Geographical Distribution of the Weevil Subfamily Ceutorhynchinae (Coleoptera, Curculionidae)

B. A. Korotyaev

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia

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Abstract—A brief general characteristic and review of distribution of the subfamily Ceutorhynchinae over zoogeographical realms are given, with an emphasis on the distribution within the Holarctic and Palaearctic. The potential of exploiting landscapes of all natural zones of the Holarctic by a low-rank taxon is exemplified by the Holarctic *Ceutorhynchus cochleariae* (Gyll.) species-group comprising ca. 20 species evenly distributed between the Palaearctic and Nearctic. Although neighboring with the powerful centers of tropical biota, the Holarctic fauna of the subfamily Ceutorhynchinae is formed mostly of endemic and subendemic genera which are especially abundant in the Palaearctic. This region possesses the most diversified generic and species composition of the fauna consisting of predominantly endemic and subendemic genera (in the Mediterranean and Saharo-Gobian regions, also of the highly diversified tribe Oxyonychini) up to its southern border. The existence of characteristic transitional faunas in the zones of contact of the Holarctic fauna with the faunas of the tropical regions in East Asia and Mexico is shown. These transitional faunas include a considerable number of endemic taxa of the genus and species groups. A conspicuous feature of the Palaearctic ceutorhynchine fauna is the rather numerous complex of the upland and high-latitude species.

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This study is based on examination of the voluminous material of the subfamily Ceutorhynchinae in the collections of the American Museum of Natural History, New York, U. S. A. (AMNH); Natural History Museum, London, U. K. (NHML); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Museum für Tierkunde, Dresden, Germany (MTD); Zoological Museum, University of Copenhagen, Denmark; California Academy of Sciences, San Francisco, California, U. S. A. (CAS); Canadian Museum of Nature, = CMN, and Canadian National Collection of Insects and Mites, = CANACOL, Ottawa, Ontario, Canada; Ch. W. O'Brien collection, Green Valley, Arizona, U. S. A.; Museum A. Koenig, Bonn, Germany (ZFMK); Bishop Museum, Honolulu, Hawaii, U. S. A.; Natural History Museum, Stockholm, Sweden (NHRM); Naturhistorisches Museum, Humboldt Universität, Berlin, Germany (NMHU); Snow Entomological Museum, University of Kansas, Lawrence, U. S. A.; Museum of Comparative Zoology, Harvard, Massachusetts, U. S. A. (MCZ); Zoologische Staatssammlung, München, Germany (ZSM); Museum national d'Histoire naturelle, Paris, France (MNHN); National Museum of Natural History, Washington, D. C., U. S. A. (USNM); Deutsches Entomologisches Institut, Müncheberg, Germany (DEI); Texas Agricul-ture and Machinery University, College Station, Texas, U. S. A. (TAMU), and University of Suwon, Republic of Korea. Data on the fauna of Russia and adjacent countries are based mainly on the collection of the Zoological Institute, Russian Academy of Sciences (ZIN) and results of my own research during 40 years.

For Palaearctic entities, limits and names proposed by Emeljanov (1974) are adopted in this paper. For description of the extra-Palaearctic distribution of the subfamily Ceutorhynchinae the scheme by Kryzhanovskii (2002) is followed here; the Palaearctic and Nearctic are treated as the ‚not in scale' entities in their traditional concepts. In the analyses of generic distribution the occurrence of species outside their native ranges is ignored.

