

CHARACTER DISPLACEMENT AND EVOLUTION OF THE JAPANESE *MNAIS* DAMSELFLIES (ZYGOPTERA: CALOPTERYGIDAE)*

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Arguments are presented for the 3 generally recognized taxa of the genus *Mnais* Selys occurring in the Japanese Islands to be regarded as independent spp., viz. *M. costalis* Selys, *M. pruinosa* Selys, and *M. nawai* Yamamoto. It is pointed out that the *M. pruinosa* populations occurring in central Honshu (the Setouchi Group) are also possibly an independent sp. to be distinguished from those occurring in southwestern Japan (the Nankai and Saikai Groups). Essentially the same combination of forms (a heterochromatic orange-winged, occasionally pale-orange- or dark-brown-winged male, a homoeochromatic hyaline-winged male, and a homoeochromatic hyaline-winged female) seems to occur in most districts of the Japanese Islands. Based on the taxonomic arrangement of the known forms, the evolution of the Japanese *Mnais* spp. is discussed. The present geographic distribution of the taxa and the combination of forms in various districts are interpreted by a working hypothesis based on the so-called "competitive exclusion (or displacement) principle" and a consequent "character displacement".

INTRODUCTION

The Japanese *Mnais* damselflies have hitherto been recorded from four main islands, viz. Hokkaido, Honshu, Shikoku, and Kyushu, and besides, from the Oki Islands, Tsu-shima Island, Gotô Islands, and from Koshiki Islands. They have long been considered to be very difficult to classify because of their remarkable polyphenism including polychromatism of wings. A number of forms have so far become known from various districts in the Japanese Islands (HIURA, 1972; ASAHINA, 1975a, 1975b, 1976; SUZUKI et al., 1980). They

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seem to be suitable objects for the following types of investigations: (1) The species showing intraspecific variability or the species group consisting of closely related species are very suitable for studying evolution and speciation; — (2) Japanese *Mnais* species may be compared with the calopterygid taxa from other continents, as similar problems are also known for other calopterygid species or species groups in Europe (e.g., HEYMER, 1973), Middle East (e.g., BUCHHOLTZ, 1951, 1955), and North America (e.g., JOHNSON, 1962; WAAGE, 1973, 1975); and — (3) they may be compared with some other insect species or species groups occurring in the Japanese Islands (e.g. *Henosepilachna* spp. of Coccinellidae, cf. KATAKURA, 1981; *Chrysolina aurichalcea* (Mannerheim) of Chrysomelidae, cf. SUZUKI & SAKURAI, 1979; *Neope* spp. of Satyridae, cf. TAKAHASHI, 1970; *Nezara viridula* (L.) of Pentatomidae, cf. KIRITANI, 1970; *Masakimya pustulae* Yukawa & Sunose of Cecidomyiidae, cf. SUNOSE, 1979; and so on).

Subsequent to ASAHINA's (1975a, 1975b, 1976) comprehensive revision of the genus, numerous workers have studied the Japanese *Mnais*, in various districts and from various standpoints. Nevertheless, many problems still remain unsolved.

The purpose of the present paper is (1) to propose a rational classification system of the Japanese members of the genus, (2) to discuss critically several opinions presented by a number of workers on possible evolutionary pathways, (3) to present a working hypothesis on the evolutionary processes within the Japanese taxa, and (4) to formulate several unanswered questions.

CLASSIFICATION AND GEOGRAPHIC DISTRIBUTION OF THE JAPANESE *MNAIS*

Prior to ASAHINA's (1975a, 1975b, 1976) taxonomic revision, the classification of the Japanese *Mnais* had long been confused (for a review cf. SUZUKI et al., 1980). Many workers have recognized the existence of three taxa and there seems to be no objection to this understanding. In the following discussion, the author will call them "*costalis*", "*pruinosa*", and "*nawai*", referring to them as a matter of convenience and to the extent there is no fear of misunderstanding.

