A PROPOSAL FOR THE UNIFORM TREATMENT OF INFRASUBSPECIFIC VARIATION BY LEPIDOPTERISTS

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The binomial system of zoological nomenclature dates back to Linnaeus' 10th edition of *Systema Naturae* in 1758. The trinomial was not conceived by Linnaeus, however, and did not come into extensive use until the last half of the 19th century. While Linnaeus created the binomial system, he did not propose any sort of rules for the naming of animals. A great deal of confusion resulted and in the early 19th century a number of codes were proposed, mostly imposing a basic philosophy for priority of names, in attempts at solution. At the First International Congress of Zoology, held in Paris in 1889, Raphael Blanchard submitted a proposed set of international rules for naming animals. Blanchard's rules were formally adopted at the Second Congress in Moscow in 1892 and have been subsequently revised until the present *International Code of Zoological Nomenclature* was adopted by the Fifteenth Congress in London in 1958 and was officially published in 1961.

Under the present Code (1961) the trinomial is restricted in usage to geographical subspecies and all other types of infraspecific variation are considered as infrasubspecific and are removed and excluded from the provisions of the Code. This decision, by the International Commission, was not meant to imply that the study of infraspecific categories other than the subspecies is unimportant, but to emphasize the fact that subspecific variation is essentially different from any of the others. Subspecific variation is generally considered to be the first stage of the speciation process and those populations which are currently treated as subspecies are so treated subjectively and may be, in any later revision, elevated to the species level. Because the subspecies names is subject to elevation to the species level (and conversely, species names are subject to reduction to the subspecies level), it is essential to retain it in the species-group where it is liable to those rules and criteria, including priority, which apply to the species name.

The geneticist, and many others, may regard other types of infraspecific variation as more important than subspecies; however infrasubspecific variants are not subject to elevation to the species category and there was deemed to be no need to conserve priorities or other protection under the provisions of the Code.

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INFRASUBSPECIFIC VARIATION

Other than a general agreement that infrasubspecific names should not be placed in italics, as are the species-group names, lepidopterists have not given them anything approaching a standard treatment in the last decade. There has been, however, a very sharp decrease in the publication of formal names to apply to infrasubspecific variation during the last twenty years. While a few names still appear, most authors are content to describe examples of infrasubspecific variation without attempting to formally name them.

Designations for many types of infrasubspecific variation seem at least useful, if not necessary, and if they are to be designated, it is highly desirable that a consistent and uniform method be used for citing them. It is not necessary that priorities or rules of Latin word formation be followed, nor is it essential that usage in Lepidoptera be consistent with that in other orders of insects or in other classes of animals. The opportunity is clearly present for lepidopterists to develop a system of designation suitable for present day needs without concern for the stigmas of priorities and validities that have made this impossible in the past. With the vacilation of the I.C.Z.N. in the area of infrasubspecific designation, it is unlikely that mandatory rules will ever be adopted. Consistent usage can only come through common acceptance of the majority of lepidopterists. It is my hope that this proposal for a rational, uniform treatment of infrasubspecific categories will eventually lead to a standard and uniform treatment by lepidopterists around the world.

Infrasubspecific designations in Lepidoptera have been employed for an assortment of variations, all of which involve maculation (phenotype expression), some, but not all, of which involve genotype and none of which, at least directly, involve physiotype. For practical purposes, they all can be grouped into four distinct categories: (1) polychromatic or polymorphic forms, (2) mutant or aberrational forms, (3) seasonal or brood forms, and (4) hybrids. Each of these presents an entirely different set of circumstances and the criteria for designation must be dealt with individually.

Polychromatic or Polymorphic Forms

Ford (1940) defined the condition of polymorphism as "the occurrence together in the same habitat of two or more discontinuous forms, or phases, of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation." Polymorphic forms are perhaps best known to North American lepidopterists in the yellow or white color phases of female *Colias* species. They are most pronounced

in the various mimetic female forms of certain African and Indo-Australian *Papilio* species, e.g. *Papilio dardanus* Brown or *Papilio polytes* Linnaeus. These are clearly genetic situations and, in fact, the genetics of many of them have been carefully studied and worked out by breeding in the laboratory. The discontinuous factor is important for considerations of polymorphism, for continuous variation that could be plotted on a curve of normal distribution, such as the length of forewings, is excluded. (For detailed discourse on the genetic aspects of polymorphism, see Ford (1965).)

