

# Genetic Nomenclature for Loci Controlling Mouse Lymphocyte Antigens

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There are now over fifty serologically defined mouse lymphocyte cell-surface antigens. Of these, more than thirty are polymorphic and have been shown to be controlled by a single genetic locus. These loci have mostly been designated by the symbol Ly- followed by a number assigned more or less in order of discovery of the locus (Table 1). However, there has been no mechanism for orderly assignment of symbols or numbers, with consequent use of a variety of symbols, duplication of numbers, and use of different symbols or numbers for the same locus. The authors recently met at the National Institutes of Health, Bethesda, Maryland, to discuss means of overcoming these problems. A preliminary draft of nomenclature rules for the Ly loci was prepared and circulated among colleagues. In this paper we present a revised version of the rules in which we (1) reallocate duplicated Ly numbers, (2) provide a definition of Ly loci, and (3) establish a central Ly nomenclature registry that will be responsible for coordinating the allocation of new Ly numbers. In establishing this nomenclature, we have tried to maintain the status quo and have only reallocated duplicated numbers or renamed loci with grossly misleading names in order to cause minimum alteration of the existing system. Thus, for example, Lna, Tind, Tsu, Thb, and Pca-1, which are informative names, have not been altered.

## **Definition of Ly Locus**

The designation Ly, italicized, should be allocated to a gene encoding a molecule that can be shown by an appropriate technique to be present on the surface of lymphocytes or to be shared by lymphocytes and other cell types. The antigenic molecule is designated by the same symbol unitalicized. The criteria for recognizing such genes have been broadened considerably since the first Ly loci were described, in order to accommodate new information ob-

tained from major technical advances, such as molecular genetic techniques, which have led to the identification of new loci for lymphocyte surface antigens. In particular, (a) somatic cell hybridization techniques have led to the mapping of several loci not exhibiting genetic polymorphism, and must be considered with conventional segregation analysis to identify and map genes; (b) biochemical techniques not involving the use of antibody can be used to identify cell-surface molecules; (c) molecular cloning can be used to identify Ly genes not showing genetic polymorphism; and (d) genes can be identified by use of cDNA probes from other species. Genes for which no cell membrane molecule has been found in the mouse can be isolated by this technique using cDNA probes for genes encoding cell membrane molecules identified in other species. These genes can be given the Ly designation followed by the gene name (in brackets) in the original species from which the gene was isolated. For example, human T3 can be detected by antibody but has no known mouse counterpart. However, the gene coding for a human T3 chain was used to isolate a corresponding mouse T3 gene. This gene should be known as Ly-[T3]. Placing the name in brackets indicates that the symbol is reserved pending evidence that the gene encodes a lymphocyte cell-surface molecule in the mouse.

It should be noted that these criteria do not distinguish between loci expressed only on lymphocytes, e. g., *Ly-1*, *Ly-2*, and *Ly-7*, and those shared with other cell types, e. g., *Ly-5* and *Ly-6*. It is not practical to make this distinction, as experience has taught us that, with time and more extensive tissue distribution analysis, many molecules have a wider tissue distribution than first reported.

#### Specificities and Alleles

Alleles are designated with lowercase letter superscripts and specificities with Arabic numerals separated from the antigen symbol by a period. The allelic superscript a is

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Table 1. Strain distribution of Ly specificities

