, the reuse of the name on a different organism could be considered to be against the rules of nomenclature. This matter is somewhat unclear.

In 1920 Holland (237) placed Morax and Axenfeld's organism in *Haemophilus* under the name *H. lacunatus*. In 1939 Lwoff (354) proposed the new name *Moraxella* for the reasons that the organisms neither resembled the haemophils morphologically nor required the X or V factors.

In view of the uncertainties about the status of the generic name the JC, after a request from Henriksen (237) and supported by the *Moraxella* Subcommittee, issued an opinion to conserve *Moraxella* against *Diplobacillus*. *Moraxella*, therefore, is the correct generic name.

Chester in 1897 (237) was the first to propose a formal name, *Bacillus conjunctivitis* (sic) on the Morax-Axenfeld organism. Two objections could be raised against this name: it was grammatically wrong (Chester corrected it to *conjunctivitidis* in 1901), and it was applied to two different organisms at the same time, the second being *B. conjunctivitis* (Koch-Kartulis), an organism of very uncertain identity, probably a mixed culture. This is against the rules, and gives a subsequent author the right to choose a new name for one of the organisms. This was done by Lehmann and Neumann (237), who proposed the epithet *duplex*. This appears to be the first validly published and legitimate specific epithet on this species.

Eyre proposed the name *Bacillus lacunatus* at a scientific meeting in 1898 (149), but did not

TABLE 3. *Taxonomy and nomenclature of the Neisseriaceae*

| | |
|---|---|
| Genus I. *Neisseria* | |
| Species: *N. gonorrhoeae* and others | |
| Genus II. *Moraxella* | |
| Species: | Alternative: |
| *M. lacunata* | *M. lacunata* subsp. *lacunata*<br>*M. lacunata* subsp. *liquefaciens* |
| *M. nonliquefaciens* | |
| *M. bovis* | |
| *M. osloensis* | |
| *M. phenylpyrouvica* | |
| *M. kingii* | |
| (*M. urethralis*) | Alternative:<br>Genus III. *Branhamella*<br>Species: |
| *M. catarrhalis* | *B. catarrhalis* |
| *M. ovis* | *B. ovis* |
| *M. caviae* | *B. caviae* |
| Genus III. *Acinetobacter* | Genus IV. *Acinetobacter* |
| Species: | Species: |
| *A. calcoaceticus* | *A. calcoaceticus*<br>*A. lwoffi* |

publish the name until 1900 (150). In 1920 Holland (237) proposed the name *Haemophilus lacunatus*, which was used in the first four editions of Bergey's Manual, but was substituted by *H. duplex* in the 5th edition. Then, in 1939, Lwoff (354) proposed the name *Moraxella lacunata*, which has been in common use ever since, so, although *M. duplex* may be the correct name, nobody uses it any more on this organism.

Lwoff applied the epithet *duplex* to the species of Petit and of Scarlett, with the varietal epithets *liquefaciens* and *nonliquefaciens*, respectively. Because the epithet was first proposed for Morax and Axenfeld's organism, it is contrary to the rules to apply it to a different species in the same genus. Also, according to the rules, in a species with two varieties or subspecies, one of them should have the same subspecific epithet as the species, i.e., one of them should have been *M. duplex* var. *duplex*. The names *M. duplex* var. *liquefaciens* and var. *nonliquefaciens* thus are contrary to the present rules.

The situation today seems to be that all authors use the names *M. lacunata* and *M. liquefaciens* (if they recognize the latter as a separate species), which is a satisfactory solution.

Scarlett (487) used the name *bacillus duplex non liquefaciens* on one of his diplobacilli. It is clear that the form of this name is illegitimate and, also, that the epithet *duplex* was unavailable, having been used on a different species in the same genus. The name *Moraxella non liquefaciens* was first used in the 6th edition of Bergey's Manual and in the paper of Murray and Truant (392). Because this, if the epithet is corrected to *nonliquefaciens*, seems to be the first name on this organism which is in accord with the rules of nomenclature, it is the correct name.

Flamm in 1956 (165) described *M. polymorpha*. Bøvre and Henriksen (69), working with a number of strains of an apparently new species characterized by possession of urease and phenylalanine deaminase, screened a large number of strains for these characters and found that Flamm's strain deaminated phenylalanine, although it lacked urease. In other characters it was as for the strains under study. It appeared to belong to the same species as the other strains. If so, *M. polymorpha* was the correct name. However, they felt that this name would cause confusion and that it might be a later homonym, and therefore illegitimate. DeBord (125–126) had described the organism *Mima polymorpha* with an oxidase-positive variety, *oxidans*. The identity of this organism is unknown, but it might well have been a *Moraxella* species.

A stronger argument was that the literature is full of reports on isolation of *Mima polymorpha*, including the variety *oxidans*, from various pathological conditions, and the use of the epithet *polymorpha* on a rather similar organism would be bound to perpetuate the confusion caused by the use of the names proposed by DeBord. On the basis of these arguments Bøvre and Henriksen (69) proposed a new name, *M.*

*phenylpyrouvica*, and requested an opinion of the JC about conserving this name against *M. polymorpha*. Such an opinion was issued by the JC in 1971 (292).

There is no doubt about the correctness of the name *M. osloensis* Bøvre and Henriksen 1967 (69). The name *M. kingii* Henriksen and Bøvre 1968 (244) has been validly published and is legitimate according to the rules of nomenclature. However, Berger (37b) has rightly pointed out that, according to recommendation 27f of the current edition of the Code, this epithet ought to have been given a feminine gender. Because this is only stated in a recommendation and not in a rule, it may not have the force of law. But this situation will be changed if the proposed revision of the International Code of Nomenclature of Bacteria is approved. If so, it seems that the name will have be changed to *Moraxella kingae*, since it was named after a female scientist.

The name *M. urethralis* (325) has not yet been formally proposed and has no standing in nomenclature.

The nomenclature of the organisms known as *Acinetobacter* has been in a highly confusing state until recently. It is now known that Beijerinck (31) had studied strains of these organisms and that in 1911 he named them *Micrococcus calcoaceticus*. He did not describe the species, and consequently its identity was not realized until very recently, when one of his strains was reexamined and found to have the same characters as the organisms known as *B. anitratum* or *M. glucidolytica*. This, therefore, is the first name to be published for an organism of this group.

In 1937 Henriksen (232) described some very strongly hemolytic gram-negative coccobacilli, which he named *Alcaligenes haemolysans*. The description agrees on nearly all points with later descriptions of the hemolytic variety of *A. calcoaceticus* (*A. lwoffi*, *Achromobacter haemolyticus* subsp. *alcaligenes* [370, 571]). The strains have unfortunately been lost, and a direct comparison with other strains is impossible. The name *A. haemolysans* was later used only in a couple of publications (180, 398, 399) and is unknown to most bacteriologists.

Among the species described by DeBord in 1939 (125), *Mima polymorpha* probably was the same organism as *M. lwoffi* (16). DeBord's description was extremely short and probably would not satisfy the requirement of the Code of Nomenclature that a publication of a name must be accompanied by a description to be valid. DeBord in 1942 (126) published a somewhat more adequate description, but in the meantime Audureau (16) had published her description of *Moraxella lwoffi*. The question of the priority therefore was uncertain (at least until Beijerinck's *M. calcoaceticus* was rediscovered), and therefore, after a request by Henriksen (238), the JC issued an opinion (290) rejecting the generic name *Mima* and the epithet *polymorpha* in this combination.

DeBord's *Herellea vaginicola* (126) has for a long time been thought to be the same organism as *B. antitratum*. A study of his description shows that it differs markedly from *B. anitratum*, particularly in attacks on sugars, and that it can not have been the same organism. Indeed, it seems to be impossible to identify it. (238). For these reasons an opinion was requested of the JC (238) to reject the name *Herellea* and the epithet *vaginicola* in this combination, and such an opinion was issued (290). Since there is general agreement that the third species of the *Mimeae*, *Colloides anoxydana*, must have belonged to a species of *Enterobacteriaceae*, probably of *Citrobacter*, the *Mimeae* have ceased to exist, and the names should not be used any more.

The organism first named by Beijerinck was rediscovered by Schaub and Hauber (491) and named *B. antitratum*. D. and M. Piéchaud and Second (438) first named it *Moraxella lwoffi* var. *glucidolytica* and later named it (439) *M. glucidolytica*. Brisou (75) proposed to include the species in *Achromobacter*. Later Brisou and Prevot (81) created the genus *Acinetobacter* for the nonmotile species of *Achromobacter*, and Brisou (77) selected *A. anitratus* (*calcoaceticus*) as the type species of this genus.

