

# The surface membrane antigen phenotype of human blood basophils

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Basophils are effector cells of allergic reactions and express a unique profile of cellular antigens (Ag). Using a combined toluidine-blue/immunofluorescence staining method, we were able to study the cell membrane Ag phenotype of normal human blood basophils with monoclonal antibodies (mAbs) against established and novel CD antigens. According to previous findings, basophils express CD9 (p24), CD11a (LFA-1 alpha-chain), CD11b (C3biR), CD11c (CR4), CD13 (aminopeptidase N), CDw17 (lactosylceramide), CD18 (beta-chain of  $\beta_2$ ), CD25 (IL-2R alpha-chain), CD26 (dipeptidylpeptidase), CD31 (PECAM), CD35 (CR1), CD38 (T10), CD43 (leukosialin), CD44 (Pgp-1), CD45 (pan-leukocyte Ag), and CD63 (basophil activation Ag). Various novel CD Ags were detected on basophils, including membrane cofactor protein (MCP) (CD46), the N-linked glycan CD47, decay-accelerating factor (DAF) (CD55), membrane attack complex inhibitory factor (MACIF) (CD59), LFA-3 (CD58), ICAM-2 (CD102), ICAM-3 (CD50), C5a receptor (CD88), MIC-2/E2 (CD99), and the interleukin-1 (IL-1) R type II (CD121b). These data provide further evidence that basophils express a unique profile of surface membrane receptors for cytokines and immunomodulating compounds, as well as adhesion molecules and surface glycolipids.

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Blood basophils and mast cells are hemopoietic cells involved in allergic reactions. These cells store multi-functional mediators and vasoactive substances and release their products on specific cell activation (13, 20). A number of immunomodulating compounds and their respective receptors are involved in the activation of basophils for mediator release and consecutive allergic responses. Major basophil agonists include various interleukins (interleukin (IL)-3, IL-5, granulocyte/macrophage colony-stimulating factor (GM-CSF) and other cytokines, peptide mediators (IL-8, MCAF), and complement components such as C5a (2, 9–11, 29).

Basophils are derived from multipotent hemopoietic progenitor cells and usually complete their differentiation in the bone marrow. In contrast, mast cells complete their differentiation in extramedullary organs (7). Differentiation of human basophils is inducible by distinct hemopoietic growth factors including IL-3, IL-5, and GM-CSF (6, 19, 22, 32). IL-3 is the most potent basophil agonist. Negative regulators of basophil growth and differentiation include tumor necrosis factor-alpha (TNF- $\alpha$ ) and the interferons (IFN- $\alpha$  and IFN- $\gamma$ ) (22).

Although basophils are usually circulating granulocytic cells, they may leave the bloodstream under certain circumstances; in particular, in the course of inflammatory and allergic reactions (12). Molecules involved in the regulation of basophil chemotaxis, adherence to the endothelium, and transmigration include peptide mediators such as chemokines, as well as adhesion receptors (3–5).

The CD system is a useful tool for the evaluation of cell-membrane antigens on various human leukocytes. This study provides an extensive summary of CD antigens expressed on human blood basophils.

## Material and methods

### *Isolation of basophils*

Human blood basophils were obtained from the peripheral blood of 24 nonallergic subjects. Mononuclear cells (MNC) were prepared by Ficoll density centrifugation. The MNC contained 3.5–5.5% basophils as assessed by Giemsa staining. After isolation, the MNC were washed in cold PBS (phosphate-buffered saline) and used immediately for cell typing with monoclonal antibodies (mAbs).

*Monoclonal antibodies (mAbs)*

The mAbs used in this study were obtained from the Fourth or Fifth International Workshop and Conference on Human Leukocyte Differentiation Antigens, Vienna, 1989 and Boston, 1993, respectively. The mAbs are specified in Tables 1–4.