| Strain       | Ly-1  | Ly-2  | Ly-3  | Ly-5  | Ly-6  | Ly-7 | Ly-8 <sup>†</sup> | Ly-9 | Ly-10 | Ly-11 | <sup>5</sup> Ly-12 | Ly-13 | Ly-14 | Ly-15 | Ly-16 | Ly-17          | Ly-18  | Ly-19  | Ly-20 <sup>§</sup> | Ly-21 |
|--------------|-------|-------|-------|-------|-------|------|-------------------|------|-------|-------|--------------------|-------|-------|-------|-------|----------------|--------|--------|--------------------|-------|
| C57BL/6      | 2     | 2     | 2     | 2     | 2     | _    | 2                 | 2    | _     | 2     |                    | _     | 2     | 2     |       | 2              | 2      | 2      | 2                  | 2     |
| C57L         | 2     | 2     | 2     | 2     | 2     | 1*   | 2                 | 2    | 1     | 2     | 1                  | 1     | 2     | 2     | 1     | 2.             | 2      | 2      | 2                  | 2     |
| C57BR/cd     | 2     | 2     | 2     | 2     | 2     | 1*   | 2                 | 2    | 1     | 2     | î                  | 1     | 2     | 2     | NT    | 2              | 2      | 2      | NT                 | 2     |
| C58          | 2     | 1     | 1     | 2     | 2     | _    | 2                 | 2    | _     | 2     | _                  | _     | 2     | 1     | 1     | 2              | 2      | 2      | 2                  | 2     |
| A            | 2     | 2     | 2     | 2     | 1     | 1    | 2                 | 1    | -     | -     | -                  |       | 2     | 2     | NT    | 1              | _      | 2      | 2                  | _     |
| BALB/c       | 2     | 2     | 2     | 2     | 1     | 1.3  | 2                 | 1    | -     | _     | -                  | -     |       | 1     | 1     | 2              | -      | 2      | 2                  | 2     |
| NZB          | 2     | 2     | 2     | 2     | 1     | 1    | 2                 | 1    | -     | -     | -                  | _     | NT    | 1     | NT    | 1              | NT     | 2      | 2                  | 2     |
| SJL          | 2     | 2     | 2     | 1     | 2     | 1    | 2                 | 1    | _     | 2     | -                  |       | _     | 1     | -     | 1              | 2      | -      | 2                  | 2     |
| SWR          | 2     | 2     | 2     | 2     | 2     | 1*   | 2                 | 1    | NT    |       | 1                  | _     | -     | 1     | NT    | 1              | 2      | 2      | 2                  | 2     |
| 129          | 2     | 2     | 2     | 2     | 2     | 1*   | 1                 | 1    | -     | 2     | -                  | NT    | -     | 2     | NT    | 1              | -      | 2      | 2                  | 2     |
| LP           | 2     | 2     | 2     | 2     | 1     | 1*   | 1                 | 1    | NT    | NT    |                    | NT    | -     | 2     |       | 1              | NT     | 2      | NT                 | 2     |
| C3H/HeJ      | 1     | 1     | 2     | 2     | 1     | 1    | 2                 | 1    |       | -     | -                  |       | 2     | 2     | NT    | 11             |        | 2      | NT                 | 2     |
| CBA/J        | 1     | 1     | 2     | 2     | 1     | 1    | 2                 | 1    | 1¶    | -     | -                  |       | 2     | 2     | -     | 2 <sup>¶</sup> | -      | 2      | 2                  | 2     |
| CBA/N        | 1     | 1     | 2     | 2     | 1     | 1,3  | NT                | 1    | 1     | NT    | NT                 | NT    | NT    | NT    | NT    | 1              | -      | 2      | NT                 | NT    |
| CE           | 2     | 1     | 2     | 2     | 1     | 1,3  | 2                 | 1    | -     | -     |                    | -     | 2     | 2     | NT    | 1              | 2      | -      | 2                  | NT    |
| DBA/1        | 1     | 1     | 2     | 2     | 2     | 1,3  | 2                 | 1    | 1     | 2     | -                  | -     | 2     | 2     | NT    | 2              | 2      | 2      | NT                 | 2     |
| DBA/2        | 1     | 1     | 2     | 2     | 2     | 1,3  | 2                 | 1    | 1     | 2     | -                  | -     | 2     | 2     | NT    | 2              | 2      | 2      | 2                  | 2     |
| AKR          | 2     | 1     | 1     | 2     | 2     | 1,3  | 2                 | 1    | -     | 2     | -                  | -     | -     | 1     | NT    | 2              | -      | -      | 2                  | 2     |
| PL           | 2     | 1     | 1     | 2     | 2     | 1*   | NT                | 1    | -     | 2     | NT                 | NT    | NT    | NT    | NT    | 1              | NT     | 2      | NT                 | 2     |
| RF           | 2     | 1     | 1     | 2     | 2     | 1*   | NT                | 1    | NT    | NT    | NT                 | NT    | NT    | 2     | NT    | 1              | -      | -      | 2                  | 2     |
| BDP          | 2     | 1     | 2     | 2     | 2     | 1*   | NT                | 1    | NT    | NT    | NT                 | NT    | NT    | NT    | NT    | 1              | NT     | -      | 2                  | NT    |
| RIII         | 2     | 2     | 2     | 1     | 1     | 1,3  | NT                | 1    | NT    | NT    | NT                 | NT    | NT    | NT    | NT    | 1              | NT     | 2      | NT                 | NT    |
| Old          | Lyt-1 | Lyt-2 | Lyt-3 | Lyt-4 | Ly-27 |      | Ly-11             |      |       |       |                    |       |       | LFA-1 | Ly-18 |                | Lym-18 | Lym-19 | Ly-22              |       |
| Nomenclature |       |       |       |       | Ly-28 |      |                   |      |       |       |                    |       |       |       |       |                |        |        |                    |       |

