The solitary population wave, a physical phenomenon accompanying the introduction of a chrysomelid

Oleg V. Kovalev

Laboratory of Biosystematic Bases of Beneficial Organism Introduction, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia

Introduction

When working in the Northern Caucasus on the introduction and acclimatization of the North American *Zygogramma suturalis* F. (Chrysomelinae) imported to the Old World as a biological control agent against the common ragweed *Ambrosia artemisiifolia* L. (Asteraceae), we discovered an undescribed phenomenon – the formation of a stable undampened wave of the high population density, which spreads without changing its shape and with a constant velocity. In a previous paper (Kovalev & Vechernin 1986, 1989), we proposed a mathematical model of this phenomenon and coined the term 'solitary population wave' (SPW). The SPW can be characterized by an enormous concentration of adult insects (up to 5000 beetles or more per square meter) within a narrow zone (Figs. 1 to 3). As this SPW advances, it causes 100% extermination of the ragweed, which also follows from the mathematical model. The wave velocity is up to three meters per 24 hours. In our case, the stable high density of the SPW (tens of millions of beetles per several hundred hectares) led to the temporary suppression of the nidi[1] of the ragweed, the decrease of the stock of ragweed seeds in the soil, and the increase in the abundance of some crops. For instance, about ten million beetles were concentrated within the wave in an 80-hectare sainfoin field *C* (Fig. 3). The wave front was 1.5 km in length, while the number of beetles amounted to 5300 per one meter of the front. The wave was in motion until the insects remained within the wave zone. Such
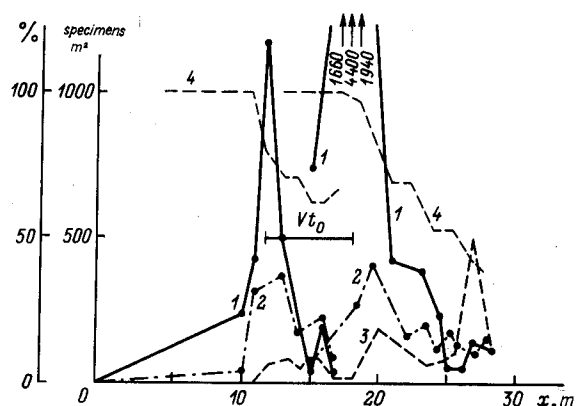

Fig. 1. Detailed structure of the SPW of *Zygogramma suturalis*. The position of the SPW as of July 4th and 6th, 1985 (based on the experimental observations on the sainfoin field *B*, see Fig. 2). $t_s = 48$ hours, which corresponds to the wave velocity (V) of about three meters per 24 hours. *Axis of abscissa:* the distance from the control point (measured perpendicularly to the wave front); *ordinate axes: left,* reduction of the common ragweed; *right,* the number of beetles per a square meter. *1.* SPW of beetles; *2.* density of the larvae involved in the SPW; *3.* density of eggs in this area; *4.* reduction of the common ragwed. *Arrows with numbers:* number of beetles in the SPW (after Kovalev & Vechernin, 1986)

a wave process in the ecosystem was not previously known in the biology of populations.

Paradoxically, the insects participating in such a wave, change their behavior dramatically and tend not to leave the SPW even during enormous population densities or severe food shortages. The be-

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[1]Merriam-Webster defines *nidus* as "1: a nest or breeding place; especially: a place or substance in an animal or plant where bacteria or other organisms lodge and multiply; 2: a place where something originates, develops, or is located." By nidi (plural from singular nidus) we mean hereafter the stable groups of the adventive plants blocking the process of succession in the areas of their invasion (including the adventive species capable of formation of a dense coverage of the surface of the freshwater reservoirs).