Adding to many forms defined by ASAHINA (1976), SUZUKI & EGUCHI (1979) and SUZUKI et al. (1980) used the name "♀-f. *typica*" for homoeochromatic hyaline-winged female forms of both "*costalis*" and "*pruinosa*". Consequently, all the known forms may be listed as follows:

(1) "*costalis*"

♂-f. *costalis*: a heterochromatic orange-winged form

♂-f. *ogumai*: a homoeochromatic hyaline-winged form

♀-f. *typica*: a homoeochromatic hyaline-winged form

♂, ♀-f. *edai*: a form with wings tinted by opaque pigments

(2) "*pruinosa*"♂-f. *pruinosa*: a heterochromatic dark-brown-winged form♂-f. *esakii*: a heterochromatic orange- to pale-orange-winged form♂-f. *strigata*: a homoeochromatic hyaline-winged form♀-f. *typica*: a homoeochromatic hyaline-winged form♂, ♀-f. *shirozui*: a homoeochromatic hyaline-winged form with considerably smaller body size(3) "*nawai*"♂-f. *nawai*: a heterochromatic orange-winged form♂-f. *sahoi*: a homoeochromatic form with pale-brownish wing-veins♂-f. *kadowakii*: a homoeochromatic hyaline-winged form with black wing-veins♀-f. *nawai*: a homoeochromatic form with orange wing-veins♀-f. *taketoi*: a homoeochromatic hyaline-winged form with black wing-veins.

Concerning the classification, three main views have been formulated as the one-species, the two-species, and the three-species hypothesis. The first of these was postulated by ASAHINA (1976), who considered the Japanese *Mnais* representing a single species, *M. pruinosa*, consisting of three "subspecies". The second one was proposed by HIURA (1972), who recognized the independency of "*nawai*" from the other two taxa. The third hypothesis was put forward by the present author (SUZUKI, 1981), who distinguished at least three independent species. Table I shows these three classification systems.

Table I
Three main classification systems of the Japanese *Mnais*

Taxon	ASAHINA, 1976	HIURA, 1972	SUZUKI, 1981
" <i>costalis</i> "	<i>M. pruinosa costalis</i>	<i>M. pruinosa costalis</i>	<i>M. costalis</i>
" <i>pruinosa</i> "	<i>M. pruinosa pruinosa</i>	<i>M. pruinosa pruinosa</i>	<i>M. pruinosa</i>
" <i>nawai</i> "	<i>M. pruinosa nawai</i>	<i>M. nawai</i>	<i>M. nawai</i>

The shift of taxonomic rank of a taxon or taxa directly influences the structure of a classification system and the interpretation of phylogenetic relationships of the group in question (cf. SUZUKI, 1976). Such a shift should not be considered merely a simple convenient treatment; one of the essential problems of phylogenetic systematics lays here.

Cladogenesis is assumed to have occurred dichotomously. In the case of the three taxa of the Japanese *Mnais*, three hypothetical cladograms may be automatically supposed (Fig. 1). If one gives an equivalent "species" or "subspecies" rank to each of these, all of the three classification systems as shown in Table I are logically possible, and it is quite arbitrary to choose one among them. However, if one recognizes a taxonomic independency of one or two of these taxa, the number of possible cladograms becomes limited. For example, if

one recognizes only "*nawai*" (N) as an independent species, only one case (a) is logically possible, since only in this way the classification system is in agreement with the assumed phylogenetic relationships towards the neighboring taxa, while the ranking provides for the hierarchic balance in the system.

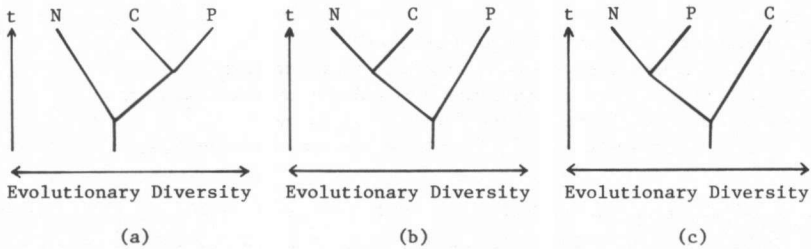


Fig. 1. Three hypothetical cladograms logically deduced for the three taxa of the Japanese *Mnais*. — (N: "*nawai*"; — C: "*costalis*"; — P: "*pruinosa*"; — t: relative evolutionary time).

