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Neurospora genetic nomenclature

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NEUROSPORA GENETIC NOMENCLATURE
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Table of Contents

Introduction

Rules for the genetic nomenclature of *Neurospora crassa* have been evolving since 1941. This document is a guide to present usage. The basic Neurospora conventions antedate genetic nomenclature of bacteria and other microorganisms and follow Drosophila nomenclature more closely. Rules for Neurospora were last summarized in 1982 (reference 16). The expanded version given here incorporates subsequent refinements and changes (e.g., 5, 7, 13). It aims to provide a system that is adaptable to new developments in molecular genetics while retaining the gene names and working vocabulary that have become established over the years.

Most of the existing Neurospora nomenclature conforms to the rules set forth here, but some does not. To avoid confusion, we have usually refrained from changing established names and symbols that do not conform to current usage. Past practice and the continued retention of names and conventions that flout the present rules should not be taken as an excuse for bad practice in the future.

What may be considered standards for Neurospora nomenclature are provided by usage in the current compendium and in the latest lists and maps published by the Fungal Genetics Stock Center (FGSC). The present document has benefitted from recent descriptions of Drosophila and maize nomenclature (6, 2). The detailed rules for Drosophila published by *Flybase* (6) may provide guidance for problems that are not considered here.

http://newprairiepress.org/fgr/vol46/iss1/15
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1. Gene names and symbols

1.1. *Names.* Like Drosophila, Neurospora has a relatively well defined wild-type phenotype. In the formative years with both organisms, existence of a gene was recognized when a mutation occurred that deviated from the wild type. The gene was then named using a word that described the mutant phenotype. Gene loci recognized on the basis of naturally occurring variants (e.g., mating type idiomorphs, vegetative incompatibility genes, isozyme markers) were named according to the phenotype affected. Descriptive gene names were given in preference to using numbers or nondescriptive names. They are informative, easier to remember, and less likely to result in confusion with other loci.

In choosing what aspect of the phenotype to use as a basis for naming a mutant gene, preference was given to the most convenient and useful manifestation. For example, all arginine auxotrophs were named "arginine" rather than being given different names based on the earliest utilizable precursor (citrulline, ornithine, etc.) or on the enzyme that was rendered nonfunctional. A gene specifying the molybdenum cofactor that is shared by nitrate reductase and xanthine dehydrogenase was named "nitrate-8" rather than "molybdenum cofactor" or "xanthine dehydrogenase" because the mutant is scored as a nitrate nonutilizer. These considerations still hold.

Gene names should be concise and informative. Each name must be unique and must not have been used previously for a Neurospora gene. Gene names or symbols should not be prefixed with word *Neurospora* or the letters *n* or *nc* to indicate that a gene is from Neurospora. To do so would be redundant. Sequence-database identification-code entries, which often begin with NC or NEU, are not gene names or symbols, nor do they establish priority.

Different loci bearing the same name and the same base symbol should be numbered sequentially beginning with one, e.g., *arg-1, arg-2, arg-3*, etc. If a name applies to only one locus, use of the number 1 is optional. For example, the gene that specifies invertase is symbolized *inv* rather than *inv-1*. Arbitrary strain-identification numbers should not be converted into locus numbers.

Regulatory genes have usually been given the same name and symbol as the structural genes they regulate (e.g., *nit-2, leu-3, cys-3*), but this is not always true (e.g., *pcon, pgov, scon, ty*).

When new names, symbols, locus numbers, or allele-number prefixes are to be assigned, it is essential to avoid duplication by consulting the most recent FGSC stock list and the lists that accompany the current genetic maps.

1.2. *Symbols.* Symbols are preferably three-letter abbreviations of the gene name, but they may consist of two letters or (rarely) one or four. Symbols are written in lower case italics (e.g., *inv*) except when the name is based on a mutant allele that is dominant. The first letter is then capitalized (e.g., *Asm*). Nonallelic genes that have the same descriptive name and symbol are distinguished from one another by numbers that are separated from the base symbol by a hyphen (e.g., *al-1, al-2, al-3*). This use of hyphens in Neurospora and Drosophila differs sharply from the convention in many other organisms, where a locus number (or letter) is not separated from

the base symbol. Hyphens are used only to separate the locus number from the base symbol to which it is appended.

