TERTIARY HOMOPTERA OF STAVROPOL AND A METHOD OF RECONSTRUCTION OF CONTINENTAL PALAEOBIOCOENOSES

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ABSTRACT. The fossil remains of insects from Vishnevaya Balka are the principal basis for studies of the entomofauna of the Caucasus in the Miocene period. The representatives of the Homoptera (monophagous and oligophagous) which are closely associated with certain genera and species of plants, have been carefully studied. The wealth of species of Psyllidea (mainly monophagous) allows us on the basis of biocoenotic relationships to enlarge the list of plants existing in the Stavropol region in Karagan times.

The geological section of Vishnevaya Balka comprises a considerable portion of the Karagan horizon from above the Chockrack boundary. It shows some regularity in the burials of the representatives of different orders of insects by layers. Diptera recorded in the lower layers as only 17%, rise to 48% in the upper layers. Homoptera dominate in the lower layers, with 35%. The beetles and Hymenoptera make up no more than 3–10%; Trichoptera 15–24%, falling in the upper layer I to 7–8%. The biocoenotic relationships of Homoptera and Diptera enable us to estimate the changes of biocoenoses in time. During the deposition of the lower layers a woody vegetation (trees and shrubs) prevailed while herbaceous vegetation was characteristic of the upper layers, pointing to the gradual steppization of the area.

IN 1939 a large collection of fossil insects (3,600 specimens) was found near the town of Stavropol. They were obtained from the Karagan strata (the Middle Miocene of the Caucasus). A detailed study of the Miocene entomofauna and the description of the locality Vishnevaya Balka enable us to define the environmental conditions of biocoenoses and to trace their modifications during that geological period. This paper is an extension of the discussion included in my earlier paper (1964); it considers a new method of reconstructing palaeobiocoenoses using the 'Principle of Actualism' and citing many examples of the ecology of different orders of modern insects.

The insects are the most numerous class of animals and the representatives of different groups are adapted to diverse environmental conditions. Among them are phytophagous insects feeding on some certain food plants, as monophagous and oligophagous species; predators and parasites each adapted to its respective species or groups of animals, either vertebrates or invertebrates.

The Homoptera are a group of suctorial plant-feeding insects closely connected with their host-plants. Metcalf (1946) has pointed out that most of the species in the Homoptera are limited to a single or a narrow range of host-plants. This characteristic feature together with their insufficient powers of flight makes them very valuable as geographical indices. Their food associations being constant, changing of the host usually leads to morphological modifications and the emergence of new forms. Among Homoptera, Psyllidea are generally monophagous. Aphidea change their host during a season, either from a woody plant to a herbaceous one, or from one woody plant to another. As a rule these host-plants are of a quite definite genus and species. With the loss of one of the two hosts, heterocyclic species became anholocyclic leading only to parthenogenous generations of apterae (pseudohiemosistens or pseudofundatrix) and alatae (alata exsulans or alata non migrans).

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Most of the psyllids described belong to recent forms whose host-plants are well known. In such cases we may confidently say that in that locality there were in existence plants of the same genus and closely related in species to the modern representatives. In other cases some new species of psyllids closely related to modern forms are found as well; so we may suppose that they might have inhabited some plants closely related to the modern representatives of the same or a related genus of the same family.

The study of phytophagous Homoptera (monophagous and oligophagous) enables us to make up a preliminary list of plants which were probably included in the phytocoenoses of the Stavropol region in Karagan times. Generally it comprises all the species which were identified by Palibin (1936) for that locality. Only in a few cases were there plants unknown for the Stavropol region of Karagan times, but found in the Chockrack strata of the Caucasus, or plants belonging to genera which are at present found in the Caucasus. The latter are perhaps of the Caucasus–Middle Asia, or of Asia Minor origin. Consequently the representatives of those genera might have existed there from the Tertiary period. The list given above has been partly confirmed by the data of spore-pollen analysis (Grossheim and Gladkova 1950).

The collections of insects from Vishnevaya Balka serve now as the basis for the understanding of the Caucasus Miocene entomofauna. Water insects, plant feeders, and saprophages, form the greater part of entomofauna making up almost equal groups; predators and parasites occur in lesser number (Rohdendorf 1939).