Seeliger, Schubert, and Schlieber (501), assuming that *B. antitratum-M. glucidolytica* was the same organism as *D. mucosus*, which was very briefly described by von Lingelsheim (341), proposed the transfer of this species to a new genus, *Lingelsheimia*. None of the strains of von Lingelsheim exist, and the description is too vague to identify the species with certainty.

One of the arguments for the transfer of this species to *Lingelsheimia* is that Brisou, in a letter to these authors, is said to have expressed the opinion that he prefers to follow a proposal by Prévot (451) to recognize *A. stenohalis* as the type species of *Acinetobacter*. According to Seeliger et al., the latter species should not be in the same genus as *A. calcoaceticus*. They further make this statement: "Since the original author has thus withdrawn his earlier proposal as made in 1957, *A. stenohalis* becomes the legitimate type species of the genus *Acinetobacter* Brisou and Prévot 1954."

It may be objected that Brisou's alleged withdrawal of his proposal from 1957 was made only in a private letter, which can not be

considered as valid publication. Furthermore, even if Brisou should publish his support of Prévot's proposal to make *A. stenohalis* the type species, such a change of mind probably could not be accepted, since the Code of Nomenclature has no provision for such a change of mind. It thus seems that Brisou's original proposal stands and that *A. anitratus* (*calcoaceticus*) remains the type species. As long as this genus is recognized, it will be impossible to transfer *A. calcoaceticus* to another genus, and if *A. stenohalis* can not be in the same genus, it is the latter species which will have to be transferred.

The situation therefore appears to be that the generic name *Acinetobacter* has been validly published and is legitimate.

The epithet *calcoaceticus* is the first published name for an organism of this genus. Because Beijerinck did not publish any description of this species, the publication of the name is not valid according to the Rules of Nomenclature, but the fact that some of his original strains exist and that an increasing number of authors are now using the name *A. calcoaceticus* are strong arguments for accepting this name in spite of the objections that can be made. Another very great advantage is that acceptance of this name would remove all questions of priority and at the same time would make all the many other names which this species has been known under illegitimate.

If somebody should wish to consider the varieties which do not produce acid from sugars in the usual media, as a separate species, two epithets might be available, Henriksen's *haemolysans* and Audureau's *lwoffi*. Of these *haemolysans* has priority, but it was only intended for use on the hemolytic strains of this biotype, and it has only been used very rarely and had best be forgotten. The epithet *lwoffi* would be preferable. It has been in common use in the literature. Conservation of the epithet *calcoaceticus* against all synonyms, perhaps also of *lwoffi* against *haemolysans*, might clarify the situation.

## TWITCHING MOTILITY, COLONY VARIATION, FIMBRIATION, COMPETENCE IN TRANSFORMATION, AND CAPACITY FOR PARASITISM

In 1961 Lautrop (322) demonstrated a peculiar form of surface translocation in strains of *B. anitratum*, which he first interpreted as gliding motility, and he suggested the transfer of the organism to *Cytophaga*. Later (323) he found that this motility could better be described as "twitching" and withdrew the proposal to transfer the species to *Cytophaga*. Piéchaud (437) demonstrated a form of motility not due to flagella in all *Acinetobacter* and *Moraxella* species that were studied. Ryter and Piéchaud (483) by electron microscopy demonstrated long, thin appendages on some of these bacteria, which they called proflagella. They did not consider them as flagella. Halvorsen (212) confirmed Lautrop's demonstration of twitching motility in strains of *Acinetobacter* (sugar acidifying and "asaccharolytic"), but failed to demonstrate this motility in *M. nonliquefaciens*.

Henriksen (239) found that *M. kingii* occurred with two different colony types, one of which was of the ordinary convex, round, smooth type, and the other of which was irregular, spreading, and caused "pitting" and "corrosion" of the agar surface. Henriksen and Bøvre (245) demonstrated the same two colony types in *M. nonliquefaciens*, and Pedersen (416, 417, 418) and Bøvre and Frøholm (64, 66) demonstrated the same phenomenon in *M. bovis*. Bøvre, Bergan, and Frøholm (61) found that these colony forms, spreading-corroding (SC), and normal (N), and an intermediate form (NSC), could be shown to vary both from SC to N and vice versa, usually with low frequency. Some N forms appeared to be stable. By electron microscopy they found that the SC cells had numerous long, thin fimbriae, whereas the N cells had only occasional fimbriae or, usually, none. NSC cells appeared to have fewer fimbriae than SC cells. The authors found some inconclusive indications of the presence of a special antigen in the SC form, possibly associated with the fimbriae. Bøvre and Frøholm (63) demonstrated a close association of presence of fimbriae with competence in genetic transformation in *M. nonliquefaciens*, and later (64, 66) they found the same correlation between colony type, fimbriation, and competence in *M. kingii* and *M. bovis*, as well as in *M. nonliquefaciens*.

Henrichsen, Frøholm, and Bøvre (230) demonstrated close association of twitching motility with the SC (and NSC) colony type and with fimbriation in these species.

Pedersen, Frøholm, and Bøvre (419) found that the ability of *M. bovis* to colonize the bovine conjunctiva, and to cause experimental keratoconjunctivitis, was associated with the SC colony type and with fimbriation, competence in transformation, and twitching motility. Thus in these three species there is an, apparently firm, association of these characters. This suggests that these associated characters may be related to parasitism and pathogenicity. It remains to be seen whether the ability to colonize mucous membranes is similarly associ-

ated with these characters in other *Moraxella* species. It may be mentioned that it seems (personal observations) that the SC type of colony may be the usual type in recently isolated strains of *M. nonliquefaciens* and that there is a tendency to a change to the N type on prolonged subcultivation. It can also be mentioned that the tendency to produce pitting of agar surfaces appears to be common in other parasites on mucous membranes (*N. catarrhalis* and alpha streptococci).

Whether the proflagella demonstrated by Ryter and Piéchaud (483) in two species of *Moraxella* (*M. liquefaciens and M. nonliquefaciens*) and two of *Acinetobacter* (*A. lwoffi* and *A. glucidolytica*) are analogous with the fimbriae demonstrated by the other authors cited above remains to be shown, but the association with twitching motility is suggestive. The variability of these characters demonstrated by Bøvre and associates could explain some discrepancies between observations made by different authors.

It seems reasonable to suggest that such phenomena as described in this chapter may be of more widespread occurrence than realized today. It remains to be shown that they occur in other *Moraxella* and *Acinetobacter* species or outside these genera. Fimbriation has been demonstrated in a number of other bacterial species.

It may be recalled that Bøvre (55) did not succeed in finding *Acinetobacter* strains which were competent in transformation. After Juni and Juni and Janik (293–296) found competent strains of this genus, the possibilities for studying the association of competence with other characters opened.

Associations of characters such as described in this chapter appear to be of considerable interest in general and medical microbiology.

## SEROLOGY

The literature on the serology of *Moraxella* and *Acinetobacter* reflects the confusion that has been reigning in the taxonomy and nomenclature of these organisms. In some cases the identity of the strains used in the serological studies has been uncertain, and the results obtained are consequently difficult to interpret.

Haug and Henriksen (215, 216) studied a limited number of strains of all recognized *Moraxella* species. A few *Acinetobacter* strains were included for comparison. Agglutination tests with live and heated suspensions and gel precipitation tests with ultrasonic bacterial extracts were used. *M. lacunata*, *M. bovis*, and *M. nonliquefaciens* showed cross-reactions in agglutination tests, but also heterogeneity between the strains. *M. phenylpyrouvica* and *M. osloensis* showed mainly strain-specific reactions and did not cross-react with other species. *M. kingii* did not cross-react with other *Moraxella* species. By the use of three immune sera, 11 out of 14 strains could be assigned to three serotypes.

There were no cross-reactions between *Acinetobacter* strains and *Moraxella* strains. *M. kingii*, *M. bovis*, and *M. nonliquefaciens* appeared to have a nonantigenic or poorly antigenic surface component which inhibited agglutination of live cells, but was removed by heating. In the *M. phenylpyrouvica*, *M. osloensis*, and *Acinetobacter* strains, agglutination was unchanged or reduced by heating.

Gel diffusion tests showed marked cross-reactions between *M. lacunata*, *M. bovis*, and *M. nonliquefaciens* with one to several shared precipitin lines in all combinations, whereas the other species did not cross-react significantly. *M. kingii* did not cross-react with other *Moraxella* species, but appeared to share some antigens with *Bacteroides* (*Eikenella*) *corrodens*. The results suggest that the serology of *Moraxella* is complex and that much additional work would be needed to clarify it. It seems questionable whether such additional efforts would be worthwhile.

In the review of the literature on *Acinetobacter* serology, the names employed by the authors have been used. Henriksen (232) studied 16 strongly hemolytic strains of *Alcaligenes haemolysans* and found that 14 of the strains showed marked cross-reactions. Two strains deviated from the others.

