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NOTES ON THE LIFE HISTORY OF *SEPHISA PRINCEPS* IN EASTERN RUSSIA (LEPIDOPTERA: NYMPHALIDAE)

ALEXANDER DANTCHENKO [1], ANDREI SOURAKOV [2], AND THOMAS C. EMMEL [3]

[1]Avangardnaia St. 11-160, ROS-125493 Moscow, Russia;
[2]Dept. of Entomology and Nematology, University of Florida, Gainesville, Florida 32611; and
[3]Dept. of Zoology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.– Descriptions of immature stages and adult and larval behavior of *Sephisa princeps* Fixsen (Lepidoptera: Nymphalidae) are provided from the Russian Far East. The larvae feed in groups and exhibit an elaborate communal behavior. The overall distribution and biology are discussed in relation to the species' supposed endangered status, which is not confirmed in the present work: only complete destruction of the habitat can actually thrust a *S. princeps* population into endangered existence. The geographic range of each of the four species of the genus *Sephisa* is correlated with the range of different species of the larval hostplants of the oak genus *Quercus*. The ranges of different subspecies of *S. chandra*, are found to correspond with the ranges of different subspecies of *Q. glauca*, allowing one to suppose a possible co-speciation between these two taxa.

KEY WORDS: *Apatura*, Apaturinae, behavior, biology, China, Coleoptera, conservation, egg, *Euripus*, Europe, Fagaceae, Far East, Hainan, *Hestina*, *Hestinalis*, hostplants, immature stages, India, Japan, Korea, larvae, Lycaenidae, Malaysia, Nepal, oviposition, Primor'e, pupae, Russia, Salicaceae, *Sasakia*, *Sephisa*, Taiwan, Yunnan.

The nymphalid butterfly, *Sephisa princeps* (Fixsen, 1887), was described from two males collected on Mount Pung-Tung, Korea, in August, 1884. For a long time, the population of this species from the Russian Far East was considered as a subspecies of *Sephisa dichroa* Kollar (Kurentzov, 1970; Tuzov, 1992), even though the morphological differences between these taxa were previously recognized (Seitz, 1909). Thus, the genus *Sephisa* was mistakenly viewed as monotypic (see Anon, 1984: *Red Book of the USSR*).

The study of the collections of the Berlin Museum, Germany, and Zoological Museum of Kiev, Ukraine, did not reveal any specimens collected prior to 1900, even though such renowned collectors as the Dorries brothers, Graeser, and Christoph made exhaustive collections in the area (Staudinger, 1901). This apparent scarcity can only be explained by extremely low populations of this species at that time. The first specimen of *S. princeps* in the Zoological Institute collection in St. Petersburg is labeled August 1, 1915, Sedanka (near Vladivostok), Col. Delle. From 1927-1930 this species became abundant: 28 males and 8 females were collected by Kotshubej at Ussuri, Sutchan, Jul 24-Aug 3. Moltrecht's specimens come from approximately the same location (Moltrecht, 1929).

In recent work by Masui and Inomata (1994), the genus was revised and included in the *Euripus* group, which contains five genera: *Euripus, Hestina, Sephisa, Sasakia*, and *Hestinalis*. The biology of *Sephisa princeps*, which is the most northern species of the group, was largely unknown except for the short mention that the foodplant was *Quercus mongolica* Fisch (Fagaceae) (Masui and Inomata, 1994). Last instar larvae and pupae of the closely related *S. chandra androdamas* Fruhstorfer, from Taiwan, are illustrated and their host- plant recorded as *Quercus morii* Hay. (Kubo and Cang, 1985). Appearance of the larvae and pupae are superficially similar to those of *S. princeps*, however, we are providing a more elaborate description of all the immature stages in the present work. Uchida (1991) and Lin (1994) record *Q. glauca* as a hostplant of *S. chandra androdamas* in Taiwan.

Males of *S. princeps* can be found locally in the Russian Far East, particularly in the Prichankaiskiy region of the Primor'e area. However, females are extremely rare in museum collections. Our observations during 1988-1995 in the vicinity of Barabash-Levada town, of the Pogranichniy region, showed that the density of *S. princeps* is never as high as that of other Apaturinae in the area, but its numbers are more stable through the years. For example, in late July 1991 on the road along the Komissarovka River at Barabash-Levada, one male could be found along each 30-50m section of the road. Unlike other Nymphalidae, males never formed puddling groups. When chased off the road, they would fly up and land on the branches of oak trees. They displayed territorial behavior by perching and attacking passing butterflies. In the second half of July 1994, we observed large numbers of males and, a little later, females (Fig. 7N), feeding on tree sap in the canopy.

DESCRIPTION OF LIFE HISTORY

Egg: On 24 Jul 1994, we obtained 28 eggs from a caged female. A block of 26 glued-together eggs was laid into a rolled leaf of a