Among the Homoptera studied the groups inhabiting woody plants prevail. From 30 species and over 300 specimens of psyllids only 3 specimens (belonging to 3 species) inhabited herbaceous plants. The fact that only a few leaf-hoppers, the inhabitants of herbaceous vegetation of moist meadows and flood plains (*Cicadella viridis* L., *Eupteryx*, *Paramesus*), were found, confirms the insufficient development of those phytocoenoses. On the other hand among Diptera the inhabitants of herbaceous vegetation (Chloropidea) occur together with those of deciduous forests and shrubs (Sciaridae and Agromyzidae).

The geological section of Vishnevaya Balka comprises a considerable portion of the Karagan horizon above the Chockrack boundary. Throughout the section the fossil insect remains occur in the interlayers of the same fine-grained marl. The insects studied are of similar small to medium size. The phenomenon of taphonomic character such as a size selection of insects in the marly interlayers, cannot influence considerably the quantity of the representatives of separate orders. The burials of the relatively large Trichoptera are consistent throughout the marly interlayers of the whole section, while small psyllids prevail in the lower layers and Diptera (including also small forms) in the upper layers. All this enables us on the basis of the number and variety of fossil remains to speak about the changes in the composition of the entomofauna in the course of the deposition of the sediments and to estimate the changes in the composition of respective plant associations.

In the entomofaunal assemblage Coleoptera and Hymenoptera are almost constant in number in all layers at about 3–10%; Trichoptera vary from 15 to 24% with the exception of layer I where they are reduced to 7–8%. It is quite different with Diptera and Homoptera. Diptera increase to 17–24% in the upper layers (XVI–X), amounting to 30% in layer V, to 33% in layer I and even to 48% in exposure 4 which is the slide of several layers in the geological section of Vishnevaya Balka; it is situated above layer I. Thus in the upper layers Diptera become a dominant group.

On the contrary Homoptera dominate in the lower layers (layer XVI), making up about 35%. They are present in various assemblages where willow and rosaceous groups of psyllids prevail. There occur also single representatives of psyllids from high cranberry (*Viburnum*), *Caragana* or acacia, cinnamon, and pistachio (*Pistacia*). The whole composition of Homoptera fauna points to the existence of woody vegetation. In layer XI the number of Homoptera sharply decreases, falling as low as 8–10%, and of the whole rich psyllid assemblage only two species feeding on Leguminosae are left, one from *Caragana* or acacia, the other from lucerne (*Medicago*). In layer IX Homoptera increase, and again groups of willow and rosaceous psyllids appear but with smaller number of species. Separate representatives of psyllids from high cranberry (*Viburnum*), *Astragalus*, *Elaeagnus*, and two species from *Ulmus* are also found. In the upper layers (VIII, V, III) and exposure 4, Homoptera make up no more than 3–5%; only in layer I do their numbers rise to 16%, but consist almost exclusively of Aphididea. In the upper layers (exposure 4) side by side with numerous psyllids from legumes and aphids, small cicades (plant-hoppers, frog-hoppers, and leaf-hoppers) are found.

The above analysis shows a change of biocoenoses in the course of the Karagan strata formation conditioned by one or another kind of plant association. In the lower layers insects connected with arborescent plant associations prevail while in the upper layers insects related to herbaceous plants dominate. It is possible that during the period of the Upper Karagan strata formation herbaceous vegetation developed sufficiently and that forest plant associations were replaced by those of steppe character.

Summing up the material on the composition of entomofauna and flora we appear to have contradictory data. On the one hand there occur the inhabitants of arid areas, psyllids from *Astragalus*, *Valerianella*, and *Pistacia*, and also psyllids from *Medicago*. The latter plant, owing to its long roots (about 3 m.), can grow in relatively arid areas. The existence also of evergreen plants is confirmed by the presence of fossil remains, and by the burial of psyllids inhabiting those plants in Karagan times.

On the other hand there are indications of the existence of deciduous forests in the occurrence of Sciaridae (Diptera) whose larvae live in leaf litter and are associated with the formation of humus. The presence of Agromyzidae whose larvae mine leaves shows that there was an abundance of angiospermous plants, mainly trees and shrubs and partly herbaceous vegetation.

Finally there is evidence of the existence of wet meadows with herbaceous vegetation. For instance there are the remains of Tipulidae (Diptera) and a leaf-hopper (*Cicadella viridis* L.) whose larvae and imagines inhabit wet meadows, and Chloropidea (Diptera) inhabiting exclusively herbaceous vegetation. The presence of Chironomidae and Culicidae and some remains of water-plants point to the existence of open fresh-water lakes, rivers, and lagoons. This is also indicated by the presence of Dolichopodidae whose larvae inhabit wet meadows, but whose imagines are predators feeding on small insects.