Schaub and Hauber (491) found that 15 encapsulated strains of *B. anitratum* had the same capsular antigen. Stuart, Formal, and McGann (524), on the other hand, found that their strains of B5W were serologically heterogeneous. Live suspensions were agglutinated to high titers as loose floccules. After heating in boiling water they were nearly inagglutinable, but after heating to 120 C for 2.5 h O agglutination with the same titers as with live antigens was obtained. Ferguson and Roberts (160) found that suspensions heated to 100 C for 1 to 3 h were nonagglutinable. Heating to 121 C for 2 to 3 h produced variable results. Agglutination with live antigens gave confusing results but by capsular swelling 10 serotypes were established. Attempts to establish O groups failed.

Aiken et al. (4) produced immune sera against 25 strains and tested them against 291 strains. Ninety-five percent of "*Herellea*-like"

and 39% of "*Mima*-like" strains were agglutinated by one or more sera.

Cary, Lindberg, and Faber (106) used the precipitation test with Maxted extracts of the bacteria. Only type-specific reactions were obtained, and nine new serotypes were established in addition to the 10 of Ferguson and Roberts. The same authors (107) prepared a polyvalent serum against *Mima* and one against *Herellea*. The antigens were alkali treated, the cells were used for slide agglutination, and the supernatants for precipitation. All *Mima* strains were agglutinated by the *Mima* serum and all *Herellea* strains by the *Herellea* serum. The fact that the 10 type strains of *B. anitratum* (generally considered to be a synonym of *Herellea*) reacted with the "*Mima*" serum and not with the "*Herellea*" serum is difficult to explain.

Cary (105) in a later study included strains of *Moraxella*, *N. winogradskyi*, *D. mucosus*, and *B. anitratum*. The same polyvalent sera and sera against the 10 serotypes were used. Alkali-treated bacteria were used for slide agglutination and Maxted extracts for type precipitation. Because the exact identity of some of the strains is uncertain, interpretation of the results is difficult. Cross-reactions between *Moraxella* and *M. polymorpha* var. *oxidans* were found.

Mannheim (368) studied 40 strains of *A. chromobacter conjunctivae* and *A. haemolyticus*. He demonstrated three kinds of antigen: K antigens apparently different from capsular antigens, giving loose, floccular agglutination with high titers. The antigen was heat stable, but could be removed by washing heated cells. It did not appear to be a fimbrial antigen. O antigens were demonstrated in heated and washed cells. After heating to 120 C for 2 h, other antigens ("Tiefenantigene") could be demonstrated. All strains of *A. conjunctivae* were found to be serologically equal, whereas *A. haemolyticus* was heterogeneous.

Biegeleisen et al. (42) found it possible to identify *Herellea* strains by the use of pools of fluorescein-labeled antibodies. Cross-reactions with other species did not appear to be a problem.

Mitchell and Burrell (382–383) worked with strains labeled *H. vaginicola*, *M. polymorpha*, *M. polymorpha* var. *oxidans*, *M. nonliquefaciens*, *M. lwoffi*, *B. anitratum*, and *M. liquefaciens*. They immunized with sonic extracts and used gel precipitation tests. *H. vaginicola* extracts gave five precipitate bands, four of which were common to both strains. *M. polymorpha* extracts gave five bands, two of which were common to both strains. Three of four strains of *M. polymorpha* var. *oxidans* seemed to be identical, and one differed from the others. Some serological relationship was demonstrated between *Mima-Herellea* and *Moraxella* and between *M. liquefaciens* and *M. nonliquefaciens*.

Marcus et al. (371) demonstrated 28 serotypes of *H. vaginicola*, most of which differed from those of *Mima*. By means of fluorescein-tagged pools of type-specific sera 79% of *Herellea* strains could be identified.

The results of these serological studies are difficult to interpret. Different methods have been used and different antigens have been studied. There are some striking discrepancies. Schaub and Hauber (491), e.g., found that all of their 15 strains had the same capsular antigen, whereas Ferguson and Roberts (160) found 10 different serotypes, and Marcus et al. (371) found as many as 28. The serological identity of all strains of *A. conjunctivae* found by Mannheim (368) also seems to be in contrast to the general impression of heterogeneity. In order to interpret such discrepancies, it might be useful to know something about the origin of such homogeneous strain collections. Possibilities such as nosocomial spread, contaminated eye drops, or some similar common source suggest themselves.

It seems reasonable to conclude that the serology of *Acinetobacter* is very complex, with great heterogeneity. It seems to be clear that a great deal more work would be needed to achieve a serological classification as in the *Enterobacteriaceae*. In view of the limited role these bacteria play in medicine, the amount of work would probably be out of proportion to the possible benefits of such a classification.

## DESCRIPTION OF INDIVIDUAL TAXA

### Genus Moraxella

**M. lacunata.** Micromorphology: In eye coid to coccobacillary or short to medium rods, with rounded or with nearly square ends, gram-negative, often with some tendency to resist decolorization, marked tendency to arrangement in pairs and sometimes in short chains. No swimming motility, no flagella, no endospores. Show twitching motility (230, 437) when in the fimbriated state.

Physiology: With one exception (*M. osloensis*), complex growth requirements (29). Aerobic. Mesophilic. Parasitic.

Biochemical reactions: Oxidase reaction positive with dimethyl- and tetramethyl-*p*-phenylenediamine. With one exception (*M. kingii*), catalase positive. With one exception (*M. kingii*), asaccharolytic. Comparatively inactive

biochemically. Do not produce indol or $H_2S$.

Antibiotic sensitivity: Strongly to moderately (*M. osloensis*) sensitive to penicillin. Sensitive to streptomycin, chloramphenicol, tetracyclines, and erythromycin.

DNA compositions and genetic compatibilities are shown in Tables 1 and 2.

**M. lacunata.** Micromorphology: In eye secretions, plump diplobacilli about 2 × 1 to 1.5 μm. In culture plump diplobacilli. In older cultures tendency to formation of filaments and other "involution forms."

Colonies: On blood agar or ascites agar, colonies are small, flat, translucent, resembling pneumococci (18). Old laboratory strains may have irregular, rough colonies. Nonhemolytic.

Physiology: Does not grow on simple peptone media, due to a toxic effect of certain components of peptone. This toxic effect can be counteracted by biological fluids, cholesterol, (356), oleic acid, or by dilution of the media with water. Poor or no growth at room temperature, optimal growth at 33 to 37 C.

Biochemical activities: Liquefies coagulated serum and, if the medium contains serum, gelatin. Nitrate reduced to nitrite. Urease, phenylalanine, and tryptophan deaminase not produced.

Habitat: Mostly isolated from inflamed human eyes. Some authors claim to have found it in the nose (40, 118, 147) and throat (403), but details of identification procedure are usually not given. Appears to have been very common from the time of the first isolation (1896) to about 1920. Rarely mentioned in the literature in later years.

Type strain (neotype) Morax 260 (ATCC 17967) (240). *M. liquefaciens* may be considered as a biotype or as a subspecies of *M. lacunata* (*M. lacunata* subsp. *liquefaciens*), which differs from it only in being able to grow on media without serum and, consequently, to liquefy the usual gelatin media, due to insensitivity to the toxic factors which affect *M. lacunata*.

Habitat: As for *M. lacunata*. Has also been isolated from guinea pigs' eyes by Ryan (482) and from bovine eyes by Wilcox (570).

Reference strain (or neotype strain) NCTC 7911, ATCC 17952 (240).

Pathogenic activities of *M. lacunata* and *M. liquefaciens*: *M. lacunata* was first described (18, 387) as the cause of a mostly mild, subacute to chronic, angular conjunctivitis, which appeared to be of world-wide distribution. *M. liquefaciens* (426) was first described as the cause of keratitis. The pathogenic activities of these bacteria seem to be very similar, although *M. liquefaciens* appears to have been more often considered to be the cause of keratitis than *M. lacunata*. In much of the literature on these bacteria no distinction has been made between them. In the years following the first descriptions of this particular type of conjunctivitis and of the diplobacilli, a large number of reports on the occurrence of the disease were made from all over the world (2, 3, 7, 9, 21, 34, 41, 85, 138, 142, 144, 147, 149, 150, 158, 183, 194, 195, 206, 253, 257, 259, 277, 284, 315, 316, 339, 340, 342, 344, 346, 347, 348, 378, 384, 385, 387, 388, 390, 396, 397, 406, 410, 413, 423, 424, 425, 426, 427, 429, 444, 446, 472, 476, 487, 488, 493, 494, 496, 497, 512, 513, 523, 535, 540, 541, 550, 552, 564, 573, 574).