*Combined toluidine-blue/immunofluorescence staining method*

Expression of CD antigens on human blood basophils was assessed by a combined toluidine-blue/immunofluorescence staining method, as described previously (23, 24, 26, 31). In brief, cells were incubated with mAbs at 4°C for 30 min, washed in PBS, exposed to a fluorescein-conjugated, second-step antibody (IgG + IgM), and washed in PBS. Then cells were fixed in glutaraldehyde (0.025%) for 1 min, washed in PBS, and stained with toluidine blue (0.0125%) for 8 min at room temperature. In each experiment, nonspecific staining was excluded by using PBS instead of a first-step mAb, and by using an isotype-matched control antibody. Moreover, in all experiments, cells were exposed to AB serum before staining with mAbs, to inhibit nonspecific binding. Cells were examined under bright-field and immunofluorescence light by two independent observers.

**Results and Discussion***Expression of cytokine receptors on human basophils*

Various cytokines have been identified as basophil regulators. Human basophils, in turn, express cytokine-binding sites. As assessed by mAbs against previously defined or novel CD antigens, human blood basophils expressed IL-1 R type II (CD121b), the IL-2 R alpha-chain (CD25), and CD40 Ag (IL-4 costimulatory cytokine R, member of NGF R family). A minority of basophils (<10%) displayed (weak) reactivity with mAbs against GM-CSF R (CD116) and IFN- $\gamma$  receptor (CD119). Similar results have recently been obtained by radioreceptor assay. In particular, enriched human basophils (obtained from chronic myeloid leukemia patients) express low-affinity receptors for IL-2 (25), and high-affinity receptors for IL-3 (29, 30), IL-4 (27), IL-5 (16), GM-CSF (16), IFN- $\gamma$  (unpublished), and IL-8 (CD128) (15, 30).

Basophils were found to lack G-CSF R, c-kit/SCF R (CD117), CSF-1/M-CSF R (CD115), IL-1 R type I (CD121a), the 75-kDa IL-2R beta-chain (CD122), TNF-R (CD120), IL-6 R (CD126), IL-7 R (CD127), and gp130 (CD130) (Table 1). These observations are consistent with the functional responses of human basophils to recombinant cyto-

Table 1. Cytokine R expression on basophils and mast cells

| Cytokine R               | mAb                            | CD   | Reactivity with mAbs |             |
|--------------------------|--------------------------------|------|----------------------|-------------|
|                          |                                |      | Basophils            | Mast cells* |
| IL-1 RI                  | hIL-1R1                        | 121a | –                    | –           |
| IL-1 RII                 | hIL-1R2                        | 121b | +                    | –           |
| IL-2 R                   | Anti-TAC                       | 25   | +                    | –           |
| IL-2 R $\beta$           | Mik- $\beta$ 1, Mik- $\beta$ 2 | 122  | –                    | –           |
| IL-3 R $\alpha$          | nt                             | 123  | nt                   | nt          |
| IL-4 R $\alpha$          | nt                             | 124  | nt                   | nt          |
| IL-6 R $\alpha$          | B-H23                          | 126  | –                    | –           |
| IL-7 R $\alpha$          | hIL-7R                         | 127  | –                    | –           |
| IL-8 R                   | B-G20                          | 128  | –/+                  | nt          |
| AP01/FAS                 | 7C11, anti-FAS                 | 95   | –                    | –           |
| Endoglin, TGF-R          | PN-E2, E9                      | 105  | –                    | –           |
| CD40-ligand R            | B-E10                          | 40   | +                    | –           |
| M-CSF R/c-fms            | 7-7A3-17                       | 115  | –                    | –           |
| GM-CSF R                 | hGM-CSF R                      | 116  | –/+                  | –           |
| G-CSF R                  | Anti-G-CSF R                   | nc   | –                    | –           |
| SCF R/c-kit              | YB5.B8, SR-1                   | 117  | –                    | ++          |
| TNF RI                   | htr-9, MR1-3                   | 120a | –                    | –           |
| TNF RII                  | MR2-1, utr-1                   | 120b | –                    | –           |
| gp 130                   | AM64                           | 130  | –                    | –           |
| IFN R $\alpha$ , $\beta$ | IFN- $\alpha$ R3               | 118  | nt                   | –           |
| IFN R $\gamma$           | GIR-208                        | 119  | –/+                  | nt          |

