

EGG STRUCTURE AND NOTES ON BIOLOGY OF THECLINAE FROM PRIMOR'E, RUSSIAN FAR EAST (LEPIDOPTERA: LYCAENIDAE)

ALEXANDER DANTCHENKO, ANDREI SOURAKOV, and THOMAS C. EMMEL

Leninskiy Prospect 33, Inst. of Evolutionary Morphology and Ecology of Animals, Moscow, Russia;
Dept. of Entomology and Nematology, University of Florida, Gainesville, Florida 32611; and
Depts. of Zoology and Entomology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.—The biology and systematics of hairstreak butterflies of the genera *Artropoetes*, *Araragi*, *Strymonidia*, *Neozephyrus*, *Wagimo*, *Ussuriana*, *Fixsenia*, *Thecla*, *Chrysozephyrus*, *Japonica*, *Shirozua*, and *Antigius* from the Russian Far East are discussed. The life histories and especially the morphology of the eggs are useful in drawing taxonomic conclusions.

KEY WORDS: Amur, *Antigius*, *Aphnaeus*, *Araragi*, *Arhopala*, *Artropoetes*, Asia, behavior, Betulaceae, China, *Chrysozephyrus*, ecology, Eumaeini, Fagaceae, *Fixsenia*, hostplants, immatures, *Japonica*, Juglandaceae, Korea, larvae, *Loxura*, Manchuria, morphology, *Neozephyrus*, Oleaceae, Palearctic, Papilionidae, Rhamnaceae, Rhopalocera, Rosaceae, Rutaceae, *Shirozua*, *Strymonidia*, systematics, *Thecla*, Theclini, Ulmaceae, Umbelliferae, Ussuri, *Ussuriana*, *Wagimo*.

Primor'e is a small area of the Russian Far East, located in the very southeast of Russia, next to Korea and Manchuria. Due to its warm local climate, it contains a high diversity of animal and plant life. This study considers the biology and egg morphology of several species of Theclini which occur sympatrically in the southern Primor'e.

There have been no studies on the biology of Theclini of the Far East since the end of the last century (Graeser, 1888-92). In a sense, this situation is the result of the typological concept which dominated systematics during the last century. It would be unjust to say today that systematists completely ignore biological data: on the contrary, it is very common to list, for example, food plants. Often, this information is transferred from one work to another, forming whole lists of foodplants, which sometimes are not even found in the region studied. Such works can reduce the desirability of using biological information in taxonomy, due to a great amount of misleading information in the literature. Interest in life history studies is on the rise now in general, due, undoubtedly, to their importance for conservation. However, the use of this kind of information for taxonomic purposes is more the exception than the rule (Saigusa, 1993). Life history studies, of course, are not a substitute for regular taxonomic study of adult characters, but in groups with few morphological differences in the imago, they might be very essential. Tree-feeding Theclinae represent a group where morphological details can be quite useful in taxonomy.

In 1991-93, we studied the systematics and biology of Theclini in two regions of Primor'e: at the very southern end of the region, in the delta of the Riazanovka River and in the Prihankaiskiy area, in the vicinity of the town Barabash-Levada. The South Primor'e site includes hilly habitat at 100-600m elevation, with domination of *Quercus mongolica* Fish. (Fagaceae) and

sandy dune habitat along the coast where *Quercus dentata* Thunb. dominates. This area is the most northern border of the distribution of *Quercus dentata*, which is found mostly in subtropical Asia. The Prihankaiskiy region is different not only because of its climate (autumn in this place is unusually warm), but also because of its steppe-type landscape, which is more characteristic of the Amur region. Mid-elevation forest of the regional Pogranichniy mountain chain consists mostly of *Quercus mongolica*.

Our studies were conducted from early April to the end of September. They consisted of collecting eggs and larvae in nature and breeding butterflies from the eggs obtained from the females in the laboratory. The objects of our study were mostly tree-feeding Lycaenidae of the Theclini and Eumaeini groups. All species of these groups are associated with trees or shrubs and overwinter in the egg stage. Collecting eggs in nature allowed us to estimate habitat preferences, as well as to obtain information on the oviposition pattern of different species.

SPECIES ACCOUNTS

Strymonidia ilicis ilicis (Esper) (Fig. 1L) is found only in the European part of Russia, associated with young oak growth in open areas. The female lays eggs on the fresh shoots. First instar larvae bore into the buds. The last instar larva's coloration resembles the color of the young oak leaves on which it feeds, sitting on the lower surface of the leaf (Fig. 3I). The larva pupates on the ground, or occasionally on the shoots. Adults hatch at the end of June.

Strymonidia latior latior (Fixsen) (Fig. 1K). The larva feeds on *Rhamnus ussuriensis* Vassil (Rhamnaceae). This species is often considered a subspecies of the European *Strymonidia spini* (Fabricius), to which it is closely related. There are significant differ-

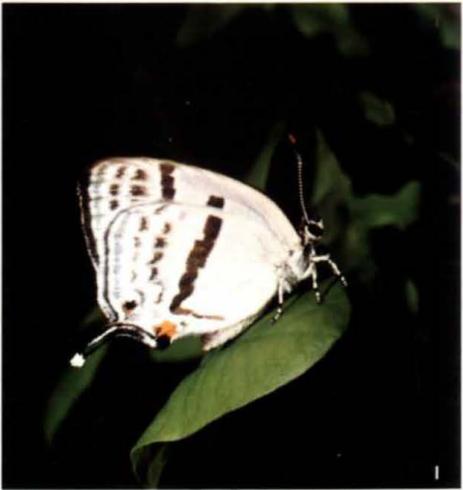




PLATE 2. (1) *Neozephyrus ultramarinus* Fixsen: (a) male; (b) male underside; (c) female; (2) *N. taxila* Bremer: (a) male; (b) male underside; (c) female; (3) *N. saphirinus* Staudinger: (a) male; (b) male underside; (c) female; (4) *N. quercus* L.: (a) male; (b) male underside; (c) female; (5) *Wagimo signata quercivora* Staudinger: (a) male; (b) male underside; (6) *Fixsenia pruni* L., male.

PLATE 1. (A) *Neozephyrus saphirinus* Staudinger; (B) *Antigius butleri* Fenton; (C) *Neozephyrus quercus* L.; (D) *N. aquamarinus* Dubatolov & Sergeev; (E) *Strymonidia eximia* Fixsen; (F) *Neozephyrus taxila* Bremer; (G) *N. japonicus* Butler; (H) *Thecla betulae crassa* Leech; (I) *Antigius attilia* Bremer; (J) *Japonica onoi* Murayama; (K) *Strymonidia latior* Fixsen; (L) *Strymonidia ilicis* Esper.