When a gene name contains a number that is necessary for identifying the product or phenotype, the product-identifying number is included as an integral part of the base symbol, with digits unseparated from the letters by a hyphen (e.g., *tom22*; *nuo78*). A hyphen can then be used if it is needed to distinguish locus numbers from numerals belonging to the gene name (e.g., *hsp70-1, hsp70-2*; see reference 13).

Roman numerals should be avoided in gene symbols.

Suppressors are symbolized using the letters *su,* followed immediately by the symbol of the suppressed gene in parentheses. If nonallelic suppressors of the same gene are known, locus numbers follow the parentheses (e.g., *su(met-7)-1, su(met-7)-2*). As in Drosophila, su^{+} designates the wild-type gene, *su* the mutant suppressor allele. For allele-specific suppressors, the allele number is included as a superscript of the locus symbol (e.g., *su(trp-3*^{td201}*)-2*). Enhancers are symbolized in a similar way (e.g., *en(am)-1*).

The mating type genes, formerly called *mt*, are now symbolized *mat* (reference 7). The *mat* locus is occupied by either of two nonhomologous sequences, *mat A* or *mat a.* These are called idiomorphs rather than alleles (10). In most contexts, the abbreviated symbol *A* or *a* is used. Only when the context requires specifying the idiomorph completely is it necessary to use the more ponderous symbols *mat A-1 mat A-2 mat A-3* (for *A*) or *mat a-1* (for *a*). Unless the context requires that *mat* be shown in the actual order of its location on the map, the mating type symbol follows all other symbols when multilocus genotypes are written, (e.g., *leu-3 cr-1 al-2 A* or *cot-1 a*)

Chromosomal loci other than genes usually have the initial letter of the symbol capitalized (e.g., *Cen, Tel, In, T*). Also, the initial letter is usually capitalized in symbols for active or relic transposons (e.g., *Tad, Pogo*).

1.3. *Dominance and recessiveness*. When a gene is named for a mutant phenotype that is recessive to the wild type, the name and symbol are written in lower case letters (e.g., *al*: *albino*). The initial letter is capitalized when the mutant phenotype is dominant (e.g., *Ban*: *Banana*). The initial letter is not capitalized when a gene is named for alleles that show codominance (e.g., *het*: *heterokaryon incompatibility*).

Mutant phenotypes may be expressed either in the vegetative phase or in the sexual phase, or in both. Some mutant genes are known to be dominant in the sexual phase but recessive in vegetative tissues. The initial letter of the name and symbol is then capitalized if the gene name is based on the dominant mutant phenotype (e.g., *R, Asm*) but the the initial letter is not capitalized if the name is based on the recessive mutant phenotype (e.g., *mei-3, pk*^{D}).

Dominance or recessiveness is usually not known at the time new vegetative-phase mutants are named. In the absence of that information, lower case symbols are routinely used because recessive loss-of-function mutations are the most common type to be detected phenotypically.

http://newprairiepress.org/fgr/vol46/iss1/15
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Tests for dominance in the vegetative phase may employ either heterokaryons or heterozygous partial diploids. Partial diploids are preferred because they ensure a 1:1 allele ratio, whereas the ratio of nuclear types in heterokaryons may depart widely from equality. Partial diploids are obtained as duplication progeny from crosses heterozygous for insertional or quasiterminal rearrangements.

Mutant genes that are recognized by their expression in the perithecia of heterozygous crosses are immediately known to be dominant (e.g, *R, Asm*). Recessive sexual-phase mutations are less likely to be detected because they must be present in both parents of a cross in order to be expressed. Many of the known sexual-phase recessives were recognized in crosses homozygous for mutant genes affecting mutagen sensitivity and DNA repair (e.g., *uvs, mus*). These had already been detected and named as recessive vegetative-phase mutants. Other recessive sexual-phase mutants have come from backcrosses in experiments specifically designed to detect them (9). Still others were discovered accidentally in crosses between inbred parents (e.g., *mei-1, mei-3*).