Numbers in the body of the table are the specificities defined by antibody. The "-" means that no serologically detected specificity has been defined for the indicated strains. NT, not typed. Allelic designations have been changed to conform to convention, i. e., CS7BL/6 has the *b* allele and therefore the .2 specificity. Ly-6A-Ly-6E have identical strain distributions except for Ly-6B; NZB is Ly-6A.1, Ly-6C.1, Ly-6D.1, and Ly-6E.1. Three alleles but only two specificities have been defined for the Ly-7 locus. The Ly-7.1 and Ly-7.3 specificities are both expressed in some strains and Ly-7.1 only in others. CS7BL/6 had CS8 express neither specificity

\* Strains which have not been tested for Ly-7.3

Ly-11 of Potter and McKenzie (1981)

<sup>∓</sup> Ly-11 of Meruelo and co-workers (1981)

Ly-m20 is the Ly-17.2 specificity

Variations among C3H and/or CBA sublines have been reported

used for specificity .1, *b* is used for specificity .2, etc. The uniform practice of designating the C57BL/6 allele with the superscript *b* and specificity with the number .2 is recommended, e. g., for *Ly-1*, C57BL/6 mice have the allele *Ly-1<sup>b</sup>* and the specificity Ly-1.2. This convention requires a change of two alleles and specificities, for the *Ly-5* and *Ly-7* loci (see below).

# **Monoclonal Antibodies**

Since the advent of monoclonal antibodies, it is possible to produce many different antibodies recognizing the same molecule, including antibodies detecting different epitopes present on one molecule. In the absence of any coordinated effort to determine if such epitope differences have any significance in terms of function or differentiation, we do not consider it necessary to distinguish between specificities defined by independently derived monoclonal antibodies (Tables 2 and 3). However, where possible, a monoclonal antibody should be used to define an antigen. Some Ly antigens defined by monoclonal antibodies have been designated Ly-m, e. g., Ly-m10. Since the vast majority of antigens are now defined by monoclonal antibodies, the "m" should no longer be used. Thus Ly-m10 is now Ly-10.

#### **Xenogeneic Antibodies**

Lymphocyte antigens can often be detected by xenogeneic antibodies. In some cases, these antibodies can distinguish between specificities determined by different alleles at the particular locus; in others, they react equally well with all specificities. In the latter case, e. g., with an antibody recognizing the Ly-1 antigen, the antigenic determinant recognized by the antibody is not assigned a specificity number, but can be referred to as a "framework" determinant or as a molecule carrying the Ly-1 specificity. Antibodies with framework specificities are listed in Table 3.

#### **Requirements for Designating a New Ly Locus**

A cell-surface molecule must be identified and shown to be present on lymphocytes. The molecule will usually be identified by serological methods, preferably by a monoclonal antibody, often combined with biochemical characterization.

Evidence for genetic control of the molecule must be shown. If genetic variation is found, crosses should be made to show that the variation is controlled by a single gene and, if possible, to find the chromosomal location of

<sup>§</sup> C57BL/10 (not in table) is the only identified Ly-20.1 (Ly-22.1, old nomenclature) strain