A study of this literature seems to lead to the conclusion that these organisms did play a role in the pathogenesis of eye infections. But the exact role, whether as a primary cause or as secondary invaders, is difficult to assess. Several authors reported the isolation of these species from eyes of healthy persons, from the nose or the throat (41, 118, 147, 534), or in eyes affected by trachoma (139, 210, 378, 390, 424). The importance of predisposing factors has also been pointed out: underprivileged living conditions (41), alcohol abuse (158), trauma to the eyes (413, 540, 573), and various factors (310).

Attempts to produce the disease by inoculation of pure cultures have given variable results. Both Morax (387) and Axenfeld (19) obtained positive results. Inoculation of animals in the eyes or parenterally have given negative results.

The reason why these bacteria, which caused such a great interest in the years up to about 1920, hardly have been mentioned in the literature since then is obscure.

Reports of isolation of these organisms from other pathological conditions are few and uncertain: two cases of meningitis, one of polyserositis, and a case with symptoms suggesting typhoid fever (155, 414). The fact that these strains were penicillin resistant suggests that the diagnoses may not have been correct.

There is one more reliable report of the isolation of *M. liquefaciens* from a case of endocarditis (504) and one of repeated isolation from a case of sinusitis (519).

The occurrence of related organisms in animals does not seem to have been much studied, but Ryan (482) found strains which were very closely related to *M. liquefaciens* (52) in guinea pig eyes, and Wilcox (570) found similar strains in bovine eyes. The association of this group of organisms with eyes is striking.

**M. nonliquefaciens.** Micromorphology: Plump rods of short or medium length with rounded or often nearly square ends. Marked tendency to arrangement in pairs, occasionally in chains. Often marked variation in size, shape, and stainability. Giant cells and filaments sometimes occur, particularly in cultures incubated for more than 1 day or under unsuitable conditions (dry atmosphere).

Colonies: After 20–24 h colonies are from about 0.5 to 1.5 to 2 mm in diameter, low convex, sometimes with a domed center and a flat periphery, semitranslucent to opaque, often with an opaque center and a more translucent periphery. Soft to friable consistency. Nonhemolytic. When colonies in primary cultures from pathological material are scraped off blood agar plates, marked pitting of the agar is usually seen, and if cultures are incubated for a few days in a humid atmosphere, the SC-type of colony often develops with irregular margins, which often are surrounded by thin, granular films of spreading growth, with marked "corrosion" under the colonies. Rare strains (245) at first appear as depressions ("craters") in the agar with a central papilla. After repeated subcultures, this colony type often changes to the regular, smooth, convex N type.

No swimming motility, but twitching can be demonstrated in cultures in the SC phase. Fimbria are found in this phase.

Some strains, mostly (or always) isolated from nose or sputum of patients suffering from ozaena (231, 233, 246, 379), are encapsulated and grow with large mucoid colonies resembling the most common type of *Klebsiella ozaenae* (serotype 4). The capsular antigen appears to be the same in all such strains. In these cases, atoxic *C. diphtheriae* of the mitis type is regularly present.

Physiology: Growth is poor or fails on simple peptone media, e.g., Clark & Lubs' medium or Hugh & Leifson's O-F medium. Moderate growth on nutrient broth or agar of good quality (brain-heart infusion, Todd-Hewitt broth). Growth is improved by addition of serum or ascites fluid. Slight growth at room temperature. Optimal growth at 33 to 37 C, but some strains fail to grow or grow very poorly at the latter temperature if the atmosphere is dry. Killed by exposure to 49 C for 10 min or less. Keeps alive on blood agar at room temperature for at least 27 days.

Biochemical reactions: Nitrates reduced to nitrites. Gelatin and serum not liquefied. No growth in Koser's citrate medium. Some strains split urea immediately after isolation, but this property is lost in subculture. Phenylalanine and tryptophan are not deaminated.

Habitat: Respiratory tract of man (37, 45, 60, 235, 300, 302, 404, 421). Very common (about 10 to 20%) in the nose, where it is most easily detected. Occurs in the throat, but is more difficult to detect. Apparently rare in other localities. Not yet known to occur in animals.

Pathogenicity: *M. nonliquefaciens* seems to be a quite harmless commensal in the respiratory tract. Only extremely rarely does it seem to cause disease. It may be recalled that the first strain to be isolated (490) was believed to be the cause of keratitis. In view of the very large number of cases of diplobacillary eye infection that have been studied, it is remarkable the *M. nonliquefaciens* has only been identified once. However, the diagnoses were frequently only made by microscopy or by inadequate cultural methods, and one may suspect that some of the organisms encountered in such infections may actually have been *M. nonliquefaciens*. It can hardly have been a common organism in eye infections, however.

Hurez et al. (270, 283) reported a case of purulent meningitis in a 3-year-old boy where *M. nonliquefaciens* was cultivated from spinal fluid and blood. Another case in a 20-year-old man was reported by Reynaud, Le Noc, and Massat (465). Lapeysonnie et al. (320) reported a mild epidemic of meningitis where *M. nonliquefaciens* was isolated from several cases. They discussed the possibility that it might have been secondary invasion in virus infections. Lapeysonnie (319) reported nine cases—probably from the same outbreak. At the time when these reports were made, the differentiation of *M. nonliquefaciens* from organisms such as *M. osloensis*, *M. phenylpyrouvica*, and *M. urethralis* was impossible. The identity of the isolated strains, therefore, is uncertain.

Some cases of infections with isolation of *Mima polymorpha* var. *oxidans* have been reported (91, 123, 314). These, also, might have been any of the mentioned *Moraxella* species.

Mucoid strains of *M. nonliquefaciens* have been found to be associated with chronic disease of the nose and bronchi by several authors (45, 231, 233, 246, 379). In most, if not all these cases (246, 379), the patients were found to suffer from ozaena or from a corresponding bronchial infection. The pathogenic role of these bacteria is unknown. The reason why these mucoid strains, like *K. ozaenae* and mucoid strains of *Acinetobacter* (379), should be associated with ozaena and, in the case of the two former species apparently exclusively with this disease, is an

unsolved mystery. The regular presence of atoxic *C. diphtheriae* in this disease suggests the possibility that the whole thing may have started with nasal diphtheria with secondary invasion of the mucoid organisms. There is little reason to think that the latter are the cause of the disease.

Type strain (neotype) is 4663/62 (NCTC 10464, ATCC 19976) (68).

**M. bovis.** Micromophology: Plump diplobacilli of similar appearance as *M. nonliquefaciens*. Some strains have more slender rods. Chains not uncommon. Nonencapsulated. No swimming motility, but twitching can be demonstrated in the SC or NSC phase.

Colonies: Small, comparatively flat, greyish, semitranslucent, soft colonies can appear with the SC, NSC, or N type of colony as described for *M. nonliquefaciens*. Strains freshly isolated from bovine eyes are in the SC phase. Hemolytic, but nonhemolytic variants occur (452).

Physiology: Poor or no growth on ordinary fluid media: indol medium, nitrate medium, and Clark & Lubs' medium. Fair growth on nutrient agar. Good growth on media containing blood, serum, or ascites fluid. Feeble growth on the surface of Hugh & Leifson's O-F medium. Little or no growth at room temperature. Optimal growth from about 32 to 37 C.

Biochemical reactions: Nitrate not reduced to nitrite in customary media. Wilcox (570) found that his strains reduced nitrates in Trypticase-soy broth. No deamination of phenylalanine or tryptophan. No urease. No growth in Koser's citrate medium. Gelatin and serum are liquefied.

Habitat: Isolated from the eyes of cattle suffering from infectious keratoconjunctivitis and, less frequently, from eyes of normal cattle.

Pathogenicity: *M. bovis* is associated with infectious bovine keratoconjunctivitis (IBKC), or at least with many outbreaks of this syndrome, as shown by numerous reports (1, 6, 23, 26, 153, 156, 175, 189, 247, 281, 285, 417, 461, 563, 568, 569, 570). Some authors have not found evidence of any such association (168, 514). Thus Spradbrow (514) studied 25 outbreaks and could only find *M. bovis* in two herds, and only in one of them was *M. bovis* frequently found. Some authors report finding the organism more or less frequently in the eyes of healthy animals (1, 204, 569), whereas others do not (23, 26, 156, 281).