1. GENERAL CHARACTERISTIC OF THE SUBFAMILY CEUTORHYNCHINAE

The subfamily Ceutorhynchinae (ceutorhynchines) is one of the most clearly defined (Thompson, 1992) taxa of the long-nosed weevils (Curculionidae Phanerognatha). It is usually grouped together with the subfamilies Conoderinae (= Zygopinae) and Baridinae, which have a similar structure of the mesothorax with

apices of the epimera projecting beyond the contour of the pronotum and elytra, and even (Zherikhin and Gratshev, 1995) separated together with these subfamilies in the family Barididae. Preliminary analysis of the principal characters of the external structures of the adults and the distribution of the subfamily Ceutorhynchinae and allied taxa was carried out by Korotyaev et al. (2000) for clarifying the systematic position of the subfamily Orobitidinae, formerly included in the Ceutorhynchinae. This analysis, as well as the recent comparative morphological study of the peculiar structures of the weevil vestiture (Lyal, 2006), did not support combining ceutorhynchines in one subfamily with other taxa or their separation from the family Curculionidae. There have never been any conflicts between taxonomists as to which of the subfamilies Ceutorhynchinae, Conoderinae or Baridinae a particular genus should be placed, even if identification of a weevil of these taxa to the genus level is a very complicated task. No detailed morphological description of the Ceutorhynchinae is available in the literature which may be largely responsible for conflicts in the estimation of the affinities of this subfamily with similar taxa. A catalog of the world fauna of the subfamily Ceutorhynchinae with data on the host plants, key to genera, and comprehensive bibliography has been published by Colonnelli (2004); a brief review of the morphology, classification, distribution, and trophic specialization of ceutorhynchines is given by Korotyaev (2006).

Weevils of the subfamily Ceutorhynchinae mostly have a small (1.2–7, usually 1.5–3 mm long), typically broad and convex ventrally, often also dorsally, body. The length of elytra of the species from temperate regions is usually only slightly greater than their width; in many species from tropical regions their width is greater than their length. Such proportions of the body are not very common in weevils and are associated with powerful development of the indirect flying musculature. Thus, the general appearance of the adults by itself characterizes the subfamily Ceutorhynchinae as a peculiar and highly advanced taxon. Apices of the mesepimera in most Ceutorhynchinae slightly project between the posterior angles of the pronotum and elytral humeri and are visible dorsally. The rostrum in all the species is placed between coxae in repose and may be tightly clasped to the body. In many species with a moderately long rostrum the meso- and metasternum are more or less deeply depressed for reception of the rostrum, but the margins

of the rostral channel do not form high keels characteristic of another weevil subfamily with a well-developed rostral channel, the Cryptorhynchinae.

In addition to their well-developed flight, Ceutorhynchinae is the only family-group taxon of the Curculionidae (except for the tribes Rhamphini and Anoplini of the Curculioninae), whose members possess a highly developed ability to jump, which is also reflected in the appearance of the adults. The development of the ability to jump is correlated with the thickening of the hind femur, shortening of the hind tibia and outcurving its apex; the body in species capable of jumping is usually convex and compact.

Furthermore, Ceutorhynchinae is one of the few subfamilies widely represented in the aquatic habitats. In the profoundness of morphological adaptations to aquatic habitats and in the swimming abilities (Egorov, 1988) they have matched the largest and most highly specialized taxon of aquatic weevils, the subfamily Bagoinae. The ability to jump and aquatic habit have probably arisen independently in several tribes of Ceutorhynchinae which implies a high level of the general organization of this subfamily.

The host range of the subfamily Ceutorhynchinae is very wide. The majority of ceutorhynchines develop on dicotyledons, but species of several genera from different tribes are associated with monocots, and all species of the Ancient Mediterranean tribe Oxyonychini with 20 genus-group taxa develop on Ephedra (classis Pinophyta). Species of Ceutorhynchinae are generally highly specialized herbivores; in the relatively well-known Palaearctic fauna, narrowly oligophagous species are predominant, and many species are monophagous [classification of the trophic specialization after Emeljanov (1967)]. The vast majority of species of the Holarctic fauna develops on herbaceous plants. Preference for dominants of the vegetation as hosts characteristic of oligophagous insects in general (Emeljanov, 1967) is manifested by ceutorhynchines as well. For example, species of the nominotypical subgenus of the genus *Coeliodes* Schoenh., one of the three largest endemic Palaearctic genera and the largest dendrophilous genus of ceutorhynchines, are associated mostly with oaks that are the main members of the arboreal cenoses of the nemoral and Mediterranean vegetation. Yet most of the Palaearctic and, apparently, Nearctic species develop not on edificator plant species, but on cenophobes (Razumovskii, 1981), i.e., species with low