Since ASAHINA (1975a, 1975b, 1976, 1980) recognizes but a single species in Japan (*M. pruinosa*), his system admits logically all the three cases (a-c) of Figure 1. His fundamental idea seems to have been accepted by e.g. INOUE (1980) and (?) OBANA (1983). HIURA's (1972) hypothesis, supported also by e.g. HIGASHI (1981), seems to agree with cladogram (a). According to it, the other two cladograms (b, c) are not accepted logically. OBANA's recent opinion (1983) seems to agree with cladogram (b), though his explanation has no logical consolidation; that is, he is of the opinion that "*pruinosa*" and "*costalis*" have a common ancestor and that "*nawai*" might have originated from "*costalis*"(!). The present author has insisted that the Japanese *Mnais* consist of at least three independent species. His hypothesis completely agrees with cladogram (a) induced from Hiura's hypothesis, but, as discussed below, its evolutionary significance is quite different from the latter. YAMAMOTO's (1956) hypothesis agrees with cladogram (b).

Asahina's hypothesis is not consistent with the generally accepted species and/or subspecies concepts. *M. "pruinosa"* and "*nawai*" have wide distributional ranges in common and occasionally coexist in the same stream or creek. Since, according to the generally accepted subspecies concept, two or more subspecies of a given species do not coexist in the same habitat, Asahina should give some positive reasons for considering these two taxa as "subspecies" rather than "species".

MNAIS EVOLUTION IN THE JAPANESE ISLANDS

ARRANGEMENT OF THE KNOWN FORMS

It seems that the existence of a number of forms has complicated *Mnais* problems. The discrimination and naming of a distinct entity are the first and fundamental step in taxonomic inquiry. However, the author considers that the following non-essential forms should be eliminated from the discussion, though they occasionally show biogeographically significant features.

- (1) ♂, ♀-f. *edai* of "*costalis*"

It is obviously an aberrant which might have originated by means of mutation (cf. EDA, 1965; ASAHINA, 1976).

- (2) ♂-f. *sahoi* of "*nawai*"

This can be regarded as the individual of ♂-f. *nawai* without opaque areas along the costal margins of wings. The frequency of occurrence of the form seems higher in southwestern Japan, especially in northern Kyushu (cf. ASAHINA, 1976; YOSHIDA & MATSUURA, 1978), while it has been but seldom recorded from other districts (e.g., SUZUKI & EGUCHI, 1979; Suzuki unpublished). There seems to be a tendency for the size of the opaque areas on male wings of "*nawai*" (and also in ♂-f. *esakii* of "*pruinosa*") to be largely conditioned by the fluctuation of body size.

- (3) ♀-f. *taketoi* of "*nawai*"

The typical individual of this form can be easily discerned from the nominate f. *nawai*. However, intermediate individuals in varying degrees between both forms occasionally occur within the same population. The relative frequencies of both forms in a given population vary from population to population, at least so in the Hokuriku District (SUZUKI & EGUCHI, 1979; SUZUKI, 1980).

- (4) ♂, ♀-f. *shirozui* of "*pruinosa*"

This seems to be merely an ecotype, confined to cool, high-altitude habitats (cf. ASAHINA, 1976). ASAHINA (1976) emphasized the diagnostic importance of the pterothoracic poststernum coloration in the "form" classification of the Japanese *Mnais*. However, this character is inadequate in the case of "*nawai*" and "*pruinosa*" from the Hokuriku District (cf. SUZUKI & EGUCHI, 1979). Recently, OBANA (1983) revealed that the coloration of the pterothoracic poststernum of this form changes with maturation.