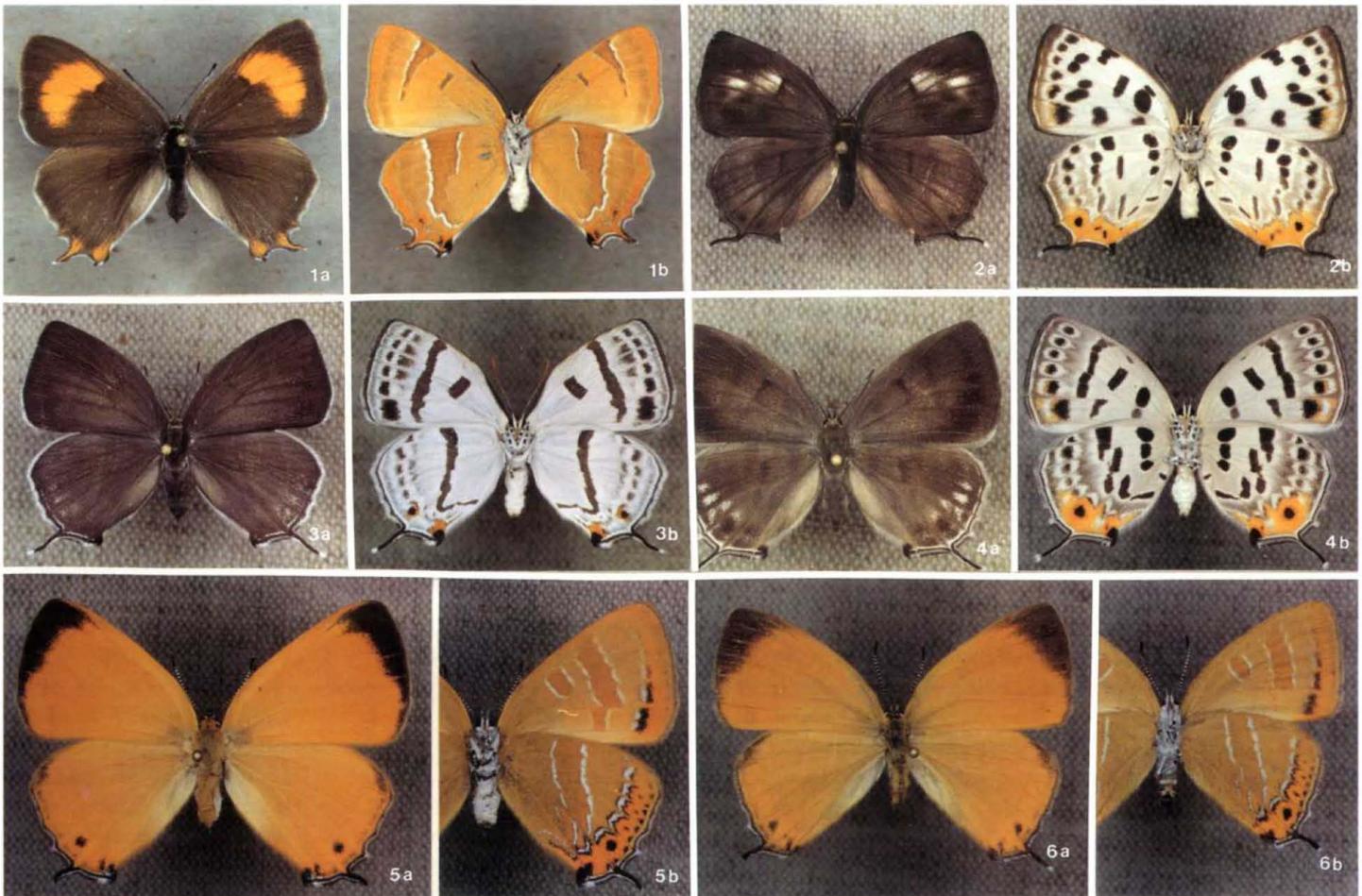


PLATE 4. (1) *Thecla betulae* L. (a) male; (b) male underside; (2) *Araragi enthea* Janson; (a) upperside; (b) underside; (3) *Antigius attilia* Bremer; (a) upperside; (b) underside; (4) *Antigius butleri* Fenton; (a) upperside; (b) underside; (5) *Japonica onoi* Murayama; (a) upperside; (b) underside; (6) *Japonica lutea* Hewitson; (a) upperside; (b) underside.

ences, however, in the morphology of males, females, and larvae of *S. s. latior* and all other European subspecies of *S. spini*. Besides, the distributional areas of these taxa do not overlap, nor do the distributions of their food plants: *S. spini* feeds on *Prunus spinosa* L. (Rosaceae) or *Rhamnus cataractica* L. (Rhamnaceae). These facts are probably the reasons that *S. l. latior* is listed in Tuzov's *Synonymic List of Butterflies from the ex-U.S.S.R.* as a separate species (Tuzov, 1993). The adults fly in open areas. Females lay egg clusters of two (in the branching points of thin branches) to 80 (at the bases of the trunk) (Fig. 6D). The larva bores into a just-opened bud and later stays inside the developing flower clusters. The last-instar larva pupates in the litter on the ground. Under laboratory conditions, it pupates in the container's layer of dry leaves, attaching itself to the leaf with a silk thread. Adults hatch in the middle ten days of July.

***Strymonidia eximia eximia* (Fixsen)** (Fig. 1E). Larvae feed on *Rhamnus diamantiaca* Nakai (Rhamnaceae). Eggs are laid in clusters of one to four on the uneven surface of shoots. The food

PLATE 3. Last instar larvae: (A) *Araragi enthea* Janson; (B) *Neozephyrus ultramarinus* Fixsen; (C) *N. aquamarinus* Dubatolov & Sergeev; (D) *Wagimo signata* Staudinger; (E) *Thecla betulina* Staudinger; (F) *Neozephyrus japonicus regina* Butler; (G) *Strymonidia eximia* Fixsen; (H) *S. latior* Fixsen; (I) *S. ilicis* Esper; (J) *Antigius butleri* Fenton; (K) *Thecla betulae* L.; (L) *Antigius attilia* Bremer; (M) *Japonica onoi* Murayama; (N) *Neozephyrus saphirinus* Staudinger; (O) *N. taxila* Bremer.

plant is found mainly in the understory of the forest. Thus *S. eximia* is separated from *S. latior* ecologically. An egg of *S. eximia* was found on *Rhamnus ussuriensis* Vassil only once (Fig. 5I). In the laboratory, larvae were raised on *Rhamnus cataractica*. Adults hatch several days later than *S. latior*. The larva is shown in Fig. 3G.

***Strymonidia w-album w-album* (Knoch)** is found in the European part of Russia. Here the egg is considered for comparison with the Far East subspecies. The egg is shown in Fig. 6H.