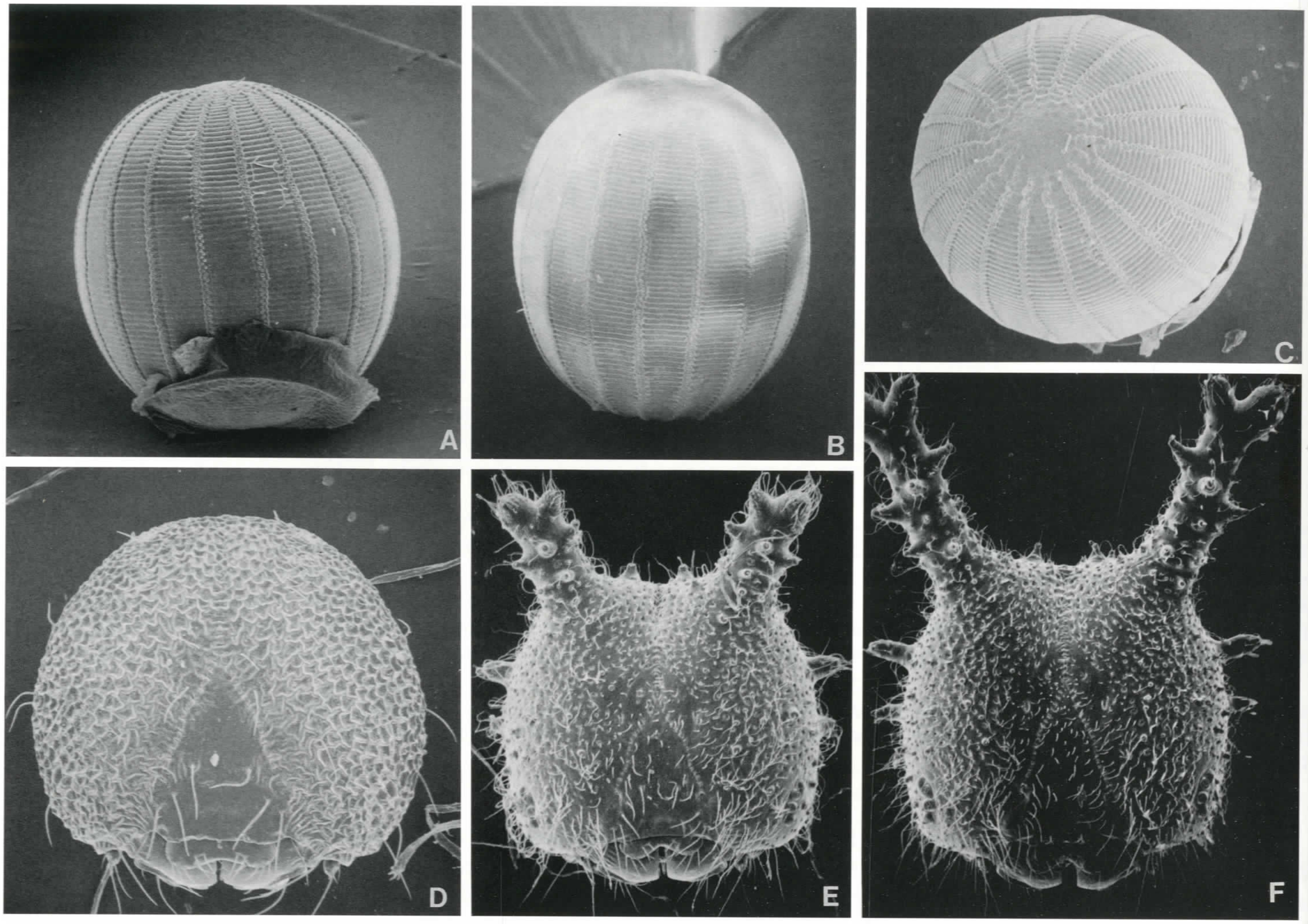


Fig. 1. *Sephisa princeps*: (A) Egg with 18 vertical ribs (X50); (B) Eggs with 17 vertical ribs (X50); (C) Egg, dorsal view (X50); (D) Head of the 1st instar larva (X75); (E) Head of the 2nd instar larva (X38); (F) Head of the 3rd instar larva (X30) (by A. Sourakov).

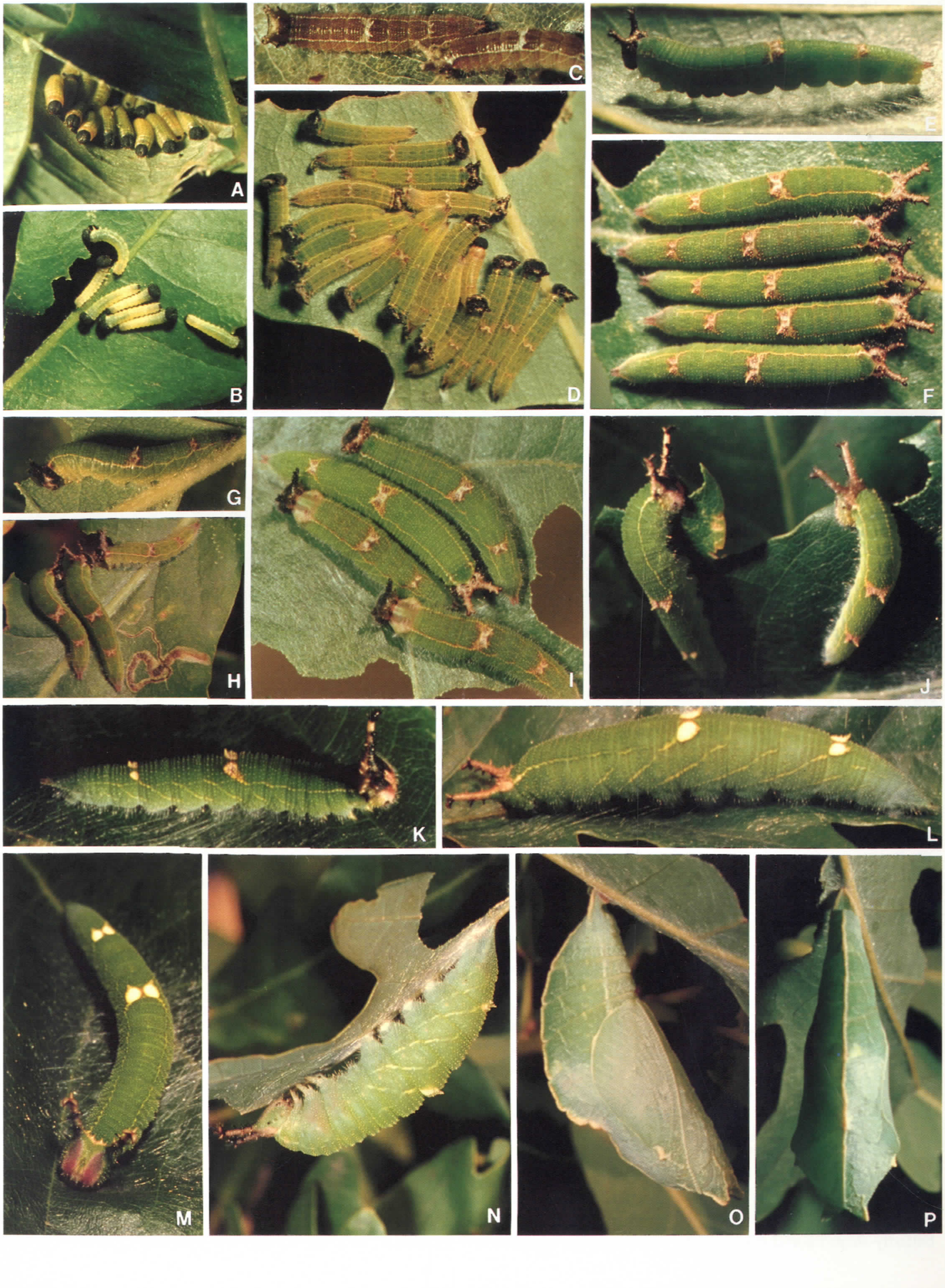
new shoot of *Quercus mongolica* Fisch (Fagaceae). The female died in six days and upon opening her abdomen, we found another 24 fully formed eggs.