Address for correspondence: Oleg V. Kovalev, Laboratory of Biosystematic Bases of Beneficial Organism Introduction, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, 199034, Russia. *Email:* kovalev@ok11495.spb.edu
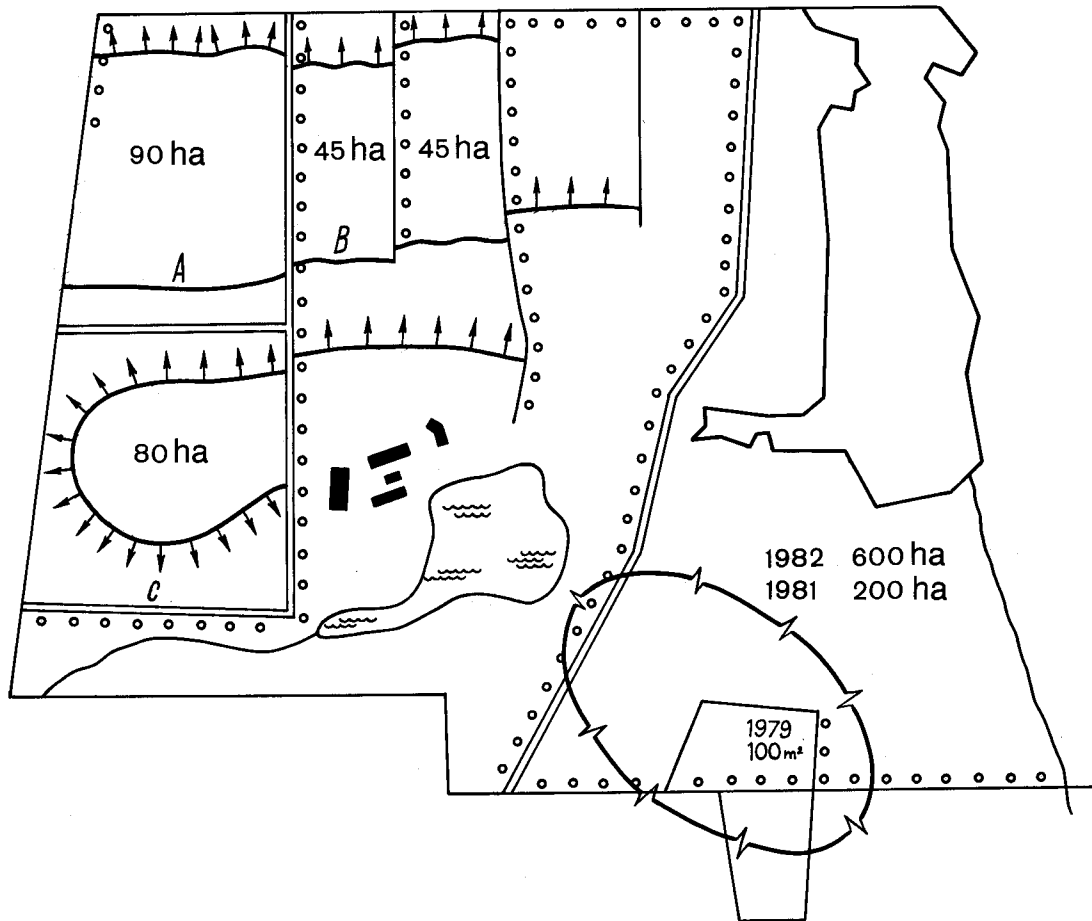
Fig. 2. Formation and advancement of the SPW of *Z. suturalis* in the fields of the farm 'Pelagiadskii' (Stavropol region, Northern Caucasus) in which the common ragweed, *Ambrosia artemisiifolia*, is growing. *A.* alfalfa (90 hectares); *B.* sainfoin (45 hectares); *C.* sainfoin (80 hectares). The wave front as of June 15th, 1985. *Oval:* extension of the territory occupied by *Z. suturalis*, released in 1978, by 1981 (200 hectares). *Arrows:* direction of the spread of the SPW (after Kovalev, 1989a).
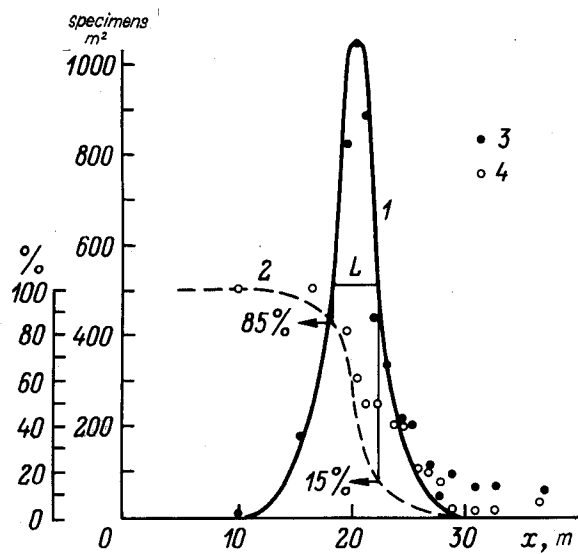

Fig. 3. Solitary population wave of *Z. suturalis* (1, 3) and the induced wave of the reduction of the common ragweed (2, 4): 1, 2. theoretical estimate based on the model; 3, 4. results of the experimental observations on the sainfoin field *C* (see Fig. 2) on June 9th, 1985. *Axis of abscissa:* distance from the control point (measured perpendicularly to the wave front); *ordinate axes:* left, reduction of the common ragweed; *right,* number of beetles per square meter; *L,* width of the wave (after Kovalev & Vechernin, 1986).

havior of insects forming the SPW in the terrestrial and freshwater ecosystems follows the same scenario as that of the ordered wave structures generated spontaneously according to the laws of physics for self-organization. In the physics, chemical, and biological media, such nearly undampened bunches of energy can be described by using a mathematical model of the *autosolitons* – the waves that resemble particles in their behavior (Kerner & Osipov, 1991). The most similar phenomenon is the autowave of fire, which causes the 'burning out' of the food resource, an irreversible change in the environment by the total extermination of the food plant. Just as it is in the case of the formation of the solitons, an initial impulse of supercritical amplitude is needed to provoke the SPW. For the spread of insects by means of an SPW, the density of the population has to reach some critical level to provide the necessary quantity of insects per meter of width of the wave front.

The formation of an SPW frequently accompanies the introduction of beneficial phytophagous insects to new continents and, in my opinion, some of the most efficient campaigns against adventive weeds owe their success to the efficiency of the SPW. The formation of an SPW has not yet been studied

by entomologists. The formation of an SPW in the homeland of these insects is not possible. The formation of an SPW most frequently accompanies the introduction of chrysomelids, it is less frequent in Curculionoidea, and very rare in other insect orders.

Formation of solitary population waves accompanying the introduction of chrysomelids

Exotic species of Chrysolina and their target, klamath weed or Saint John's wort, Hypericum perforatum

We found the most impressive formation of an SPW in an outstanding campaign aimed at the suppression of *Hypericum perforatum* L. (Clusiaceae) in North and South America, Australia, New Zealand, and the Republic of South Africa with the aid of species of *Chrysolina* (Chrysomelinae) introduced from Europe (Huffaker, 1957, 1967; Harris *et al.*, 1969; Julien & Griffiths, 1998). The most efficient species *C. quadrigemina* (Suffrian) managed "to depress weed density by approximately 99%" (Julien & Griffts, 1998). Within the limits of the ancestral distribution area in the Old World, these species never reach such population densities and never experience such explosions in mass reproduction. However, entomologists not only did not study the phenomenon of the SPW in detail, but also they did not even notice the unusual features of the biological processes, even though an extremely high concentration of insects, analogous to the SPW in the ragweed nidi, was sometimes shown in photographs and diagrams. The first photograph in which an SPW can be identified was published by Huffaker (1957) to illustrate the spread of *C. quadrigemina* (= *gemellata*) in California. The characteristic constancy of the SPW shape can clearly be seen in the photograph: the insects do not leave the wave front despite the food shortage within the moving SPW.

The similarity in the dynamics of growth of the population density in the SPW of *C. quadrigemina* in California and of *Z. suturalis* in the Northern Caucasus can easily be seen. Huffaker (1967) notes: "By the fourth year, almost complete destruction over a distance of one mile occurred and not a single living plant could be found within a quarter mile of the original release site". In the fourth year of acclimatization, the area of the SPW of *Z. suturalis* in the Northern Caucasus comprised 200 hectares, and the common ragweed was totally exterminated (Fig. 2).