1.4. *Gene loci recognized by DNA sequence.* We need no longer depend on mutant differences. cDNA libraries and sequencing now make it possible to recognize genes for which no variant product or phenotype has been detected. These "anonymous" genes can be placed on the genetic map by using them as probes in RFLP mapping. In absence of a known mutant phenotype, gene names may be based on the time or site of expression (e.g. *con*). The null mutant of such a gene may (e.g., *asd-1*) or may not (e.g., *con-11*) reveal a conveniently recognizable mutant phenotype on which to base a descriptive name. If the null mutant is lethal (as with *tom19* and *tom22*, for example), or if it is phenotypically wild type, or if the mutant phenotype remains undetermined, it is appropriate and informative to base the name on sequence-homology with a gene or gene family the function of which is known in another organism (e.g., *ras*: *ras-like*, *pzl*: *phosphatase-z-like*). This should be done, however, only if the sequence makes a strong prediction of function. A Neurospora gene should not be named for the overt phenotype of its homolog in another organism if that phenotype is developmentally complex and far removed from the primary gene product. Manifestation of the genes may have diverged in the two organisms, resulting in quite different phenotypes. For example, mutations in homologous genes appear to be responsible for cerebrohepatorenal anomalies in humans and for failure of premeiotic nuclear fusion in the croziers of Podospora (3) and Neurospora (K. Howe and M. A. Nelson, personal communication).

If neither phenotype nor homology is known, a gene may be given a generic symbol indicating anonymity. The symbol *anon* is used in Drosophila, with some distinguishing suffix, and this is recommended for Neurospora. An alternative that has been proposed is *eat* (*encodes anonymous transcript*) (17). The meaning of *eat* is not obvious from the symbol, however. Generic names and symbols of this type, that represent a category of mutants rather than a specific mutant, have a long history of use in Neurospora. Best known is the use of *un* for temperature sensitive genes of unknown function. Other generic categories are *ccg* for clock-controlled genes, *con* for genes expressed during conidiation, and *sdv* for genes expressed under conditions favoring sexual development

When a mutant phenotype or a definitive sequence-homology is discovered for an anonymous mutant, the option exists of changing the name to something more definitive. For example, if the null allele of a gene initially called *anon(NP6C9)* were found to result in restricted colonial growth, the name could be changed to *col-x*.

Different *anon* genes are best distinguished using isolation numbers, as in the example, because if the genes were numbered serially, a clearing house would be needed to avoid using the same number repetitively.

1.5. *Genes in ectopic positions.* A Neurospora gene that has been integrated ectopically is designated by appending *(EC)* to the gene symbol, e.g., *am(EC).* The genotype of a strain with a gene deleted from its normal position and a wild type copy of the same gene inserted elsewhere in the genome would thus be symbolized *am; am*$^{+}$*(EC).*

1.6. *Gene fusions and transposable-element insertions.* A double colon is employed to indicate the genes or elements that have been joined. For example, *mtr::Asm-1*$^{+}$*(EC)* or *am::Tad*. Symbols cannot be expected to convey full information about complex constructs or genotypes. This is best done in the text or using a figure.

1.7. *Priority. Synonyms.* Where differences exist in published names for the same gene, the symbol and name are adopted that were used when the gene was first reported to be at a previously unknown chromosomal locus -- usually when the gene was first mapped. For example, when sequence comparisons and allelism tests revealed that mutations called *ccg-2* and *bli-4* are allelic with the alraady established gene *eas*, the two newly coined names became inactive synonyms of *eas.* Inactive synonyms should never be used later for another gene.

Where the same symbol has inadvertantly been used for two genes with different names, the symbol that was published first is retained and a different symbol is assigned to symbolize the name of the other locus. For example, if the long-established symbol *nd* (*natural death*) were accidentally used for a gene that specified NADH ubiquinone reductase, it would be necessary to find a new symbol for the latter.

Priority is established by publication in a refereed journal or book, or in an article in Fungal Genetics Newsletter. Use of a gene name or symbol in conference abstracts, in Dissertation Abstracts International, or in unpublished theses does not establish priority, although names and symbols reported there may be adopted in the absence of any conflict. Sequence-databank codes are not gene symbols and do not confer priority.

1.8. *Changing gene names and symbols.* The name and symbol of a mutant gene should be changed only for compelling reasons, as when the original name is found to be incorrect or misleading. Reasons for making the change should be clearly stated, as was done in changing *met-4* to *cys-10* or *ol* to *cel*. For examples, see reference 13.