- (5) ♂-f. *esakii* of "*pruinosa*"

The author assumes that the ♂-f. *pruinosa* of "*pruinosa*" is a form where the wing coloration of ♂-f. *esakii* becomes remarkably darker. Since YOSHIDA & MATSUURA (1978) reported several populations from northern Kyushu in which both ♂-f. *pruinosa* and ♂-f. *esakii* and various intermediate colour forms were seen, these two forms should be essentially regarded as referable to the same entity.

Based on the above considerations, the following revised arrangement of the essential Japanese *Mnais* forms is proposed:

<i>"costalis"</i>	<i>"pruinosa"</i>	<i>"nawai"</i>
♂-f. <i>costalis</i>	♂-f. <i>pruinosa</i> (+ ♂-f. <i>esakii</i>)	♂-f. <i>nawai</i> (+ ♂-f. <i>sahoi</i>)
♂-f. <i>ogumai</i>	♂-f. <i>strigata</i>	♂-f. <i>kadowakii</i>
♀-f. <i>typica</i>	♀-f. <i>typica</i>	♀-f. <i>nawai</i> (+ ♀-f. <i>taketoi</i>)

It may be easily noticed that all three taxa consist of the same combination of forms, viz. a heterochromatic orange-winged (rarely pale-orange- or dark-brown-winged) male form, a homoeochromatic hyaline-winged male form, and a homoeochromatic hyaline-winged female form. This is the starting point for the following discussion.

A PROPOSED WORKING HYPOTHESIS

ASAHINA (1980, p. 107) asserted as follows: "It seems advisable to assume a hypothetical stock "*protocostalis*" in North Japan from which the western subspecies *nawai*, and the eastern subspecies *costalis* originated. The subspecies *costalis* seems to be situated between "*protocostalis*" and southwestern ssp. *pruinosa*. There is also a possibility that ssp. *costalis* developed from ssp. *pruinosa*". His statements include the following four assumptions: (1) there was a hypothetical ancestor "*protocostalis*" in northern Japan, (2) "*nawai*" and "*costalis*" originated from "*protocostalis*", (3) "*costalis*" is an intermediate form of "*protocostalis*" and "*pruinosa*", and (4) "*costalis*" developed from "*pruinosa*". Of these, the first three assumptions require evolutionary or cladogenetic relationships among the three taxa, "*protocostalis*", "*nawai*", and "*costalis*";

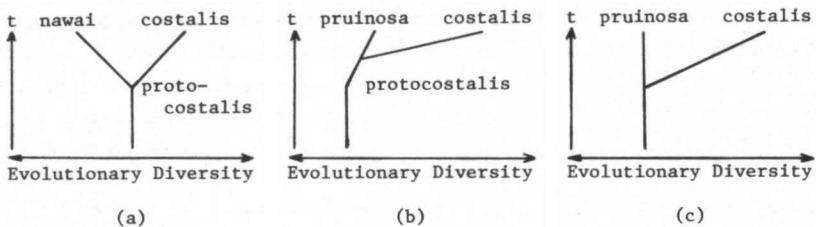


Fig. 2. Graphic interpretation of cladogenesis of the Japanese *Mnais*, as suggested by ASAHINA (1980). — (t: Relative evolutionary time).

shown in Figures 2a and b. The fourth assumption admits the cladogenetic relationship between "*pruinosa*" and "*costalis*"; shown in Figure 2c. The fourth assumption denies the existence of a common ancestor of "*pruinosa*" and "*costalis*". It also insists that "*costalis*" originated from a part of "*pruinosa*"; in other words, "*costalis*" originated from "*pruinosa*" after the establishment of the latter. The cladograms (b) and (c) are consistent with each other but they do not admit the cladogram (a). Apparently, thus ASAHINA (1980) postulated two contradictory, mutually exclusive cladogenetic processes. His preliminary hypothesis, therefore, can not be maintained.