Many attempts have been made to transmit the disease to healthy animals. Some authors report successful transmission by means of eye secretions (6, 153, 281, 461), which proves very little, whereas many authors report successful transmission of the disease, often in mild form, by instillation of cultures of *M. bovis* into the eyes (1, 23, 26, 175, 247, 281, 285, 418, 419, 461). Others have failed in this (6, 153, 204, 563). Of the latter authors, one (153) used an old laboratory culture, and another (563) states that his culture had become rough before he used it for the experiments. Attempts to produce the disease in other animals have given negative results in some cases (23, 153, 175). Pugh, Hughes, and McDonald (455) managed to establish *M. bovis* in the eyes of sheep and mice, but not of rabbits, rats, or guinea pigs. Thirteen of 18 inoculated mice developed conjunctivitis, and 10 developed keratitis. Henson and Grumbles (248) found that *M. bovis* produced pathological changes in chicken embryos, rabbits, and mice. They also (249) found a labile hemolytic toxin bound to the cells and a dermonecrotic toxin resembling an endotoxin. Although there thus is considerable evidence to show that *M. bovis* plays a pathogenic role in many outbreaks of IBKC, its etiological role is far from clear. It seems possible that IBKC may be a syndrome which can be due to different causes. Thus mycoplasma (317), viruses, e.g., infectious bovine rhinotracheitis virus (509, 528, 529, 568), and rickettsia-like organisms (568) have been suggested as possible causes of the disease.

It also seems possible that simultaneous infection with two different agents may play a role. Pugh, McDonald, and Packer (457) showed experimentally that an infection with infectious bovine rhinotracheitis virus enhanced the pathogenic effect of *M. bovis*. It also appears that its pathogenic effect may be enhanced by other factors. In some countries the disease only occurs in the summer season (168, 568), and agents such as ultraviolet light and the activities of flies (168, 522, 568) may play a role. Hughes, Pugh, and McDonald (263–266, 452) in a series of papers studied the enhancing effect of ultraviolet irradiation on experimental infection with *M. bovis*. It proved easier to produce experimental infection after preceding irradiation.

Variations in virulence may explain some of the discrepancies between the results of different attempts to produce experimental infection. Hemolytic activity may be one virulence factor, as suggested by Pugh and Hughes (452). They found that nonhemolytic variants appeared to have a reduced capacity for causing keratoconjunctivitis and that a superinfection of eyes harboring a nonhemolytic variant with a hemolytic variant could produce disease symptoms.

Some authors have mentioned S to R dis-

sociation as a possible cause of variations of virulence (153, 247, 281, 563). The studies of Pedersen, Frøholm, and Bøvre (419) and Bøvre and Frøholm (66, 67) throw some light on this. They found that freshly isolated strains grew with the SC type of colony mentioned above, which was characterized by fimbriation, twitching motility, and the capacity to colonize the bovine eye and to cause conjunctivitis. The N type, which tended to arise on continued subcultivation, lacked these characters.

In summary, although there is strong evidence for the pathogenic role of *M. bovis* in IBKC, in fact rather more convincing than in the case of *M. lacunata* and human conjunctivitis, there are still many unsolved problems.

Type strain (neotype) ATCC 10900 (241).

**M. osloensis:** Bøvre and Henriksen 1967 (68).

Micromorphology: Often as for *M. nonliquefaciens*. Some strains have a more fusiform or lanceolate shape of the cells, others show a predominance of diplococcal cells.

Colonies: Usually slightly smaller than of *M. nonliquefaciens*, with entire edges and glistening surface. Soft or coherent consistency. No pigment, nonhemolytic.

Physiology: Simple growth requirements. Will grow in a defined medium with ammonium ions as source of nitrogen and a simple organic compound as source of carbon (29, 68, 251). Fair growth on all the usual media. Grows within the range from room temperature to 37 C. Is somewhat more resistant to heat than *M. nonliquefaciens* (killed by exposures from 53 C for 20 min to 65 C for 10 min). Grows on Hugh and Leifson's O-F medium. Keeps alive at room temperature on blood agar for at least 27 days. Accumulates poly-$\beta$-hydroxybutyrate inclusions.

Biochemical reactions: Nitrates may or may not be reduced to nitrates. No urease except for irregular reactions which may be seen in freshly isolated strains. According to Pickett and Pedersen (433), acid is produced from ribose and xylose. Other biochemical reactions are as for *M. nonliquefaciens*.

Antibacterial agents: Less sensitive to penicillin than other *Moraxella* species (sensitive to about 0.1 unit/ml). Sensitive to the other commonly used antibiotics.

Habitat: Uncertain. Strains have been isolated from the genitourinary tract, blood, spinal fluid, and nose, but it appears to be rare in the respiratory tract.

Pathogenicity: Probably low. Strains have been isolated from cases of serious infection, but only rarely. A case of septic arthritis has been described (159).

Type strain: A 1920 (NCTC 10465, ATCC 19976) (68).

**M. phenylpyrouvica.** Bøvre and Henriksen 1967 (69).

Micromorphology: Short rods, mostly occurring as diplobacilli of slightly smaller dimensions than in *M. nonliquefaciens*. Often somewhat irregular in thickness and shape of the individual cells. May occasionally be encapsulated.

Colonies: On blood agar colonies are from pin-point size to 1 mm in diameter after 20 h, smaller than those of *M. nonliquefaciens*, low convex with a tendency to form an irregular edge with a raised center on prolonged incubation. Semitranslucent to moderately opaque. Unpigmented. Soft, mucoid, or friable consistency. No hemolysis, but sometimes a greenish discolorization of blood agar. After incubation for 2 to 3 days blood agar plates turn brown (more rapidly than with other *Moraxella* species).

Physiology: Growth requirements not known in detail, but apparently fastidious. Poor growth in fluid peptone media without aeration, but grows well on the surface of Hugh and Leifson's O-F medium. Usually no growth on Koser's citrate medium or in Audureau's defined medium with ethanol (16). Slight growth at room temperature. Optimal growth at 33 to 37 C. Less sensitive to heat than *M. nonliquefaciens*, resisting exposure to 53 C for 30 min, and being killed by exposure to 57 C for 20 min. Remains alive on blood agar at room temperature for at least 40 days.

Biochemical reactions: Nitrates usually reduced to nitrites, with some exceptions and some weak reactions. No acid from carbohydrates. Gelatin and serum not liquefied. Usually rapid splitting of urea. Phenylalanine and tryptophan strongly deaminated.

Habitat: Uncertain. Strains have been isolated from the genitourinary tract, blood, spinal fluid, and pus from various lesions. A case of brain abscess ascribed to *Moraxella polymorpha* has been reported (343). Whether this was *M. phenylpyrouvica* is uncertain.

Pathogenicity: Probably low.

Type strain 2863 (ATCC 23333, NCTC 10526) (69).

**M. kingii.** Henriksen and Bøvre 1968 (244).

Micromorphology: Cells are somewhat smaller than those of other *Moraxella* species, with square ends in pairs and chains. The tendency to chain formation is more marked than is usual in other species. Nonencapsulated.

Colonies: May occur in the SC type or the N

type. The latter is small, delicate, low convex, and nearly translucent, with a circular, entire edge and a glistening surface, 0.1 to 0.5 mm in diameter after 20 h on blood agar.

The SC type colony starts growth as tiny depressions in the agar with a raised central papilla and a granular surface. After 2 to 4 days the size increases to 4 to 5 mm. In the first 2 to 3 days several concentric zones with finely granular surfaces may be seen. The central part of the colony gradually becomes filled with growth and becomes raised with an irregular or a smooth surface. Old cultures may be highly pleomorphic. When the growth is gently removed, "corrosions" of the agar surface become apparent. The SC type is fimbriated, shows twitching motility, and is competent in transformation. Both colony types are surrounded by narrow zones of beta hemolysis.

Physiology: Fastidious growth requirements. Little or no growth in peptone media. Moderate growth on nutrient agar. No growth on Hugh and Leifson's O-F medium. Practically no improvement of growth by addition of serum. No need for X or V factors. Slight or no growth at room temperature. Optimal growth at 32 to 37 C. On blood agar kept at room temperature, different strains keep alive for 6 to 23 days.

Biochemical reactions: Catalase negative. Nitrates reduced to nitrites by some strains. Acid from glucose and maltose on ascites agar slants, a trace of acid from galactose. No acid from fructose, lactose, saccharose, arabinose, xylose, rhamnose, mannitol, dulcitol, sorbitol, or glycerol. Gelatin and serum not liquefied. No urease or deamination of phenylalanine and tryptophan.

Habitat: Many of the strains were isolated from the human throat. Strains have also been isolated from nose, blood, bone lesion, and joint.

Pathogenicity: Probably low.

Type strain 4177/66 (ATCC 23330, NCTC 10529).

### Candidates for the Genus Moraxella

**M. urethralis.** (325) Although the name of this species has not been validly published, nor its taxonomic position determined, it seems reasonable to describe it here.

Micromorphology: Small gram-negative rods, 0.6 × 1 to 1.5 μm coccoid to short rods. More irregular forms also occur. Predominant arrangement in pairs and aggregates. Flagella, endospores, and capsules absent.