\* Data for human mast cells have been presented at Fifth International Workshop on Human Leukocyte Differentiation Antigens, Boston, 1993.

nt, not tested; nk, not known; nc, not yet clustered; ++, very strong reactivity of mAb with all basophils/mast cells; +, more than 90% of basophils/mast cells positive; +/–, 50–80% (subset) of basophils/mast cells positive; –/+, 10–50% (small subset) of basophils/mast cells positive; –, less than 5% of basophils/mast cells positive.

kines. Thus, recombinant human IL-3, IL-5, IL-8, and GM-CSF, as well as the interferons, are basophil agonists promoting mediator secretion (10, 29), whereas no effect is obtained with G-CSF, M-CSF, TNF, IL-6, or IL-7. Moreover, SCF (c-kit ligand) does not cause basophil mediator release unless very high (nonphysiologic) concentrations are used. IL-1 $\beta$  has also been found to promote histamine secretion from human blood basophils (9, 17). The functional role(s) of IL-2 R and IL-4 R on human basophils remain(s) unknown. Human mast cells express functional SCF-binding sites (1, 2, 21, 33) but lack high-affinity receptors for IL-3 (28). A summary of cytokine receptors expressed on basophils and mast cells is given in Table 1.

*Immunoglobulin (Ig) receptor expression on basophils*

Basophils typically express high-affinity receptors for IgE (Fc $\epsilon$ RI; not yet clustered) (13, 18). Allergen binding, as well as the consecutive secretory responses, is mediated via this cell-membrane surface receptor. Basophils also bind IgG molecules on their surface (14) and, unlike mast cells, react with mAbs against IgG/Fc $\gamma$ RII (CDw32) (24, 26, 31). Basophils lack Fc $\gamma$ RI (CD64) and -III (CD16) and the low-affinity IgE receptor (Fc $\epsilon$ RII = CD23). In addition, basophils do not react with mAb against the

Table 2. Immunoglobulin R expressed on basophils and mast cells

| Fc Receptor        | mAb      | CD  | Reactivity with mAbs |             |
|--------------------|----------|-----|----------------------|-------------|
|                    |          |     | Basophils            | Mast cells* |
| Fc <sub>γ</sub> R  | A62      | 89  | —                    | —           |
| Fc <sub>ε</sub> R1 | IgE+algE | nc  | +                    | +           |
| Fc <sub>ε</sub> R2 | MHM6     | 23  | —                    | —           |
| Fc <sub>γ</sub> R1 | 32.2.22  | 64  | —                    | —           |
| Fc <sub>γ</sub> R2 | CIKM5    | w32 | +                    | —           |
| Fc <sub>γ</sub> R3 | VEP13    | 16  | —                    | —           |

\* Data for human mast cells were presented at Fourth and Fifth International Workshop on Human Leukocyte Differentiation Antigens, Vienna, 1989 and Boston, 1993, respectively.  
nc, not yet clustered.

IgA/Fc<sub>α</sub>R (CD89). Table 2 shows a summary of immunoglobulin receptors expressed on human basophils and mast cells, as assessed by immunostaining.