Eggs are white, ellipse-shaped. Micrographs of the two eggs we examined show some differences in proportion of the eggs, which can be correlated with differences in the number of vertical ribs: there are 18 vertical ribs on one egg (Fig. 1A,C) and 17 on the other (Fig. 1B). Their sizes are 1.24mm wide and 1.32mm high, and 1.14mm wide and 1.34mm high, respectively. There are more than 60 horizontal ribs between the vertical ribs and there is a pore on both sides of the vertical rib for each of the horizontal ribs. Ribs disappear when they reach the rosette-shaped micropylar area (Fig. 5A), which is 0.25mm in diameter.

First instar: The leaf with 26 eggs was placed into a cage with fresh branches of *Quercus robur*. Hatching began on the 16th day after oviposition and 23 eggs hatched within 24 hours. Three eggs were infertile. Upon hatching, larvae were white and 3 mm long. During the first 24 hours, the larvae kept together, feeding on their egg shells and building a silken nest around the leaf with the original batch of eggs. Later, larvae went out on the leaves in groups of 5-8 and returned into the nest after feeding. Two days later, larvae moved to another leaf and formed a new nest at its base (Fig. 2A), from where they went to its tip or to another leaf to feed (Fig. 2B). In ten days, larvae started molting into the second instar. Almost all of them formed one compact group at this time.

Larvae are green, with a black, 1.0mm wide and 0.8mm high head. Body length at maturity is 5.5-6.0 mm. The entire head except frontoclypeus is covered with raised reticulation (Fig. 1D). The shape of the body and chaetotaxy can be seen on the micrograph (Fig. 3). The prothoracic shield (Fig. 5B) is divided in two: one portion for each lateral side of the body, and each bearing four setae. Unfortunately, part of the body setae were broken off in the only first instar larva we preserved. However, from observations on the intact setae as well as on the second instar chaetotaxy, we can conclude that dorsal setae are all modified into short

Fig. 2. *Sephisa princeps*: (A) 1st instar larvae in the nest; (B) 1st instar larvae feeding; (C) Several of the larvae have turned dark and gone into diapause; (D) Larvae have just molted into 2nd instar; (E) 3rd instar larva building a nest; (F) 3rd instar larvae resting in the nest; (G) 2nd instar larva feeding; (H) 3rd instar larvae feeding; (I) 3rd instar larvae molting into 4th instar; (J) 4th instar larvae feeding; (K) 4th instar larva building a nest; (L) Full-grown 5th instar larva; (M) Newly molted 5th instar larva building a nest; (N) 5th instar larva before pupation; (O) Pupa, lateral view; (P) Pupa, dorsal view (by A. Dantchenko).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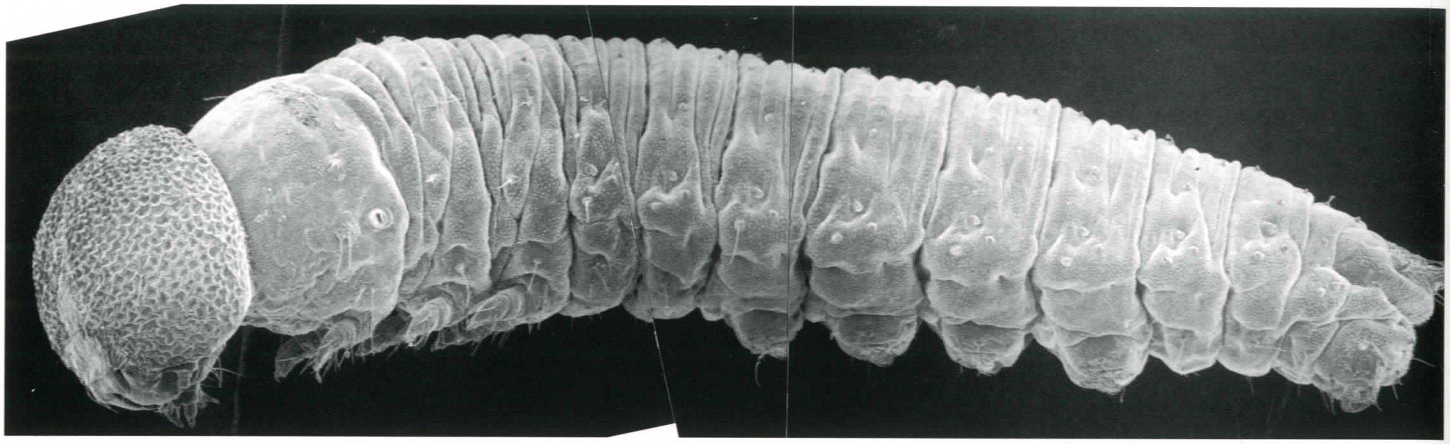

Fig. 3. *Sephisa princeps*: Micrograph of the 1st instar larva, lateral view (by A. Sourakov).

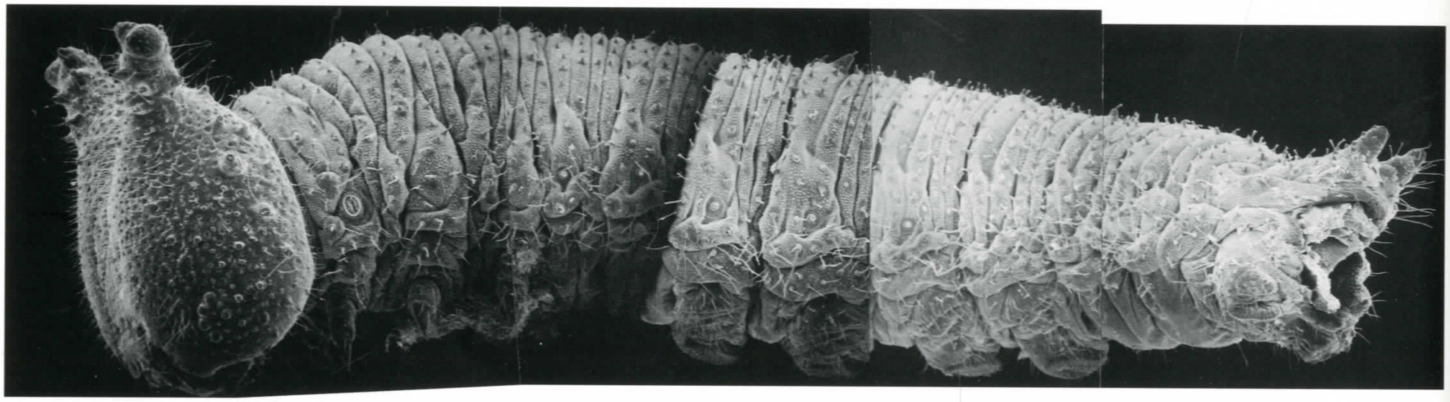

Fig. 4. *Sephisa princeps*: Micrograph of the 2nd instar larva, lateral view (by A. Sourakov).