Nearly all of the North American *Colias* species exhibit dimorphic yellow vs. white female color phases (for detailed information, see Hovanitz, 1950), and many names have been proposed to refer to the white form: "alba" Strecker, "albida" Chermock, "canescens" Comstock, "flavocincta" Cockerell, "hatui" Barnes & Benjamin, "neri" Barnes & Benjamin, "medi" Gunder, "lambillioni" Dufrane, "martini" Gunder, "pallida" Cockerell, "pallida" Skinner, "pallidice" Scudder, "pallidissima" Bowman, and "shastae" Barnes & Benjamin. While roughly 50% of these names are more or less descriptive of the color condition, the genetic factors creating the white or yellow phases are identical, or nearly so, for all of the species in the genus and there is no reason why a single descriptive name should not be employed as a *nomen collectivum* to apply to the equivalent forms in each species. However, since both white and yellow forms are normal genetic components of the population, it would not be proper to apply a designation to the white form without an equivalent designation for the yellow form. It is my proposal that the name "alba" be employed as a descriptive and collective name for the white color phase in *Colias* species, and that "flava" be similarly employed to designate the yellow phase. If desired, "chrysa" could be added to distinguish those populations with an orange phase from those with a yellow phase.

The use of a collective-descriptive designation, as cited in the example of *Colias*, seems to be the most practical way to deal with polymorphic variation. To avoid confusion with species-group names, these names should be enclosed in quotation marks but not italicized. Since they are not subject to the laws of priority and since they are descriptive, there is no need to append an author's name. (Author's names are appended to species-group names to facilitate the reference to an original description, not to honor the author.) The use of Latin to derive the collective-descriptive names seems preferable to a contemporary language because it will have equal meaning in international usage and will discourage translation into vernacular vocabulary. There is, of course,

some loss of descriptive value in the Latin derived names, as most biologists in the present day are not Latin scholars. With slight modification, collective-descriptive designations can be adapted to polymorphic as well as polychromatic situations.

Additional examples of polychromatic situations are: *Heliconius doris* (Linnaeus) which is sympatrically trichromatic in both sexes with red, green and blue color phases which could be referred to, respectively, as "erythro," "chloro" and "cyano." Similarly, the dimorphic female color phases of *Papilio glaucus* Linnaeus could be treated as "flava" for the yellow examples and "atrata" for the dark ones. The blue and brown color phases of certain female Lycaenidae, e.g. *Plebejus saepiolus* (Boisduval), could be collectively indicated as "cyana" and "atrata." Similarly, "cyana," "atrata" and "bicolor" could be used in reference to the brown, blue and mixed females of *Morpho aega* Hübner. The silvered and unsilvered varieties of *Speyeria* and related genera might be referred to as "argentamaculosus" and "flavomaculosus" respectively.

For non-chromatic polymorphic forms, the system is not as simple for there may be no simple descriptive term that could be used to designate the various forms. In many of these cases, the various polymorphic forms are apparent mimics of other species and it is appealing to compose a compound name of the prefix "pseudo-" along with the specific name of the model species.[2] As an example of non-chromatic polymorphism consider the various polymorphic females of *Papilio dardanus cenea* Stoll in South Africa. Van Son (1949) lists eleven distinct named forms of the female of *Papilio dardanus cenea* all of which show a remarkable phenotype expression and all of which are strikingly distinct from the male phenotype. All of these forms are apparent mimics of distasteful or protected species of Danaidae or Craeidae, which allows us to coin a collective-descriptive name based on the model-mimic relationship. *Papilio d. cenea* form "hippocoonides" Haase, which mimics *Amauris niavius dominicanus* Trimen, would be designated as *Papilio d. cenea* "pseudodominicanus" which is both simpler and more meaningful; similarly, form "trophonius" Westwood, which is a mimic of *Danaus chrysippus* Linnaeus, would become "pseudochrysippus"; and the other forms could be similarly named for the species they mimic.