#### Complement-related antigens on human basophils

Complement receptors on human blood basophils include C3biR/CR3 (CD11b), CR4 (CD11c), and CR1 (CD35). Basophils also react with mAbs against C5aR (CD88). Basophils are not recognized by mAbs against C3dR (CR2 = CD21). Interestingly,

Table 3. Complement receptors expressed on basophils: comparison with tissue mast cells

| Complement R | mAb        | CD  | Reactivity with mAbs |             |
|--------------|------------|-----|----------------------|-------------|
|              |            |     | Basophils            | Mast cells* |
| CR1          | E11, To5   | 35  | +                    | —           |
| CR2          | B1         | 21  | —                    | —           |
| CR3          | VIM-12     | 11b | +                    | —           |
| CR4          | 3.9, Kim-5 | 11c | +                    | —           |
| C5aR         | W17 S5/1   | 88  | +                    | —           |

\* Presented at Fifth International Workshop on Human Leukocyte Differentiation Antigens, Boston, 1993.

human lung mast cells do not express detectable amounts of CR1, CR2, CR3, CR4, or C5aR. Activation of basophils via C5aR (CD88) (anaphylatoxin) is a well-recognized phenomenon (11). CD Ags involved in complement deactivation were also detected on human basophils in this study. Thus, basophils expressed membrane cofactor protein (MCP = CD46), decay-accelerating factor (DAF = CD55), and membrane attack complex inhibitory factor (MACIF = CD59). A role for these Ags on human basophils has not been described so far, but it is tempting to speculate that these Ags prevent

Table 4. Adhesion receptors expressed on basophils and mast cells

| C   | mAb       | Adhesion R     | Natural ligand(s) | Reactivity with mAbs |             |
|-----|-----------|----------------|-------------------|----------------------|-------------|
|     |           |                |                   | Basophils            | Mast cells* |
| 02  | T11       | LFA-2          | LFA-3/CD58        | —                    | —           |
| 09  | BA2       | p24            | p24?              | ++                   | ++          |
| 11a | MHM-24    | LFA-1a, β2     | ICAM-1/2          | +                    | —           |
| 11b | VIM-12    | Mac-1a/C3biR   | C3bi;Fb;FX        | +                    | —           |
| 15  | VIM-D5    | 3-FAL          | selectins?        | —                    | —           |
| 18  | MHM-23    | beta-chain, β2 | ICAM,Fb           | +                    | —           |
| 29  | 4B4, K20  | beta-chain, β1 | Lm,Co,Fn          | +                    | +           |
| 31  | SG134     | PECAM          | PECAM?            | +                    | —           |
| 36  | 5F1       | Tsp-R          | Tsp               | —                    | —           |
| 41  | C17/27    | IIb/IIIa, β3   | Fb, Fn, vWF       | —                    | —           |
| 43  | G19-1     | leukosialin    | ICAM              | ++                   | ++          |
| 44  | F10-44-2  | Pgp-1          | hyaluronate       | ++                   | ++          |
| 50  | IC1-1D2   | ICAM-3         | LFA-1             | +                    | +/-         |
| 51  | NKi-M9    | VNRa           | Vn, Fb, Tsp       | —                    | +           |
| 54  | 84H10     | ICAM-1         | LFA-1             | +                    | +/-         |
| 58  | BRIC5     | LFA-3          | LFA-2             | +                    | +           |
| 61  | AP6       | beta-chain, β3 | Vn, Fb, Tsp       | —                    | +           |
| 62  | G1        | PADGEM         | SLX               | —                    | —           |
| 102 | CBR-IC2/1 | ICAM-2         | LFA-1             | +/-                  | +/-         |
| 103 | LF61      | HML-1          | nk                | —                    | —           |
| 104 | 439/93    | β4 integrin    | nk                | —                    | —           |
| 106 | E1/6      | VCAM-1         | VLA-4             | —                    | —           |

\* Data for human mast cells were presented at Fourth and Fifth International Workshop on Human Leukocyte Differentiation Antigens, Vienna, 1989 and Boston, 1993, respectively.  
nk, not known; Fb, fibrogen; Fn, fibronectin; Lm, laminin; Co, collagen; Tsp, thrombospondin; Vn, vitronectin; ++, very strong reactivity of mAb with all basophils/mast cells; +, more than 90% of basophils/mast cells positive; +/-, 50–80% (subset) of basophils/mast cells positive; -/+, 10–50% (subset) of basophils/mast cells positive; —, less than 5% of basophils/mast cells positive.

excess complement activation and lysis at the basophil surface membrane. Table 3 provides a summary of complement-related CD Ags expressed on human blood basophils.