mushroom-shaped setae on chalazae (Fig. 5F). Spiracles are elevated. The prothoracic ostium is shown in Fig. 5C. Legs are short, with laterally flattened tibia and tarsus, bearing few setae (Fig. 5E). The last abdominal segment is bifurcate. The dorsal setae on the last segment are longer than the rest of the dorsal setae, and have a few teeth distally (Fig. 5D).

Second instar: The behavior of the second instar was similar to that of the first instar: larvae came out in groups to feed for 3-4 minutes (Fig. 2G), and then return into the nest for 15-20 minutes (Fig. 2D). This stadium lasted 5 days for most of the larvae. In twelve days, these larvae molted into the third instar. However, five larvae were darker than the rest and grew slower (Fig. 2C). They then went into diapause but did not survive overwintering.

Head is black, 1.57mm wide, 1.25mm high in the middle. It bears horns of 0.66mm (30% of the total head height), giving short branches in all directions. There are two larger and several smaller projections coming off the lateral side of the head, and on the occiput between the horns. The surface of the head except for the frontoclypeus is pitted, with numerous thin setae covering it (Fig. 1E). Secondary segmentation of the body is expressed much more strongly than in the first instar (Fig. 4). Anal forks become larger. The body is covered with numerous secondary setae. Setae below the spiracular line are long, thin, and spinose. Those that are above the spiracular line are mostly short, stout, widened distally, and bearing spines and positioned on the large pinacula (Fig. 5G). The body is green. There are two brown-and-white butterfly-shaped dorsal marks on the fourth and tenth abdominal segments, located between white-brown subdorsal lines (Fig. 2D,G). The subdorsal line gives rise to similarly colored lines, which diagonally cross the lateral side of two segments, going forward and down. These lines are present on all abdominal segments. Body length at the end of instar is 10 mm.

Third instar: There were three separate leaf nests of larvae. Larvae were spending up to 30 minutes together on the upper surface of the leaf (Fig. 2F) and then abruptly going out in groups of 4-6 larvae to one of the leaves on the same branch (Fig. 2H). After feeding for 4-6 minutes, they were returning to the nest following their silky track. This stadium lasted 4 days.

The head is black with reddish frontoclypeus and reddish area around the stemmata. It is 2.1mm wide and 1.75mm high in the middle. There is a pair of horns, 1.5mm (52% of the total head height) each (Fig. 1F). Thus, relative to the head size, the horns are significantly longer than in second instar. Otherwise, the larva is similar to the second instar.

Fourth instar: The behavior was similar to that described for earlier instars. The larval nest was always positioned so that the feces rolled out of the nest. After reaching a body length of 28 mm following 5 days, the first larva started to molt to the fifth instar.

Head is 3.36mm wide, 2.83mm high. Reddish area around stemmata increases (Fig. 2J,K). Horns are 2.69mm (50% of the total head height) long and are lightly colored posteriorly.

Fifth instar: The larvae were too big to have more than five fit in one leaf nest. When a nest was transferred to a new plant, the