Such apparent contradictions depending on different environmental conditions of biocoenoses (either arid or humid) may be explained by differences in biotopes, conditioned by the meso-relief of the area and the existence of basins.

It must be noted that only one specimen of a cockroach was found, the optimal conditions for cockroaches being thickets in tropical forests with a high degree of humidity (Bey-Bienko 1950). On the basis of floral composition Palibin has defined the average annual temperature of the area as greater than 20° C. Consequently temperature could not have been a limiting factor for the distribution of cockroaches; it must have been low humidity with sparse vegetation cover.

It should be pointed out that of all the psyllids described there is only one species of the subfamily Aphalarinae, *Agonoscena marmorea* B.-M., whose related Recent species, *Agonoscena targionii* Licht., lives on pistachio. Other representatives of this subfamily which are characteristic of the wormwood plant associations of desert and semi-desert are completely absent.

The above facts show that the climate of the Stavropol region in Karagan times was by no means of desert character but only slightly arid or moderately humid. The part of the Karagan basin described was considerably diluted with fresh water from the rivers. These conditions were favourable for life of some insects, such as the larvae of Trichoptera, water beetles (Dytiscidae and Hydrophilidae), Diptera-Culicidae and Chironomidae, and surface bugs (Gerridae), while land was characterized by a considerable variety of biocoenoses.

LITTORAL AND INLAND BIOCOENOSES OF STAVROPOL IN KARAGAN TIMES

On the basis of the palaeobotanical material, the study of the Homoptera, and the analysis of the composition of entomofauna and ecological data of present-day plants and insects, we may outline the following bioceoneses:

1. Biocoenoses of littoral and coast plant associations of the sea and brackish lagoons.
2. Biocoenoses of submerged and waterside plant associations of fresh-water basins.
3. Biocoenoses of flood-plain forests and tugai thickets.
4. Biocoenosis of deciduous-evergreen forest.
5. Biocoenosis of light, dry pine forest.
6. Biocoenoses of light, dry deciduous forests of savanna type and steppe shrub-growths.
7. Biocoenosis of coniferous forest.

BIOCOENOSES OF LITTORAL AND COAST PLANT ASSOCIATIONS OF THE SEA AND BRACKISH LAGOONS

From a description of the insect locality in the Stavropol region it may be concluded that the continental deposits of the Karagan layers in Vishnevaya Balka and Temnoles-skaya were formed in the conditions of fresh-water lagoons with salinity no more than 5‰. These conditions were favourable for the existence and development of water insects, as for instance, larvae of Trichoptera, may-flies (Ephemeroptera), dragon-flies (Odonata), surface bugs (Gerridae), water beetles (Dytiscidae, Hydrophilidae), larvae of Diptera-Chironomidae, and Culicidae. On the bottom of the parts of basins with quiet or sub-mobile water, as well as the larvae of benthic insects a great number of small *Spaniodontella* lived. These bivalves are found associated with *Unio*, *Planorbis*, and other fresh-water forms. They have no adaptation for burrowing and no siphons which are characteristic of the sub-littoral bivalve infauna.

The remains of marine plants are very rare. They have been found only in Temnoles-skaya and Vlasova Balka and have been identified by Dr. I. V. Palibin as marine brown algae (*Cystoseira* sp.) and red algae (*Sphaerococcites* sp.).

The first inhabitants of the sandy coasts where the recession of the sea took place were herbaceous plants. Due to the tidal conditions of the sea-coast the majority of the species were probably halophytes which were unharmed by occasional submergence in sea-water and by the high salt content of the soil. The burial of herbaceous plants is very rare and there is but little chance of preservation of the imprints of plants so rare and few as the herbaceous pioneers of sandy shoals; the association corresponds to the *Pes-caprae* formation described by Richards (1952, p. 296).

Some of these plants penetrated inland, forming in places the biocoenosis of sandy dunes. Above the tidal zone and on steep slopes small and crooked trees and shrubs grew, scattered and in groups. In the formation of such biocoenoses the species of *Salix* played an important part, as well as grasses and other herbaceous mono-cotyledons which were the first to colonize the barren sandy coasts, shoals, and cliffs. These biotopes might have been occupied by *Myrica*?, *Elaeagnus*?, *Astragalus*?, various other trees and shrubs which could grow on poor soils, and also a herbaceous legume *Medicago* L.