In an attempt to advance our understanding of the *Mnais* evolution in the

Japanese Islands, the author is proposing here a new working hypothesis, which can be briefly summarized as follows:

- (1) There are three (or more than three) independent *Mnais* species in Japan, viz. *M. costalis* Selys (= "*costalis*" in the preceding discussion), *M. pruinosa* Selys (= "*pruinosa*"), and *M. nawai* Yamamoto (= "*nawai*").
- (2) The present geographic distribution of these has been brought about by the operation of the so-called "competitive exclusion principle" (HARDIN, 1960) or "competitive displacement principle" (DE BACH, 1966) and a consequent "character displacement" (BROWN & WILSON, 1965; WAAGE, 1975).

The author should like to mention the fact that in both *M. costalis* (UBUKATA, 1977, 1979) and *M. pruinosa* (HIGASHI, 1976, 1981) there are some differences in territorial behavior between the two male forms: orange-winged males (f. *costalis* of the former species and f. *esakii* of the latter) establish conspicuous territories, but hyaline-winged individuals (f. *ogumai* of the former and f. *strigata* of the latter) do not. UBUKATA (1979) interpreted such differences as strongly related with those in their mating strategies; viz. orange-winged males develop a territory-occupying mating strategy in open environments, as to the searching strategy in mainly closed environments, employed by hyaline-winged individuals. Ubukata's interpretation of this phenomenon seems quite plausible: the occurrence of two male forms, which differ from each other in their environments or niches favorable for adult activities, especially mating behaviour, is important for the prosperity and maintenance of the species; it must cause the increase of reproductive efficiency or mating chance for both sexes and the extension of habitats. The situation in *M. pruinosa* may be essentially similar to that in *M. costalis*. Moreover, the above mentioned interpretation seems essentially applicable to the situation in the Nankai (and probably Saikai) Group(s) of *M. pruinosa* as observed by HIGASHI (1976, 1981).

HIURA (1972) discriminated the following seven groups in the Japanese *Mnais*: (1) Tōhoku Group, (2) Bōsō Group, (3) Setouchi Group, (4) Nankai Group, (5) Saikai Group, (6) Chūgoku Group, and (7) the "Nawa" Group. Though his hypothesis is attractive and apparently includes some far-sighted ideas (discussed later), it has probably caused a delay in the solution of the *Mnais* problems. Hiura recognized the independence of *M. nawai* (his "Nawa Group"), but did not discriminate *M. costalis* and *M. pruinosa*; his Tōhoku and Bōsō Groups are included in the former species and the remaining groups in the latter. Of the four groups corresponding to *M. pruinosa*, the definition of the Chūgoku Group is quite vague and its nature cannot be comprehended.

The nature and the geographic distribution of the remaining three groups may be understood as follows: (1) the Setouchi Group corresponds to the populations in the central Honshu (Kantō, Kōshin'etsu, and Kinki Districts) and consists of the combination of a homoeochromatic hyaline-winged ♂-f. *strigata* and a homoeochromatic hyaline-winged ♀-f. *typica*; — (2) the Nankai Group corresponds to the populations occurring in the area SW of the Kinki District