Exotic Agasicles hygrophila and their target, alligator weed, Alternanthera philoxeroides

The formation of an SPW can be very efficient in the case of the spread of chrysomelids in aquatic habitats. *A. hygrophila* Selman et Vogt was successfully introduced into Australia, New Zealand, Thailand, and the USA to control the South American *Alternanthera philoxeroides* (Martius) Grisenbach (Amaranthaceae) (Julien, 1981, 1987). In Australia,

the species "quickly established and spread rapidly throughout the aquatic habitat. Substantial reduction in the area of floating mats occurred within 14 months of release"(Julien, 1987). It should be noted that the details of the formation of the SPW in the aquatic habitat are identical to those in the terrestrial ecosystems.

European species of Galerucella and their target weed, purple loosestrife, Lythrum salicaria

Galerucella calmariensis L. and *G. pusilla* Duftschmidt were released as classical biological control agents against the Eurasian *Lythrum salicaria* (Lythraceae) in Canada and the USA (Julien & Griffits, 1998). It was not until this case that entomologists (Corrigan *et al.,* 1998) noticed the formation of an SPW accompanying the spread of insects, referring to our work (Kovalev 1990a). Unfortunately, the use of the term 'waves' instead of 'SPW' is unsatisfactory because it lacks the necessary information. The formation of an SPW is accompanied by the growth of "Extremely large populations of beetles (>500 egg masses/m^2) with up to 95% reduction in flower density and 90% reduction in stand density" (Corrigan *et al.*, 1998; Julien & Griffits, 1998).

Therefore, reduction of the food plant by up to 90% or higher in an SPW is a characteristic feature of the phenomenon and follows from the mathematical model of the process (Kovalev & Vechernin, 1986). Why then is the phenomenon of an SPW so infrequent, only taking place sporadically?

Regularities in the formation of an SPW in ecosystems

While the autowave-like processes in the population structures only remain in the life cycles of lower organisms (bacteria, amoebae, Myxomycetes, etc.), the SPW phenomenon in higher organisms was only discovered during the course of the purposeful importation of an infrageneric oligophage (Kovalev, 1995a) (an insect of which the range of food plants is restricted to a single genus) into the population of an adventive weed. It should be noted that all the representatives of the co-evolutionary 'insect-plant' system found in the SPW belonged to phylogenetically young taxa (Kovalev, 1992), leaf beetles from the subfamilies Chrysomelinae and Galerucinae, in particular. All adventive weeds are apoplast herbaceous plants, 'Neogene herbs' (Kovalev, 2000). Such aggressive weeds are able to block the process of succession in ecosystems disturbed by humans (Kovalev, 1995b). The homogenous structure of the phytocoenose of the dominating food plant is a necessary precondition for the formation of an SPW. The formation of an SPW during the introduction of *Ch. quadrigemina* to the pastures of California dominated by *Hypericum perforatum,* was so effi-

cient exactly because the cattle homogenized the coenotic structure of the herbage. Likewise, the adventive weeds invading freshwater reservoirs (*e.g.*, alligator weed) form homogenous floating mats that allow the rapid formation of an SPW in the case of the successful introduction of *A. hygrophila*.

The study of SPWs is interdisciplinary. The regularity of the manifestation of SPWs constitutes a phenomenon of nonlinear physics. Unfortunately, entomologists consider these processes as unusual population states. In the English translation of our paper (Kovalev & Vechernin, 1986) by Scripta Technica, the term "solitary population waves", reflecting the peculiarities of the nonlinear processes, was replaced by a new term, "isolated population waves". The use of the necessary theoretical approaches to study SPWs could be of practical importance, because they could artificially create the conditions favorable for the formation of an SPW in the course of the introduction of chrysomelids.

Homogenous coenotic structure of adventive weeds

The conditions for the formation of an SPW are rarely favorable in disturbed ecosysems, even when one weed dominates. Such favorable conditions can be created in special testing areas.

In order to provoke the formation of an SPW in a population of *Z. suturalis* in the Northern Caucasus, the soil in the testing area was cultivated several times before the necessary density of a pure stock of the common ragweed (10,000-12,000 young plants per square meter) was achieved. The velocity of an SPW depends on the density of beetles per meter of the wave front. For example, if the density of the common ragweed is 200 g/m² and the density of the beetles 1000 beetles per 1 m, then the velocity of the SPW is only 0.1 m per 24 hours, which makes it look as if the SPW does not advance at all. The maximum SPW velocity reported for *Z. suturalis* is 3 m per 24 hours. When the areas of *Z. suturalis* concentration were destroyed, the conditions for the formation of an SPW were no longer favorable, and the population structure returned to a state of low density. A small area of concentration (four hectares) allowed an SPW to form in the agrocoenoses, even in a vast area of 300,000 hectares.

Peculiarities regarding the reduction of the food source in an SPW

Perhaps the most unusual regularity connected with the formation of an SPW is the peculiarity regarding the reduction of the food source: the wave only moves after the complete elimination and death of the plants within the wave structure. For example, the large plants (1.5 m) of the common ragweed, *Ambrosia artemisiifolia* (Asteraceae), survived by exuding cell juice from the tips of shoots, even after the leaves had been completely reduced by the beetles. The beetles stood on the plant until the death

of the latter and did not attempt to move to plants whose leaves were intact, and which were situated along the front of the wave (Fig. 5). No such behavior has been described in the literature dealing with the mass reproduction of phytophages. These regularities can be explained by the general laws of the spread of autosolitons (Kerner & Osipov, 1991). Such 'population waves' could well have a catastrophic effect on ecosystems. Therefore, selection supports mechanisms that prevent the formation of conditions that are favorable for the formation of an SPW (Kovalev, 1990, 2002).