Gene loci that bear generic names such as *anon*, *ccg, con, eat, sdv,* or *un* present a special case. When a definitive phenotype, function or homology is discovered for such a gene, the question arises whether to propose substituting a more informative name for the generalized original. An

http://newprairiepress.org/fgr/vol46/iss1/15
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investigator may propose to abandon the generic name, as was done for example when *un(STL6)* was changed to *fls, sdv-10* to *asd-1*, and *con-8* to *phr*. On the other hand, the decision may be to retain the generic name, as was done when gene products were identified for *un-18* and *un-24*. The decision whether to rename an *un* mutant may be influenced by the consideration that scoring and recognition is best accomplished on the basis of temperature sensitivity. Decisions whether to change will depend not only on anticipated usefulness of a more specific name but also on how firmly the original name is established and how widely it has been used.

1.9. *Multilocus genotypes.* When more than one locus in the same linkage group is to be shown, symbols are written in the linear order of loci on the conventional linkage map and are separated from one another by single spaces, e.g., *cr-1 al-2 nic-1*. Commas are not used. When a genotype includes markers from different linkage groups, the groups are separated by semicolons and spaces, e.g., *cr-1 al-2; am inl; nic-3*, for markers in linkage groups I, V, and VII. In designating multilocus genotypes, wild type is implied for a specific gene if no symbol is given for the locus. For example, *cr-1 al-2 A* X *nic-1 a* implies *cr-1 al-2 nic-1*$^{+}$ *A* X *cr-1*$^{+}$ *al-2*$^{+}$ *nic-1 a*. If there is no ambiguity when genotypes are written out, a simple unraised + sign may be used to indicate the relevant wild type allele, for example, *cr-1 al-2 + A* X *+ + nic-1 a*. Acronyms may be used to represent complex genotypes, e.g., *alcoy, multicent*.

1.10. *Species other than N. crassa.* Names and symbols for genes in other Neurospora species should be identical to those of their *N. crassa* homologs when the homology is securely known. A nonconforming name should be changed unless this seems inadvisable because of long-established usage in the other species.

2. Alleles

2.1. *Symbols.* Where there is a standard wild-type allele in a defined laboratory strain, the locus symbol without a superscript represents the mutant allele. The same symbol with a plus superscript designates the wild-type allele (*Bml*$^{+}$). In designating genotypes, the symbol + is reserved for the wild type allele. Multiple alleles, or alleles differing in resistance to a toxic agent, or allelic genes having no definitive wild type, are distinguished by appropriate superscripts (e.g., *frq*^{1}*, frq*^{2}*, frq*^{3}; cyh-*1*^{R}, *cyh-1*^{S}; *het-6*^{OR} , *het-6*^{PA}*; a*^{m1}*,* ^{am33}). Intragenic deletions are treated as alleles at the gene locus. Deletions of an entire single gene or a large portion of it are designated by prefixing the symbol with a capital Greek delta, e.g., *am*.

When superscripting is impossible, as in ASCII, superscripted text is enclosed in square brackets. Thus, *frq*^{7} would be written *frq[7]*.

2.2. *Pseudogenes.* If DNA sequence indicates that a locus is occupied by a defective member of a gene family, the locus is named as a member of that gene family. If it is a pseudogene, that fact may be shown by appending the letters *ps* to the base symbol as a superscript (e.g., *Fsr63*^{ps}, a 5S RNA pseudogene). An active gene may later be found that is allelic with such a pseudogene (see for example *Fsr33*).

2.3. *Isolation numbers (allele numbers)*. Allelic mutations bear identical locus symbols and locus numbers. Each independently originating new mutation at a gene locus is assigned a unique

isolation number (often called allele number) even though it is phenotypically indistinguishable from the mutants previously known. Isolation numbers are commonly prefixed by letters indicating the laboratory of origin. A list of letters already used as prefixes is published in the FGSC catalog following the section of single-mutant stocks. Isolation numbers are not part of the gene symbol and are not displayed except when necessary to distinguish between alleles. The number may then be shown in parentheses after the full locus symbol, e.g., *pyr-3*(KS43). When a new mutant gene has not yet been assigned a locus number, pending tests for allelism with similar genes at previously established loci, the mutant may be designated temporarily by an appropriate letter-symbol followed immediately by the allele number in parenthesis, e.g., *ilv(STL6).*

2.4. *Culture collection accession numbers*. Culture collections assign an arbitrary number to each stock as it is acquired. This number is usually prefaced by initials of the organization -- e.g., FGSC, ATCC, CMI, or CBS. The same strain may have more than one accession number if it is included in two or more collections. Care should be taken to distinguish accession numbers from isolation (allele) numbers. The culture collection accession number may be provided to identify the exact source of a strain that was used. It should not be used in place of the isolation number to identify what allele was used.