For situations where males and females are dimorphic with respect to each other but constant within the same sex, e.g. *Neophasia terlootii* Behr, with white males and brick orange females, no infrasubspecific designation is required or desirable. For species which display a great

[2] The Code (recommendation D13) advises against the use of the prefix pseudo- with non-Greek nouns or adjectives; however this is the simplest procedure to use in collective-descriptive designation and infrasubspecific usages are clearly not governed by the Code in any case.

deal of random variation, e.g. *Parnassius phoebis* Fabricius, collective-descriptive names could be utilized to refer to the various individual variants. Eisner (1955) (see also Brown, 1956) proposed a total of 66 collective-descriptive names for application to variation that he had observed in the genus *Parnassius.* Many of the variants referred to by Eisner represent aberrations rather than polymorphisms and are treated in the following section. Unless a variant is fairly regular in occurrence and there is good reason to suspect a genetic cause for it, I see no reason or need for an infrasubspecific designation.

In using collective-descriptive names for polymorphic forms, setting the names in another typeface (e.g. **boldface**), but not italics, could be considered as an alternative to enclosing them in quotation marks. Intervening qualifying phrases (e.g. form as in *Colias gigantea* ♀ form "alba") would be optional usage.

Mutant or Aberrational Forms

Aberrations, mutants or "sports" are encountered with fair frequency among Lepidoptera. Many of these forms (mutants) have genetic cause but, unlike polymorphic forms, they are extremely rare in occurrence and not a normal part of the population. If the same sort of mutant reappears from time to time, it is assumed to be maintained by recurrent mutation rather than by selection. Other aberrational forms are produced by environmental causes. For example, it is well known that aberrant specimens of *Euphydryas phaeton* (Drury) can be artificially produced by exposing pupae to near freezing temperatures at a critical time in their development. As a general rule, these forms are much rarer in occurrence than are polymorphic forms; in the majority of cases their actual percentage of occurrence in a population would be less than 0.01% (one in 10,000). A polymorphic form may be this rare in a local population, but not throughout its entire range and, in some cases, an environmentally induced aberrant may be considerably more common than this during a single brood, but not on a continuing basis.

In the not too distant past, there was a strong tendency to adorn each mutant or aberrational form with a formal name. At present, they are rarely named, but are frequently described and reported in the literature. Whether genetic or non-genetic in cause, aberrants normally are not an integral part of any population; each specimen is an individual without direct continuity with any succeeding individuals which may resemble it. Putting a name, formally or informally, on aberrant specimens serves no useful purpose, and might serve to confuse them with polymorphic forms. It should be kept in mind, however, that mutant forms are the

raw material for evolution and that they may become established as polymorphic forms through selection.

Sexual mosaics and gynandromorphs are considered by me to fall into this category of aberrational forms.

Seasonal Forms

Seasonal forms are most pronounced in the areas of Africa where there is a considerable seasonal variation in rainfall. The "wet" and "dry" season forms of some species, particularly of the genus *Precis* (Nymphalidae), are so completely distinct in appearance that they were described as distinct species. In North America, seasonal forms are best known in the distinct brood forms of *Eurytides marcellus* (Cramer) (Papilionidae), *Celastrina argiolus* (Linnaeus) (Lycaenidae), various *Pieris* species (Pieridae) and various *Polygonia* species (Nymphalidae).

Seasonal forms may be considered environmental in nature, as the changes in appearance are brought about in response to environmental conditions, in most cases differences in solar radiation or differences in humidity, and not by genetic change. Of course genetic factors control the seasonal changes, since some species have seasonal forms while closely related ones may not. In some cases, changes in active genes may be responsible for the phenetic differences, but both forms are identical in terms of total genome, one form flowing from the other via direct inheritance.

A great deal of nomenclature has been expended, in the past, in treatment of seasonal variation where the variation involved is clearly the result of common factors. For instance, *Pieris sisymbrii* Boisduval, *Pieris protodice* Boisduval & LeConte, *Pieris occidentalis* Reakirt, *Pieris napi* (Linnaeus) and *Pieris rapae* (Linnaeus) have, in common, a situation in which the early spring brood is heavily marked on the ventral hindwing while summer or fall broods are relatively immaculate. Many names have been formally proposed to cover this situation in *Pieris* (including "transversa" Barnes & Benjamin, "vernalis" Edwards, and "nasturtii" Edwards for the spring forms; and "acadica" Edwards, "cruciferarum" Boisduval, "aestiva" Harris, "castoria" Reakirt, "iberidis" Boisduval, "pallida" Scudder, "pallidissima" Barnes & Benjamin, and "yreka" Reakirt for the summer forms). All of these could readily be eliminated by using "vernalis" as a descriptive-collective name for all of the spring broods and by using "aestivalis" as an equal descriptive-collective name for the summer broods. This same system could be used in the case of all species having seasonal or brood forms; the descriptive

names "autumnalis" and "hyemalis" could be added to cover fall or winter forms as required.