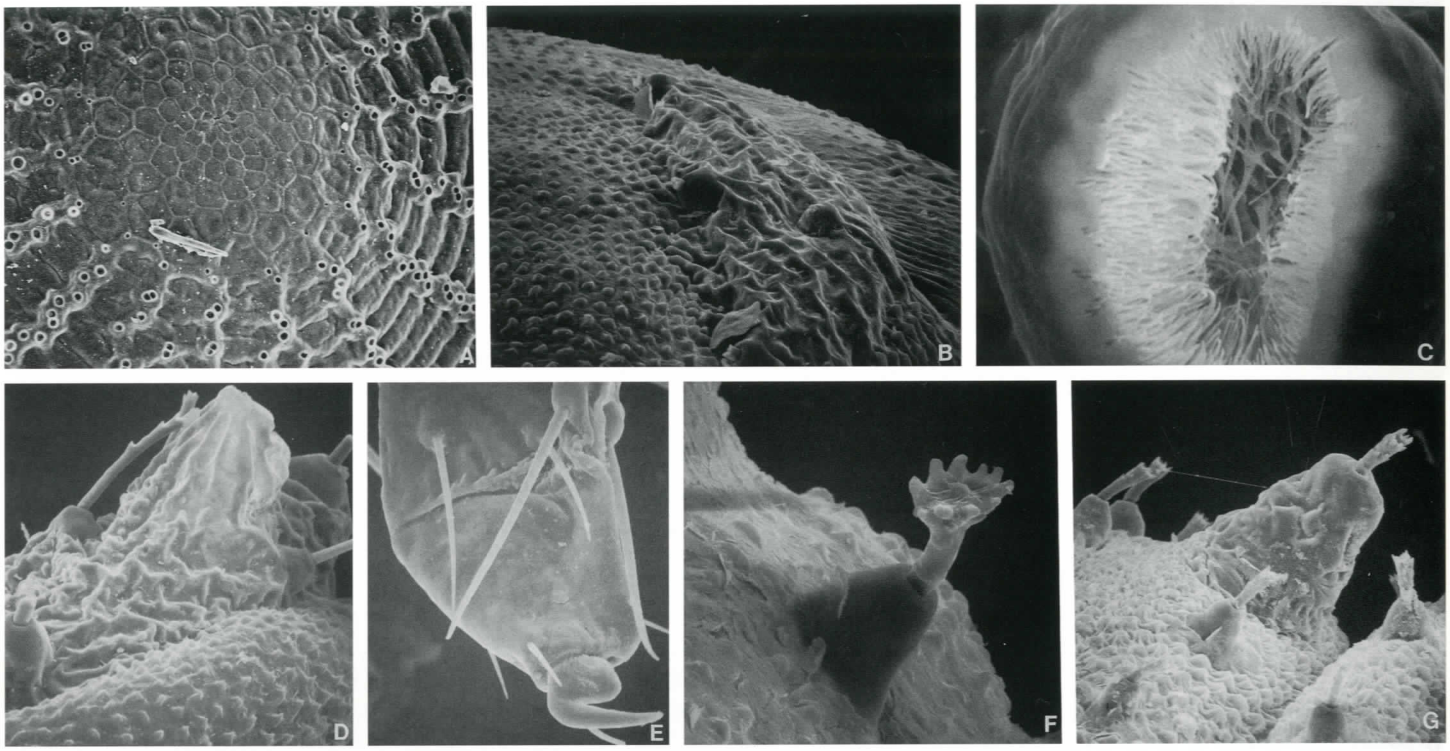

Fig. 5. *Sephisa princeps*: (A) Micropylar area of the egg (X250); (B) Prothoracic shield of the 1st instar larva (X500); (C) Prothoracic ostium (X2000); (D) Anal segment, 1st instar larva (X500); Prothoracic leg, 1st instar larva; (F) Dorsal seta of the 1st instar larva (X1500); (G) Dorsal setae, 2nd instar larva (X500) (by A. Sourakov).

larvae continued living gregariously. When placed singly on different branches of the same plant, each larva made a separate nest and went out to eat at different times. After feeding, they sometimes would return into the new nest, but more often ran around until bumping into another larva's nest. Then the guest larva would abandon its nest and move into a new-found one. In this manner, all the larvae ended up together in one nest (Fig. 7K-M). Each of the newly arriving larvae would add some silk to a communal nest.

When a visiting larva tried to enter a nest built by another larva, both exhibited a rather complex behavioral ritual which was repeated time after time. The host larva usually occupied the center of the leaf, facing its base (petiole end). When a visitor larva tried to enter, it faced a host's head and both moved synchronously, as if the host was trying to catch the guest's head with his own (Fig. 7A-F). In most cases, this "dance" resulted in a visitor joining the host in the nest (Fig. 7H-J), after the host "invited" the guest by moving its head out of the way (Fig. 7G). Sometimes, however, the guest was chased away, which would be preceded by an imitation of a fight. In general, the behavior of grown larvae seemed to be complex, which, besides the ritual described above, is expressed in the following routine. A larva exercised very precise choice for a place for the nest and always followed the same route, covered with silk threads, when going to feed. After choosing the leaf on which it was going to feed, a larva attached this leaf strongly to the branch with many layers of silk. Upon being irritated by a pin, a larva attacked the pin vigorously, attempting to crush the pin between its mandibles. At the same time, larvae were very tolerant of each other while in the nest.

On the eleventh day of the fifth instar, the first larva changed its color, turning light green with a purple spot on the side of the third segment. While looking for a place to pupate, the larva studied the underside of all the leaves; the larva sometimes hung itself from the anal segment, as if measuring the sufficiency of available space for a pupa. After finding a leaf suitable for pupation, the larva covered a surface of 10mm width with a layer of silk and, after resting several hours with its head up, turned its head down and remained attached to the silky area for about 2 hours (Fig. 2N).

Head is 4.96mm wide, 4.36mm high, green, with light-brown tips of the horns and the occipital stripe connecting them light-brown. Horns are 4.85mm (55% of the total height of the head) long. The reddish marks are now occupying most of the anterior surface of the head, leaving only a triangular area of the frons green (Fig. 2M). The dorsal side of the head, including horns, is brown (Fig. 2L). The epicranial notch is deeper than in the 4th instar and the head surface is concave along the epicranial suture, so that the horns appear longer. The horns have a number of short branches, and are trifurcate apically. There are numerous noticeable projections on the lateral, posterior and dorsal sides of the head (Fig. 6J). The body coloration remains the same as in earlier instars, except for dorsal butterfly-shaped marks, which become larger. Only the "body" of the "butterfly" remains brown, with the entire "wings" turning white (Fig. 2L,M). The length of most larvae at the end of instar is 55mm, but the last larvae to pupate are larger, up to 60mm long and obviously females.

Pupa: All the larvae pupated in 10 days after becoming fifth-instars. Pupal stage lasted about 12 days.

Pupa is 33-36 mm long. It is flattened laterally, and its dorsal margin resembles the shape of the oak leaf margin (Fig. 2O).

When viewed dorsally, the mid-dorsal stripe resembles the central vein of the oak leaf and there are thin stripes coming off it which resemble peripheral veins (Fig. 2P).

General Comments: Only five out of 23 larvae went into diapause. The diapausing larvae did not survive overwintering. We think, however, that the second generation of 14 butterflies obtained by us as a result of this rearing represents an artifact, provoked possibly by the absence of the day-night fluctuation in temperatures. The day length was natural through the time of the rearing, but temperatures, especially at night, were much higher than at the *S. princeps* natural habitat. The fact that daylight triggers the second-generation emergence of *Apatura ilia* (Denis & Schiffermüller) is known from earlier work, in which both *A. ilia* and *A. iris* (Linnaeus) were reared under a regime of prolonged daylight. *Apatura iris*, however, had one generation a year. Occasionally, individuals of the second generation of *A. ilia* can be found in nature in the environs of Moscow (Dantchenko, pers. observ.). We cannot prove absence or presence of the second generation of *Sephisa princeps* in nature. However, it is possible to speculate that *S. princeps* has one generation a year, based on the length of the development time and cold winter temperatures throughout all of its area. It is possible that a long autumn, with long cold nights, is necessary for starting the larval diapause. If that is so, it would explain the rarity of this species in areas close to the ocean. Warmer weather in these areas would provoke a second generation of the butterflies, without providing sufficient hostplant feeding-source, and temperature-regime resources, for its survival.

Length of Life Cycle: The whole rearing cycle from egg laying to adult emergence took 60 days to complete at 18-20°C.

SEPHISA PRINCEPS AS AN ENDANGERED SPECIES

Sephisa princeps was not included in the *Red Book of Russia* (Anon., 1983), but it appeared in the *Red Book of the USSR* (Anon., 1984) under the name *S. dichroa princeps*. While not criticizing the principles by which insect species are included on endangered species lists, we would like to note that in this particular case, previous authors have never collected *Sephisa princeps* themselves, and their information on ecology and factors contributing to decreasing numbers of this species is not confirmed by our observations. Indeed, the density of populations in Primor'e was never previously studied. Thus, there are no data supporting the placement of *S. princeps* on the endangered species list; it is instead a relatively rare but widespread species in the Russian Far East.

