Commonwealth Institute of Entomology, London.
Huelsenbeck, J. R., and F. Ronquist. 2001. Bioinformatics 17: 754-755.
Linnavuori, R. 1959. Suomalaisen Elain-ja Kasvitieteellisen Seuran Vanamon Elaintieteellisia Julkaisuja 20: 1-370**.**
Linnavuori, R. 1965. Zoologische Beiträg 11: 137-150.
Linnavuori, R. and D. M. DeLong. 1977. Brenesia 12 & 13: 163-267.
Linnavuori, R. 1979. Revue de Zoologie et de Botanique Africaine 93: 647-747.
Linnavuori, R. and K. T. Al-Neamy. 1983. Acta Zoologica Fennica 168: 1-105.
Oman, P. W., W. J. Knight, and M. W. Nielson. 1990. Leafhoppers (Cicadellidae): a bibliography, generic check-list and index to the world literature 1956-1985. CAB International Institute of Entomology, Wallingford, U.K. 368pp.
Rakitov, R. A. 1998. Russian Entomological Journal 6: 7-27. [
Ross, H. H. 1957. Systematic Zoology 6: 87-97.
Swofford, D. L. 2000. PAUP* 4. Phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Sunderland, MA.
Wagner, W. 1951. Commentationes Biologicae 12: 1-44.

Phylogeny and Evolution of the Subfamily Orgeriinae (Homoptera, Dictyopharidae)

A.F. Emeljanov & **V.G. Kuznetsova,** Zoological Institute of the Russian Academy of Sciences, Universitetskaja nab., 1, St. Petersburg 199034, Russia; hemipt@zin.ru; **C. Nokkala** & **S. Nokkala,** Laboratory of Genetics, Department of Biology, University of Turku, FIN-20014, Turku, Finland; seppo.nokkala@utu.fi

The subfamily Orgeriinae is interesting for an evolutionary study because its recent representatives demonstrate successive stages of adaptation to conditions of mild to extreme aridity. The subfamily comprises 185 species in 38 genera of four tribes: Ranissini (7 genera, 43 species), Colobocini (1 genus, 1 species), Almanini (20 genera, 104 species), and Orgeriini (10 genera, 37 species). It is restricted to the arid regions of the Holarctic: the first three tribes are Palearctic, and Orgeriini are Nearctic. Some non-holarctic groups of independent origin (Lyncidinae, Strongylodematinae, Capeninae, and Risiinae) have been erroneously assigned to the subfamily in the past.

The knowledge of the taxonomy and biogeography of the group is fairly complete, except at the southern extremes of the range. Emeljanov (1969) published a taxonomic revision of Orgeriinae and analyzed their phylogeny and evolution with traditional methods in 1980. Kuznetsova (1985) clarified the karyology of the tribes Ranissini and Almanini and suggested that the karyotype of Ranissini with 2n = 26+XO had arisen from the modal for Dictyopharinae (2n = 28+XO) by the fusion of two large autosomal pairs with formation of a huge chromosomal pair. The karyotype of Almanini (2n = 24+XY) in its turn had originated from that of Rinissini by X-autosomal fusion involving the huge chromosomal pair mentioned above. Nokkala et al. (in preparation) investigated the molecular phylogeny of the same tribes and constructed a cladogram based on the 16S rDNA. The morphology- and DNA-based trees show only minor differences.

The tribal taxonomic rank of the intercontinental disjunction and the association of the subfamily with the xeric habitats indicates the Eocene age of this disjunction. The presence of a member of the advanced tribe Almanini (*Tilimontia*) on the Canary Islands, isolated since the Miocene, also attests to the at least Miocene age of this tribe.

The Palearctic branch of Orgeriinae demonstrates progressive adaptation to the more xeric and cooler environments parallel to the climatic changes during the Cenozoic: dry meadows (subtropical savannahs), tomillares, sagebrush semideserts, saltwort and other subshrub deserts, and cold steppes.

The analysis of the geographic distribution of particular genera and species reveals them being restricted to particular vegetation types within the framework of individual climatic types (as determined by the thermal regime, humidity level and dynamics, and continentality).

