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# Hemagglutinin Typing as an Aid in Identification of Biochemically Atypical *Escherichia coli* Strains

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Tests for the presence of mannose-sensitive and mannose-resistant, eluting hemagglutinins and fimbriae were helpful in indicating whether biochemically atypical strains of the tribe *Escherichieae* might be escherichiae or shigellae.

In the examination of clinical specimens, biochemically typical strains of *Escherichia coli* are readily differentiable from shigellae; biochemically atypical strains, however, such as anaerogenic, nonmotile, lactose-nonfermenting strains of *E. coli*, may so mimic shigellae that their identification is troublesome, a difficulty often exacerbated by the extensive sharing of O antigens between *Shigella* and *Escherichia* (10).

Biochemically typical strains of *E. coli* are usually hemagglutinating and fimbriate (8, 9). Thus, for example, 258 (84%) of 306 biochemically typical strains of *E. coli*, primarily of urinary origin (P. B. Crichton, Ph.D. thesis, University of Dundee, Scotland, 1980), possessed a mannose-sensitive (MS) hemagglutinin (HA) that agglutinated fowl and guinea pig erythrocytes in the absence, but not in the presence, of D-mannose and was invariably associated with the presence of type 1 fimbriae (5); in addition, 162 (53%) of the 306 strains possessed one of a series of mannose-resistant and eluting (MRE) adhesins (6, 9) that agglutinated different erythrocyte species in the presence and absence of D-mannose and better at low than at high temperatures. In *E. coli*, many different patterns of MRE hemagglutinating activity have been detected (4, 6, 9, 14, 15, 23); the majority are associated with the presence of type MRE fimbriae (6, 8, 9). A few exceptional strains of $MRE^+$ *E. coli* that agglutinated a narrow range of erythrocyte species, e.g., humans or fowl only, were nonfimbriate (6, 9, 13, 19).

The O antigens 1 through 8 of the Alkalescens-Dispar (A-D) strains investigated are identical or closely related to O antigens 1, 2, 4, 7, 9, 25, and 81 of *E. coli* (10) and less closely related to certain *Shigella* O antigens (10). We wished to establish whether the A-D strains produced adhesins and fimbriae like the biochemically typical strains of *E. coli* to which they have been shown to be related as judged by polynucleotide sequence analysis (2).

## MATERIALS AND METHODS

**Bacterial strains.** The 40 A-D strains of *E. coli* used in this study (see Table 1) included 4 strains that we isolated from urine (2 strains), diarrheal feces (1 strain), and a fallopian tube (1 strain). The other 36 strains from national reference collections, and hence unselected with reference to their clinical origin, were: (i) 16 strains of unknown source from the National Collection of Type Cultures, London, England, which represented all available A-D cultures from that collection, none being of O serogroups 6, 7, or 8; (ii) 10 fecal strains of *Escherichia alkalescens* from the Division of Enteric Pathogens, London, defined by the donor as nonmotile, anaerogenic strains of *E. coli* O1, i.e., the most common serogroup (10; B. Rowe, personal communication); (iii) 10 strains, previously described by Kauffmann (22), which were obtained from the State Serum Institute, Copenhagen, Denmark and included one or two cultures from the less common A-D O serogroups 2 through 8, but were of unknown source.

**Biochemical tests.** The reactions of these biochemically atypical strains were determined by standard procedures (10).

**Media.** Nutrient broth no. 2 and nutrient agar CM3 were from Oxoid Ltd., London, England. Phosphate-buffered broth and agar were, respectively, nutrient broth and nutrient agar with 0.35% (wt/vol) $KH_2PO_4$ and 0.65% (wt/vol) $Na_2HPO_4$ (pH 7.0) per liter. Media were dispensed as previously described (6).

**Production of HA.** For MS HA, bacteria were grown serially in static 48-h broths (nutrient broth) at 37°C. Strains were judged to be $MS^-$ if they gave negative MS HA results in each of 10 serial broth cultures (6). For MRE HA, bacteria were grown at 37°C on phosphate-buffered agar for 24 h, or in phosphate-buffered broth for 48 h; they were also tested after growth at 18°C on phosphate-buffered agar for 48 h, or in phosphate-buffered broth for 7 days (6).