However, I feel that a preferable treatment for seasonal or brood forms would be to assign the successive generations a Greek letter designation. Thus the spring broods of the *Pieris* species cited above, could be given the designation α (alpha), and the summer broods could be designated by β (beta).

Compare the following methods of designating the two distinct spring and summer broods of *Eurytides marcellus*.

Method I, using commemorative names with priorities:

Eurytides marcellus (Cramer) form "walshii" (Edwards) [early spring brood]
Eurytides marcellus (Cramer) form "telamonides" (Felder & Felder)
Eurytides marcellus (Cramer) form "lecontei" (Rothschild & Jordan) [summer brood]

Method II, using collective-descriptive names:

Eurytides marcellus (Cramer) "monovernalis" [early spring brood]
Eurytides marcellus (Cramer) "bivernalis" [spring brood]
Eurytides marcellus (Cramer) "aestivalis" [summer brood]

Method III, using Greek-letter designations:

Eurytides marcellus (Cramer) α brood [early spring brood]
Eurytides marcellus (Cramer) β brood [spring brood]
Eurytides marcellus (Cramer) γ brood [summer brood]

It is my feeling that method III is preferable, as there would be no ambiguity such as might result if collective-descriptive names, albeit different ones, were used for both polymorphic and seasonal form designations.

Hybrids

In Lepidoptera, hybrids are not excessively rare in nature and, in some cases, can be produced with a degree of efficiency in the laboratory. We must, however, recognize four distinct classifications of hybrids: (1) hybrids between two subspecies of the same species, (2) hybrids between two distinct species of the same genus, (3) hybrids between two species of different genera, and (4) hybrid populations that are viable and breeding, although resulting from the hybridization of two distinct species.

Where both parents are known, a hybrid can be readily designated by joining the two species-group names with a multiplication sign (×).

(1) For hybrids between subspecies of the same species, such as between *Limenitis arthemis arthemis* (Drury) and *Limenitis arthemis astyanax* (Fabricius), the designation would be *Limenitis arthemis* (*arthemis* × *astyanax*) or *Limenitis arthemis* (*astyanax* × *arthemis*). The name of the male parent, if known, should precede that of the female parent.

(2) For hybrids between two species of the same genus, such as *Limenitis arthemis* and *Limenitis archippus* (Cramer), the combination would be *Limenitis arthemis* × *archippus* or *Limenitis archippus* × *arthemis.*

(3) For the much rarer situation of hybrids between two species of distinct genera, e.g. hybrids between *Phyciodes tharos* (Drury) and *Chlosyne nycteis* (Doubleday), the designation would be simply *Phyciodes tharos* × *Chlosyne nycteis*, or *Chlosyne nycteis* × *Phyciodes tharos.*

(4) In Lepidoptera there are, albeit very rarely, viable, breeding populations resulting from hybridization between two closely related species. *Papilio kahli* Chermock & Chermock is one of the better known examples of these, and has been treated in detail by Remington (1958), who concluded:

"1) Riding Mountain is the locus of origin of *P. kahli*, an isolated, distinctive offshoot of *P. polyxenes* with black wings, spotted abdomen, and large acentric 'pupil.' 2) In relatively recent times *P. machaon* arrived on the plateau, perhaps carried from Alberta in hay or straw during the development of the National Park or of highways or railroads. 3) These two *Papilio* at first lacking behavioral and other isolating mechanisms, hybridized rather freely; the distinctive genotype of *P. kahli* allows the F_1 heterozygotes to show some yellow-wing characters never seen in laboratory crosses of *machaon* with true *polyxenes.* 4) Since *P. kahli* and *P. avinoffi* belong to separate species, one expects that isolating mechanisms are evolving in Riding Mountain populations and that eventually natural hybrids will no longer be produced. Meanwhile, each species may be incorporating into its genotype new adaptive alleles from the other species (introgression). There is little basis for regarding *kahli* as dimorphic in the sense of *P. glaucus* females. For the present, these Riding Mountain swallowtails may be called *P. kahli* (or *P. polyxenes kahli*), *P. machaon avinoffi* and their hybrids."