| Ly-22 | Ly-23 | Ly-24 | Ly-25 | Ly-26 | Ly-27 | Ly-28 | Ly-29 | Ly-30 | Ly-31 | Ly-32 | Lyb-2 | Lyb-3 | Lyb-4 | Lyb-5 | Lyb-6 | Lyb-7 | Lyb-8 | Thy-1 | Thy-2 | Lna-1 | PCA-1 |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 2     | 2     | 2     | _     | _     | 2     | 2     | 2     | 2     | -     | 2     | 2     | 2     | 2     | 2     | _     | _     | 2     | 2     | 2     | 2     | _     |
| 2     | 2     | 2     | -     | -     | 2     | NT    | -     | 2     | -     | NT    | 1     | 2     | 2     | NT    | NT    | NT    | NT    | 2     | -     | 2     | -     |
| 2     | 2     | 2     | 1     |       | NT    | NT    | -     | 2     | -     | -     | 1     | 2     | NT    | NT    | NT    | NT    | NT    | 2     | -     | 2     | -     |
| 2     | 2     | 2     | -     | -     | 2     | 2     | -     | -     | -     | -     | 1     | 2     | NT    | NT    | 1     | NT    | 2     | 2     | 2     | 2     | -     |
| 2     | -     | 2     | -     | -     | -     | 2     | -     | 2     | 1     | 2     | 2     | 2     | 2     | 2     | -     | -     | 2     | 2     | 2     | -     | 1     |
| 2     | -     | 1     | -     | -     | -     | 2     | 2     | 2     | 1     | 2     | 2     | 2     | 2     | 2     | -     |       | 2     | 2     | 2     | -     | 1     |
| 2     | 2     | 2     | -     | 1     | 2     | 2     | 2     | 2     | 1     | 2     | NT    | NT    | NT    | NT    | NT    | NT    | -     | 2     | -     | NT    | 1     |
| -     | 2     | 2     | 1     | -     | 2     | 2     | -     |       | 1     | -     | 3     | 2     | 2     | 2     | -     | -     | 2     | 2     | -     | -     | 1     |
| -     | _     | 2     | 1     | -     | 2     | 2     | -     | 2     | 1     | -     | 1     | 2     | 1     | 1     | 1     | NT    | 2     | 2     | -     |       | 1     |
| 2     | 2     | 2     | -     | -     | 2     | 2     | 2     | 2     | -     | 2     | 2     | 2     | 2     | NT    | -     | NT    | NT    | 2     | -     | NT    | -     |
| 2     | 2     | NT    | -     |       | 2     | NT    | 2     | NT    | NT    | NT    |
| 2     | NT    | 2     | ~     |       | -     | 2     | 2     | 2     | 1     | 2     | 2     | 2     | 1     | 1     | -     | 1     | 2     | 2     | NT    | NT    | 1     |
| 2     | -     | 1¶    | -     | NT    | NT    | 2     | 2     | 2     | 1     | -     | 1     | NT    | 1     | 2     | 1     | -     | 2     | 2     | NT    | -     | NT    |
| NT    | NT    | NT    | NT    | NT    | NT    | 2     | NT    | NT    | 1     | 2     | 2     | -     | NT    | NT    | -     | NT    | 2     | 2     | NT    | -     | NT    |
| 2     | -     | 2     | 1     | 1     |       | NT    | -     | -     | 1     | NT    | 3     | 2     | 2     | 1     | -     | 1     | 2     | 2     | NT    | -     | 1     |
| -     | 2     | 1     | -     |       | 2     | 2     | -     | 2     | -     | -     | 1     | 2     | NT    | 1     | 1     | 1     | -     | 2     | 2     | NT    | NT    |
| -     | 2     | 1     | -     | -     | 2     | 2     | -     | 2     | 1     | -     | 1     | 2     | 1     | 1     | 1     | 1     | -     | 2     | 2     | -     | -     |
| 2     | -     | 2     | -     | -     | 2     | -     | -     | 2     | 1     | -     | 3     | 2     | 2     | 2     | -     | -     |       | 1     | 2     | -     | 1     |
| 2     | 2     | NT    |       | -     | 2     | NT    | NT    | NT    | 1     | NT    | 2     | NT    | NT    | NT    | NT    | NT    | -     | 1     | NT    | ~     | 1     |
| -     | 2     | 2     | NT    | -     | 2     | -     | -     | 2     | 1     | -     | 3     | 2     | 2     | 2     | NT    | -     | 2     | 1     | NT    | NT    | 1     |
| -     | NT    | NT    | NT    | NT    | NT    | 2     | NT    | NT    |       | -     | NT    | 1     | NT    | -     |       |
| -     | NT    | NT    | NT    | -     | NT    | NT    | NT    | NT    | -     | 2     | NT    | 1     | NT    |       | 1     |
| Lym-2 | 2     | Pgp-1 |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |

the gene. A unique strain distribution of the alleles or a unique chromosomal location can be taken as evidence for a new Ly locus. If variation in the antigen is not found, it may be possible to identify the gene controlling the antigen by somatic cell hybridization, by molecular cloning, or by discovery of other variation in the gene such as a restriction fragment length polymorphism.

If the presumed new locus shows no recombination with a previously known locus, it should not be given a new locus symbol until more definitive evidence is available that the two genes are indeed distinct. Such evidence may include different tissue distributions or different molecular weights. Neither are entirely reliable, however, since apparently different tissue distributions may result from use of different antibodies or different methods of quantifying presence of the antigen, and different molecular weights may result from posttranslational modifications of the antigen.

### Ly Nomenclature Registry

This registry has been established at the National Institutes of Health and will be administered by H. C. Morse III. New *Ly* gene numbers will be allocated in order of receipt of requests, which should be accompanied by a copy of the evidence demonstrating a new *Ly* locus. All applications should be addressed to Dr. H. C. Morse III, Laboratory of Immunopathology, National Institute of Allergy and Infectious Diseases, Building 7, Room 304, National Institutes of Health, Bethesda, MD 20892, USA.

#### **Designation of Loci and Specificities**

The suggested nomenclature is shown in Table 1, where the strain distribution is also shown. Several points should be made.