#### *Adhesion receptors expressed on blood basophils*

Human basophils express a number of recognition molecules involved in cell–cell interactions, in binding to endothelial cells, or in binding to matrix molecules. According to previous findings (3–5, 23, 31), basophils express  $\beta$ 1 (CD29,CD49d,CD49e) and  $\beta$ 2 (CD11a,b,c/CD18) integrins. Basophils were found to lack  $\beta$ 3 (CD41,CD51/CD61) integrins and the  $\beta$ 4 integrin CD104. Human mast cells express  $\beta$ 1 and  $\beta$ 3, but not  $\beta$ 2 integrins (1, 8, 23, 31). The  $\beta$ 1 and  $\beta$ 2 integrins (in particular, LFA-1 and VLA-4) on human basophils bind to activated endothelium, a process involving the adhesion receptors VCAM-1 and ICAM-1 on the endothelial cell surface (3–5). Other adhesion receptors expressed on basophils are the aggregation receptors CD9 (p24 Ag) and CD31 (PECAM) as well as the intercellular adhesion receptor ICAM-1 (CD54). Basophils also express ICAM-2 (CD102) and ICAM-3 (CD50) antigen. In addition, basophils react with mAbs against leukosialin (CD43, a receptor for ICAMs) and the Pgp-1 homing R (CD44) (31). The x-hapten (CD15 = 3-FAL, a putative R for selectins) is located on the surface of basophils, but is masked by gangliosides. Thus, basophils do not react with mAbs against CD15 unless pretreated with sialidases or exposed to neuraminidase-producing virus (24). Basophils lack CD2 (LFA-2), CD22 (p130/14, R of CD75), and the thrombospondin R CD36, and do not bind mAbs against the homing molecule HML-1 (CD103) and CD106 (VCAM-1, R of VLA-4/CD29/49d). Table 4 shows a summary of adhesion receptors detectable on human basophils, in comparison with human tissue mast cells.

#### *Cell-surface enzymes on basophil granulocytes*

Unlike mast cells, human blood basophils contain the FMLP-degrading enzymes CD13 (aminopeptidase N) (24, 26) and CD26 (dipeptidyl-peptidase) (31), as well as the leukocyte phosphatase Ag CD45 (24). Basophils lack the endopeptidase Ag CD10 (CALLA-Ag).

#### *Surface gangliosides and glycolipids*

Various gangliosides are expressed on human basophils. Basophils typically display huge amounts of CDw17 (lactosyl-ceramide) and can be purified to homogeneity by FACS-sorting with CDw17 mAbs. Basophils also express CD43 (leukosialin) (31) and

the ceramide dodesaccharide Ag CDw65 (VIM-2 epitope), but lack CDw60 (Neu-Ac-Neu-Ac-Gal-linked Ag). In this study, basophils were found to express the N-linked glycan CD47 and to lack CD77 (globosialylceramide).

#### *Virus-binding sites*

Recently, several CD Ags have been identified as binding sites for viral epitopes. Human basophils express the rhinovirus binding site CD54 (ICAM-1 Ag) and, in this study, they were found to expose the measles virus binding site CD46. Basophils lack the human immunodeficiency virus (HIV) receptor T4 (CD4) and the Epstein-Barr virus receptor CD21 (31).

#### *Summary*

Knowledge of CD cell-surface antigens expressed on human basophils should lead to a better characterization of these cells, to new isolation methods providing pure cell populations, and to a better understanding of how basophils interact with surrounding epitopes and thus contribute to allergic and inflammatory reactions.

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