Richer biocoenoses existed evidently on the banks of low-salinity lagoons and lemans and also river deltas. Some aquatic and riverside plants have been found in the Karagan layers of Stavropol: *Najadopsis dichotoma* Heer, *Phragmites oeningensis* A. Br., and *Dryopteris stiriaca* Ung. The present-day representatives of these genera also occur in the littoral associations of the sea and in river deltas (L. A. Sokolova *et al.* 1956, pp. 541–3). In the littoral zone reeds often form a 'sudd' (the term is used by Richards 1952) or floating sward on which *Dryopteris* and some other plants begin to settle. Besides the last named, *Carex* and *Nymphoides* most probably took part in the associations of deltas, and *Phragmites oeningensis* A. Br. grew on the margins of deltas and lemans. Further on along the river banks it was joined by *Dryopteris stiriaca* Ung., *Equisetum parlatorii* Schimp. and ?*Carex*. These were subsequently replaced by alder and willow over-growths and finally the latter gradually merged into the association of flood-plain humid forest.

BIOCOENOSES OF SUBMERGED AND WATERSIDE PLANT ASSOCIATIONS OF FRESH-WATER BASINS

Some fossil plants recorded from the Karagan layers of Stavropol enable us to assume the existence of several successive stages in the development of the vegetation of fresh-water basins, deltas, and low-salinity lagoons. This is also indicated by the composition of the entomofauna. The following three stages may be traced:

1. 'The association of the pond lily', the stage of bottom-rooted aquatic plants in which *Najadopsis dichotoma* Heer may be included. This biocoenosis of fresh-water basins (rivers and lakes) comprises also various groups of Karagan insects whose larvae or adults are associated with reservoirs; may-flies (Ephemeroptera), dragon-flies (Odonata), surface bugs (Gerridae), water-beetles (Dytiscidae, Hydrophilidae), caddis-flies (Trichoptera), and some Diptera-Culicidae, Chirono-midae, and also predators Dolichopodidae.

2. 'The reed-swamp association.' This consists of a reed, *Phragmites oeningensis*, and sometimes also the sedge (*Carex*). A leaf-hopper *Chloriona stavropolitana* B.-M. found in this biocoenosis is closely related to the present-day representatives of this species existing on *Phragmites communis* L. Although *Carex* has not so far been found among the Stavropol fossil plant remains, a leaf-hopper *Cicadella viridis* L. which has been recorded from Karagan strata can be seen on the recent species of *Carex*.

   Richards (1952, p. 284) has noted that ferns occur in the 'Emergent aquatic associes'. In the river-side 'reed-swamp association' of the flood-plain in Middle Asia a fern *Dryopteris thelypteris* is found. It is possible that a fern *Dryopteris stiriaca* (Ung.) Palib. found in the Karagan layers and a horsetail *Equisetum parlatorii* Schimp. also formed part of this biocoenosis.

   Again Richards (1952, pp. 293–4) noted: '. . . in the earlier phases of the hydrosere herbaceous plants are generally dominant; later they are replaced by woody plants. Both in temperate and tropical hydroseres monocotyledons play an important part in the intermediate stages. In temperate regions they dominate the reed swamp stage. . . .' Many herbaceous plants, chiefly grasses (identified by I. V. Palibin under uncertain name *Culmis graminis*) formed part of this assemblage. The progress of this association stimulated the development of rich and varied groups of insects related to herbaceous plants. Thus the Tipulidae and Dolichopodidae whose larvae live either in water-logged soils or wet meadows were widespread with the development of the swamp meadow stacio.

3. 'Shrub association.' (This is the temperate zone analogue of the tropical 'Marsh shrub association'.) It consists of willow and alder thickets (*Salix lavateri* Heer and *Alnus kefersteinii* Goepp.). According to Richards's statement: '. . . in this process of *Verlandung*, or formation of new land from water, vegetation plays an essential part' (1952, p. 283). This association may be regarded as the last stage in the hydrosere and the beginning of the development of the forest association. It is the waterside character of this plant association that explains the wealth in species of willow psyllids.

As well as these plant associations of lakes and rivers on silty and clay soils, it is very probable that there were phytocoenoses on sand in whose formation the species of the genus *Salix* played an important part in addition to grasses and other herbaceous monocotyledons which were the first to colonize the sandy shores and cliffs. The variety of biocoenoses and the fact that the willow is not very particular about the soil is manifested by the number and variety in species of willow psyllids in the Karagan layers of Vishnevaya Balka.