(a) The numbers have been reassigned where necessary, in most cases with the approval of the appropriate authors. Some of the reassignments have broken the timehonored practice of the lowest numbers being allocated to the earliest described locus. These reassignments were made to fill in gaps in the numbers, or in some cases to leave a locus with its original designation rather than to alter it to indicate priority.

(b) The major duplications have been eliminated, e. g., three *Ly-11s*, two *Ly-15s*, and two *Ly-20s*.

(c) The *Lyt* designation will no longer be used, as newer techniques, particularly flow cytometry, have demonstrated that the antigens occur on cells other than T cells. *Lyt-1*, *Lyt-2*, and *Lyt-3* will now be *Ly-1*, *Ly-2*, and *Ly-3*, as originally defined. *Lyb-2* to *Lyb-8* will remain as such, since they would otherwise have to be changed to quite different numbers.

(d) The Ly-6 gene complex requires special rules. At this complex, there appear to be four to six closely linked loci not separated by recombination, but nonetheless coding for molecules with different tissue distributions. We have adopted a nomenclature similar to that used for the H-2 complex, allocating separate letters to the presumed separate loci (see below).

(e) Symbols such as *Lna-1* and *Thy-1* have been retained for convenience. We recommend that if such genes are described in the future, they be given an Ly number.

Table 2. Monoclonal antibodies defining Ly alloantigens

Table 4. Chromosomal locations

| Specificity | Ig class   | Origin                     |
|-------------|--|----------------------------|
| Ly-1.1      | IgG <sub>20</sub>  | Hogarth et al. 1980a       |
| Ly-1.2      | IgM  | Mark et al. 1982           |
| Ly-2.1      | IgG <sub>1</sub> , IgG <sub>2</sub> , IgG <sub>2</sub> , IgM | Hogarth et al. 1982        |
| Ly-2.2      | IgM  | Gottlieb et al. 1980       |
| Ly-3.1      | IgM  | Gottlieb et al. 1980       |
| Ly-5.1      | IgG <sub>20</sub>  | Shen 1981                  |
| Ly-5.2      | IgG <sub>20</sub>  | Shen 1981                  |
| Ly-6A.2     | IgG <sub>20</sub>  | Kimura et al. 1984         |
| Ly-6B.2     | IgG <sub>20</sub>  | Kimura et al. 1984         |
| Ly-6C.2     | IgM  | Kimura et al. 1984         |
| •           | IgG2, IgG2, IgM  | Hogarth et al. 1984c       |
| Ly-6D.2     | IgM  | Kimura et al. 1984         |
| •           | IgG  | Hogarth et al. 1984c       |
| Ly-6E.1     | IgG  | Kimura et al. 1984         |
| Ly-7.2      | IgG <sub>1</sub> <sup>2a</sup>                               | Lanier and Warner 1982     |
| Ly-7.3      | IgG  | Lanier and Warner 1983     |
| Ly-9.1      | IgG <sub>2a</sub> (rat)                                      | Ledbetter et al. 1979      |
| Ly-9.2      | IgG <sub>2a</sub>  | Hogarth et al. 1980b       |
| Ly-10.1     | - 54   | Kimura et al. 1980b        |
| Ly-12.1     | IgG <sub>2a</sub>  | Hogarth and McKenzie       |
|             |  | 1984                       |
| Ly-15.2     | IgG <sub>2a</sub>  | Potter and McKenzie 1981   |
| Ly-17.2     | IgM, IgG <sub>2a</sub>                                       | Kimura et al. 1981a        |
| Ly-18.2     | IgM  | Kimura et al. 1981b        |
| Ly-19.2     | IgG <sub>2b</sub>  | Tada et al. 1981           |
| Ly-21.1     | IgG <sub>2a</sub>  | Kennard and Meruelo 1982   |
| Ly-22.2     | IgG <sub>2b</sub>  | Tada et al. 1983           |
| Ly-23.2     | IgM  | Gasser et al. 1983         |
| Ly-24.1     | IgM (rat)  | Lesley and Trowbridge 1982 |
| Ly-24.2     | IgM (rat)  | Lesley and Trowbridge      |
|             | IgG <sub>2</sub> , (rat)                                     | Colombatti et al. 1982     |
| Lv-25.1     | IgG <sub>2</sub>   | Hogarth et al. 1984a       |
| Ly-26.1     | $IgG_{2}$ , $IgM$  | Hogarth et al. 1984b       |
| Ly-27.2     | $\lg G_{2a}$   | Matsushima et al. 1986     |
| Ly-29.2     | IgM  | Gonez et al. 1985a         |
| Ly-30.2     | IgM  | Gonez et al. 1985b         |
| Ly-31.2     | IgGn   | Tada et al. 1984           |
| Lvb-2.1     | IgG <sub>2</sub>   | Yakura et al 1980          |
| <b>,</b> –  | IgG <sub>2b</sub>  | Subbaro and Mosier 1984    |
| Lyb-8.2     | IgG  | Symington et al. 1982      |
| PC.1        | IgG (rat)  | Dumont et al. 1985         |
|             | IgG  | Stearne et al. 1985        |
|             | 0  |                            |