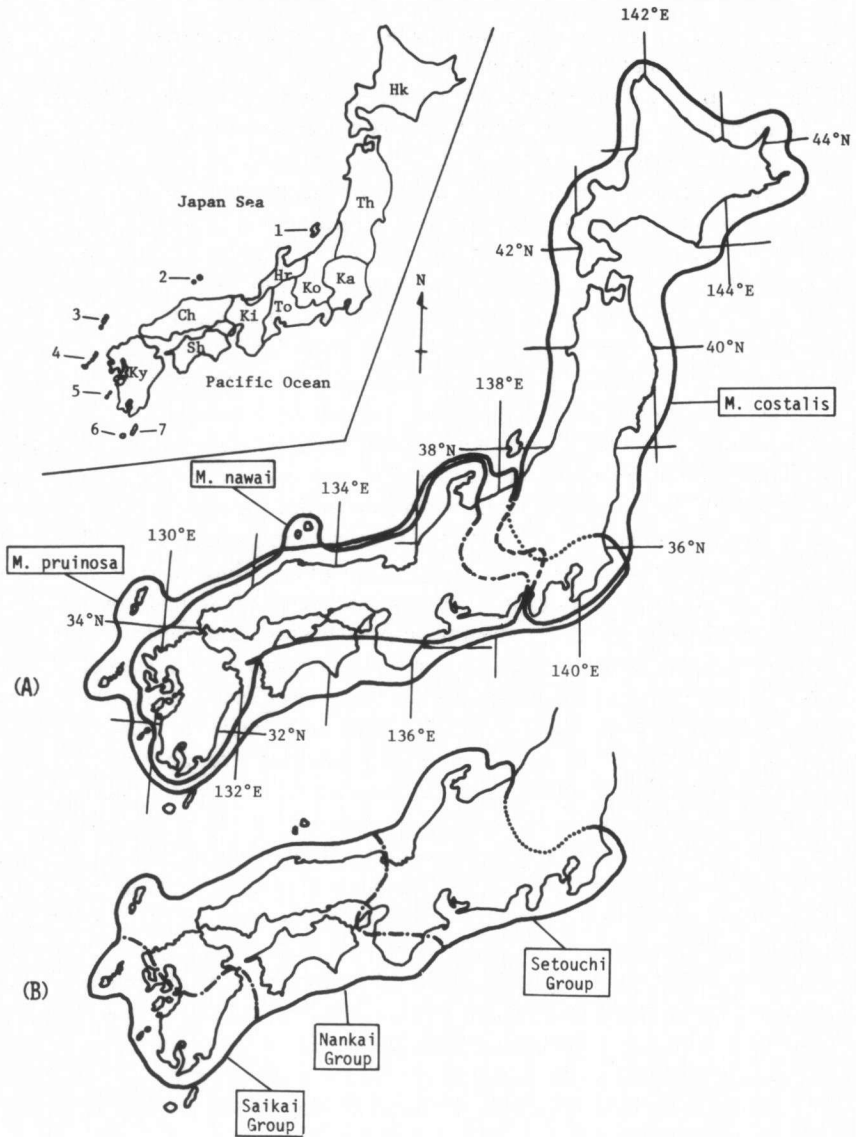


Fig. 3. Geographic distribution of the Japanese *Mnais* species. (A) *M. costalis*, *M. pruinosa*, and *M. nawai*. (Districts and the main islands are indicated in the insert, viz. districts: Hk: Hokkaido, —Th: Tôhoku, —Ka: Kantô, —Ko: Kôshin'etsu, —Hr: Hokuriku, —Tk: Tôkai, —Ki: Kinki, —Ch: Chûgoku, —Sh: Shikoku, —Ky: Kyushu, —Ko+Hr+Tk: Chûbu; — islands: 1: Sado-ga-shima, — 2: Oki, — 3: Tsushima, — 4: Gotô, — 5: Koshiki, — 6: Yaku-shima, — 7: Tane-ga-shima). — (B) Geographic distribution of the Setouchi, Nankai, and Saikai Groups of *M. pruinosa*.

(Kinki, Chûgoku, Shikoku, and Kyushu Districts) and contains heterochromatic orange- to pale-orange-winged ♂-f. *esakii*, homoeochromatic hyaline-winged ♂-f. *strigata*, and homoeochromatic hyaline-winged ♀-f. *typica*. It should be noticed that the geographical distribution of this group in the Kinki District is restricted to Kii Peninsula of the Kino-kawa River (cf. INOUE, 1977, 1980; OBANA, 1983); — (3) the Saikai Group corresponds to the populations in the Kyushu District and consists of heterochromatic dark-brown-winged ♂-f. *pruinosa* (including heterochromatic orange- to pale-orange-winged ♂-f. *esakii*), homoeochromatic hyaline-winged ♂-f. *strigata*, and homoeochromatic hyaline-winged ♀-f. *typica*. His Chûgoku Group is interpreted as being almost included in the Nankai Group. Though his grouping of *M. pruinosa* has been occasionally referred to by many workers, the author would like to propose the abolition of Hiura's "Tôhoku", "Bôsô", and "Chûgoku" Groups.