**Hemagglutination tests.** The methods for preparation of erythrocyte suspensions and the performance of the HA tests have been described (6, 9). The species of erythrocytes tested were: domesticated fowl,

TABLE 1. *HA and fimbriae in biochemically atypical strains of E. coli*

| Strain reference no. | Source[a] | O (A-D) serogroup | Biochemical reactions[b] | | | | | | | | | | | | | Production of HA[c] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Lac | Mel | Dul | Raf | Suc | Xyl | Rha | Sbl | Lys | Orn | Arg | Ind | Onp | MS | MRE of type[d]: |
| 1601 | NCTC | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | MPS |
| 5183 | NCTC | 1 | − | − | − | − | − | + | (+) | + | + | − | (+) | + | − | − | GMPS |
| 5379 | NCTC | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | GMPS |
| 7925 | NCTC | 1 | − | − | − | − | − | + | − | (+) | + | − | (+) | + | − | − | MPS |
| 9775 | NCTC | 1 | − | − | (+) | − | − | + | − | (+) | + | − | (+) | + | − | + | MPS |
| 9951 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | − | − | (+) | + | − | − | MPS |
| 9980 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | MPS |
| 10498 | DEP | 1 | − | − | − | − | − | + | (+) | − | + | − | (+) | + | − | − | MPS |
| 11028 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | − | − | (+) | + | − | − | MPS |
| 11365 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | − | + | − | − | MPS |
| 11460 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | MPS |
| 11878 | DEP | 1 | − | − | (+) | − | − | + | (+) | − | + | − | (+) | + | − | − | MPS |
| 12310 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | MPS |
| 13090 | DEP | 1 | − | − | (+) | − | − | + | − | (+) | − | − | (+) | + | − | − | MPS |
| 14062 | DEP | 1 | − | − | (+) | − | − | + | (+) | (+) | + | − | (+) | + | − | − | MPS |
| 54(38949) | SSI | 1 | − | − | (+) | − | − | + | − | (+) | + | − | − | + | − | − | MPS |
| 70348 | DU | 1 | − | − | − | − | − | + | − | − | + | − | − | + | − | + | MPS |
| 7345 | DU | 1 | − | − | − | − | − | + | − | (+) | + | − | (+) | + | − | − | MPS |
| 7926 | NCTC | 2 | − | − | − | − | − | + | − | (+) | + | − | (+) | + | − | − | MPS |
| 9776 | NCTC | 2 | − | − | − | − | − | + | − | − | + | − | (+) | + | + | − | MPS |
| 82 (A-193) | SSI | 2 | − | − | − | − | − | − | − | − | − | − | − | + | − | + | MPS |
| 7927 | NCTC | 3 | − | + | − | − | − | − | + | + | − | + | (+) | + | − | − | − |
| 9777 | NCTC | 3 | − | + | − | + | (+) | + | − | + | + | + | (+) | + | + | + | − |
| 83 (2-193) | SSI | 3 | − | − | − | − | − | − | + | + | − | + | − | + | − | − | − |
| 117 (54a) | SSI | 3 | + | + | + | − | − | + | + | + | + | + | − | + | + | + | − |
| 4168 | NCTC | 4 | (+) | + | − | + | (+) | + | + | + | + | + | (+) | + | + | − | − |
| 7921 | NCTC | 4 | − | + | − | − | − | + | − | + | − | + | (+) | + | + | − | − |
| 7928 | NCTC | 4 | − | − | (+) | − | − | + | − | (+) | + | − | (+) | + | − | − | MPS |
| 9778 | NCTC | 4 | − | − | − | − | (+) | + | + | + | − | + | (+) | + | + | − | − |
| 119 (2605) | SSI | 4 | − | − | − | − | − | + | + | + | − | + | − | + | + | − | − |
| 4169 | NCTC | 5 | (+) | + | − | + | (+) | + | + | + | + | + | (+) | + | + | − | M |
| 128 (5513) | SSI | 5 | + | + | − | + | (+) | (+) | + | + | + | − | − | + | + | − | − |
| 129 (145) | SSI | 5 | − | + | − | + | (+) | (+) | + | + | + | − | − | + | + | − | − |
| 131 (2801) | SSI | 6 | + | + | − | − | − | + | + | + | − | − | − | − | + | − | − |
| 132 (2278) | SSI | 7 | + | + | (+) | + | + | + | − | + | + | − | (+) | + | + | + | MPS |
| 133 (187) | SSI | 8 | − | − | (+) | − | − | + | + | (+) | + | + | − | + | + | − | − |
| 7922 | NCTC | NT[e] | − | + | − | + | (+) | + | − | (+) | + | + | − | + | + | + | − |
| 7923 | NCTC | AA[e] | + | + | − | − | − | + | + | + | − | − | − | − | + | − | − |
| 55222 | DU | AA | − | − | − | − | − | + | (+) | (+) | + | − | − | + | − | − | MPS |
| 75019 | DU | AA | − | − | + | − | − | + | (+) | (+) | + | − | − | + | − | − | GMPS |

[a] NCTC, National Collection of Type Cultures, Central Public Health Laboratory, London, U.K.; DEP, Division of Enteric Pathogens, Central Public Health Laboratory, London, from B. Rowe (all were isolated from human feces); SSI, State Serum Institute, Copenhagen, Denmark, from F. and I. Ørskov; DU, Bacteriology Department, University of Dundee Medical School, Dundee, U.K., original isolates by the authors (strains 70348 and 75019 from urine; 7345 from feces; 55222 from a fallopian tube).