Our observations show that the practice of spring burning of grass is the most dangerous factor influencing many Far East insect populations (Soule, 1987). This particular factor does not, however, affect *S. princeps* and other Apaturinae populations because their larvae overwinter high in the canopy of oak trees. This makes Apaturinae the most common nymphalids in secondary oak forests regenerating after forest fires (Fig. 7O). Only complete destruction of the habitat can actually "endanger" these species.

Interestingly, the inclusion of poorly-known species on endangered taxa lists, and the subsequent prohibition of their collection and study, is a quite common phenomenon. This propensity for over-reaction is well illustrated among students of the European Lycaenidae in a recent edited book, *Conservation Biology of Lycaenidae* (e.g., see the article by Bálint, 1993). The more information on the ecology of a species there is available, the more ecologically oriented is the approach to its conservation. The less information that people have, the more bizarre the protective measures which are proposed (a total prohibition on collection, for example, which discourages virtually all field work on a species to learn its true status, its biology, and what might be done to save it if it truly is "endangered"). Another example of unprofessional conservation effort is listing close relatives of *Sephisa*, such as *Apatura iris* and *A. ilia*, as "endangered" species. Both of these species are often most common in disturbed habitats, due to increased availability of their foodplants there: *Salix caprea* L. and species of *Populus*, respectively. *Apatura ilia* can even be found 50m above the most polluted areas of Moscow, flying in the canopies of *Populus* trees planted for landscaping decoration of the city!

DISCUSSION

Masui and Inomata (1994) provide notes on biology and foodplant records for the species of *Sephisa*. We were able to compare the distributional area of the different species of this butterfly genus with the known distributions of their foodplants, using a monograph on oaks of Asia (Menitskiy, 1984):

1. *Sephisa dichroa* Kollar (TL: Kashmir, India)

Moore (1986) indicates that *Quercus incana* Roxb. is a foodplant of this species. According to Menitskiy (1984), *Q. incana* is a typical dominant tree of the outer slopes of the Himalayan mountains at elevations of 1200-2000m. It prefers moist and cold ravines with sufficient rainfall and reasonable snowfall. Trees blossom in May and produce acorns about 15-17 months later. The distribution of *Q. incana* perfectly overlaps with the distribution of *S. dichroa*, so that we can suppose the existence of a monophagous host/herbivore relationship between these two species (Fig. 8).

2. *Sephisa daimio* Matsumura (TL: Horishan, Taiwan)

This is an endemic species of Taiwan. It would be logical to assume, therefore, that the foodplant is an endemic native species of Taiwanese oak. Indeed, an endemic oak, *Quercus morii* Hayata, is found in the subtropical zone and dominates in the temperate zone (1600-2400m) of the island's mountains, and is recorded as a foodplant for *S. daimio*. This tree blossoms in April and produces acorns by October-November.

3. *Sephisa chandra* Matsumura (TL: Darjeeling, India)

The area of distribution for this species is very extensive: from northern India to Taiwan in the east, and to Malaysia in the south. There are several distinct geographic subspecies: *S. c. androdamas* Fruhstorter (TL: Taiwan); *S. c. hainanesis* Miyata and Hanafusa (TL: Hainan Island); *S. c. stubbsi* Corbet (TL: Phahang, Malay peninusula). The biology of this species is des-

Fig. 6. *Sephisa princeps*: (A)-(J) Molting into the 5th instar: (A) 4th instar larva before molting; (B) Old skin starts moving backward; (C) The larva breaks the old skin with its legs; (D) The new capsule is free, with skin still moving backward; (E) The anal segment is freed; (F)-(H) Vigorous movements of the head result in freeing mandibles from the old capsule; (I) The old mandible is pushed off the leaf; the horns are still soft and discolored, but straight; (J) Fully formed head. (K)-(Q) Process of pupation: total time of pupation is eight minutes; pupa gains its color and hardens to the stage shown in Fig. 2O within next 24 hours. (R)-(V) Hatching of male adult; total time of hatching is 1 minute (by A. Dantchenko).