Dalbergia bella Heer which occurred in the Stavropol flora of Karagan times might have been a relic of the previously mentioned 'Marsh scrub associes' (Richards 1952, p. 284) which in tropical conditions included some other species of the same genus. And yet we cannot place *Dalbergia bella* Heer in this particular phytocoenosis with certainty, as the species of this genus occur in the hylea and in dry *Shorea* forests. If *Dalbergia bella* Heer was a part in the 'Marsh scrub associes', it must have grown in the plant association *Salix–Alnus*, together with *Salix lavateri* Heer and *Alnus kefersteinii* Goepp.

Among the plants which may also be considered as belonging to the riverside biocoenosis it is possible to name the representatives of the family Myricaceae, two species of which occurred in Temnolesskaya (*Myrica olgae* Palib. and *M. salicina* Palib.) and one in Vishnevaya Balka. Probably there was also a representative of the *Elaeagnaceae* (*Elaeagnus*). In Recent times the representatives of the genus *Myrica* occur in the fringes of swamp forest, on seaside swamps, sandy shores, along streams, and on peaty bogs.

In the river-bank plant association *Terminalia miocaenica* Ung. might have been present as some species of this genus occur in riverside phytocoenoses, for instance in India. According to Richards this genus could have been a relic of the tropical riverside association. However, the presence of this plant does not give any reason to suppose that in Karagan times anything similar to a mangrove might have existed in the Stavropol region (Mchedlishvili 1951, pp. 921–3), because the species of the genus *Terminalia* grow above the tidal zone and are most frequently met with in biocoenoses of dry deciduous savanna and monsoon forests. There was no typical component of the 'Mangrove forest association' among the fossil plant remains.

BIOCOENOSES OF FLOOD-PLAIN FOREST AND TUGAI THICKETS

As has been said the thickets of *Salix* and *Alnus* are the primary stage in the development of a forest association. On the low sides of rivers, lakes, and river-deltas in particular, the association of swamp forest might have developed as humid flood-plain forest and growths of shrubs on peaty soils. The floristic composition of such phytocoenoses most probably consisted of *Salix lavateri* Heer, *Alnus kefersteinii* Goepp., *Taxodium dubium* Sternb., and perhaps some species of the genera *Myrica* and *Ulmus*.

The group of willow psyllids is largely represented in the entomofauna of Vishnevaya Balka. Some Recent species live in light humid forests, on peat bogs, and on wet meadows along the watercourses. These are *Trioza striola*? Flor, *Psylla abdominalis*? M.-D., *Ps. pulchra*? (Zett.), *Ps. saliceti*? Forst., *Ps. moscovita*? Andr. Probably *Psylla adjuncta* B.-M. and *Ps. subambigua* B.-M. also inhabited similar biotopes.

The presence of psyllids inhabiting the humid stacio and peat bogs is good evidence that the light, humid deciduous forest on the flood plain might have existed.

In this biocoenosis, as well as willow psyllids, certain other forms might have lived: *Psylla ulmi*? Forst., a leaf-hopper of the genus *Eupteryx* (Cicadellidae), an arboreal mesophyte living on *Salix*, *Alnus*, etc.; a frog-hopper of the genus *Aphrophora* (Cercopidae), a habitant of trees and shrubs (*Salix*, *Alnus*), and herbaceous vegetation; also Tipulidea, soil gnats (Sciaridae), fungus gnats (Fungivoridae), scorpion flies (Mecoptera), etc.

On drier biotopes the river-bank vegetation changed considerably in the composition of forms and assumed most probably the character of the tugai thickets of the Middle Asian steppe areas. The composition of tugai associations apparently included willow and *Elaeagnus* thickets, and herbaceous plants such as grasses and legumes. The biocoenosis most probably consisted of willow psyllids (except those inhabiting peat-bogs) common to steppe and mountain regions: *Psylla klapaleki*? Sulc., *Ps. praevia*? Log., *Ps. moscovita* Andr., *Ps. propinqua*? Schaefer, *Ps. medicaginis*? Andr., *Trioza salicivora*? Reuter, *Tr. magnisetosa*? Log. The families Agromyzidae, Empididae, Syrphidae, and Sciaridae appear with a richer development of herbaceous vegetation. This presumed phytocoenosis evidently alternated with meadow associations of grasses and legumes.