Colonies: 1.5 to 2 mm after 48 h, uncharacteristic, nonhemolytic, more overtly white than the described *Moraxella* species.

Physiology: Aerobic. Simple growth requirements. Slow growth in a simple mineral medium with ammonium ions as nitrogen source and acetate or hydroxybutyrate as the only source of carbon. Poly-β-hydroxybutyrate inclusions occur regularly.

Biochemical reactions: Oxidase positive with both reagents, catalase positive. No acid from carbohydrates and alcohols, except slowly and weakly from ethanol. Gelatinase, urease, phenylalanine deaminase, and nitrate reductase are absent. Indol, acetoin, and $H_2S$ are not produced.

Antibacterial agents: As sensitive to penicillin as the known *Moraxella* species.

Habitat: Isolated from human sources, mostly from urines and specimens from the female genital tract.

Pathogenicity: Probably low.

Genetic compatibilities: Incompetent in transformation. DNA from streptomycin-resistant mutant does not transform *M. nonliquefaciens*, *M. osloensis*, *N. catarrhalis*, *N. ovis*, or *N. elongata* (70).

This organism seems to be indistinguishable from certain cultures labeled *Mima polymorpha* var. *oxidans*, but other strains with the same label differ from this organism.

**M. anatipestifer.** In 1954 Bruner and Fabricant (86b) studied a strain, isolated from duckling, thought to belong to the species named *Pfeifferella anatipestifer* by Hendrickson and Hilbert in 1932 and renamed *Pasteurella anatipestifer* in the 6th edition of Bergey's Manual. The strain was a short gram-negative, nonmotile rod occurring singly and in pairs. It grew on ordinary media, but serum improved growth.

Sugars were not fermented, but gelatin and coagulated egg and serum were liquefied.

In contrast to the organism of Hendrickson and Hilbert, the strain at first required $CO_2$ for growth, but could be adapted to growth without $CO_2$.

The authors question the pathogenicity of the strain for ducks. They believe the organism belongs to the genus *Moraxella* and that it should be named *M. anatipestifer*. They state, however, that the strain had been studied by R. G. E. Murray of the University of Western Ontario and that he did not find it to be "a morphological relative of the Moraxella cultures that he has examined." Additional studies would be needed to decide the relationship of the organism to *Moraxella*.

### Unnamed Species of Uncertain Taxonomic Position

Two other strains thought to represent new *Moraxella* species have been described. One of them was the "new *Moraxella* strain" of van

Bijsterveld (43), the other a strain described by Sutton et al. (526). Although they have not been named, and their taxonomic position is undecided, a description of these apparently similar strains is given here.

Van Bijsterveld's strain (43):

Micromorphology: Straight rods with rounded ends, 2 to 5 × 0.5 to 1 μm, usually arranged in pairs and, during active growth, often in chains. On prolonged incubation pleomorphism appears with ovoid bodies and filaments, which usually do not stain well. Circular or oval areas in the cytoplasm which do not stain well were usually prominent in these cells. No swimming motility. "Gliding" motility was observed. Gram-negative, but some cells are slow in decolorizing. Capsulated.

Colonies: After 24 h colonies are 0.1 to 0.5 mm in diameter, circular, low hemispherical or low conical, isolated colonies often being twice as large. The colony differentiates into a raised, slightly opaque center and a flattened, translucent periphery. The structure is amorphous to finely granular. The colony is smooth and glistening, of butyrous consistency, and easily emulsified, with a tendency to autoagglutination in saline. No beta hemolysis, but some hemolysis is seen after 3 days on a 1-mm rabbit blood overlay agar. Alpha hemolysis is seen on sheep blood agar and sometimes on horse blood agar.

Physiology: Strict aerobe. $CO_2$ does not improve growth. No growth at 20 C. Optimal growth between 33 and 37 C. A humid atmosphere enhances growth. Apparently complex growth requirements. No growth in Koser's citrate medium or in Audureau's medium (16). No growth on MacConkey's agar, Endo agar, or desoxycholate-citrate agar. Poor growth on peptone media. Growth on simple media is improved by addition of serum. No requirement for hematin or nicotinamide adenine dinucleotide. Very light brown pigment formed on Loeffler's serum. Viable after 5 to 9 days at 37 C, for 11 to 21 days at 33 C, for 14 to 21 days at 20 C and for 32 to 40 days at 4 C. The strain is killed after 5 min at 51 C.

Biochemical reactions: Catalase negative, oxidase reaction strongly positive with tetramethyl-*p*-phenylenediamine and weakly positive with the dimethyl reagent. Acid formed by oxidation from glucose, mannose, fructose, saccharose starch, dextrin, and maltose. A trace of acid from galactose, trehalose and xylose. No acid from adonitol, arabinose, cellobiose, dulcitol, glycerol, inulin, lactose, mannitol, melibiose, melizitose, mesoinositol, raffinose, rhamnose, salicin, and sorbitol. Ten percent lactose not attacked. Indol positive. Methyl red negative. Acetylmethylcarbinol not produced. Nitrate and nitrite not reduced. No urease. No reduction of methylene blue. Weak gelatinase.

Arginine, hippurate, and esculin not hydrolyzed. Thyrosine and xanthine not decomposed. Slight casein digestion. No beta galactosidase activity. Oxidative deamination of DL-norleucine and L-phenylalanine. Reactions with L-leucine, DL-methionine, and L-tryptophan were dubious (negative reaction with L-tryptophan and weak positive reaction with phenylalanine (unpublished data). Negative decarboxylase reactions with L-arginine, DL-ornithine, and glutamic acid.

Antibacterial agents: Highly sensitive to penicillin, chloramphenicol, streptomycin, oxytetracycline, erythromycin, and many other antibiotics.

Habitat: Isolated from a case of angular conjunctivitis. Pathogenicity unknown. DNA base composition 49 mol% G+C. The designations of the strain in type culture collections are ATCC 25869 and NCTC 10717.

The strain of Sutton et al. (521). This organism appears to share the great majority of characters with van Bijsterveld's strain. It therefore only seems necessary to state the points which appear to differ from the latter strain.

Colonies: Slow growth. After 24 h at 37 C, colonies are 0.1 to 0.5 mm. The colonies tended to grow down into the medium, resulting in indentations of the surface immediately beneath it. After 48 to 72 h colonies were 1 to 1.5 mm in diameter with an occasional colony twice this size, smooth, glistening, many with a raised, slightly opaque center and a flat, translucent periphery. The colonial appearance resembled that of *Bacteroides corrodens*. No hemolysis after 24 h, but after 48 h, there was incomplete hemolysis on sheep blood agar.

Biochemical reactions: Does not deaminate phenylalanine. No liquefaction of gelatin.

Habitat: Isolated from a corneal abscess in man. Pathogenicity unknown. DNA base composition 49.9 mol% G+C. The strain has been deposited in the National Collection of Type Cultures, London.

Comment: These strains resemble *Moraxella* species in some respects, but there are some objections to their classification as *Moraxella* species. One objection is the extensive attack on sugars. It is true that *M. kingii* also attacks some sugars. Other sugar-decomposing strains have also been described. *M. saccharolytica*

Flamm 1956 (163) has been shown by Lautrop (324) to be identical with *Flavobacterium meningosepticum* and is no *Moraxella*. A strain described by Chiu (117) may or may not have been a *Moraxella*. It would need to be studied further to clarify its taxonomy. As for *M. kingii*, it has been placed in this genus for the time being, but it differs from the other *Moraxella* species in several respects: DNA composition, lack of genetic compatibility with other species, and morphology, and there is considerable doubt whether it really belongs in *Moraxella*.

A second objection is the indole production, which is unknown in the genus *Moraxella*. The morphology also is atypical of *Moraxella*. If the difference in DNA base composition (49 and 49.9 mol% G+C) can be verified, it is a further strong argument against classifying these strains as *Moraxella*. However, in the paper of Sutton et al. (526) the DNA base composition of *M. kingii* is given as 49 mol% G+C instead of the 44.5 mol% found by Henriksen and Bøvre (244). This discrepancy needs an explanation.

Sutton et al. (526) compare their strain with *M. kingii*, *B. corrodens*, and van Bijsterveld's strain and find that their strain resembles the latter strain most closely. In fact, the resemblance may be greater than realized by Sutton et al. The differences they list are motility and phenylalanine deaminase (both positive in van Bijsterveld's strain) and colony appearance. The motility reported by van Bijsterveld, however, was of the "gliding" (twitching?) type, which the strain of Sutton et al. apparently was not checked for. In view of the fact that their strain grew with typical SC colonies, observed in several *Moraxella* species, it is reasonable to guess that this strain would also show twitching motility. Also, in analogy with the *Moraxella* species, the fact that van Bijsterveld's strain showed twitching motility might tempt one to guess that this strain may have grown with SC-type colonies when freshly isolated. Thus the difference between the colonies of the two strains may be no more than a difference in the phase of the SC to N variation.