Influence of an SPW on the dynamics of vegetation

A characteristic of an SPW is the constant shape and velocity that the wave maintains for a relatively short phase of the lifecycle of the chrysomelid. Although the SPW 'blurs' when egg-laying females emerge, the migrating beetles and, later, larvae (Huffaker, 1967) strongly influence the dynamics of the vegetation. The process of succession enhances the efficiency of the chrysomelid in weakening the domination of the adventive weed. For example, within the SPW zone of *Z. suturalis* in the Northern Caucasus, the first and second stages of succession took place within the same period as that in North America (Kovalev *et al.,* 1989). In the spring, when the density of the hibernating beetles was low, in areas of the SPW young plants of the common ragweed *(Ambrosia artemisiifolia)* only died within reach of the 'phytogenic field' around young plants of weeds in the first stage of succession. In May, the extermination rate reached 64% in young plants of the common ragweed under an average density of three beetles per square meter, and 80%, under the maximum observed density of nine beetles per square meter (Kovalev *et al.,* 1989). In this territory, a special role in the change of the vegetation in the first stage of succession was played by *Conyza canadensis* (L.) Cronq. (Asteraceae), the most widely distributed companion of the common ragweed in its homeland, North America (Kovalev & Onosovskaya, 1989). Within the SPW area of *Z. suturalis*, the course of succession, which existed before the advent of *Ambrosia*, has normalized again (Fig. 4; Kovalev *et al.*, 1989).

Possibilities regarding the widening of the host range of an agent in an SPW

During the past few years, there has been a tendency not to limit the circle of potential biocontrol agents to infrageneric oligophages. Instead, nowadays, the circle includes infratribal oligophages, which feed on several genera of plants (Kovalev, 1995a). This is probably based on the assumption that species not change the co-evolutionary connections developed within the ancestral distribution area. We suggested that these strategies can be changed (Kovalev, 1995a). For example, *Z. suturalis* is an infrageneric
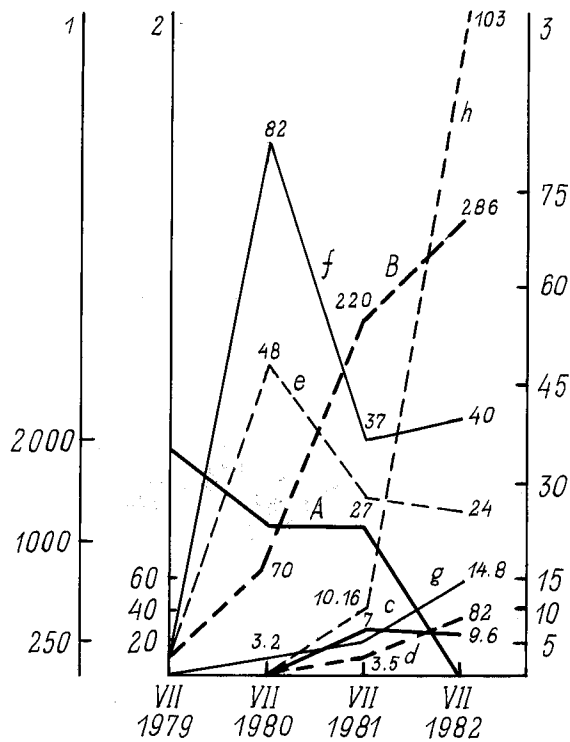
Fig. 4. Dynamics of the vegetation within the zone of the SPW of Z. suturalis in the Northern Caucasus. A. Ambrosia artemisiifolia; B. Zygogramma suturalis; C. Cirsium arvense (L.) Scop.; D. Hypericum perforatum L.; E. Chenopodium album L.; F. Conyza canadensis (L.) Cronq.; G. Daucus carota L.; H. Elytrigia repens (L.) Nevski. Ordinate axis: 1. common ragweed; 2. Zygogramma suturalis; 3. other plants (natural logarithm); axis of abscissa: registration time (after Kovalev & Onosovskaya, 1989).

oligophage with a limited range of food plants – A. artemisiifolia and A. maritima L. (=psilostachya DC). Within the area occupied by the SPW of Z. suturalis in the Northern Caucasus, the association of the adventive weed Iva xanthiifolia (Nutt.) Fresen. (Asteraceae), represented by large plants (70-150 cm), has been totally exterminated. Naturally, this could not happen within the ancestral distribution area of the phytophage and the plant in the New World, even though both Ambrosia and Iva belong to the tribe Heliantheae. After the beetles had fed on I. xanthiifolia, they ceased to lay eggs, because the sesquiterpene lactones of all Asteraceae, except Ambrosia, act upon Z. suturalis as juvenoids, analogues of the juvenile hormone of insects. This is the basis for the formation of an infrageneric oligophagy in this coevolutionary system. A different situation may take place in the case of the infratribal oligophages, which are capable of widening the range of food plants under experimental conditions. It should be taken into account that, as a result of selection, the cultivated forms of Helianthus annuus (Asteraceae) lose the protective properties of the sesquiterpene lactones.

Unusual variation of the phenotype of Z. suturalis in the SPW

During the formation of the SPW of Z. suturalis, an unusual variation of the color pattern has been reported (Figs. 6 to 35), including melanistic forms (Figs. 15 to 23, and 25) which do not occur even in other species of the genus (Kovalev & Medvedev,