***Strymonidia w-album sutschani* (Butler)**. The taxonomic status of this taxon is unclear. It is considered a synonym of the subspecies *S. w. fentoni* in the latest literature. However, we consider this taxon as a valid species. The actual position of this taxon could be determined only by comparing the biology and morphology of all the available taxa in the group. We have not observed its oviposition behavior in nature; however, this species, as with other species of the group, is likely to be associated with *Ulmus* sp. (Ulmaceae). In the laboratory, larvae were raised on *Ulmus levis* L. Adults feed on Umbelliferae together with *S. eximia* and *S. latior*, and fly in the second half of July. The egg is shown in Fig. 6I.

***Fixsenia pruni pruni* (Linnaeus)**. Larvae of this species bore into the buds of *Prunus padus* L. (Rosaceae) after hatching from the egg. Adults fly in open areas in the middle of June.

Fixsenia herzi herzi (Fixsen) lays eggs on *Pyrus ussuriensis* Maxim. (Graeser). (Rosaceae) In the laboratory conditions, it lays eggs and feeds on *Malus mandshurica* (Maxim.) Kom. (Rosaceae). Adults are often seen on flowers in mid-June.

Wagimo signata (Staudinger) (Fig. 2(5)). The larva of this species shows more specialized features (Fig. 3D). It is found only on *Quercus mongolica* Fischer (Fagaceae). Eggs are laid mostly on the large flower buds found in the upper part of the oak-tree canopy, and in clusters of one to six eggs (Fig. 5F). The larva of the first instar bores into the bud. Later instars feed on flowers and fresh leaves. Under laboratory conditions, the larva pupates on the stem. According to Yokoyama and Wakabayashi (1967), this species pupates inside a shelter which the larva nibbles out of the bark. Adults hatch in the middle of July.

Antigius attilia (Bremer) (Fig. 1I and Fig. 4(3)) and *Antigius butleri* (Fenton) (Fig. 1B and Fig. 4(4)). Adults, larvae (Fig. 3J,L), pupae and genitalic structures are very similar. The egg of *A. butleri* is similar to that of *A. attilia*, though in the egg of *A. attilia*, the projections are longer and the egg is flatter (Fig. 5A,B). These features probably have been selected as part of the different ecologies of oviposition. *A. attilia* lays a solitary egg into the gaps and folds in the bark of *Quercus mongolica* (Fagaceae). *A. butleri*, on the other hand, lays eggs in clusters of 6 to 12 eggs under the old bark where it is separated from the trunk of *Quercus mongolica*. In the zones of overlap of *Q. dentata* Thunberg and *Q. mongolica*, eggs of both species have been found occasionally on *Q. dentata*. This shared intermediate-host situation does not happen in species in which the female lays eggs on shoots or buds. In those species, survivorship of the larva strongly depends on the precision with which the female places the egg. Buds of *Q. dentata* open two weeks later than those of *Q. mongolica*. Such timing often determines the ecological ties between oak species and the insects feeding on them.

Araragi enthea enthea (Janson) (Fig. 4(2)). Larvae (Fig. 3A) feed on *Juglans manchurica* (Juglandaceae). The eggs are laid singly, or sometimes in pairs on young shoots, from the bases to the bud. Larvae, which are green in all of the instars, hatch at the end of May and feed on the underside of leaves until the end of June. Larvae pupate on the leaves. Adults fly at the end of July.

Japonica lutea (Hewitson) (Fig. 4(5)) and

Japonica onoi Murayama (Fig. 4(6)). The relationship between these two species resembles that between *A. attilia* and *A. butleri*. The differences in these sympatric species are ecological rather than morphological. *Japonica lutea* lays eggs (Fig. 6G) solitarily on buds of young shoots of *Quercus mongolica* (Fagaceae). The female of *J. onoi* lays eggs in a similar manner, but uses *Quercus dentata* and deposits clusters of three to 15 eggs. In both species, the female conceals the egg after it is laid by rubbing its abdomen against the freshly laid egg and masking it with hairs and a waxy secretion. It makes it almost impossible for us to find the egg on the similarly colored, hairy shoots of the foodplant. However, these cryptic eggs do not escape parasitic wasps: 40% of the eggs collected in nature were parasitized. These observations are similar to those of Saigusa (1993), who studied Japanese populations of these species. We support his view of this group as being differentiated on the basis of ecological rather than morphological characters. A larva of *J. onoi* is seen in Fig. 3M.

Neozephyrus taxila (Bremer) (Fig. 1F and Fig. 2(2)). The study of Bremer's type material by Dubatolov and Sergeev (1987) showed that *N. taxila* is conspecific with *N. cognatus* (Staudinger), which then became a junior synonym. *Neozephyrus taxila* feeds on an oak, *Quercus mongolica* (Fagaceae). The egg (Fig. 5J) is laid next to the bud, the female preferring the side shoots. Hatching of the larva from the egg is synchronized with the opening of the bud. Thus it is likely that the fully formed larva overwinters inside the egg. The first instar larva molts on the inner side of the bud scales. The last instar larva (Fig. 3O) stays next to the bud area and phenotypically resembles the bud scales. Among congeners, this species appears earliest: the end of June. *Neozephyrus japonicus japonicus* (Butler) (Fig. 1G). The authors of the work in which the lectotype of *N. taxila* (Bremer) was designated (Dubatolov and Sergeev, 1987), proposed to apply the name *N. japonicus* to butterflies associated with species of *Alnus* (Betulaceae). While our purpose here is not to propose a taxonomic revision, and we cannot confirm the identity of these names, we can make these observations. To determine whether these taxa are good species, one would have to see their types, and preferably also compare modern samples of populations from their type localities. There is no firm evidence that the population we are dealing with in Primor'e belongs to this species, or even a single species. The eggs (Fig. 6N) were collected from several different species of *Alnus* and were mixed together. The later study of the structure of 150 eggs showed that all the eggs fall into one of two morphological groups, with almost no overlap. The adult butterflies are quite variable. Eggs are laid on different parts of the plant: shoots, buds, and old branches. That behavior is not typical for the group as a whole, for each species is usually very particular about the place in which the egg is laid by the female. All these facts suggest that there could be several sibling species involved in our samples. To determine that definitively, one would have to rear separately eggs of different ecotypes and compare populations of butterflies obtained from each ecotype. The larva in Fig. 3F was photographed on a cultivated species of *Alnus*. In nature, however, the shape of the larva is congruent to the shape of the leaf margin, a feature which is typical for all the larvae of the species in the group. The last instar larva rolls the leaf and spends most of the time inside the resulting tube. It pupates on the lower surface of the leaf, or inside the several tied-together leaves. Adults hatch at the end of July. They appear as the last species to fly in the group of green Theclinae in Primor'e.