The Orgeriinae evolution was reconstructed based on the following assumptions: (i) New groups of generic or higher rank originate in the process of colonization of novel environments. (ii) Elements of the local fauna undergo gradual transformation. (iii) Groups evolving in particular conditions colonize all the available territories where these conditions exist and follow the fate of this area. Disappearance of such conditions results in disappearance of a corresponding group (genus, tribe) due to its extinction or transformation. (iv) In a genus with a wide range of ecological types of species, the more mesophilous representatives are the ancestral ones. An evolutionary return to more favorable conditions is unlikely.

The main source of the paleoclimatic data for the following reconstruction is the comprehensive work by Sinitsyn (1965).

(1) The origin of the tribe Ranissini (i.e., of the subfamily Orgeriinae) is associated with the formation of the initial subtropical savannah center in Central Asia (Kashgaria) after a more humid epoch of dry savannah meadows (Paleocene – Eocene). The ancestor of Ranissini is unclear (Dictyopharini or Orthopagini).

(2) The origin of the tribe Colobocini and of the common ancestor of Almanini and Orgeriini is associated with the formation of protomediterranean landscapes in the northwestern part of the arid center (territory of Kazakhstan) in the Early Eocene.

(3) A short period of partial aridization of the North-Atlantic land bridge permitted migration of the ancestral Orgeriini into Sonoran North America in the Middle Eocene. The Beringian land bridge was permanently humid up to the glacial time.

(4) With the progressive continentalization and cooling of climate in the Oligocene, the (proto)mediterranean environments shifted to the west and south-west; the ranges of Colobocini and ancestral Almanini (Almanae) shifted accordingly. The vacated eastern territory was occupied by the group Nymphorgerii, a direct descendant of Almanae. Probably, this is the first group of Orgeriinae that shifted onto semixerophilous dicot herbs, and then to xerophiles like *Artemisia*.

(5) During the Messinian Miocene crisis (drying up of the Mediterranean Sea), the group Almanae reached the Atlantic and the Canary Islands, which were connected to Africa.

(6) Also in the Miocene, due to the appearance of the Central-Asian center of maximum aridization with desert conditions, the next group, Scirtophacae, shifted to desert Chenopodiaceae and analogous semishrubs with succulent leaves.

(7) In the Pliocene, Scirtophacae expanded their range as the desert area expanded, and branched into the steppes in connection with cooling at the northern border of the arid center.

(8) At the same time, in the western (Middle-Asian) part of the arid area, Scirtophacae gave origin to a more halophilous desert group Tigrohaudae and psammophilous Orgamarellae and Ototettiges.

(9) Superaridization and progressive cooling of the Central-Asian desert region (i.e., the eastern part of the large Asian arid area) resulted in the retreat to the west (i.e., to a more acceptable Middle-Asian area) of all orgeriine groups (Ranissini, Nymphorgerii, Tigrahaudae, Orgamarellae), except some tolerant Scirtophacae (*Mesorgerius* in steppes, *Scirtophaca* in deserts).

(10) The tribe Ranissini retains the association with the climate characterized by summer rainfalls. Under the pressure of the gradual aridization, this tribe retreated from the lowland savannah meadows into low mountain elevations (Tien Shan center) and colonized the arising steppes (South Siberian center). Further cooling of the main steppe area pushed the steppe Ranissini (*Ranissus, Schizorgerius*) westward up to the Balkan region.

(11) The evolution of the North American Orgeriinae, represented by the tribe Orgeriini, proceeded from dry subtropical meadows to colonization of the chapparal (i.e., vegetation of the Mediterranean type) and diverse kinds of semidesert and desert vegetation (sagebrush, saltbush, yucca, agave) independently in several lineages.

Acknowledgements

The work was supported by the Russian Foundation for Basic Research (Grant no. 05-04-48387) and by the Grant from Turku University Foundation.

References

Emeljanov A.F. 1980. Phylogeny and evolution of dictyopharine planthoppers of subfamily Orgeriinae (Homoptera, Dictyopharinae). Lectures in memory of Nikolai Alexandrovich Cholodkovsky, XXXII: 1-96. Publishing House "Nauka" Leningrad branch. (In Russian).

Kuznetsova V.G. 1985. Phylogenetic analysis of chromosome variability and karyosystematics of Cicadina of the family Dictyopharidae (Homoptera, Auchenorrhychna). Entomologicheskoe Obozrenie. 65(3): 539-553. (In Russian).

Sinitsyn V.M. 1965. Ancient climates of Eurasia. Part I. Paleogene and Neogene. Publishing House of Leningrad University. 167 pp. Leningrad. USSR. (In Russian).