Fig. 5. Peculiarities of the distribution of Z. suturalis on Ambrosia artemisiifolia plants within the solitary population wave in the Northern Caucasus (after Kovalev & Vechernin, 1986).
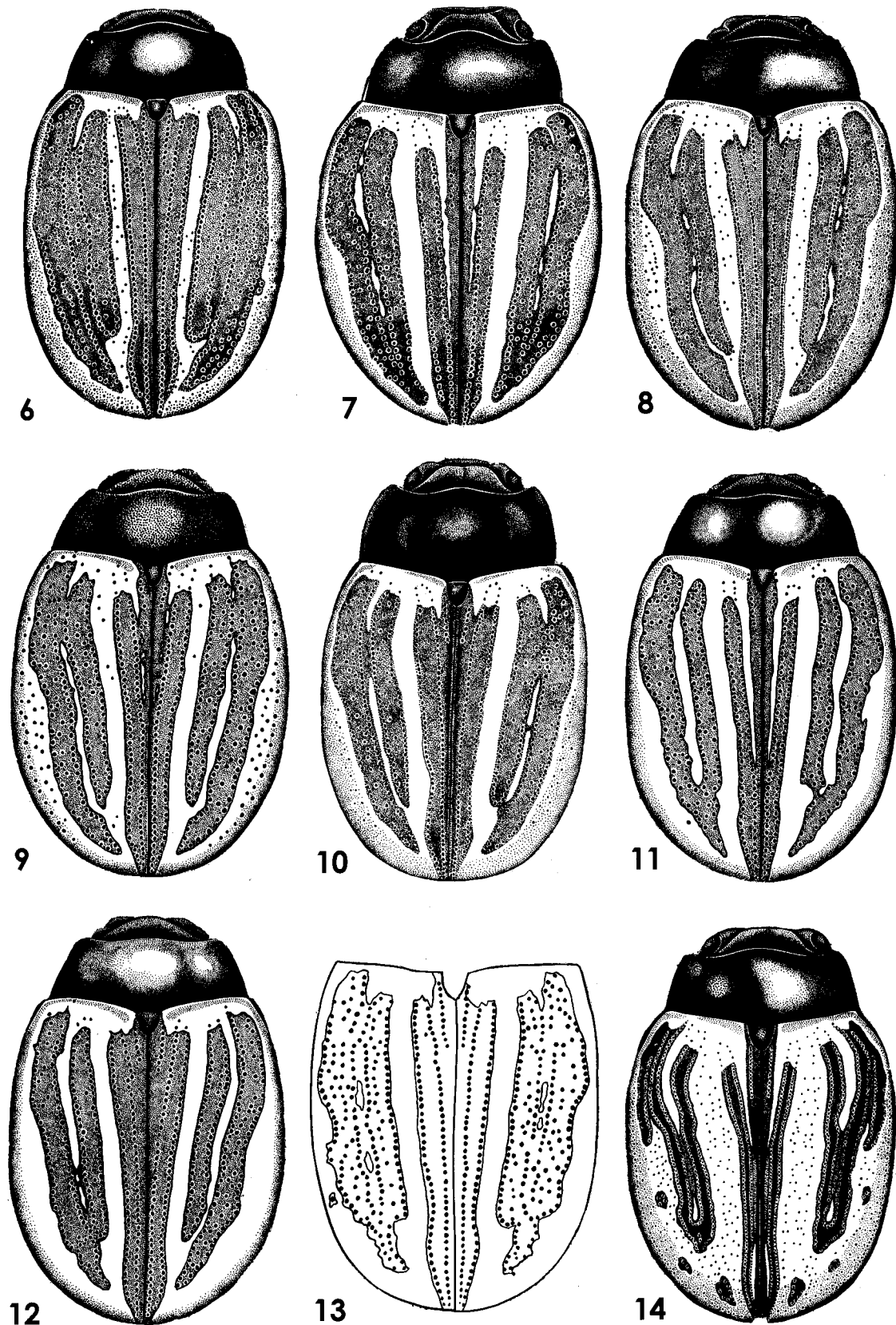
Figs. 6 to 13. Variations in *Z. suturalis* from the SPW in the Northern Caucasus.
Fig. 14. Zygogramma disrupta Rogers (after Kovalev, 1989b).

1983). The role of the tracheae in this variation is clearly visible (Fig. 24). The unbroken series of gradual melanization (Figs. 6 to 14) ends with the complete melanization of the cuticle (Fig. 25). All

this happens within an area of several thousand hectares occupied by the SPW of *Z. suturalis* in the Northern Caucasus. The complete melanization of the cuticule of *Z. suturalis* is so unusual for the genus
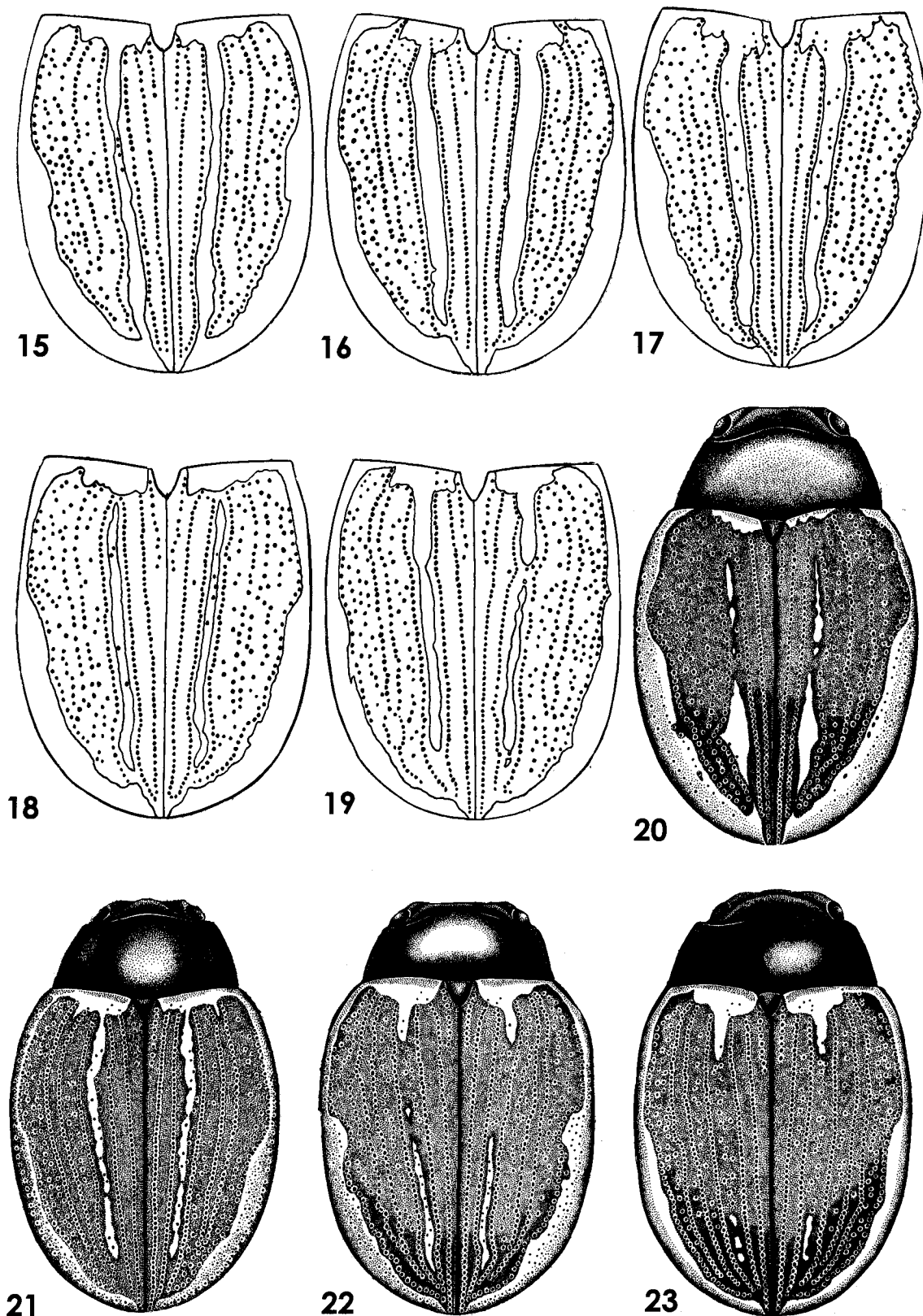
Figs. 15 to 23. Unbroken variation series of growing melanization in *Z. suturalis* from the SPW (after Kovalev, 1989b).