Neozephyrus ultramarinus ultramarinus (Fixsen) (Fig. 2(1)). In Fig. 3B, one can observe the presence of sexual dimorphism in the larval stage: the female larva is darker than the male larva. Eggs are laid in the folds of the bark of thick branches of *Quercus dentata* (Fagaceae). Eggs (Fig. 5H) can be occasionally found on *Quercus mongolica* as well, especially in the areas where *Q. dentata* is absent. This is a typical case of "areal food plant" (a term proposed by Leonid Nikolaevskiy, pers. comm.). When a butterfly evolves together with its food plant, it acquires extreme ecological and biochemical compatibility with it. A new, closely related plant might subsequently move into the area. This new plant does not always become a new foodplant of our butterfly, even though its larvae are potentially capable of feeding on it. It might be used by a butterfly as an alternative source of

food in case of a crisis with the original foodplant population. A similar example of such an occurrence in North America would be the Schaus swallowtail (*Papilio aristodemus ponceanus* Schaus) (Papilionidae) in southern Florida. Butterflies of this species normally lay eggs only on torchwood (*Amyris elemifera*) (Rutaceae), which is rather rare in its usual hardwood hammock habitat. Larvae are capable of feeding on wild lime (*Zanthoxylum fagara*) (Rutaceae), present in the area in abundance. However, wild lime is utilized as a foodplant in nature only occasionally.

***Neozephyrus quercus* (Linnaeus)** (Fig. 1C and 4(4)). This species is found in the European part of Russia. The larva feeds on *Quercus robur* L. (Fagaceae); the female lays solitary eggs, usually in the corner formed by the union of the bud and the stem (Fig. 7I). The first instar larva bores into the bud, which is still closed. In later instars, the larvae (Fig. 8B) strongly resemble the scales of the bud and stay next to them. Flight period of adults varies geographically, but usually occurs in the second half of the summer. In the present work (see following), this species is compared with its eastern analogous species, *Neozephyrus saphirinus* (Staudinger).

***Neozephyrus saphirinus* (Staudinger)** (Fig. 1A) is very similar to *N. quercus* in appearance and biology (Fig. 2(3) and Fig. 3N). The food plant of *N. saphirinus* is *Quercus dentata* (Fagaceae), which leafs out two weeks after the leaf-sprouting of *Q. mongolica*, a species analogous in phenology to the food plant of *N. quercus* in Europe. So despite the morphological resemblance between the two butterfly species, *N. saphirinus* adults appear later in a particular season due to their association with the slower-leafing *Q. dentata*. The egg is shown in Fig. 5N.

***Neozephyrus aquamarinus* Dubatolov & Sergeev** (Fig. 1D). Eggs (Fig. 5N) were obtained from a live female and raised on European *Quercus robur* (Fagaceae). We have not seen type material of this species, so the identification of this species is ambiguous. The population of female adults obtained from our laboratory rearing is very close in appearance to *N. aquamarinus*. However, males are so unusual that they do not fit the description of any known taxa, including *N. aquamarinus*. Their genitalia, however, fit the description of *N. aquamarinus*. Under the laboratory conditions, females laid eggs primarily on the buds. First instar larvae are similar to other species of this group. The last instar larva (Fig. 3C) is dark grey, and most of the time this larval stage stays on thick branches, feeding only at night.

***Neozephyrus* sp.** This species is close to *Favonius macrocercus* Wakabayashi and Fukuda from Korea, but that species has not been found on the territory of Russia. Adults and immature stages of our population are significantly different. The discussion of the taxonomic status of this species will follow. Eggs were collected at the edge of the forest on large, 7-8m high, trees of *Quercus mongolica* (Fagaceae). The egg is shown in Fig. 6L.

***Chrysozephyrus brilliantinus* (Staudinger)**. The eggs are laid solitary on the flower buds of *Quercus mongolica* (Fagaceae) in the open areas and in the forest. The larva (Fig. 8C) of this species feeds on oak even though other Theclini species of this group (e.g., *C. smaragdinus*, *C. yoshikoeae*, *C. lineae*, and *C. gaoui*), are found on Rosaceae. *Chrysozephyrus brilliantinus*, described by Staudinger, was synonymized by Shirôzu and Yamamoto under the name *C. aurorinus* (Oberthür). *Chrysozephyrus aurorinus* was described from Oskold Island from a female,

which has red and blue patches on the front wings. No type specimens are known. The species described as *C. smaragdinus*, *C. brilliantinus* and *C. korshunovi* all fit the original description of *C. aurorinus*. Thus, *C. brilliantinus* is not even mentioned in Tuzov's (1993) list because its taxonomic status is not clear. In our opinion, it is a good species, whose name should be revived. ***Ussuriana michaelis michaelis* (Oberthür)**. Larvae feed on *Fraxinus rhynchophylla* Hance (Oleaceae). Eggs (Fig. 6E) were obtained under laboratory conditions. The female's ovipositor is twice as long as its abdomen and normally is hidden inside the abdomen. Before laying an egg, a female looks for a deep gap in the bark. She inserts her ovipositor into this cavity and lays an egg. The last instar larva of a Chinese population of this species is illustrated in Koiwaya (1993). We think that the population examined by Koiwaya is similar to our population. Adults fly at the end of July, feeding on Umbelliferae. Butterflies spend their non-feeding time in the canopy.

***Shirozua jonasi* (Janson)**. According to our observations, females lay eggs always on the ant paths on the trunk of *Quercus mongolica* (Fagaceae). Larvae of the last instar feed on aphids on leaves and branches. They are colored purple-brown and constantly are tended by ants. Placed in the cage together with larvae of other species of butterflies, however, the larvae of *Shirozua jonasi* attacked molting and sick individuals and consumed them. Adults hatch in the first ten days of August.

***Thecla betula crassa* Leech** (Fig. 1H and Fig. 4(1)). Larvae feed on *Prunus padus* L. and *Prunus spinosa* L. (Rosaceae) in the European part of Russia. Our population feeds on apricot, *Armeniaca manchurica* Maxim. (Rosaceae), and sometimes on *Prunus asiatica* Kom. Eggs (Fig. 5C) are laid solitary, or sometimes in pairs on the stem or at the branching point of young plants, or sometimes on the lower branches of the older trees. The larva comes out of the egg, as in most members of this group, in early spring and feeds on the leaves from just-opened buds. Later instars feed on the leaves, sitting on their upper surfaces. The mature larva (Fig. 3K) pupates in the litter on the ground. This species occurs all over Russia, but the subspecies *T. b. crassa* is restricted to the Amur and Ussuri districts.