| Gene         | Chromosome       | Linked genes           |
|--------------|------------------|------------------------|
| <br>Ly-1     | 19               | Ly-10, -12, Ea-4, ru   |
| Ly-2/3       | 6                | Igk, mi                |
| Ly-5         | 1                | Pep-3                  |
| Ly-6 complex | 15*              | Thb, Gpt-1, Gdc-1      |
| Ly-7         | $12^{\dagger}$   | Igh-1, Pre-1           |
| Ly-8         | Unknown          |                        |
| Ly-9         | 1                | H-25, Ly-17, -22, Mls  |
| Ly-10        | 19               | Ly-1, -12, Ea-4, ru    |
| Ly-11        | 2 <sup>+</sup>   | H-3, B2m, pa           |
| Ly-12        | 19               | Ly-10, -1, Ea-4, ru    |
| Ly-13        | Unknown          |                        |
| Ly-14        | 7                | с                      |
| Ly-15        | 7                | Hbb                    |
| Ly-16        | 12               | Igh-1, Pre-1, Ly-7     |
| Ly-17        | 1                | Ly-22, -9, Mls         |
| Ly-18        | $12^{\parallel}$ | Ltw-2                  |
| Ly-19        | 4                | Ly-2, -4, -6, Mup-1, b |
| Ly-20        | 4                | b, Fv-1                |
| Ly-21        | 7                | с                      |
| Ly-22        | 1                | Ltw-4                  |
| Ly-23        | 2                | H-3, B2m, Ly-4         |
| Ly-24        | 2                | H-3, B2m, Ly-4         |
| Ly-25        | 2                | Ly-24, H-3, B2m        |
| Ly-26        | Unknown          |                        |
| Ly-27        | Unknown          |                        |
| Ly-29        | 4                | Lyb-2, Mtv-20          |
| Ly-30        | Unknown          | •                      |
| Ly-31        | 4                | Akp-2                  |
| Lyb-2        | 4                | Mup-1, b               |
| Lyb-3        | Unknown          | -                      |
| Lyb-4        | 4                | Mup-1, Lyb-2, -6       |
| Lyb-5        | Unknown          |                        |
| Lyb-6        | 4                | Lyb-2, -4              |
| Lyb-7        | 12               | Igh-1                  |
| Lyb-8        | 7                | Ğpi-1                  |

\* P. M. Hogarth, L. Washburn, E. M. Eicher, and I. F. C. McKenzie (manuscript submitted)

<sup>†</sup> Hogarth et al. (1984d)

<sup>\*</sup> Map location under reevaluation (D. Meruelo, personal communication)

<sup>II</sup> B. A. Taylor, personal communication

 Table 3. Monoclonal antibodies defining framework determinants of lymphocyte antigens

| Antigen | Antibody                | References                    |
|---------|-------------------------|-------------------------------|
| Thy-1   | IgG <sub>2a</sub> , IgM | Ledbetter and Herzenberg 1979 |
| Ly-1    | IgG <sub>2a</sub>       | Ledbetter and Herzenberg 1979 |
| Ly-2    | IgG <sub>2a</sub>       | Ledbetter and Herzenberg 1979 |
| Ly-3    | - 24                    | Ledbetter et al. 1980         |
| Ly-4    |                         | Dialynas et al. 1983          |
| Ly-5    |                         | Trowbridge 1978               |
| Ly-6    | IgG <sub>2a</sub>       | Dumont et al. 1985            |
| Ly-15   | 0 24                    | Davignon et al. 1981          |
| Ly-17   | IgG                     | Unkeless 1979                 |
| Ly-24   | $IgG_{2a}$ , $IgG_{2b}$ | Trowbridge et al. 1982        |

\* All antibodies made in rats

# Description of the Ly Loci

We now present a brief description of the *Ly* loci. References are given for the more recently described loci and for potential areas of confusion. Otherwise, the information can be found in several reviews (McKenzie and Potter 1979, Hogarth and McKenzie 1984, Sutton et al. 1985). Table 1 illustrates the strain distribution, Tables 2 and 3 the availability of monoclonal antibodies, and Table 4 the linkage relationships. Nomenclature of Ly Loci

Ly-1. Formerly Lyt-1.