that a taxonomist could easily establish a new taxon if he was not aware of the circumstances under which these melanistic forms came into existence.

In North America, the homeland of *Z. suturalis,* we did not find any remarkable variations in this character, but in eleven States of the USA we found a stable frequency of the dominant alleles within the distribution areas of two very similar subspecies, *Z. s. suturalis* and *Z. s. casta* Rogers. Moreover, in museum collections examined, no specimens showing variations in these characteristics were found. At the same time, we discovered all forms of varia-
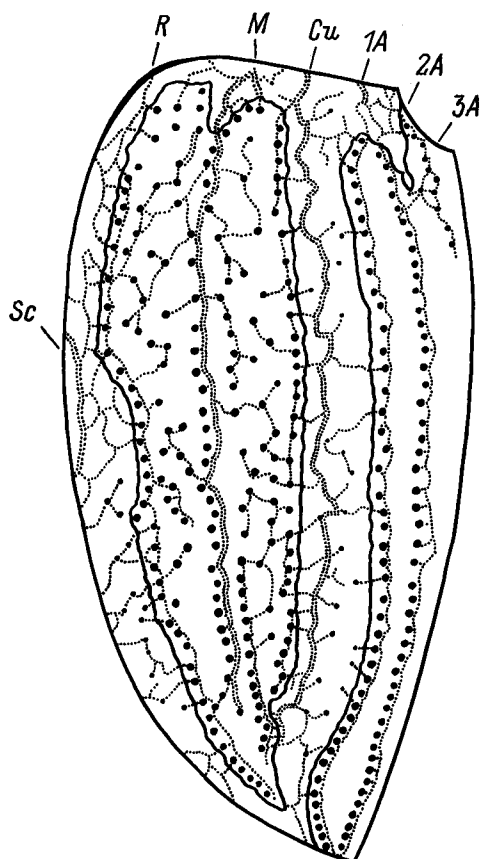
Fig. 24. Trachaeation of the elytrae in Z. suturalis and homologies of the wing venation. The outline of the sutural and marginal melanine stripes are indicated by the solid line (after Kovalev, 1989b).

Fig. 25. Melanistic form of Z. suturalis from the SPW (after Kovalev, 1989b).

tions characteristic for both subspecies represented by a single series of variations within the zone of the SPW of Z. suturalis in the Northern Caucasus (Figs. 6 to 14).

Even though Z. s. casta only differs from the nominative subspecies by the brighter color of the external longitudinal stripe of the elytrae, the frequency of these alleles remains stable throughout the whole distribution areas of each of the two subspecies. The cause of such an isolation of the subspecies could be very simple: the radius of the reproductive activity of the beetle is very small.

We have also discovered another phenomenon: the development of flight in a species, which, in its home country, lacked the ability to fly. The formation of 'flyers' had only taken place under the high population density stress within the SPW, when 'pedestrians' were completely replaced by 'flyers'. Now all populations of Z. suturalis in the palaearctics – from the south of Europe (Croatia, Serbia, and, probably, Italy) to the far eastern areas of Russia and China – possess the ability to fly. We have not found any other examples of such an extreme variation in phenotype in the many known cases of biological invasion described for very different taxa (Hengeveld, 1989).

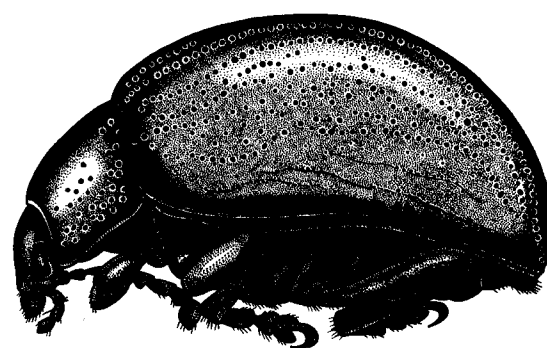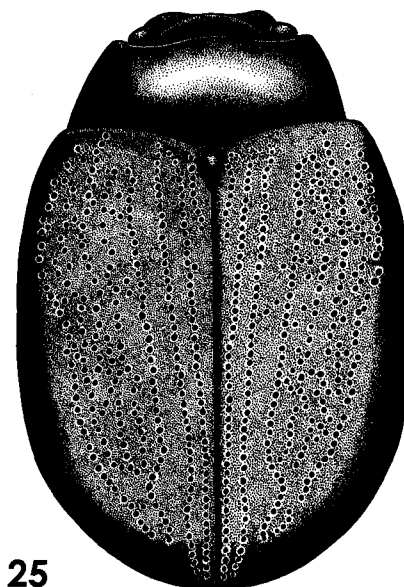The uniqueness of the processes that take place

within an SPW is connected, in the first place, with population inbreeding: a small introduced population reproduces under the stress of enormous density, when the egg-laying females change their behavior and cannot leave the SPW zone.