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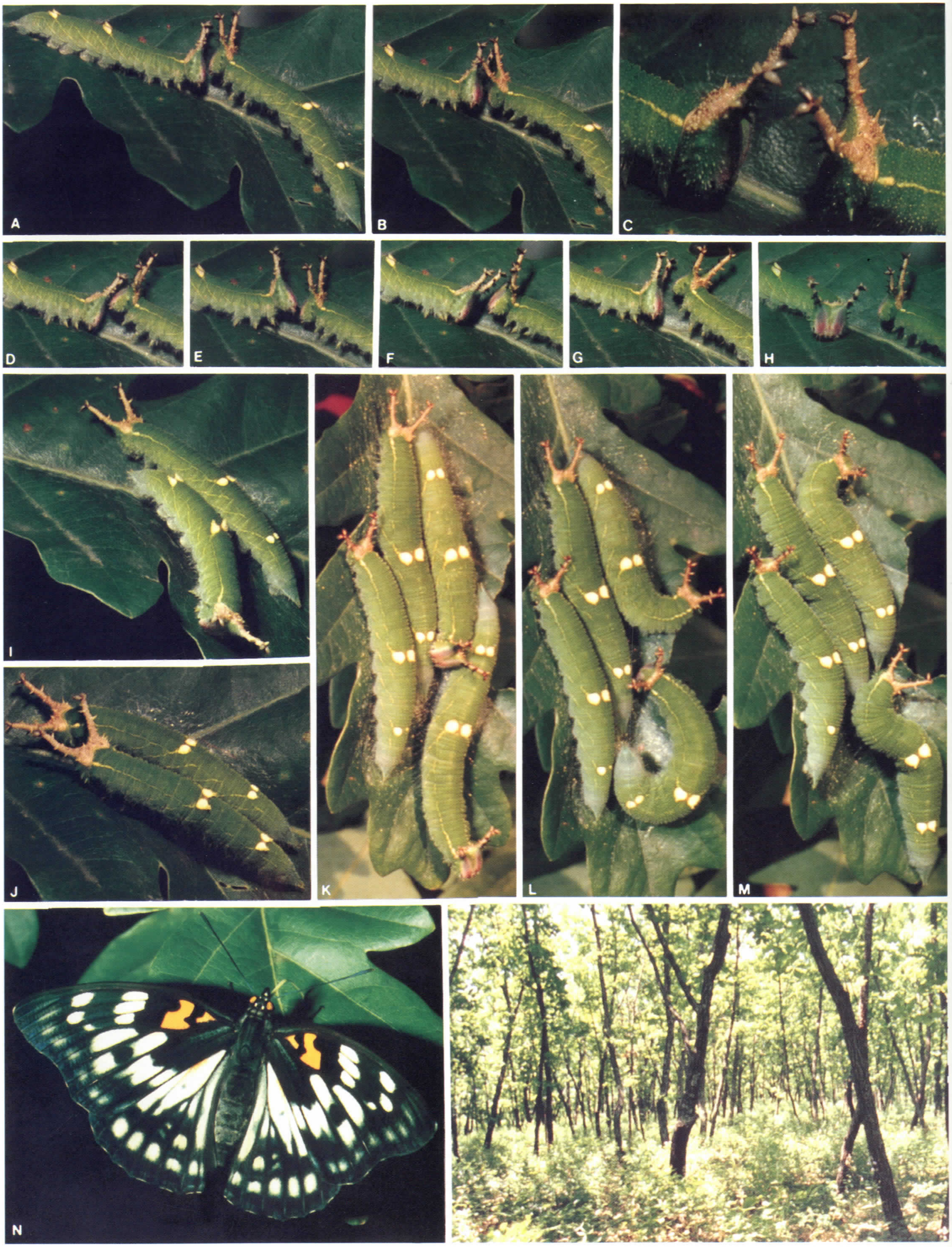
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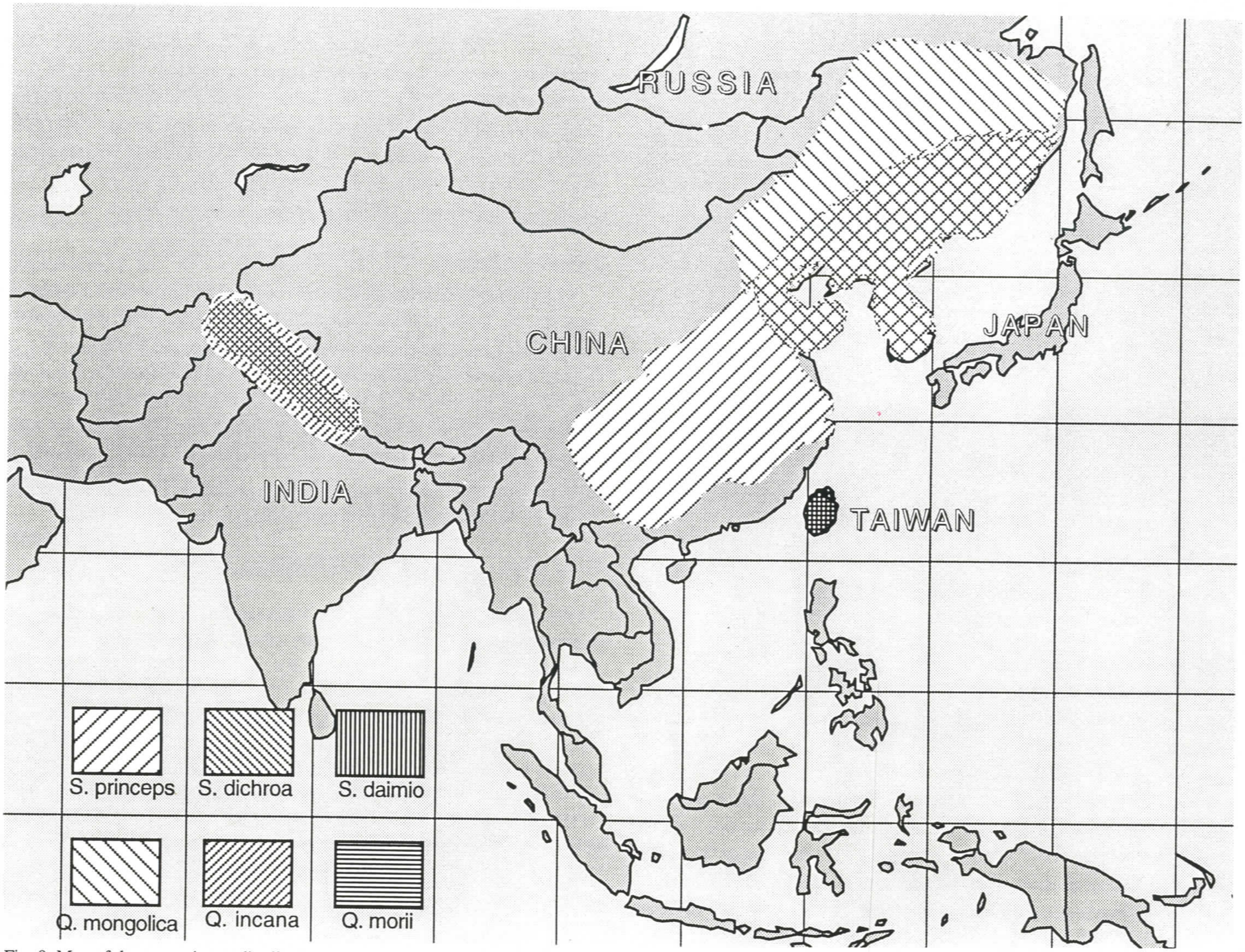

Fig. 8. Map of the approximate distributions of *S. princeps, S. dichroa,* and *S. daimio* overlapping map of the distributions of their foodplant species (by A. Sourakov).

cribed from Taiwan for subspecies *S. c. androdamas*. The hostplants include *Q. morii* (Kubo and Cang, 1985) and *Q. glauca* (Uchida, 1991; Lin, 1994). We can suppose that *Q. glauca* also serves as a hostplant for the mainland populations. It is a highly polymorphic tree, developing numerous forms within a giant area of eastern and southeastern Asia (with the sole exception of the equatorial region). Interestingly, the ranges of the subspecies of *Q. glauca* correspond with the ranges of different subspecies of *Sephisa chandra*: *Q. g. longinux* (Hayata) (TL: Taiwan) for *S. c. androdamas*; *Q. g. annulata* (Smith) (TL: Upper Nepal) for *S. c. chandra*; *Q. g. schottkyana* (Rehd. & Wils) (TL: Syntype: Yunnan, China) for phenotypically distinct populations of *S. chandra* in central China.