In the Karagan layers of Temnolesskaya the representatives of *Alnus*, *Taxodium*, *Equisetum*, and *Phragmites* have been found, also the remains of *Abies stavropolitana*, Palib. and some subtropical evergreens: Lauraceae, Myricaceae, Rosaceae (*Amigdalus*), Mimosaceae (*Acacia*), and various herbaceous plants. Evidently there was in the Temnolesskaya region a lowland area adjacent to the banks of a river-delta or perhaps a leman where a reed (*Phragmites oeningensis* A. Br.) grew near the shore and a horsetail (*Equisetum parlatorii* Schimp.) and a fern (*Dryopteris stiriaca* (Ung.) Palib.) were situated behind it, on the shore. Further inland alder thickets (*Alnus kefersteinii* Goepp.) appeared and there might have been a gradual transition from the latter to the association of a humid forest where *Taxodium dubium* Sternb. grew in the lower places and the oak (*Quercus aspera*?), *Viburnum*, *Ulmus* occupied a higher position. In the herbaceous ground flora *Dryopteris stiriaca* (Ung.) Palib. apparently alternated with grasses. The recorded frog-hopper of the genus *Aphrophora* lived on alder and willow trees and shrubs and on herbaceous plants.

This biocoenosis strongly resembles the *Colchis* alder and oak-alder lowland forests, though not so richly represented. The phytocoenosis evidently existed on clay and silty soils.

Other vegetative forms recorded from Temnolesskaya fossil plant remains by no means suggest that the continental biocoenoses were humid. These forms were *Amygdalus rodobojana* Ung., *Laurus lalages* Ung., *L. primigenia* Ung., and *Acacia parschlugiana* Ung. which were meso-xerophytic vegetative forms also taking part in other biocoenoses.

The entomofauna includes besides frog-hoppers of the genus *Aphrophora* a considerable number of butterflies (Lepidoptera, about 20%) and some bugs that may point to the existence in the Temnolesskaya region of open dry bioceonoses.

BIOCOENOSIS OF DECIDUOUS-EVERGREEN FOREST

The evergreens in the Karagan flora of Stavropol form a large proportion of the whole plant association. The present-day species of these genera are found mainly in the south subtropics of Asia and North America.

The floristic composition of the Stavropol deciduous-evergreen forest evidently comprised *Quercus aspera* A. Br., *Persea princeps* Heer, *Pinus saturni* Ung., *Sabal haeringiana* Heer, *Laurus primigenia* Ung., *L. lalages* Ung., *Cinnamomum scheuchzeri* Heer, *C. rossmasleri* Heer. Perhaps there were also *Terminalia miocaenica* Ung., *Dalbergia bella* Heer, and *Rhus obovata* Ett. Magnolias which are characteristic of humid biocoenoses are never met with in this phytocoenosis (*Flora of the USSR*, 1937, vol. 7). However, they occurred in the Karagan layers of Dagestan where they obviously formed part of more humid biocoenoses.

It is possible that in places the plant associations included also some of the Rosaceae: *Pyrus* in the shade; *Malus* and *Prunus* on exposed sites.

The biocoenosis obviously included a rich and varied fauna of insects. Among psyllids *Trioza cinnamomi*? Bos., *Tr. similis* B.-M., *Tr. interposita* B.-M., *Tr. subproximata* B.-M., *Agonoscena marmorea* B.-M., *Retracizzia andrianovae* B.-M., *Psylla loginovae* B.-M., *Ps. vasiljevi*? Suls, and *Ps. umbrata* B.-M. might have been in existence. Among other groups of insects there might have been present a plant-hopper *Dictyophara* and some families of Diptera such as the Bibionidae, Agromyzidae, Sciaridae, Empididae, and Syrphidae.

BIOCOENOSIS OF LIGHT, DRY PINE FOREST

As has been said, in drier regions on sandy soils and slopes the oak forest was evidently replaced by the light, dry deciduous pine forest with a certain proportion of evergreen and deciduous subtropical flora such as palms, laurels (laurel, avocado), and herbaceous plants. This biocoenosis might have included also *Acacia parschlugiana* Ung. and possibly *Caragana* and *Pyrus*.

Among psyllids described there are no species whose host belongs to the genus *Pinus*. However, in a number of cases some closely allied species among the Recent representatives of psyllids (whose hosts are unknown) have been mowed down together with the herbaceous vegetation in the pine forest at the altitude of 2,000–3,000 m. For instance, a recent species *Trioza bifurcata* Tuth. is related to the fossil *Trioza interposita* B.-M. It should be noted that many adults of the recent species are met with on the pine in autumn though their hosts are other plants, e.g. *Psylla pulchra* (Zett.) feeding on the willow.