When depositing strains in a culture collection, investigators should make sure that each strain is given a unique identification number and that allele numbers are provided for all mutant genes.

3. Heterokaryons

Genotype symbols for the component nuclei of a heterokaryon are separated by a plus sign. Parentheses are used to enclose symbols defining the entire heterokaryon, as for example (*col-2 A + ad-3B cyh-1 A*) (13).

4. Distinguishing generations in a pedigree

Haploid parent and progeny strains in a series of crosses are called p_1, f_1, etc., using lower case letters. Backcross generations are also designated using lower case letters, b_1, b_2, etc. (The progeny from f_1 X p_1 are designated b_1, progeny from b_1 X p_1 are b_2, etc.) This deviation from the upper case symbols used with diploid organisms (P_1, F_1, etc.) was introduced in 1924 for haploid gametophytes of the bryophyte Sphaerocarpus (1). Lower case letters were first used for Neurospora by Dodge in 1928 (4).

When subscripting is impossible, as in ASCII, subscripted text is enclosed in doubled square brackets, e.g., b_2 would be written b[[2]].

5. Genotypes and phenotypes

Genotype symbols are italicized, phenotype symbols are not. Genotype designations include not only genes but also centromeres (e.g., *Cen-VII)*, telomeres (*Tel-V)*, the nucleolus organizer (*NO*) or nucleolus organizer region (*NOR*), and chromosome rearrangements (e.g., *T(III;V)AR177), In(IL;IR)OY323), Dp(VL>IVL)AR33*; see reference 14). The locus of a gene is designated using

http://newprairiepress.org/fgr/vol46/iss1/15
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the base symbol without a superscript. Acronyms and abbreviations for complex genotypes are italicized (e.g., *alcoy, multicent*).

A phenotype symbol is obtained by converting each relevant base gene symbol to nonitalic, capitalizing the initial letter, and adding "+" , "", or another allele-designation as a superscript. For example, a strain of genotype *al-2 arg-6* is phenotypically Al Arg; a strain of genotype *al-2*$^{+}$ *arg-6*$^{+}$ is phenotypically Al^{+} Arg^{+}; a partial-diploid strain of genotype *al-2 arg-6/al-2*$^{+}$ *arg-6*$^{+}$ is phenotypically Al^{+} Arg^{+}, and a *cpl-1*^{S} strain is phenotypically Cpl^{S}. Double mutants for the same function may be designated phenotypically using the shared base-symbol. Thus, the phenotype of an *arg-2; arg-3* strain is written Arg.

6. Gene products

The protein products of genes are represented by the same characters used to designate the genes encoding them, written in nonitalic capital letters (5). For example, the protein product of the *preg* gene is PREG and that of *inv* is INV. If the name of a gene product is written in full, capitalization is unnecessary.

7. Distinguishing "locus" and "gene"

"The words "locus" and "gene" should not be treated as synonymous. A locus can be defined as a chromosomal site of variable size at or within which is located a gene, a restriction site, a knob, a breakpoint, an insertion, or other distinguishable feature." (reference 2). A gene is a DNA sequence that is regularly or conditionally transcribed at some time during the life cycle.

8. Linkage groups and chromosomes

Linkage groups, which are defined genetically, are designated by Roman numerals I through VII. These are not italicized except when they are included in the symbol for a chromosome rearrangement. Chromosomes, which are defined microscopically or physically, are designated by Arabic numerals. For correspondences between linkage groups and chromosomes, see references 15, 12. Most genes are readily assigned to a linkage group, but obtaining direct information about their physical chromosome location is difficult. Linkage group numbers are therefore used rather than chromosome numbers in the symbols for chromosome rearrangements and for identifying electrophoretically separated chromosomal DNAs (12).