***Thecla betulina* Staudinger** is similar to *T. betula* morphologically and biologically. The larva (Fig. 3E) feeds on *Malus manchurica* Maxim. (Rosaceae) and, starting from the second instar, rolls the leaf, forming a tube, inside which it spends most of the time. The larva pupates on the ground. Adults fly in August in the understory on the edge of the forest. Fig. 6J shows the egg.

***Artropoetes pryeri pryeri* Murray** lays eggs in groups of 3-5 on old shoots of 1-3m high *Syringa amurensis* Rupr. (Rosaceae). Adults fly in early July in open areas of the forest.

DISCUSSION OF EGG DIFFERENCES

In this review of a series of closely related Theclini species from the Primor'e region of Russian Far East, we found that the egg morphology is the most useful character for differentiating and grouping species. We used a Scanning Electron Microscope (SEM) to examine the egg surface and micropylar region in detail. The following similarities and differences were found.

Echinoid eggs, with sharp pointed spines and bearing aeropyles (Fig. 7A) on circular ribs, are found in the following species: *Neozephyrus quercus* (Fig. 5E, 0.85mm), *W. signata*

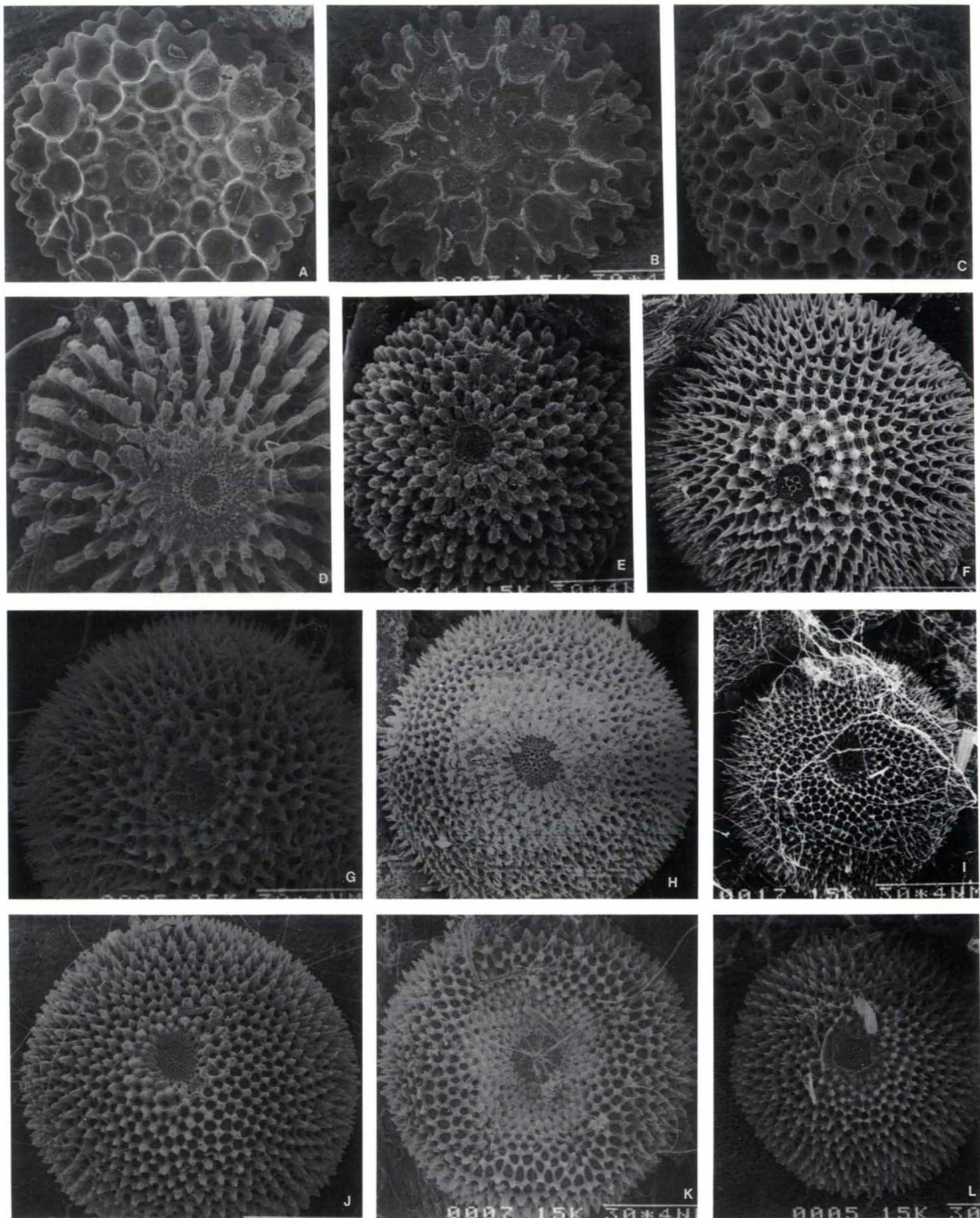


PLATE 5. Micrographs of eggs (magnification: 100x). (A) *Antigius butleri* Fenton; (B) *A. attilia* Bremer; (C) *Thecla betulae* L.; (D) *Chrysozephyrus brilliantinus* Staudinger; (E) *Neozephyrus quercus* L.; (F-G) *Wagimo signata quercivora* Staudinger; (H) *Neozephyrus ultramarinus* Fixsen; (I) *Strymonidia eximia* Fixsen; (J) *Neozephyrus taxila* Bremer; (K) *N. aquamarinus* Dubatolov & Sergeev; (L) *N. saphirinus* Staudinger.

(Fig. 5F, 0.95mm), *N. ultramarinus* (Fig. 5H, 0.89mm), *N. taxila* (Fig. 5J, 0.95mm), *N. aquamarinus* (Fig. 5K, 0.90mm), *N. saphirinus* (Fig. 5L, 0.75mm), *N. japonicus* (Fig. 6B, 0.70mm), and in the species nova of *Neozephyrus* (Fig. 6L, 0.90mm). In *N. quercus*, though, the spines are wider and less pointed. The micropyles of these eggs are 4, 5, or 6-petaled rosettes (Fig. 7E,F,G).

The closest in appearance to this group is the egg of *Chrysozephyrus brilliantinus* (Fig. 5D, 1.10mm). However, the tubercles there are not pointed. The micropylar area is a 6-petaled rosette situated in the crater, not porous and situated in the middle as in other species. The egg is larger than in other species. Cells are tetragonal in all of the above species.

In *Antigius athilia* (Fig. 5B, 0.87mm) and *A. butleri* (Fig. 5A, 0.85mm), tubercles become even wider and shorter, exposing rounded porous hexagonal cells (Fig. 7H). Eggs in these species are much flatter.