The psyllids feeding on leguminous shrubs (*Psylla longifurca* B.-M.) and on *Pyrus* (*P. vasiljevi*? Suls) as well as some frog-hoppers of the genus *Aphrophora* which are met with on conifers (*Pinus* and *Abies*) might have formed part of this biocoenosis.

BIOCOENOSES OF LIGHT, DRY DECIDUOUS FOREST OF SAVANNA TYPE AND STEPPE SHRUB GROWTHS

The composition of the Karagan flora includes a certain proportion of drought-resistant and steppe-land forms that may point to the existence of dry steppe phytocoenoses in Karagan times. Some of these plants evidently formed part in the composition of deciduous-evergreen forests on less humid biotopes preferring chiefly the margins or occupying exposed sunny mountain slopes covered with herbaceous vegetation, thus forming steppe-land shrub associations. These are *Amygdalus rodobojana* Ung., *Laurus primigenia* Ung., *L. lalages* Ung., and *Acacia parschlugiana* Ung.

Grassy legumes and leguminous shrubs such as *Caragana*, *Astragalus*, *Medicago* may also be added to this biocoenosis. Though their fossil remains are not known, the above-described psyllids live on them at present. *Pistacia*, on which may live *Agonocena marmorea* B.-M. may be included in this assemblage, as well as *Cotoneaster*, *Myrica*, and *Myrsine*.

The biocoenosis described may be subdivided into different associations depending on biotope and different soil types. It is possible to separate a group of plants growing on stony calciferous mountain slopes: *Amygdalus*, *Laurus*, *Prunus*, *Cotoneaster*, *Pistacia*, *Sorbus*, *Caragana*, *Astragalus*, *Medicago*. Some of them such as *Sorbus*, *Acacia*, *Caragana* occur on stony slopes on other substrata (*Flora of the USSR*, 1945, vol. 11). *Pistacia*, associated in places with *Amygdalus*, may belong to the driest biotopes (Korovin 1934, p. 372).

In the steppe zone the shrubs *Cotoneaster* and *Astragalus* grew in groups in the association with grasses and herbaceous legumes (*Medicago*). On sandy mountain slopes and in dry regions the drought-resistant vegetation of *Astragalus*, *Valerianella*, and *Medicago* probably grew. In addition a number of species in both tree and bush form composed some kind of low mountain woodland of Middle Asia (Korovin 1934, p. 372). The biocoenosis included psyllids living on Rosaceae, Lauraceae, and Leguminosae, including *Psylla vasiljevi*? Sulč, *Ps. loginovae* B.-M., *Ps. stavropolitana* B.-M., *Ps. umbrata* B.-M., *Ps. elongata* B.-M., *Ps. cotoneasteris*? Log., and a group of leguminous psyllids including *Ps. longifurca* B.-M., *Ps. medicaginis*? Andr., *Ps. rhombifera*? Log., and also *Trioza magnisetosa*? Log., *Agonoscena marmorea* B.-M., and *Retracizzia andrianovae* B.-M. It is possible to include in this biocoenosis aphids, many of which live on *Acacia*, and *Chanithus vishneviensis* B.-M., a mesoxerophyll of steppe regions.

BIOCOENOSIS OF CONIFEROUS FOREST

Among the fossil remains of Vishnevaya Balka only three representatives of gymnospermous plants have been found: *Taxodium*, *Pinus*, and *Abies*. *Taxodium dubium* Sternb. apparently formed part in the biocoenosis of swamp forest and humid flood-plain forest; *Pinus saturni* Ung. in the bioceonosis of dry mixed forest. The latter was evidently the main representative in the association of dry pine forest with evergreen undergrowth on sandy soils, mountain slopes, and cliffs. As to *Abies stavropolitana* Palib., it could not have grown in the community with *Taxodium dubium* as the present-day representatives of the former are not tolerant of water-logged soils with a high water-table; but it could be included in the phytocoenosis with *Pinus saturnii* Ung., which can grow on mountain slopes with sufficiently fertile soils. This may be confirmed by the fact that *Abies stavropolitana* Palib. and *Psylla abietis* Kuw. feeding on it, were met with by chance (a single specimen of *A. stavropolitana* and two specimens of *Ps. abietis*); it is known that the further from the sea, a river mouth, or fresh-water basin the biocoenosis exists, the less is the possibility of burial of the flora and fuana. There are also species among the Karagan psyllids which at present inhabit the submontane, lower montane, and sub-alpine zones. This may indicate that such types of biocoenoses, and biotopes corresponding to them, may have been in existence in Karagan times.