Ly-2. Formerly Lyt-2.

Ly-3. Formerly Lyt-3.

*Ly-4.* This specificity is reserved for the gene encoding the mouse equivalent of the human Leu-3/T4 antigen. Alleles of *Ly-4*, formerly *Lyb-1*, have essentially the same strain and tissue distributions with alleles of *B2M* and probably represent polymorphism of the same gene. The gene encoding Ly-4 antigens is defined by monoclonal antibodies (Dialynas et al. 1983, Pierres et al. 1984, Wassmer et al. 1985).

*Ly-5.* Formerly *Lyt-4.* The allele and specificity designations originally described are reversed, i. e., C57BL/6 now carries the *Ly-5<sup>b</sup>* allele and the Ly-5.2 specificity, and SJL carries the *Ly-5<sup>a</sup>* allele and the Ly-5.1 specificity.

Ly-6. Antigens determined by the Ly-6 locus were defined first by conventional antibodies and later by monoclonal antibodies. A series of monoclonal antibodies define specificities with an identical or similar strain distribution, but with different tissue distributions, and in some cases different sizes of proteins. For example, DAG, Ala-1, H9/25, ThB, Ren-1, Ly-27, Ly-28, Ly-6A to Ly-6E, and probably others have been detected by a large number of antibodies produced by different investigators. It is not clear whether Ly-6 is a gene complex or a single locus with variation due to patterns of mRNA transcription of splicing, posttranslational modification of proteins or to differing affinities of antibodies (Palfree et al. 1986). For the present, we consider Ly-6 to be a gene complex, with the individual loci identified by the addition of capital letters (after Kimura et al. 1984). The original Ly-6 locus as identified by the first described monoclonal antibody (Kimura et al. 1980a) now becomes Ly-6A, and the others are identified as listed below (Kimura et al. 1984). Gm-2.2 was described by Hibbs and co-workers (1984).

| Locus | Speci-<br>ficity | Synonyms               | Tissue distribution   |
|-------|------------------|------------------------|---|
| Ly-6A | Ly-6A.2          | Ly-6, Ly-8             | Lymph nodes, spleen, low in thymus, T>B                             |
| Ly-6B | Ly-6B.2          | Gm-2.2                 | Bone marrow, granulocytes   |
| Ly-6C | Ly-6C.2          | H9/25,<br><i>Ly-28</i> | Lymph nodes, spleen, bone<br>marrow, blast cells, granulo-<br>cytes |
| Ly-6D | Ly-6D.2          | Ly-27                  | Thymus, lymph nodes, spleen,<br>blast cells, low on bone<br>marrow  |
| Ly-6E | Ly-6E.1          | Ala-1                  | Blast cells, low on thymus,<br>spleen, lymph node, bone<br>marrow   |

The closely linked *Thb* locus should be considered a separate locus since it is a regulatory locus affecting expression of the ThB antigen, a protein whose structural locus has not been identified.

*Ly-7*. The allelic designations are changed so that C57BL/6 is Ly-7<sup>b</sup>. The specificities now defined by monoclonal antibodies are Ly-7.1 and Ly-7.3 (Lanier and Warner 1982, 1983). The Ly-7.2 specificity has not been defined by antibody.

*Ly-8.* Formerly *Ly-11* with the Ly-11.2 specificity defined by conventional alloantisera (Potter and McKenzie 1981). The former *Ly-8* (Frelinger and Murphy 1976) is considered identical with *Ly-6A*.

*Ly-9.* This locus has two specificities, Ly-9.1 and Ly-9.2 (Mathieson et al. 1980), both defined by monoclonal antibodies (Ledbetter et al. 1979, Hogarth et al. 1980b). The protein T100 or Lgp100 (Ledbetter et al. 1979) is the product of the *Ly-9* locus.

*Ly-10.* There is only one serologically defined specificity, Ly-10.1, defined by a monoclonal antibody (Kimura et al. 1980b).

*Ly-II.* One specificity only, Ly-I1.2, has been defined by a conventional antiserum (Meruelo et al. 1980, 1982). The *Ly-II* of Potter and McKenzie (1981) is now *Ly-8*, and the *Ly-mII* of Tada and co-workers (1980) is now *B2m*.

*Ly-I2.* One specificity only, Ly-12.1, has been defined by both conventional (Potter and McKenzie 1981) and monoclonal (Hogarth and McKenzie 1984) antibodies.

*Ly-13.* One specificity only, Ly-13.1, has been defined by conventional alloantisera (Potter and McKenzie 1981).