Finally, repetition of the test for phenylalanine deamination carried out simultaneously and by identical technique (unpublished data) showed that both strains gave a weak positive reaction with phenylalanine, possibly slightly stronger in van Bijsterveld's strain, but both strains gave negative reactions with tryptophan. Thus there is no significant difference in this character.

The conclusion is, therefore, that the strains of Sutton et al. and of van Bijsterveld are nearly identical and should be placed in the same species, but that it is highly questionable that this species should be placed in *Moraxella*.

### Other Possible Candidates for the Genus Moraxella

Hughes and Pugh (262) describe organisms isolated from eye infections in horses. These nonhemolytic, nonproteolytic strains appear to have the typical characters of *Moraxella*, including the oxidase reaction. Larsen, Bille, and Nielsen (321) described organisms isolated from neonatal piglets with high frequency. The piglets appeared to be debilitated or underdeveloped and died in the preweaning period, and in many cases the organisms appeared to have caused generalized infections. They are thought to belong to *Moraxella*, with good reason, to judge from the description.

Wilcox (568, 569) from infected bovine eyes isolated *Moraxella*-like strains which differed from *M. bovis*. The relationship of the organisms listed in this paragraph to *Moraxella* deserves study in order to find out if they belong to known species or represent new species. It also seems probable that an intensified search for *Moraxella*-like organisms in the eyes and respiratory tract of other animal species might be rewarding.

Withers and Davies (572) isolated an organism identified as *M. lacunatus* from cats with conjunctivitis.

Some of the strains studied by Thornley (539), in particular her phenon 3, are other possible candidates for membership in *Moraxella*. Judging from the study of a few of them, these strains have some of the characters of *Moraxella:* typical micromorphology, positive oxidase reaction, moderate growth energy, and high sensitivity to antibiotics. They deaminate phenylalanine and tryptophan nearly as efficiently as *Proteus* or *M. phenylpyrouvica* and produce urease. They differ from *Moraxella* in refusing to grow at 35 C and, like *A. calcoaceticus*, in oxidizing various aldoses (glucose, mannose, arabinose, xylose, and lactose). Some strains are fimbriated (539) and some produce marked "pitting" of agar surfaces. The DNA base composition is given as 44 to 44.5 mol% G+C, near to the range of *Moraxella* and *Acinetobacter*.

Further study is needed to decide if these organisms are related to *Moraxella* or, as suggested by Thornley (539), to *Acinetobacter*.

### Genus Acinetobacter

This genus as defined by Brisou (76), by Brisou and Prévot (81), and by Prévot (451)

contains some species which are of no interest to this review, and which will not be dealt with here. We are only concerned with the organism defined as *A. calcoaceticus* in the chapter on taxonomy.

**A. calcoaceticus.** Micromorphology: On agar cultures many strains produce mainly coccoid cells with a marked tendency to occur in pairs, looking like, and easily confused with, *Neisseria*, but a careful study of the films always reveals a few rods. In fluid cultures the picture may be more pleomorphic with more abundant rods and some filaments. In some strains, rods may predominate even in agar cultures. The cells are usually rather plump and gram-negative with some tendency to resist decolorization. Many strains are encapsulated. No endospores, no flagella.

Colonies: In some strains colonies are domed and mucoid with a more or less viscous or gluey consistency. They may be 1 to 2 mm in diameter after 20 h and increase to several mm. In other strains, colonies are low convex, smooth, even, entire, more or less opaque, and usually of a butyrous consistency. Some strains produce "pitting" of the agar surface. Many strains, when studied by agar microscopy, show twitching motility (322, 323, 436), and a variation from a twitching to a nonmotile variety and vice versa can be demonstrated.

Physiology: Comparatively simple growth requirements (30). Will grow on simple, even in chemically defined media (16) with ethanol or other simple organic compounds as sole source of energy. Strict aerobes. Some strains are mesophilic, others fail to grow at 35 C. Some strains are capable of growing near 0 C (539). These organisms, in contrast to *Moraxella*, are highly versatile biochemically and nutritionally have become very popular subjects for biochemical studies (14, 15, 17, 32, 95–102, 115, 122, 161, 175, 177–179, 206, 211, 217–225, 227, 251, 256, 272, 286, 289, 297–299, 303, 304, 306, 326, 330–336, 355–361, 375, 391, 408, 409, 474, 475, 525, 546, 547, 549, 556, 565, 566).

Biochemical reactions: These are variable, and based upon different patterns the genus has been proposed to be divided into different species and subspecies by different authors. The catalase reaction is positive and the oxidase reaction is negative. Nitrate is not reduced to nitrites (or reduced only slightly, for a light pink color of questionable significance may sometimes be seen after addition of the nitrite reagents), but this is apparently not due to failure of utilizing nitrate. Jyssum and Joner (297–299) found that a strain of *B. anitratum* could utilize nitrate or nitrite as sole source of nitrogen and that hydroxylamine was a possible intermediate in nitrate reduction. Juni (294) recently found that several strains of *Herellea vaginicola* reduced nitrate. The strains transformed his competent strain of *Acinetobacter*. Many strains oxidize aldoses: glucose, mannose, galactose, arabinose, rhamnose, and often lactose in peptone water media. These strains always produce acid on 10% lactose agar slants, but fail to attack other sugars, except occasionally maltose. Glucose is oxidized to gluconic acid (108, 335, 556) and lactose to lactonic acid (555). Many strains fail to produce acid from sugars in peptone water, but do so if the medium is diluted with water, or if the bacteria are incubated in the salt solution employed by Aiken, Ward, and King (4). A minority of strains fail to show acid production even in these conditions (unpublished data). Whether this is due to inability to attack sugars or only to very low attack rates has not been determined.

The strains which produce acid in usual fermentation media correspond to *B. anitratum-M. glucidolytica*, whereas those that only produce acid under special condition correspond to *M. lwoffi*. Some strains of each of these types liquefy gelatin and serum. Some strains split urea, and citrate is utilized by some strains. Phenylalanine and tryptophan are not deaminated, and lysine, ornithine, arginine, and glutamic acid are not decarboxylated. The *o*-nitrophenyl-β-D-galactopyranoside test is negative, and indol, $H_2S$, and acetoin are not produced.

Some strains, both of the "saccharolytic" and "asaccharolytic" types, produces very strong hemolysis on blood agar, characterized by very clear, rapidly growing zones of hemolysis with very sharp borders with increased color intensity (232). The hemolysin is filterable and antigenic, and the activity of hemolysin from different strains is neutralized by the same immune serum. The hemolysin has been shown to be a phospholipase C (330–334), which also has a lytic action on leukocytes.

Antibiotic agents: The strains vary in sensitivity to antibiotics. They are rarely sensitive to penicillin.

Habitat: The main habitat appears to be soil and water. The organisms have been isolated with high frequency from soil (27, 31, 44, 556) and from water (27, 305, 376). They have also been found in milk and dairy products (93, 313, 412, 460), poultry meat (539), and frozen food (149). They have also frequently been isolated from human sources, probably as contaminants from the surroundings: skin (209, 533), saliva (503), conjunctiva (369, 407), and urine (430), as

well as from practically any possible kind of specimen of pathological material. Thus they may be considered as ubiquitous organisms, which are very frequent contaminants, but which are not, as it has been claimed, organisms indigenous to man. This has frequently not been realized by medical bacteriologists or clinicians working with these bacteria. They have frequently been isolated from animals, both as harmless commensals or contaminants and as apparent causes of disease (12, 104, 143, 197, 459, 460, 478, 508, 571).

Pathogenicity: The literature on the isolation of these organisms from clinical material and on their role as pathogens is very extensive and highly confusing. This is connected with the confusion which has been reigning about the taxonomy and nomenclature of the organisms, as well as with inaccurate description and identification, and incorrect or inaccurate naming, as well as with the fact that very frequently a pathogenic role of the organism has been assumed on doubtful grounds and on insufficient evidence.

The conclusion can not be avoided that in many cases harmless contaminants, derived from the patient or introduced by the sampling procedure, have been taken to be causative agents of disease.

There is reason to think that in the majority of cases where the organisms have been isolated from clinical material, they have only been contaminants or more or less harmless secondary invaders. Still there is no doubt that they do sometimes cause infections, even serious or fatal ones. There is some reason to suspect that such infections have increased in number in recent years. The literature indicates that many of these infections attack individuals who are particularly predisposed such as infants, particularly premature infants, or persons suffering from other serious disorders: burn patients or patients suffering from malignancies. Many cases appear to be iatrogenic: postoperative infections or infections caused by unsterile instruments, e.g., infusions through disposable catheters (121).