Absence of spines is observed in *Thecla betulae* (Fig. 5C, 0.90mm) and *Thecla betulina* (Fig. 6J, 1.0mm). The micropyle in *T. betulae* is a 3-petaled opening in the middle of the porous rosette, with pores hidden in the deep inclined pockets (Fig. 7C). Cells are hexagonal.

The egg of *Araragi enthea* is very distinct (Fig. 6C, 0.80mm). The chorion bears long tubercles with wide triangular tips, and with the aeropyle opening in the middle. The micropyle is a 6-petaled rosette with pores similar to those in *T. betulae* (Fig. 7B). Cells are hexagonal.

Egg of *Ussuriana michaelis* (Fig. 6E, 0.63mm) are spineless, with ribs and tetragonal porous cells. The micropyle is not distinct.

A similar, only larger egg, is found in *Fixsenia pruni* (Fig. 6F, 0.90mm). The egg of *F. herzi* (Fig. 6K, 0.93mm) is much more distinct, with candle-shaped tubercles on the cross-sections of the ribs, bearing aeropyles and a rosette-shaped micropyle. Cells are mostly triangular and highly porous.

The egg of *Japonica lutea* is spineless with hexagonal, highly porous cells (Fig. 6G, 0.93mm). The micropyle is a 5-petaled rosette.

Long and sharp spines found on the egg of *Strymonidia latior* are typical for this group (Allyn, 1984). Unlike eggs of *Neozephyrus*, *Strymonidia* eggs have high ribs with numerous sharp spines, which do not seem to bear aeropyles. Tetragonal cells are poreless. The micropyle is a 4-petaled rosette (Fig. 6D, 0.80mm).

The *Strymonidia eximia* (Fig. 5I, 0.63mm) egg is similar to the above, but has a 5-petaled rosette and shorter spines.

Eggs of *Strymonidia w-a. w-album* (Fig. 6H, 0.86mm) and *S. w-a. sutschani* (Fig. 6I, 0.86mm) are very distinct. The latter might be a good species, even based on this character alone. Both species' eggs have low ribs, with cell edges forming tetragonal ribs with low thin spines. The egg of *S. w-a. sutschani* is more rounded, with more distinct ribs, than in the European subspecies. The micropyle is a 5-petaled rosette.

DISCUSSION

The first attempt to use egg shape for systematics was by Doherty (1886). Unfortunately, his great collection was lost. His approach to systematics was unconventional for the time, when systematics was based entirely on adult morphology. The system

which he proposed on the basis of egg structure corresponds so well with modern systematics that it is almost inexplicable why egg structure is not commonly used in Lycaenidae systematics.

Doherty wrote: "When the ovation is studied, these genera fall into convenient groups, defined by constant and peculiar forms of eggs. I am aware that this classification is not likely to become a popular one: the student will always prefer to separate his genera by an artificial key based on venation. But that these groups of mine are natural ones, and indicate in most cases the truth of descent, I do not doubt."

Species studied in the present work fall nicely into three groups identified by Doherty:

1. *Arhopala* (eggs with tetragonal sculpture):

- a. semispheric egg with strongly developed spines: *S. ilicis*, *S. eximia*, *S. latior*, *N. taxila*, *N. japonicus*, *N. ultramarinus*, *N. quercus*, *N. saphirinus*, *N. aquamarinus*, *N. sp.*, *W. signata*, *C. brilliantinus*.
- b. disc-shaped egg with well developed ribs: *U. michaelis*, *S. w-album*.

2. *Aphnaeus/Loxura* (eggs with hexagonal sculpture)

- a. semispheric egg with well developed ribs: *A. attilia*, *A. butleri*, *A. enthea*, *T. betulae*, *T. betulina*.
- b. smooth, disc-shaped egg: *J. lutea*, *J. onoi*, *J. sapestriata*.

3. *Thecla* (trigonal or isometric hexagon): *S. jonasi*, *F. herzi*, *F. pruni*.

It seems remarkable that so many species are so similar in their life cycle. We found eggs of eight species of Theclini on a single tree of *Quercus mongolica*. This is an excellent example of a highly specialized community, in which every species is very well adapted to its particular niche. This excellent degree of adaptation can be seen in the oviposition preferences of every species, regarding the place where the egg is laid on the branch, as well as the distance from the ground of the branch chosen for oviposition.

The larval behavior is even more specialized, with the various taxa falling into distinct groups: larvae feed at night (*N. orientalis*) or during the day; larvae feed on the flowers (*W. signata*, *N. taxila*, *C. brilliantinus*, *N. orientalis*) or on the leaves (*A. attilia*, *A. butleri*, *J. lutea*); when feeding on the leaves, larvae occupy upperside (*T. betulae*, *F. pruni*, *S. ilicis*, *A. attilia*, *A. butleri*) or underside of the leaf (*J. lutea*); some larvae are associated with ants and aphids (*S. jonasi*), while others feed solitarily.

We lack detailed comparative information on the adult biology, but from what we have observed to date, there are certain particularities in the type of the forest in which each of the species is found, as well as in utilized nectar sources and the flight period.

ACKNOWLEDGMENTS

We would like to thank L. Nikolaevskiy for discussions of taxonomy and biology of the group and for providing us with valuable information; S. Sergeev, A. Chuvilin, V. Siniaev, and S. Kunitsin for help in collecting the eggs; V. Kononov for his help in our housing at Riazanovka; and U. Eitschberger and O. Gorbunov for their help in obtaining the literature. Christine M. Eliazar kindly prepared revisions of the manuscript. This research and its publication was supported by the Lepidoptera Research Fund of the University of Florida Foundation.