[b] Tests included fermentation of lactose (Lac), melibiose (Mel), dulcitol (Dul), raffinose (Raf), sucrose (Suc), xylose (xyl), rhamnose (Rha), and sorbitol (Sbl); decarboxylation of lysine (Lys), ornithine (Orn), and arginine (Arg); production of indole (Ind); and hydrolysis of *o*-nitrophenyl-$\beta$-galactoside (Onp). +, Positive reaction at 24 h; (+), positive reaction in 2 to 3 days; −, negative reaction after 3 days.

[c] All $MS^+$ strains formed type 1 fimbriae; $MRE^+$ strains, apart from strain 4169, were type MRE fimbriate.

[d] Erythrocytes of guinea pig (G), human (M), pig (P), and sheep (S) agglutinated.

[e] NT, Not typable; AA, autoagglutinable.

i.e., hen (F); guinea pig (G); horse (H); human (M), group O only; ox (O); pig (P); and sheep (S).

**Electron microscopy.** Unfixed bacterial suspensions were examined for fimbriae with a Jeol 100CX microscope at 60 kV. The bacteria, washed with distilled water by centrifugation (2,000 × *g* for 10 min) or in situ on the carbon-coated Formvar grid, were negatively stained with phosphotungstic acid (0.1%, wt/vol, pH 7.0) containing 50 μg of bacitracin per ml (17).

**Serological tests.** Pure fimbrial antisera were prepared by standard procedures (16) against vaccine strains of *E. coli* that formed either type 1 fimbriae (strain A108) or type MRE fimbriae (strain PC 32354, with MRE hemagglutinating activity against the erythrocytes of humans, pigs, and sheep, i.e., type MPS). Bacteria that produced one or both of the fimbrial types were tested against the appropriate pure fimbrial antiserum in tube agglutination tests (16).

## RESULTS

**Biochemical reactions.** In common with many strains of *Shigella* of subgroups B through D (10), each A-D strain was nonmotile and anaerogenic, fermented arabinose, glucose, and mannitol, did not ferment adonitol, amygdalin, or inositol, and did not utilize citrate in Simmons medium or hydrolyze urea. Their reactions with 13 other substrates (Table 1) showed, however, even among members of the same O serogroup, the diversity associated with this biochemically heterogeneous group (10).

**MS HA and fimbriae.** MS HA, with the same spectrum of erythrocyte specificity as other $MS^+$ enterobacteria (8, 9), was formed by 7 of the 40 strains (18%) under conditions of serial, static nutrient broth culture known to be selective for the $MS^+$ phase of enterobacteria with type 1 fimbriae (5, 8, 9, 24). In each of these seven strains, MS HA was associated with the presence of type 1 fimbriae detected (i) in agglutination tests with pure fimbrial antiserum versus type 1 fimbriae of *E. coli* A108 (6), and (ii) with the electron microscope. With the $MS^+$ $MRE^+$ strains 9775, 9980, 82 (A-193), and 132 (2278) (Table 1), type 1 fimbriae were demonstrated on cells from phenotypically $MS^+$ $MRE^-$ cultures obtained after serial nutrient broth culture (6, 8).

**MRE HA and fimbriae.** The three different types of MRE hemagglutinating activity detected in cultures of 26 of the 40 strains (65%) were: type MPS (human, pig, and sheep erythrocytes agglutinated) by 22 strains (Table 1); type GMPS (guinea pig, human, pig, and sheep) by strains 5183, 5379, and 75019; and type M (humans only) by strain 4169. These patterns conform, respectively, to 1, 1var., and 9 of the scheme of Duguid et al. (6). Strains that produced MRE HA of the type MPS or the variant type GMPS produced MRE fimbriae that reacted serologically with pure fimbrial antiserum versus the MRE (type MPS) fimbriae of *E. coli* PC32354 and were detectable with the electron microscope. The four $MS^+$ $MRE^+$ strains were examined for type MRE fimbriae in phenotypically $MS^-$ $MRE^+$ cultures obtained by serial culture on phosphate-buffered agar (6, 8). Like biochemically typical strains of *E. coli* (6), the 26 $MRE^+$ strains of A-D bacteria formed MRE HA on phosphate-buffered agar or in phosphate-buffered broth at 37°C, but were nonfimbriate and $MRE^-$ when grown on these media at 18°C. Strain 4169 was nonfimbriate, like biochemically typical strains of *E. coli* that formed the type M MRE HA (6, 13).