9. Chromosome rearrangements

Intragenic rearrangements or single-gene deletions are represented as alleles at the relevant locus. For rearrangements involving chromosome segments that contain two or more genes ("segmental rearrangements") the base symbols are: *T* (translocation), *In* (inversion), *Tp* (transposition within the same chromosome), *Dp* (duplication), and *Df* (deficiency, synonymous with deletion) (13). The base symbol is followed in parentheses by Roman numerals indicating the relevant linkage group or groups. (*L* or *R* may be added to indicate the linkage-group arm.) The final element in the symbol is an identification number. The entire symbol is italicized, with no intervening spaces. In symbols for reciprocal translocations, linkage group numbers are

separated by a semicolon (e.g., *T(IIIR;VR)P1226*). With insertional or quasiterminal rearrangements, the linkage groups are separated by an arrow indicating which is the donor and which is the recipient of the transferred segment (e.g., *T(IL>IIR)39311*). Progeny from insertional or quasiterminal rearrangements may contain two copies of the transposed segment. These are symbolized, for example, *Dp(IL->IIR)39311*.

When a rearrangement has two breaks in the same linkage group, superscripts may be used to distinguish left and right breakpoints (e.g., $In(OY323)^{L}$, $In(OY323)^{R}$; $T(39311)^{L}$, $T(39311)^{R}$. If a rearrangement breakpoint is inseparable from the mutant phenotype of an associated gene, the gene symbol follows the rearrangement symbol and is separated from it by a space with no comma (e.g., *T(IR;IIR)4637 al-1*). For further details, see reference 14.

10. Wild types

10.1. *Laboratory wild types.* Most experimental work has employed *N. crassa* markers and strains that were derived from a relatively few wild-type progenitors. Names of laboratory wild type strains are commonly abbreviated and are not italicized. Best known are Oak Ridge (OR), Standard (ST; commonly called St. Lawrence), Emerson (Em), and Rockefeller-Lindegren (RL), each of which exists in opposite mating types. Each of these has been used extensively in the past, in one or another laboratory, and each has contributed mutant alleles that are still in use as markers. Cryptic genetic polymorphisms exist between all these strains, and sometimes between *A* and *a* strains that bear the same name. The highly inbred, heterokaryon-compatible Oak Ridge strains OR23-1A and ORS-5a have been most widely used and have now been adopted as standards by most laboratores. For a pedigree showing the derivation of OR and other wild type strains, see reference 11.

10.2. *Strains from nature.* A newly acquired strain is given an identification number by the laboratory first putting it in stock. It may then be deposited in culture collections where it is given different accession numbers. For example, a *N. crassa* strain from Panama was successively numbered CZ30.7 by the original collector, QM 4839 by the U. S. Army Quartermaster Corps, and FGSC 1132 by the Fungal Genetics Stock Center. To avoid confusion, the original identification number CZ30.7 should be specified in designating what strain was used.

11. Transposable elements

Names and symbols are italicized and the first letter is capitalized, e.g., *Pogo, Punt, Tad, Tourist*. This conforms with usage for chromosomally integrated mobile or relic transposable elements in maize and in other fungi.

12. Mitochondria

12.1. *Mutant mitochondrial genomes.* The names and symbols of mutant mitochondrial genomes (and strains carrying them) are enclosed in nonitalicized square brackets to distinguish them from nuclear genes. The symbols, but not the brackets, are italicized. For example, [*mi-2*], [*poky*], [*stp*].

http://newprairiepress.org/fgr/vol46/iss1/15
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12.2. *Individual mitochondrial genes*. The symbols proposed for fungi by Hudspeth (8) are recommended. Gene symbols are written unhyphenated, using lower case italics and arabic numerals, e.g., *cox1, atp6.* The corresponding gene products are symbolized using nonitalicized upper case letters.

12.3 *Mitochondrial plasmids*. Plasmid names begin with a lower case letter "p" followed by the name in capital letters, e.g., pKALILO. When additional members of a family are found, they are assigned numbers sequentially, e.g., pKALILO-2. Symbols incorporate the first three letters of the name, e.g., pKAL-2. Names and symbols of mitochondrial plasmids are not italicized.

13. Use of italics

The following are italicized: Gene names and symbols, including superscripts. Symbols for individual rearrangements. Symbols for centromeres, telomeres, and the nucleolus organizer. Acronyms that represent genotypes. Names and symbols of mitochondrial genes and mutant mitochondria (the latter are enclosed in nonitalicized brackets). Symbols for transposable elements.

The following are not italicized: Names and symbols of phenotypes and gene products. Linkage group numbers (except when the Roman numeral is an integral part of the symbol for a rearrangement). Names and abbreviations for wild-type strains. Names of chromosome-rearrangement types ("translocation", "inversion", etc.) when written in the text. Names and symbols of mitochondrial plasmids.

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