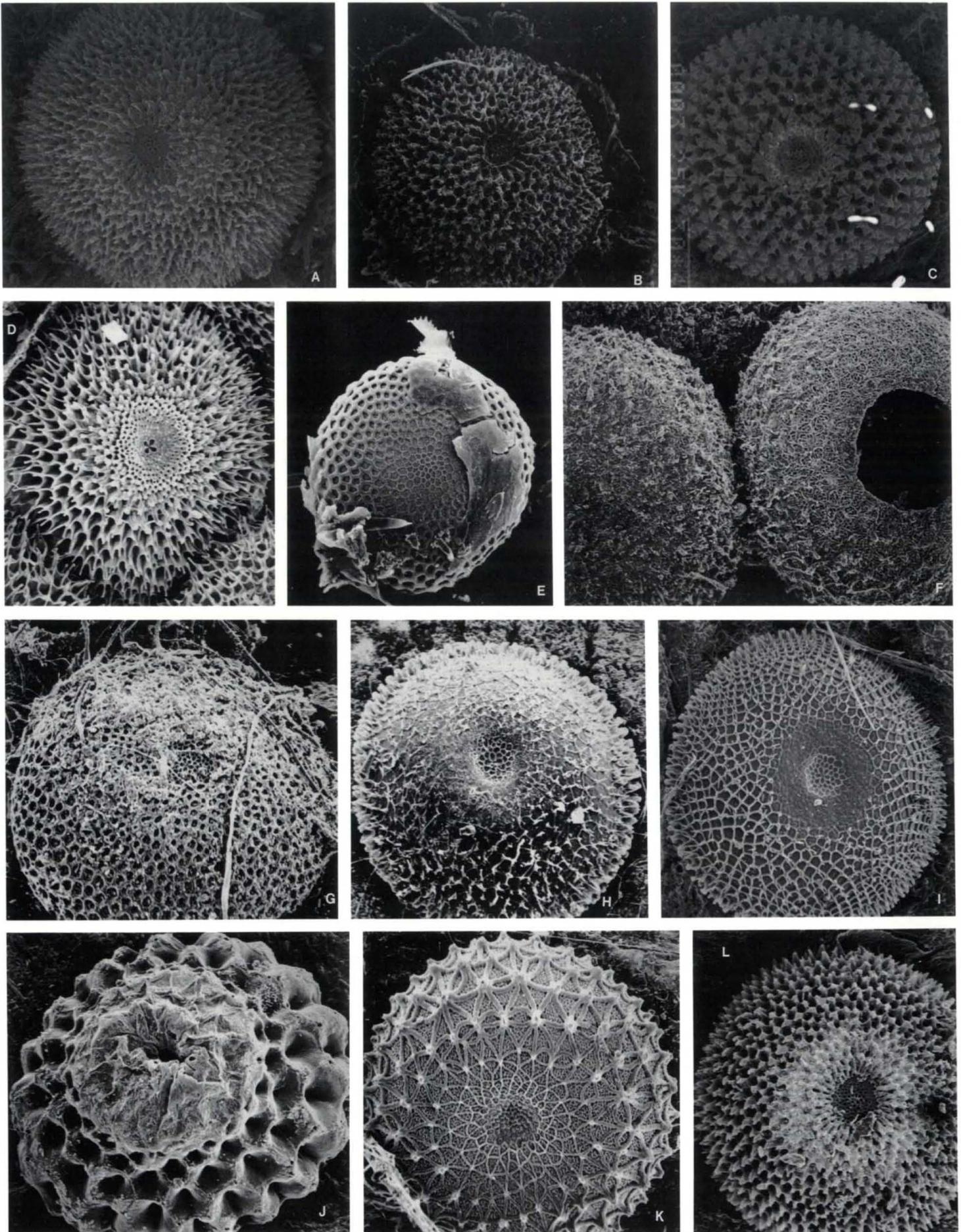


PLATE 6. Micrographs of eggs (magnification: 100x). (A) *Neozephyrus ultramarinus* Fixsen; (B) *N. japonicus regina* Butler; (C) *Araragi enthea* Janson; (D) *Strymonidia latior* Fixsen; (E) *Ussuriana michaelis* Oberthür; (F) *Fixsenia pruni* L.; (G) *Japonica lutea* Hewitson; (H) *Strymonidia w-a. w-album* Knoch; (I) *S. w-a. sutschani* Tutt; (J) *Thecla betulina* Staudinger; (K) *Fixsenia herzi* Fixsen; (L) *Neozephyrus* sp.

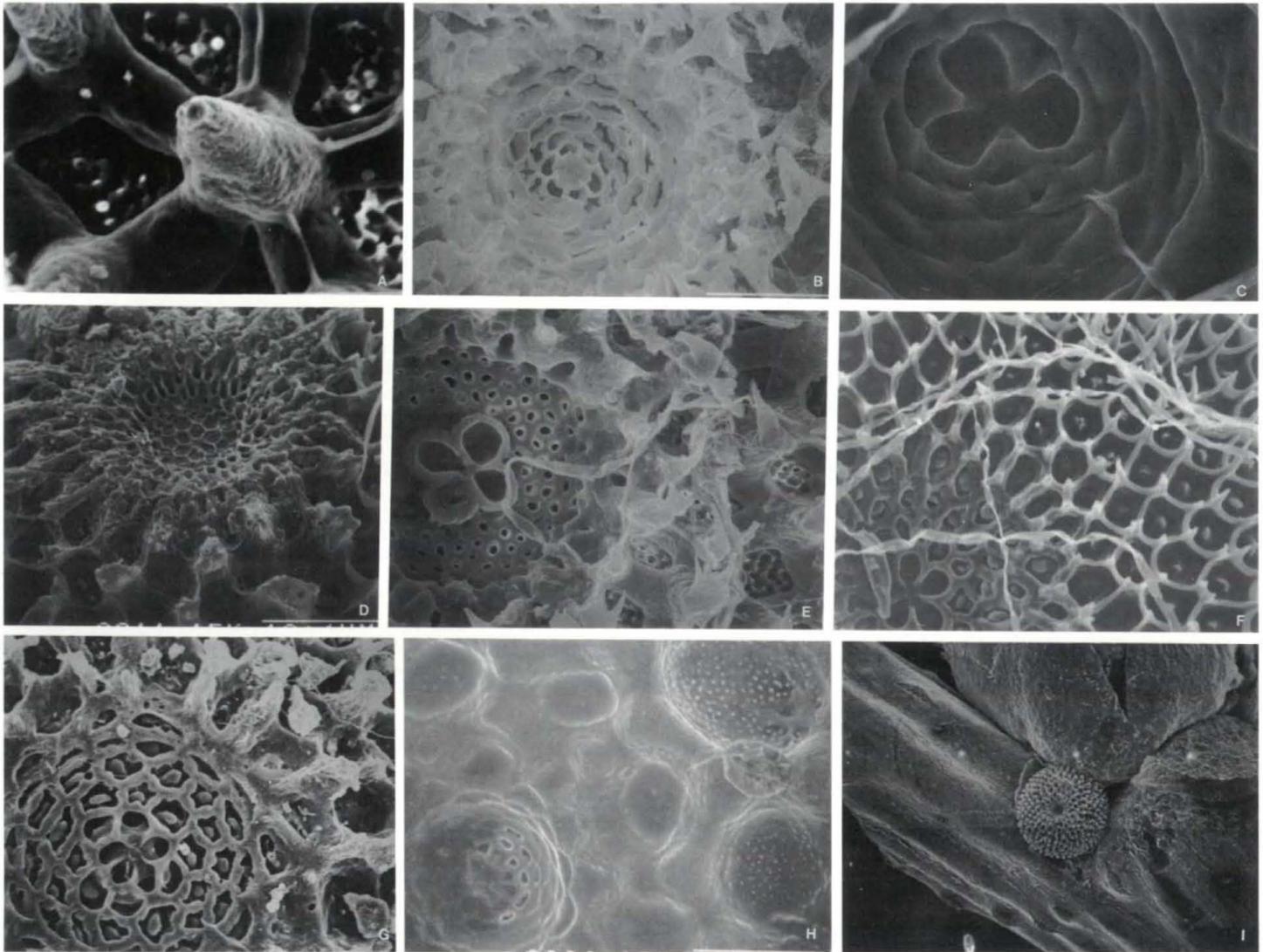


PLATE 7. (A) Aeropyle bearing spine on the egg of *Wagimo signata*; (B) *Araragi enthea*, micropylar area of the egg; (C) *Thecla betulae*, micropyle; (D) *Chrysozephyrus brilliantinus*, micropyle; (E) *Wagimo signata*, micropyle; (F) *Strymonidia eximia*, micropyle; (H) *Antigius butleri*, micropyle; (I) The egg of *Neozephyrus quercus* is laid at the bases of the bud.