## DISCUSSION

Polynucleotide sequence relatedness, guanine plus cytosine content, and genome size have indicated that strains of *E. coli* and *Shigella* species are so related taxonomically as to belong to a single genus (1, 2). Unlike the taxonomist, however, the practising diagnostic bacteriologist is likely to wish to retain the common usage of *Escherichia* and *Shigella* not least because of the clinician's familiarity with these generic terms. Problems of identification are likely to be encountered, however, when, for example, cultures of the biochemically atypical A-D strains, which have not been implicated as intestinal pathogens (10), are recovered from the feces of patients with diarrhea and mimic cultures of *Shigella*, which are established intestinal pathogens. Accordingly, for the correct identification of either genus, as many useful tests as possible—e.g., lysine decarboxylase, β-galactosidase, and utilization of acetate, citrate, and mucate (10)—will be required. The present study indicates that tests for the detection of MS or MRE HA, commonly associated with the presence of fimbrial antigens, may be further tests that aid strain identification.

The MS adhesin, associated with type 1 fimbriae, has been found in most (75 to 90%) of the strains of *E. coli* examined by others (6, 8, 9) but, among *Shigella* species, only in some serotypes of *S. flexneri* (7). Hence, among members of the tribe *Escherichieae* Bergey et al., an MS $HA^+$ culture is likely to be a strain of *E. coli* or *S. flexneri*. The MS HA findings helped little in the identification of this collection of A-D strains as escherichiae, however, since so few of them were MS $HA^+$. It is difficult to explain why the MS HA character was so rare among biochemically atypical strains of *E. coli* when it was so common among biochemically typical strains. Motility is known to be important for the selection of the MS $HA^+$ phase of enterobacteria (25),

yet lack of motility seems an unlikely explanation for the rarity of MS HA among A-D strains in view of the finding that, among a series of 306 biochemically typical strains of *E. coli* (Crichton, thesis), the frequency of the MS HA character was equally high among 187 motile strains (87%) and 119 nonmotile strains (81%).

On the other hand, MRE adhesins have been reported almost exclusively in strains of *E. coli* (6, 9, 14, 15), very rarely in a few strains of other enterobacteria (8), and not in *Shigella* (7). The incidence of MRE hemagglutinating activity in this series of A-D strains was generally similar to that reported for the series of 306 biochemically typical urinary strains of *E. coli* described (Crichton, thesis), and their MRE HA patterns were those of typical strains of *E. coli* (6, 9). To detect type MRE fimbriae either by serology or electron microscopy is probably less convenient than to demonstrate their presence by the MRE HA test, which is easy to perform, gives a result within 24 h, and detects even the rare, narrow-spectrum, nonfimbrial MRE HA. Thus, the MRE HA test should prove helpful for identification purposes.

*E. coli* MRE adhesins such as K88, K99, CFAI, CFAII, and F7 have attracted considerable interest because of their role in colonization of intestinal and urinary epithelial cells (3, 11, 12, 21, 26–28). When such plasmid-determined antigens are lost, the strain is rendered MRE HA$^-$ and nonpathogenic (8, 20). It is possible that the type MPS MRE HA so commonly encountered in this study is similarly plasmid determined. However, loss of the type MPS character was not observed at any detectable frequency either in the A-D strains, many of which had been stored for up to 30 years (J. P. Duguid, personal communication), or in larger series of biochemically typical *E. coli* (4, 23). The available clinical information about the A-D strains examined was insufficient to allow us to determine their etiological role in infection, and hence it is difficult to postulate any correlation between the presence of MRE HA and pathogenicity. Nevertheless, the suggestion that A-D strains are "opportunistic" pathogens of the urinary tract (22) is of interest in view of the findings that: (i) many of the *E. coli* O antigens with which A-D strains cross-react are recognized urinary serotypes (18), and (ii) most (65%) of our 40 A-D isolates, including all those of the most commonly recovered (A-D) serotype O1 (10), had the type MPS MRE HA, i.e., the MRE HA most frequently present in urinary strains of *E. coli* (Crichton, thesis).

Reports have appeared which show the usefulness of HA typing as an ancillary technique in the differential typing of typical strains of *E. coli* (4, 14, 15, 23). The results reported in this study on a limited series of biochemically atypical strains of *E. coli*, the identity of which we knew, suggest that tests for the presence of MS and MRE HA should be of value in the identification as *Escherichia* or *Shigella* of strains that give ambiguous results in the biochemical tests routinely used to differentiate these genera (10). A good example of its usefulness was seen with strain 82 (A-193) (Table 1), which, though biochemically as unreactive as a shigella, was clearly, on the basis of its possession of both MS and MRE adhesins, an *Escherichia* sp.

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