Fig. 7. *Sephisa princeps*: (A)-(J) "Greeting ritual" between two larvae, one of which (on the left) invades the leaf occupied by another (on the right): (A) The host (resident) larva raises its head over the leaf surface when the guest approaches; (B)-(C) Prolonged physical contact with horns, which bear numerous sensillae (Fig. 1F); (D) The host raises the head; (E) The host lowers its head, while the guest raises its head; (F) The guest moves its head to each side; (G) The host moves its head out of the way; (H) The guest accepts it as a signal to enter; (I)-(J) The guest enters and joins the host on the leaf; (K)-(M) The entrance by two guest larvae into the nest occupied by two host larvae; this event is usually preceded by the ritual shown in (A)-(H); (N) Female of *Sephisa princeps*; (O) Forest of young oak trees as a habitat for *S. princeps* (by A. Dantchenko).

We can only speculate that subspeciation of *S. chandra* went synchronously with subspeciation of its supposed foodplant. Absence of this butterfly species in the non-continental Far East (Japan) could be explained by the morphological distinctness of *Q. glauca* ssp. *glauca* var. *stenophyla*, which might be unsuitable for oviposition by females or for feeding by larvae. However, restriction of the range could also be purely for climatic reasons.

4. *Sephisa princeps* Fixsen

The range of this species is from the Amur River on the Russian-Chinese border, south to southern China, where it is sympatric with *S. chandra*. Similarly to the first three species, it is associated with particular species of oak: with *Quercus variabilis* Blume in southern Korea (Fig. 10) and with *Q. mongolica* Fisch. in northern Korea, northern China and Russian Far East (Fig. 8). Both species of *Quercus* probably satisfy requirements of *Sephisa princeps* larvae. It could also be that there are two subspecies associated with each of the foodplant species, heretofore unrecognized.

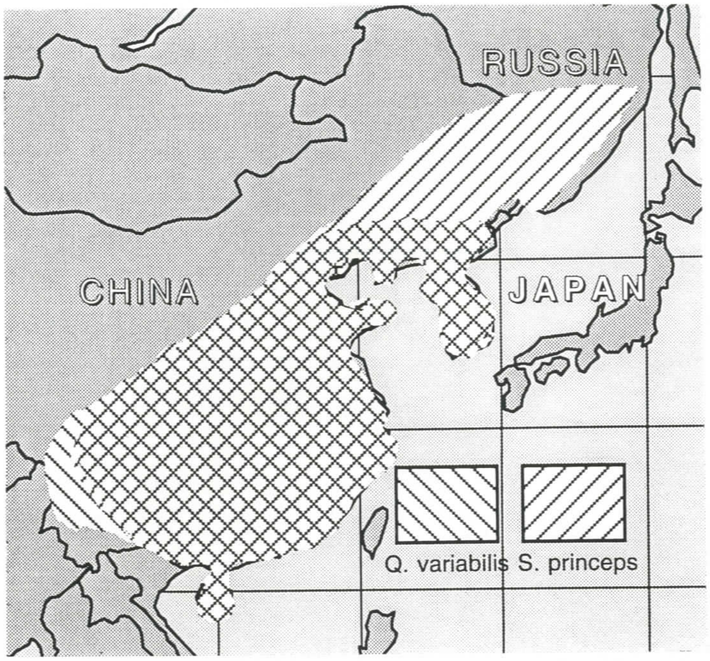

Fig. 9. Map of the approximate distribution of *S. princeps* overlapping map of distribution of its foodplant in the south, *Q. variabilis* (by A. Sourakov).

The Role of Rolled Leaves for Oviposition

In the case of *Sephisa daimio,* the leaf selected by a female for oviposition and in which eggs are laid is previously rolled into a tube by a particular species of leaf-rolling insect (Masui and Inomata, 1994). We provoked a female of *S. princeps* to lay eggs by providing artificially rolled leaves. In the wild, there are many species of Lepidoptera and Coleoptera which roll leaves for their larvae (Egorov, 1992). One example of the latter group is *Deporas unicolor* Roel. (Coleoptera: Attelabidae) (Ter-Minasian, 1950), monophagous on *Q. mongolica.* If a correlation between biology of leaf-rolling insects and oviposition of *S. princeps* exists, it might explain the discreteness of the range of *S. princeps*. Cases of similar correlation are known in Lycaenidae, where the range of a butterfly species is often determined by the range of an ant species, with which the butterfly larvae are associated.

Hostplant Relationships

According to Menitskiy (1984), the species of oaks mentioned above fall into three major subgenera of the genus *Quercus*:

1. Subgenus *Heterobalanus*: *Q. incana*. Members of this subgenus are the most primitive of the genus, which arose on the northeastern shore areas of the ancient Tethys Sea. *Q. incana* can be considered a relict species.

2. Subgenus *Cyclobalanoides*: *Q. glauca* and *Q. morii*. Members of this genus are found exclusively in eastern and southeastern Asia. *Q. glauca* seems to be the most primitive member of its section and *Q. glauca* ssp. *annulata* is the most cosmopolitan of its forms. *Q. morii* is the most divergent member of its section, which evolved as an island isolate.

3. Subgenus *Quercus*: *Q. mongolica*, *Q. variabilis*. This subgenus probably derived from mid elevation forests of southeastern Asia. Both members are the most divergent members of two different sections.

Therefore, *Sephisa dichroa*, *S. chandra*, and *S. princeps* are correlated with three separate subgenera of the genus *Quercus*. The most divergent and morphologically distinct member of the genus *Sephisa daimio* is associated geographically and biologically with the most divergent member of the genus *Quercus: Quercus morii*, an endemic of Taiwan. This finding supports the hypothesized existence of hostplant-butterfly co-evolution of the plant genus *Quercus* and the butterfly genus *Sephisa*.

CONCLUSIONS

Considering the above points, we can conclude that ranges of species of *Sephisa* correspond well with ranges of their known foodplants. In cases where no foodplant records are available, it seems possible to predict the probable foodplant species, based on the known distributions of the potential hostplant and butterfly. Therefore, lack of ecological information for any butterfly taxa can be partially compensated by speculations based on maps of plant and butterfly taxa distribution, combined with the knowledge of ecology of related taxa.

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