Now, the author should like to examine the relationships among HIURA's (1972) Setouchi, Nankai, and Saikai Groups of *M. pruinosa*. On the basis of the published records, the geographic distribution of the three groups is shown in Figure 3b. As already pointed out, the author considers there is no essential difference between the two male forms, *esakii* and *pruinosa*, though the distribution of the latter is restricted to the Kyushu District. The author judges that the Setouchi Group is quite different from the other two groups. Concerning the Setouchi Group and its relationships to *M. nawai* and to the Nankai Group of *M. pruinosa*, the attention is called to the following facts: (1) the Setouchi Group generally coexists with *M. nawai* (reported by many workers); — (2) there is complete reproductive isolation between the two species (SUZUKI et al., 1980); — (3) in the stream or creek where *M. nawai* and the Setouchi Group co-occur there is a very clear habitat segregation between them; as a rule the former inhabits the downstream areas, whereas upstream the latter almost completely dominates over the former (SUZUKI et al., 1980; SUZUKI & EGUCHI, 1979; SUZUKI & TAMAISHI, 1982); — (4) the Setouchi Group occasionally occurs downstream, provided it does not coexist with *M. nawai* (SUZUKI & EGUCHI, 1979; SUZUKI, 1980, 1981); and — (5) the Setouchi Group seems to be almost completely allopatric to the Nankai Group (INOUE, 1977, 1980).

This evidence strongly suggests that the so-called "competitive displacement (or exclusion) principle" has been operating. The circumstance that the Setouchi Group does not produce an orange-winged male form (like ♂-f. *esakii* of the Nankai Group) seems very significant. This could be interpreted as follows: the Setouchi Group cannot produce an orange-winged male form because it generally is under pressure from *M. nawai* which produces such a form in almost all the habitats. In other words, two orange-winged male forms belonging to different species cannot coexist in the same habitat. Similarly, this may be applicable to *M. nawai* that cannot produce a homoeochromatic hyaline-winged male form (f. *kadowakii*) in general, because the Setouchi Group of *M. pruinosa* generally

coexists with it in the same stream or creek.

In *Mnais*, the wing coloration is considered serving as a signal between the sexes, and/or between different male individuals in their territorial behavior (SUZUKI & TANAKA, 1980). If two very similar male forms of different species coexist in the same stream, their mating or territorial behavior, which may be genetically controlled, must be profoundly disturbed. Therefore, the existence of the ♂-f. *kadowakii* in *M. nawai* seems to become one of the important keys to resolve the *Mnais* problem. Here, the author should like to point out that in the population inhabiting the Oki Islands, the ♂-f. *kadowakii* certainly occurs together with ♂-f. *nawai* (ASAHINA, 1976). As far as the known records are concerned, no *M. pruinosa* specimen has been obtained from the islands. The author considers that if his supposition is correct, the *M. nawai* population inhabiting the islands has been able to produce both male forms only after having lived for a long time in the absence of *M. pruinosa*. In other words: *M. nawai* cannot produce both orange-winged (f. *nawai*) and hyaline-winged (f. *kadowakii*) male forms unless it is the sole occupant of an area. Consequently, coexistence with *M. pruinosa* may limit the range of habitats of *M. nawai*.

As far as the author knows, neither *M. costalis*, nor the Nankai Group (nor, probably, the Saikai Group) of *M. pruinosa* coexists with any other species in the same habitat. This fact also strongly suggests that the competitive exclusion principle might have operated in these species and, consequently, a kind of character displacement must have occurred in them since (1) *M. costalis*, which always occurs alone, can produce both orange-winged (f. *costalis*) and hyaline-winged (f. *ogumai*) males; and — (2) the Nankai Group of *M. pruinosa*, also always found alone, can also produce both orange- to pale-orange-winged (f. *esakii*) and hyaline-winged (f. *strigata*) males. The author also considers that the Setouchi Group has still preserved the genetic background able of expressing an orange- to pale-orange-winged male form as well. It is natural that the "competitive exclusion principle" does not operate in a population living alone in a stream. Consequently, the following situations are assumed to be possible for both *M. nawai* and *M. pruinosa* Setouchi Group: (1) *M. nawai* population living alone may produce a f. *strigata*-like male form, and — (2) *M. pruinosa* Setouchi Group living alone may produce a f. *nawai*-like male form. The author imagines that the existence of the f. *kadowakii* strongly suggests the occurrence of the first situation. In addition, SUZUKI (1980, 1981) has discovered several *M. nawai* and *M. pruinosa* Setouchi Group populations occurring alone in streams of the Hokuriku District, Honshu.