The most serious and most frequently reported infections are meningitis and septic infections with or without endocarditis. Reports of meningitis cases are numerous (10, 11, 20, 25, 33, 35, 36, 38, 39, 86, 87, 89, 91, 113, 114, 128, 133, 135, 136, 154, 169, 170, 181, 187, 188, 198, 202, 208, 209, 226, 250, 258, 269, 319, 328, 349, 351, 352, 373, 377, 389, 400, 401, 405, 428, 445, 450, 464, 467, 477, 498, 505, 506, 507, 510, 520, 531, 532, 543, 558, 559, 562).

Reports of septic infections are also numerous (5, 40, 88, 103, 112, 121, 132, 151, 152, 154, 155, 157, 166, 176, 182, 190, 193, 199, 201, 207, 213, 214, 229, 252, 266, 271, 279, 280, 283, 309, 366, 367, 374, 381, 395, 441, 443, 450, 468, 479, 480, 495, 502, 511, 537, 538, 544, 545, 554, 561).

Of the meningitis cases where the identity of the organism was reasonably certain, 47 were due to the "saccharolytic" biotype, and 61 to the "asaccharolytic" type. At least 8 of the cases were postoperative infections, and at least 40 of the patients were newborn infants, young infants, or very small children. In one "outbreak" (20, 169), 41 strains of *M. lwoffi* were isolated from spinal fluid and three from blood. The clinical symptoms, biphasic fever with symptoms of serous meningitis, strongly suggested an epidemic of viral infection, and the cell counts in the spinal fluids were mostly very moderate. Simultaneously there were widespread epidemics of similar infections with verified viral etiology in the same geographical region. The possibility of contamination (possibly use of unsterile "disinfectants"?) is apparent.

Of the cases of septic infection, including at least 9 cases with endocarditis, where the identity of the organism had been established, 86 were due to "saccharolytic" and 39 to "asaccharolytic" strains. At least six of the patients were infants. Many of the others suffered from predisposing diseases: cholecystitis, intestinal disease, and burns, and in many cases iatrogenic causes could be demonstrated (121), e.g., the use of disposable catheters for infusions. Several of the cases were hyperacute with the Waterhouse-Friederichsen syndrome. In other cases the symptoms were extraordinarily mild, suggesting the possibility of contamination during or after sampling. Faris and Sparling (152) obtained positive blood cultures of *Mima polymorpha* from 27 patients, only three of which had symptoms of septic infection. The positive cultures were mainly obtained from cultures with penicillinase, and probably were due to contamination of the latter. However, in septic infections as in meningitis, a sufficient number of seemingly satisfactorily verified cases remain to indicate the pathogenic potential of the organisms. These organisms have been isolated from a wide assortment of clinical specimens. This has been shown in a number of reports on the occurrence and clinical role of these bacteria (5, 13, 116, 120, 146, 167, 205, 254, 271, 275, 276, 279, 320, 329, 345, 350–353, 363, 422, 448, 449, 466, 470, 471, 481, 485, 542, 560). The attitude of the authors varies from full acceptance of the pathogenic role of the organisms to skepticism.

There are reports of isolation of the organisms

from wounds (13, 83), ulcers (13, 104, 124, 329, 536), burns (271), abscesses and cellulitis (13, 84, 113, 121, 545), brain abscesses (365, 405, 557), diseases of the chest (22, 121, 129, 136, 154, 177, 232, 329, 440, 530), cholecystitis, liver abscesses and bile (140, 280, 329), pancreatitis (280), fracture (13), joints (273, 477, 485), serous cavities (415), vaginal secretions (in some cases thought to be true infections) (72–74, 162, 318), skin infections (134, 205, 545), eyes, including conjunctivitis (84, 90, 154, 205, 368, 386), ears, including otitis media and external otitis (35, 83, 84, 192, 205), and intestinal disease (94, 205, 337). Some authors emphasize the importance of predisposing factors such as the use of respirators (462), immunosuppression, and malignancies (201).

The study of this extensive and confusing literature leaves the impression that *A. calcoaceticus* is an opportunistic organism which may, particularly when the resistance to infection is low, cause infections, even serious ones, but that in the majority of cases isolation of this organism is of slight clinical significance, representing only contamination or secondary invasion of damaged or devitalized tissues. These are views which have been expressed by many of the cited authors. But there are also authors who appear to overestimate the pathogenic role of the organism.

Examples which illustrate this point are reports on isolation of the organism from urine (135, 136, 145, 154, 205, 329, 545, 552) and from urethritis, including so-called "therapy-resistant gonorrhea" (124, 274, 307, 314, 469, 486, 527, 545). In the case of urine, some authors are skeptical and only accept cases which have been verified by satisfactory bacteriological criteria, e.g., repeated isolation in significant numbers, whereas others are uncritical.

Some observations (unpublished data) illustrate some of the diagnostic pitfalls. In a certain period there appeared to be an outbreak of nosocomial urinary infections due to a hemolytic, "asaccharolytic" strain (*A. haemolysans*). The outbreak only affected men, but contrary to expectation they were all in a medical, and not a surgical, ward. Some detective work showed that before voiding urine for bacteriological examination, the patients were instructed to wash themselves with (unsterilized) cotton and water. Examination of containers intended for this purpose showed that they contained heavy suspensions of the "offending" strain, probably derived from the cotton.

In a later period, a similar "outbreak" occurred in a gynecological ward, "due to" a hemolytic, saccharolytic strain. In this case it was found that a container with "disinfectant" used to decontaminate the catheters, containing a low concentration of a quaternary ammonium compound, actually contained a veritable culture of the strain. It may be added that in spite of the use of the contaminated catheters, no evidence was obtained that any of the women became infected with the organism.

As for urethritis, DeBord (125–127) first called attention to the occurrence of these organisms in the genitourinary tract, which, he thought, represented a pitfall in the diagnosis of gonorrheae by direct microscopy. This idea appears only to be a hypothesis, and nowhere in the papers of DeBord, or in other papers on the subject, is any proof given that this really has been a cause of diagnostic error.

Svihus et al. (527) first postulated that members of the tribe "*Mimeae*" were the cause of some cases of therapy-resistant urethritis. This postulate has been accepted by several subsequent authors and has often been mentioned in the literature, in spite of the fact that absolutely no proof has been presented that the "*Mimeae*" actually are capable of causing urethritis. The only pieces of evidence that were brought forward were that these organisms were found in the cultures and that *N. gonorrhoeae* was not detected. It is now well known that these organisms are quite common contaminants of the human body: skin, saliva, eyes, ears, urine, feces. There is no reason why they should not also occur as contaminants of specimens taken from the genitourinary tract. Isolation of "*Mimeae*" in such cultures does not prove that they cause infection.

It seems unlikely that these bacteria should be able to cause infections of the urethra, except, perhaps, as a secondary invader in damaged tissue. It is also difficult to believe that this condition could be caused by a variety of different "*Mimeae*." Of 22 strains studied, 10 were *Mima polymorpha* var. *oxidans*, 6 were *M. polymorpha*, and 6 were other, unspecified species. Also, according to general experience, the isolation of "*Mimeae*" from cases of urethritis is not nearly as common as suggested by the report of Svihus et al.

Finally, no attempt appears to have been made to transmit the infection to healthy volunteers by means of these bacteria. Thus the postulates of Robert Koch are very far from having been fulfilled in these cases.

## CONCLUSIONS

*Moraxella* is a group of parasites on mucous membranes of man and animals, mainly in the

respiratory tract, but also, for some species, in the genitourinary tract. Their pathogenic potential seems to be low, but some species are associated with conjunctivitis and keratitis in man or animals. They are mostly bacteria with fastidious growth requirements and limited biochemical activities. They appear to be closely related to the species *Neisseria* (or *Moraxella* or *Branhamella*) *catarrhalis*, *ovis*, and *caviae*. Evidence of relationship to the other *Neisseria* species has not been demonstrated.

*Acinetobacter* is a group of soil and water bacteria of wide-spread occurrence in the surroundings of man and animals. Their pathogenic potential appears to be low, but they are opportunistic bacteria which are capable of causing infections, mainly in individuals with reduced resistance to infections or as secondary invaders in diseased tissues. Their role as pathogens has frequently been overestimated. They often occur as contaminants of pathological material. Their relationship to *Moraxella* is dubious, and their taxonomic position in the *Neisseriaceae* is based mainly on morphological resemblance to *Moraxella* or to *Neisseria*. Their growth requirements are simple, and they are characterized by great nutritional and biochemical versatility.

The names of the tribe *Mimeae* and its species have been rejected by the JC of the ICSB, and should no more be used. As used in recent years, they are synonyms of *Acinetobacter* or *Moraxella* species.

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