Papilio nitra Edwards is another North American *Papilio* that represents a situation similar to that of *Papilio kahli.* Warren (1969) cited four populations of Old World *Pieris* (*dubiosa* Rober, *balcarica* W. & N., *pseudorapae* Vty. and *meridionalis* Heyne) which he considered hybrid races.

Hybrid races such as these may be referred to by specific names of the species group type—subject to priorities and other provisions of the

Code—as though they were true species; however the generic name should be preceded by the sign of multiplication, e.g. × *Papilio kahli*, or × *Pieris balcarica*.

HOW TO DETERMINE WHETHER A NAME IS SUBSPECIFIC OR INFRASUBSPECIFIC

It is necessary to recognize subspecific names and infrasubspecific names and to distinguish between them. The provisions of the Code (my treatment here is adapted from Field, 1971) are summarized here.

Subspecific Names

Article 45 (d) of the Code dictates three situations under which we are to accept a proposed name as a subspecific name.

1. The original status of any name of a taxon of lower rank than species is determined as subspecific if the author, when originally establishing the name, clearly stated it to apply to a subspecies. Obviously the best way to propose a subspecific name is to state that it is a subspecies.

2. The original status of any name of a taxon of lower rank than a species is determined as subspecific if the author, when originally establishing the name, did not state its rank. This clearly means that if an author proposed a trinomial name without explaining the trinomen in any way, we are to accept it as a proposal of a subspecies.

3. The original status of any name of a taxon of lower rank than a species is determined as subspecific if the author, when originally establishing the name, stated the taxon to be characteristic of a particular geographical area (or geological horizon) and did not expressly refer it to any infrasubspecific category. This clearly covers all names proposed in the past as races, local forms, altitude forms, and the like, provided they were proposed as trinomial names.

Infrasubspecific Names

Article 45 (d) (iii) gives two ways of recognizing when a taxon is of infrasubspecific status.

1. The original status of any name of a taxon of lower rank than species is determined as infrasubspecific if the author, when originally establishing the name, expressly referred the taxon to an infrasubspecific rank. This necessarily includes names given to all categories lower in rank than the subspecies and includes all names given to individual specimens and segments of populations such as aberrations, transition forms, seasonal forms, wet and dry forms, cold forms, color forms, sexual forms, and the names given to the separate generations of the same population.

2. The original status of any name of a taxon of lower rank than species is determined as infrasubspecific if the author, when originally establishing the name, after 1960, did not clearly state that it was a subspecies.

"Varieties" and "Forms"

Paragraph (e) of article 45, interprets the usage of the terms "variety" and "form" as follows: (i) before 1961, the use of either of the terms 'variety' or 'form' is not to be interpreted as an express statement of either subspecific or infrasubspecific rank; (ii) after 1960, a new name published as that of a 'variety' or 'form' is to be regarded as of infrasubspecific rank. (This is also stated in article 15.)

For publications dated before 1961, we must study the author's text to determine what he meant by his use of the terms "variety" and "form." If the author clearly

indicates in his text that he is writing about an individual variant (such as an aberration, color form, or the like) that is part of a population, then we have to reject the name. On the other hand, if the original author in no way shows what he meant by the term "variety" or "form," or if it is not clear that he is naming either subspecies or individual varients of such population, or if his text clearly indicates that he is describing geographical variation of the modern subspecies concept, then we have to accept any such proposed trinomial name as an acceptable trinomial under article 45 (d) (i).

Acceptable Subspecific Names

In summary, there are five types of trinomial names that should be acceptable as subspecific names under the Code.

1. Names given as trinomials (article 5), as subspecies (article 45 (d) (i)).
2. Names given as trinomials (article 5), before 1961, where no expressed category or rank is indicated (article 45 (d) (i)).
3. Names given as trinomials (article 5), before 1961, as races, local forms, altitude forms, or given as trinomials, to any other geographically based population (article 45 (d) (ii)).
4. Names given as trinomials (article 5), before 1961, as "varieties" and "forms" where the author indicates or even hints that they represent geographically based populations (article 45 (d) (ii) and (e) (i)).
5. Names given as trinomials (article 5), before 1961, as "varieties" and "forms" where the author in no way indicates what he meant by the use of these terms (article 45 (d) (i) and (e) (i)). Many authors used these terms for subspecies. Article 45 (e) (i) allows us to accept these terms as subspecific unless it is apparent that an infrasubspecific category is intended.