The melanin system of Zygogramma suturalis lacks the pigments of a different nature, and, given the many functions for which this pigment is responsible, the indicatory function of this pigment becomes very important. The areas of formation of the SPW in the Northern Caucasus thus turned out to be a unique location for the study of micro-evolution.

Zygogramma s. volatus.

A separate subspecies, Z. suturalis volatus Kovalev (Kovalev, 2002), has been established for the new intraspecific form of the species from the Old World, characterized by a number of morphological and anatomical characteristics connected with their newly developed ability to fly. For example, the structures of the thorax in the American populations differ with regard to the weak sclerotization of the hind part of the metanotum, in that they lack articulation of the third axillare, have a weaker basiradiale (resembling a sclerotized membrane with no direct connection
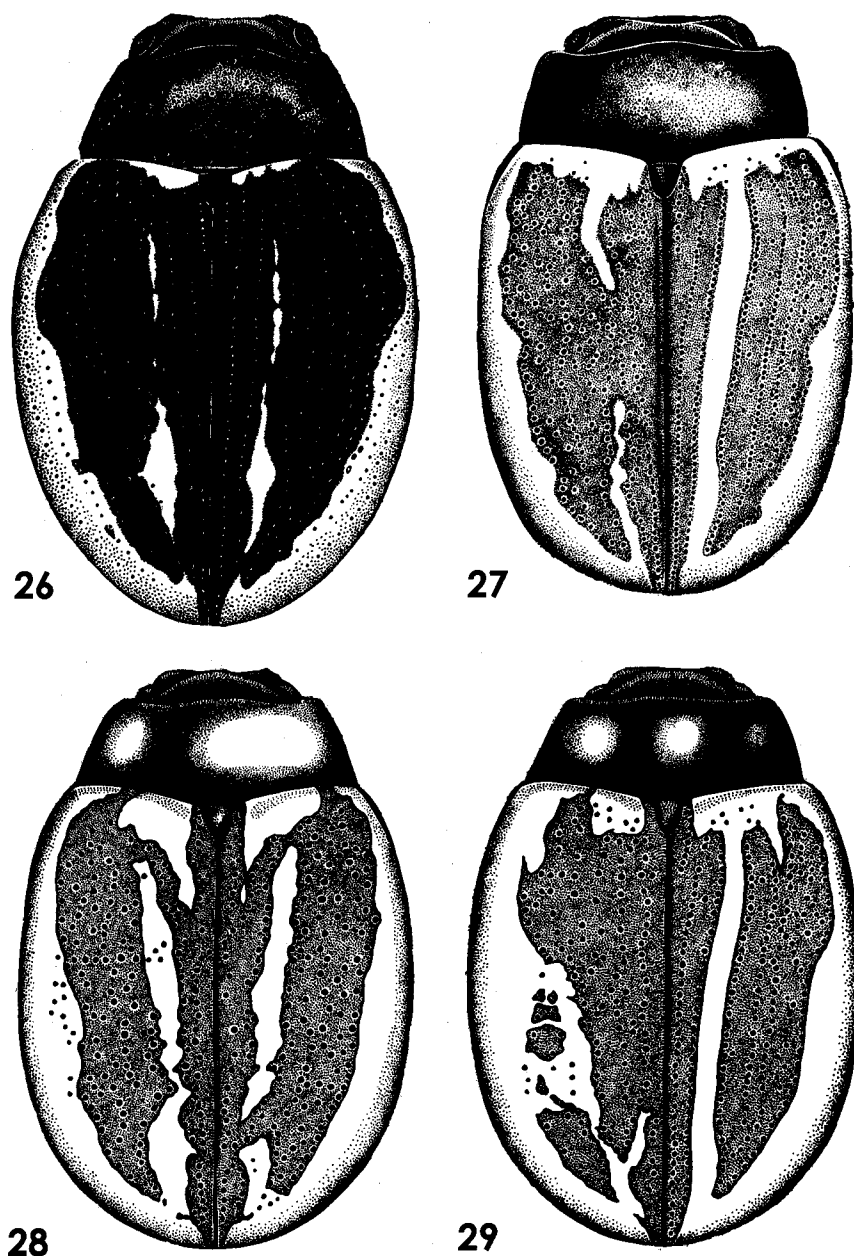
Figs. 26 to 29. Anomalous phenes of *Z. suturalis* from the SPW (after Kovalev, 1989b).

to the radial vein), and a weakly developed second axillare, which lacks a proximal medial plate. The wings of the few specimens examined were parchmentized. The flight musculature of the metathorax is reduced to thin, loose fibers. The reduction is especially remarkable in males: the oblique dorsal muscles cannot be discerned in the fat body, the longitudinal dorsal muscles are represented by four loose fibers, the dorso-ventral muscles by three thin fibers on a plate of a fat tissue, and the muscles inserted in the subalare by a single fiber (Kovalev, 2002).

The color pattern of the elytra in *Z. s. volatus* is similar to the nominative subspecies. The hind wings are strongly sclerotized (Fig. 36). The structure of the wing venation is highly variable. The hind part of the notum is strongly sclerotized. The first axillare

is connected to the notum at two points, and its end forms an articulation with the third axillare. All groups of the metathoracic muscles are well developed and consist of ten to fifteen thick, elastic fibers (Kovalev, 2002).

The development of the ability to fly in the acclimatized population can be subdivided into several phases. In the first three generations within the SPW, sclerotization of the hind wings has already begun. Up to the fourth generation when the first 'flyers' were found, so-called 'tumbling' flight was quite common (any beetle that tried to fly fell down). By the fifth generation, thousands of insects were already able to lift up into the air simultaneously.