It seems very significant that the ♂-f. *strigata* of *M. pruinosa* Setouchi Group builds a distinctive territory in the Hokuriku District (SUZUKI & TANAKA, 1980; SUZUKI & TAMAISHI, 1982). This is not consistent with the situation observed for *M. pruinosa* Nankai Group (HIGASHI, 1976, 1981). This strongly suggests that males of the f. *strigata* of these two groups differ from each other. The author assumes that the Setouchi Group of *M. pruinosa* should be distinguished

from all other Japanese forms.

The results of morphometrical analysis of the variability of the crossvein number in several areas, defined on each of the four wings, seems to support well the assumption, viz. (1) in both Setouchi and Nankai Groups, intragroup variability is very low, and (2) the latter shows higher values in crossvein number than the former and the difference between the two groups was considered statistically significant (SUZUKI & METOKI, 1983). This seems to suggest the possibility that the *M. pruinosa* Setouchi Group has already reached the status of an independent species, distinct from the Nankai and Saikai Groups. If this interpretation is correct, the Setouchi Group should be recognized as the fourth member of the genus in Japan.

Based on the present geographic distribution of the Japanese *Mnais* (Fig. 3), the author conceives their evolutionary history in the Japanese Islands as follows:

- (1) *M. costalis* was the first invader to the Japanese Islands, from northern China via Korea.
- (2) *M. nawai* and *M. pruinosa* may have invaded the Japanese Islands from northern China via Korea, in different periods, and they might have expelled *M. costalis* from southwestern Japan. This assumption seems to be supported by the fact that the two species widely occur sympatrically in the southwestern Japanese Islands, while there are several areas and islands where only one of them lives. Thus, *M. nawai* has not hitherto been known from Kii Peninsula S of the Kino-kawa River and from the Islands of Shikoku S of the so-called "Median Tectonic Line", whereas the Nankai and Saikai Groups of *M. pruinosa* do occur in these areas and in the Gotô and Koshiki (and probably Tsu-shima) Islands (cf. Fig. 3a).
- (3) In the course of the range extension, *M. pruinosa* has differentiated into 2 distinctive groups, the Saikai+Nankai Group and the Setouchi Group (cf. Fig. 3b).
- (4) Where both *M. nawai* and *M. pruinosa* coexist in the same habitat, the competitive exclusion (or displacement) principle has operated, causing the present complicated polymorphic situation.

CONCLUDING REMARKS

The present working hypothesis would be refuted, if one of the following situations, concerning the coexistence in the same habitat, would become evidenced:

- (1) *M. costalis* can coexist with *M. nawai* and/or *M. pruinosa* in the same habitat.
- (2) The Nankai and Saikai Groups of *M. pruinosa* can coexist with *M. nawai* in the same habitat.
- (3) The *M. nawai* population in which both ♂-f. *nawai* and ♂-f. *kadowakii* occur can coexist with *M. pruinosa* (either the Setouchi Group or

the Nankai+Saikai Group) in the same habitat.

If such a situation occurs, two different types of heterochromatic orange-winged (or occasionally pale-orange- or dark-brown-winged) males appear in the same habitat. In these cases, the decision that one is dealing with real coexistence should be made according to the definition of the phenomenon, "the same habitat", under which is understood the area where territorial behavior between the two types of colored males can be proven.

As the author's hypothesis rules out all of these three situations, it should be considered having a high "falsifiability" (cf. POPPER, 1959). Conclusively, future efforts should be aimed at falsifying it.

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