Names Unacceptable under the Code

There are seven types of names that are excluded as subspecific names by the Code.

1. All names proposed as quadrinomials (article 5 by recognizing only the generic name, the specific name, and, when applicable, the subspecific name).
2. All names given to aberrations as such, transitional forms as such, seasonal forms, wet and dry forms, color forms, sexual forms, generation forms as such, and similar forms (article 1; article 45 (d) (iii) and glossary of the Code: definition of the term infrasubspecific).
3. All names given to "varieties" and "forms" before 1961, where the author clearly indicates that he is dealing with an individual variant such as one of those mentioned above under number 2 (article 45 (e) (i)).
4. All names proposed as trinomials after 1960, where it is not clearly stated that such names are subspecific names (article 45 (d) (iii)).
5. All names proposed for "varieties" or "forms" after 1960 (article 15, article 45 (e) (ii)).
6. All names proposed for races, local forms, altitudinal forms, or any geographically based populations, after 1960, where they are not expressly called subspecies (article 45 (a) and article 45 (d) (iii)).
7. All names given to hybrids (article 1).

Excluded Names Becoming Available

Names rejected or excluded under the Code may later become available, for article 10 (b) states that "a name first established with infrasubspecific rank becomes available if the taxon in question is elevated to a rank of the species-group, and takes the date and authorship of its elevation."

SUMMARY

1. Taxonomic categories of lower rank than subspecies (infrasubspecies) have been removed from the protection of the "Code" (International Code of Zoological Nomenclature, 1961). This means that names proposed for infrasubspecific variation (including those proposed for polymorphic forms, aberrations, seasonal forms, sexual forms, color forms, altitudinal forms, etc.) do not have the regulation and protection of the Code under the laws of priority and uniform usage.

2. If names are to be used to designate infrasubspecific variation, they should be used in such a way as to avoid confusion with the subspecies or trinomial usage.

a. Names should be placed in quotation marks or some other typeface (such as **boldface**) and not in italics as are used for the species-group names.

b. These names should not take an author's name.

3. Since infrasubspecific names are not subject to the laws of priority or other provisions of the Code, the opportunity is clearly present for lepidopterists to develop a uniform system of designation suitable for present day needs without concern for the stigmas of priorities and validities that, ostensibly, have made this impossible in the past.

4. The following proposals are advanced to cover four major categories of infrasubspecific variation.

a. POLYCHROMATIC OR POLYMORPHIC FORMS should be described by collective-descriptive names. The use of Latin to derive the collective-descriptive names is preferred because it will have equal meaning in international usage and will discourage translation into vernacular vocabulary. The name "alba" as used to describe the white color phase of female *Colias* butterflies is an example of a descriptive name. Since a similar white color phase occurs by a similar genetic mechanism in nearly all species of *Colias*, the same name should be applied to similar color phases in all of them—thus it is a collective name.

b. MUTANT OR ABERRATIONAL FORMS are not an integral part of the population; each specimen is an individual and does not have any direct continuity with any succeeding specimen which may resemble it. Placing a name, formally or informally, on aberrant specimens serves no useful purpose and is to be discouraged entirely.

c. SEASONAL FORMS are environmental and not genetic in nature because the differing broods involved are genetically identical. Collective-descriptive names, such as are suggested for use with polymorphic variation, could be applied in this case; however, since polymorphic variation is quite distinct from seasonal variation and since a given

specimen may exhibit both polymorphic and seasonal variation, it is recommended that Greek-letter designations be employed to indicate seasonal variation. Starting with the first spring or first wet season generation, broods could be designated, successively, as α (alpha), β (beta), γ (gamma), etc. broods.

d. HYBRID INDIVIDUALS can be indicated by joining the two species-group names with a multiplication sign. In those rare situations where an actual breeding population of hybrid origin exists, a species group name may be applied, but only if the entire name is preceded by a multiplication sign.

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