Thus, the formation of the new form with distinctive taxonomic characteristics within four generations in the SPW, the displacement of the already
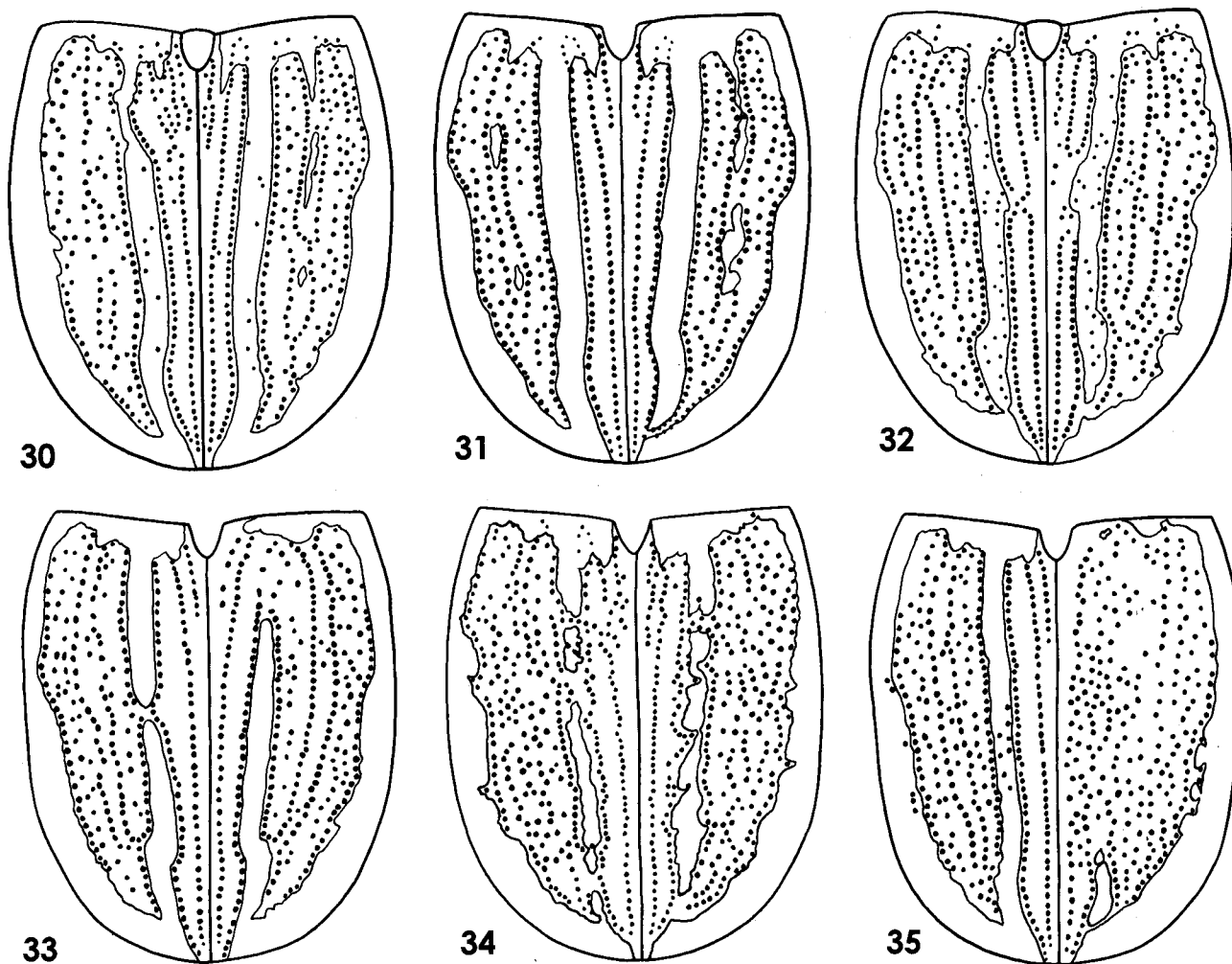
Figs. 30 to 35. Anomalous phenes of *Z. suturalis* from the SPW (after Kovalev, 1989b).
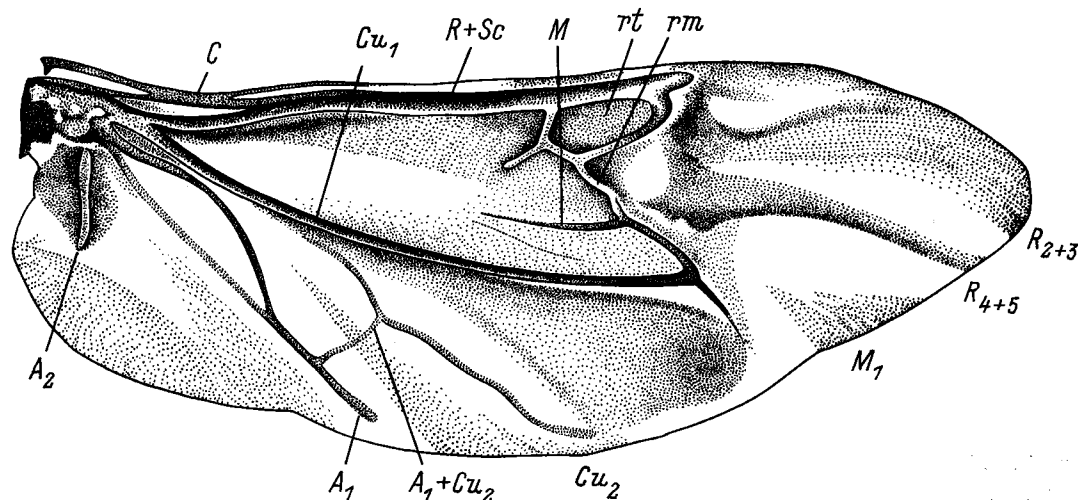

Fig. 36. The hind wing of *Z. suturalis volatus* Kovalev (after Kovalev, 1989b, 2002).

acclimatized 'pedestrians' by this new form, and the extraordinary diversity of the phenotype, cannot be explained on the basis of the notion of the synthetic theory of evolution on the gradual transformation of the population of the original species into a new population controlled by natural selection.

Concluding remarks

The very first stage of the study of SPWs in chrysomelids has already shown interesting prospects for the investigation of the phenomenon from a theoretical perspective. However, it is not yet clear why

these processes take place predominantly during the introduction of Chrysomelidae. Geneticists may be attracted by the extraordinary phenotypic variation of the introduced population achieved within few generations.

Finally, the importance of SPWs in the biological control of weeds could increase if the appropriate conditions for the formation of an SPW can be artificially created in areas of acclimatization of chrysomelids and other beneficial agents.

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