Abies stavropolitana evidently grew in the submontane zone in pure stands or with the undergrowth consisting of willow (*Salix*) and mountain ash (*Sorbus*), both of which occur in the biocoenosis of pine and coniferous forests.

Among the herbaceous vegetation besides meadow grasses there were probably numerous ferns. In this biocoenosis *Psylla abietis*? Kuw. and *Ps. sorbi*? L. might have been present as well as some species of frog-hoppers of the genus *Aphrophora* and some aphids.

CONCLUSION

The method of actualism has often been successfully employed by scientists for the reconstruction of the earth's past and in their attempts to understand the organic and inorganic processes that took place in different periods of geological history.

This may be confirmed by lithological works of N.M. Strakhov (1960) and his followers. With no less success this method has been used by R. F. Hecker and his colleagues in palaeoecological investigations at the Palaeontological Institute of the U.S.S.R. Academy of Sciences. However, these palaeoecological studies were generally concerned with the reconstruction of the environment of aquatic biocoenoses, particularly marine and more rarely those of fresh-water basins (Hecker 1948, 1965; Hecker, Osipova, and Belskaya 1963; Merklin 1950).

Fewer attempts have been made to reconstruct land biocoenoses. As a rule only the works of palaeobotanists and vertebrate specialists have been used, but of no less importance for the subject is the study in the palaeoentomology. The extensive biological relations of insects present abundant and valuable material for the indirect evidence that certain plants and animals existed though their fossil remains have not been found. The preliminary study presented in this paper is an attempt to reconstruct the phytocoenoses based not only on plant fossil evidence but also on the species of Homoptera.

Similar constant biological relationships which present plenty of material for the reconstruction of biocoenoses also exist in many other orders of insects (Hymenoptera, Diptera). For instance, phytophagous insects belonging to the subfamily Xyelinae (Hymenoptera) live only on the pine, each species of this family on a definite species of the genus *Pinus* (Rasnitsyn 1965). The same is observed among parasitic Hymenoptera: a list of hosts at whose expense one or another species of this group develops is often restricted to one or two species.

Among the representatives of Diptera there are also phytophagous insects, monophagous and oligophagous. These are various gall-flies (Cecidomyidae), leaf-mining flies (Agromyzidae), Trypetidae, and other Diptera whose larvae live either on certain species or certain genera of plants. There are also predators and parasites belonging to this order, associated with certain species of the vertebrates or invertebrates. These include various gadflies (Oestridae, Hypodermatidae, Gastrophilidae), for instance a sheep botfly (*Oestrus ovis* L.) whose larvae parasitize the nasal chamber of sheep; the species of the genus *Rhinoestrus* whose larvae occur in the nasal chamber of the horse; and the species of the genus *Gastrophilus* which parasitize the intestines of the horse.

Various species of the families Dexiidae, Calliphoridae, Phasiidae, and Tachinidae are parasites on other insects, mainly monophagous or oligophagous. The larvae of the Dexiidae parasitize the larvae of Scarabaeidae; the larvae of the genus *Protocalliphora* and *Trypocalliphora* live in birds' nests and suck nestlings' blood; various Phasiidae parasitize bugs of the family Pentatomidae; the species of the genus *Pallenia* parasitize earthworms. The representatives of the families Syrphidae and Chamaemiidae partly belong to the active predators feeding on various aphids, coccids, and psyllids.

It is of particular interest to study aphids (Aphidea) for the reconstruction of phytocoenoses, as it enables us to establish double relationships of these insects with their primary and secondary host-plants. Palaeoentomological research in the Aphidea will also help to discover the cause and nature of rising migration and life-cycles in this interesting group of insects.

Thus for the reconstruction of organic and inorganic processes in the course of different periods of the geological history of the earth it is of great importance to adopt the method of actualism in the complex study of fauna and flora and their environment. When studying certain regions in this way, numerous facts of biological relationships of different groups of animals and plants with each other and with their environment, will serve as a mutual corrective for the reconstruction of palaeobiocoenoses and their environments and will be the basis for the characteristic of climate and landscape of the past geological epochs.

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