*Ly-14.* One specificity only, Ly-14.1, has been defined by conventional alloantisera (Potter and McKenzie 1981).

*Ly-15.* Two specificities, Ly-15.1 and Ly-15.2, have been defined by conventional and monoclonal antisera, respectively (Potter et al. 1981). *Ly-15* is a polymorphism of the  $\alpha$  chain of the LFA-1 molecule (Hogarth et al. 1985, Walker et al. 1984).

*Ly-16.* Formerly *Ly-18* of Finnegan and Owen (1981). One specificity, Ly-16.1, was detected with conventional antibody.

*Ly-17.* Specificity Ly-17.1 was defined by a conventional antibody (Shen and Boyse 1980). Specificity Ly-17.2 (Kimura et al. 1981a) was originally called Lym-20.2 (Kimura et al. 1981a, Davidson et al. 1983, Kozak et al. 1984). *Ly-17* is probably identical with the Ly-M locus (Tonkonogy and Winn 1976). Ly-17 has recently been found to code for a polymorphism of the Fc gamma receptor (Hibbs et al. 1985, Holmes et al. 1985).

*Ly-18.* Formerly *Lym-18.* Specificity Ly-18.2 was defined by a monoclonal antibody (Kimura et al. 1981b).

*Ly-19.* Formerly *Lym-19.* Specificity Ly-19.1 was defined by a monoclonal antibody (Tada et al. 1981).

*Ly-20.* Originally defined by a conventional antiserum as *Ly-22* (Meruelo et al. 1983) and at one stage referred to as *Ly-15.* 

*Ly-21.* Specificity Ly-21.1 was defined by a monoclonal antibody (Kennard and Meruelo 1982) and was once referred to as Ly-20.2.

*Ly-22.* Formerly *Ly-m22.* Specificity Ly-22.2 was defined by a monoclonal antibody (Tada et al. 1983).

*Ly-23.* Specificity Ly-23.2 was defined by a monoclonal antibody (Gasser et al. 1983).

*Ly-24.* Originally designated *Pgp-1* (phagocyte glycoprotein-1) (Colombatti et al. 1982). We have changed the name of this locus with the permission of the authors. The *Pgp-1* designation is misleading because of the widespread distribution of this antigen on lymphocytes and other cells. Monoclonal antibodies recognizing the Ly-24.1 (Pgp-1.1) and Ly-24.2 (Pgp-1.2) specificities have been described (Lesley and Trowbridge 1982).

*Ly-25.* Specificity Ly-25.1 was defined by a monoclonal antibody (Hogarth et al. 1984a).

*Ly-26.* Specificity Ly-26.1 was recognized by three monoclonal antibodies (Hogarth et al. 1984b).

*Ly-27.* This number was originally used (Hogarth et al. 1984c) for the locus now defined as *Ly-6D.* It is now reassigned to a locus with one specificity, Ly-27.1, defined by a monoclonal antibody (Matsushima et al. 1986).

*Ly*-28. Originally used (Hogarth et al. 1984c) for the locus now defined as *Ly*-6C. This number is now assigned a locus defined by a monoclonal antibody to Ly-28.2 (N. Tada et al., manuscript in preparation).

Ly-29. Locus defined by a monoclonal antibody to the Ly-29.2 specificity (Gonez et al. 1985a).

*Ly-30.* Locus defined by a monoclonal antibody to the Ly-30.2 specificity (Gonez et al. 1985b).

*Ly-31.* Locus defined by a monoclonal antibody to Ly-31.2 (Tada et al. 1984).

*Ly-32.* Locus defined by a monoclonal antibody to Ly-32.2 (N. Tada et al., manuscript in preparation). Strain distribution is the same as Lyb-2.2, but the antigen is expressed on both T cells and B cells.

Lyb-2 to Lyb-8. Remain as such.

It is requested that any corrections or additions regarding the data summarized in the tables be forwarded to Dr. Morse.

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#### Note added in proof:

The allele for C57BL/6 mice at loci (e. g. Ly-l0) where no antigenic specificity is defined for the strain should always be designated as b. The Ly-7 locus will be considered provisionally to have three alleles: a for strains that are Ly- $7.1^+$ , Ly- $7.3^-$ ; b for strains that are Ly- $7.1^-$ , Ly- $7.3^-$ ; and c for strains that are Ly- $7.1^+$ , Ly- $7.3^+$ . A cDNA clone of the murine gene homologous to the human CD4 gene has been described (Tourvielle et al. *Science 234*: 610–614, 1980). The Ly-4 designation should no longer be considered to be reserved and should be used for this gene.

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