LITERATURE CITED

- Bremer, O.**
 1861. Neue Lepidopteren aus Ost-Sibirien und des Amur-Lande, gesammelt von Radde und Maak, beschrieben von Otto Bremer. *Bull. Sci. Petersburg*, 3(7):461-469.
 1864. Lepidopteren Ost-Sibirien, insbesondere des Amur-Lande, gesammelt von den Herren G. Radde, R. Maack, und P. Wulflus. *Mem. As. Sci. Petersburg*, (7) 8(1):103.
- Doherty, W.**
 1886. A list of butterflies taken in Kumaon. *J. Asiat. Soc. Bengal* (Calcutta), 55:103-140.
 1889. On certain Lycaenidae from Lower Tenasserum. *J. Asiat. Soc. Bengal* (Calcutta), 58:409-440.
- Dubatolov, V. V., and M. G. Sergeev**
 1982. New Lycaenidae of the tribe Theclini (Lepidoptera, Lycaenidae) from the fauna of U.S.S.R. *Rev. Ent. USSR* (Moscow), 61:375-381. [In Russian]
 1987. On the systematics of blues of the genus *Neozephyrus* Sibatani et Itô (Lepidoptera: Lycaenidae). In *New and poorly known species of Siberian fauna*, 18-30. Novosibirsk. [In Russian]
- Ehrlich, P. R.**
 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Kansas Univ. Sci. Bull.* (Lawrence), 39(8):305-370.
- Fixsen, C.**
 1887. Lepidoptera aus Korea. *Mem. Lepid. Romanoff* (St. Petersburg), 3:233-356, pls. 13-15.
- Graeser, L.**
 1888-93. Beiträge zur Kenntnis der Lepidopteren Fauna des Amurgebietes. *Berliner Ent. Zeit.*, 32:33-153; 33:251-268; 35:71-84; 37:209-234.
- Hemming, F.**
 1967. The general names of the butterflies and their type-species (Lepidoptera: Rhopalocera). *Bull. Brit. Mus. Nat. Hist. (Ent.)* (London), Suppl. 9:1-509.
- Higgins, L. G., and N. D. Riley**
 1970. *A Field Guide to the Butterflies of England and Europe*. London: Collins. 256pp.
- Howarth T. G.**
 1967. A revision of the genus *Neozephyrus* Sibatani and Itô (Lepidoptera: Lycaenidae). *Bull. Brit. Mus. (Nat. Hist.) Ent.* (London), 5:233-272.



PLATE 8. Last instar larvae: (A) *Neozephyrus ultramarinus* Fixsen; (B) *N. quercus* L.; (C) *Chrysozephyrus brilliantinus* Staudinger; (D) *N. saphirinus* Staudinger; (E) *N. taxila* Bremer; (F) *Antigius attilia* Bremer; (G) *Wagimo signata quercivora* Staudinger.

Janson, O. E.

1878. Remarks on Japanese Rhopalocera, with descriptions of new species. *Cist. Ent.* (Berlin), 2):269-274.

Koiwaya, S.

1993. *Studies of Chinese Butterflies*. Vol. 2. Tokyo. 230pp.

Kurentsov, A. I.

1970. *Butterflies of the Far East*. Moscow: Acad. Sci. U.S.S.R. 163pp.

Leech, J. H.

1893-94. *Butterflies from China, Japan and Corea., Part II: Lycaenidae, Papilionidae, and Hesperidae*. London. Pp. 369-393.

Murayama, S.

1978. Some butterflies from Ussuri, U.S.S.R., and Korea, with description of new species. *Tyô to Ga* (Osaka), 29:159-163.

Oberthür, C.

1880. Fauna des Lepidopteres de l'île Askold. *Études Ent.* (Rennes), 5:11-88.

Pryer, H.

1886-88. *Rhopalocera Nihonica: A Description of the Butterflies of Japan*. Part II. p. 13-15. Yokohama.

Riley, N. D.

1921. Some undescribed Rhopalocera from Mesopotamia and N. W. Persia and other notes. *Ann. Mag. Nat. Hist.* (London), 9(8): 591-600.

1939. Notes on Oriental Theclinae (Lep. Lycaenidae) with descriptions of new species. *Novit. Zool.* (Tring), 41:357.

1958. The genera of Holarctic Theclinae: a tentative revision. *Proc. 10th Internat. Congr. Ent., Montreal*, 1:281-288.

Saigusa, T.

1993. *Zephyrus Research*. No. 1 (March 5):1-22.

Scott, A. J.

1986. *The Butterflies of North America*. Stanford: Stanford Univ. Pr. 583pp.

Shirôzu, T., and H. Yamamoto

1956. A generic revision and the phylogeny of the tribe Theclini (Lepidoptera: Lycaenidae). *Sieboldia* (Fukuoka), 1(4):329-421.

Sibatani, A.

1992. Observations on the period of active flight in males of *Favonius* (Lycaenidae) in South Primorie, the Russian Federation. *Tyô To Ga* (Osaka), 43:23-34.

Sibatani, A., and S. Itô

1942. Beitrag zur Systematic der Theclinae im Kaiserreich Japan unter besonderer Berücksichtigung der sogenannten Gattung *Zephyrus* (Lepidoptera: Lycaenidae). *Tenthredo* (Kyoto), 3:318-328.

Shin, Y. H.

1970. Life history of *Ussuriana michaelis* Oberthür in Korea. *Tyô To Ga* (Osaka), 21:15-16.

Tuzov, V. K.

1993. *The Synonymic List of Butterflies from the ex-U.S.S.R.* Moscow: Rosagroservice. 73pp.

Yokoyama, M., and M. Wakabayashi

1967. *Colored Illustration of the Butterflies of Japan*. Osaka: Hoikusha. 178pp.