cenotic activity: weeds, ruderal species and members of the initial stages of the successions (the so-called pioneer groupings) (Korotyaev, 1992). This feature of the Ceutorhynchinae, developed to a varying degree in other weevils and in the leaf beetles, on the one hand, is responsible for the presence of the pests of vegetables and industrial crops, which are typical pioneer groupings, but on the other hand, provides wide possibilities of the use of ceutorhynchines for biocontrol of weeds.

Another important biological feature of the subfamily Ceutorhynchinae is a wide distribution among its members of such a highly advanced larval habit as gall inducing (Korotyaev et al., 2004). Kaplin (1981) believes that it was galling on spring ephemeral plants that enabled ceutorhynchines to adapt to the desert landscape in Middle Asia and become one of the most species-rich groups in the spring herbivore fauna of the sand deserts.

Examination of the material from most of the major world collections of weevils, first of all those of the Holarctic fauna, makes it possible to give the first brief outline of the distribution of the subfamily Ceutorhynchinae.

2. DISTRIBUTION OF THE WEEVIL SUBFAMILY CEUTORHYNCHINAE OVER THE ZOOGEOGRAPHICAL REALMS

The subfamily Ceutorhynchinae is distributed almost worldwide but has gained maximum diversity in the open and sparsely wooded landscapes of the temperate regions of the Old World, first of all in the Palaearctic and southern Africa, and also in the forests of South Asia. In the fauna of Central and South Americas, ceutorhynchines are less conspicuous. The Australian fauna comprises slightly more than 10 endemic species, most of which occur in riparian landscapes of the arid zone of the extratropical belt. There are two species of the southern Asian genus *Mecysmoderes* Schoenh. in northern Australia and two species of the almost worldwide distributed *Rhinoncus* Schoenh.; the rest of the species known from collections belong to the Palaeotropical tribe Hypohypurini with the range stretching from tropical Africa to Australia. Thus, nearly all the species of the Australian fauna (except, probably, *Rhinoncus australis* Oke, which occupies rather an isolated position in the genus and is most similar to the Nearctic *Rh. longulus* LeC.) are related to the Old World fauna, mostly that of the

Northern Hemisphere. In New Zealand, only *Rhinoncus australis* occurs; no members of the Ceutorhynchinae are known in Oceania, and few species live south of the tropical forest in South America. On the contrary, collections from South Africa, savannahs of Tropical Africa and open landscapes of the Mediterranean are always species-rich, and faunas of these regions remain poorly known. The fauna of the largely demolished tropical forests of Africa is insufficiently investigated and unlikely to be much diversified, whereas the fauna of the Indo-Malayan Region and southeastern Palaearctic, on the contrary, includes many endemic genera and species.

Predominance of a particular tribe of ceutorhynchines is characteristic of each zoogeographical realm. The Holarctic fauna is dominated by the tribe Ceutorhynchini and the genus *Ceutorhynchus* Germ., the latter comprising over 300 species associated almost exclusively with crucifers. The second position is occupied by *Mogulones* Reitt., subendemic to the Western Palaearctic, with 67 species developing on Boraginaceae. The third is *Thamiocolus* Thoms. with over 40 species on labiates, also distributed mostly in Western Palaearctic. The Palaearctic surpasses the Nearctic and all realms [other than the Holarctic] in the number of endemic genera, which is, probably, due to a better knowledge and a more elaborated classification of the Palaearctic fauna.

In the Nearctic, the tribe Ceutorhynchini also occupies the leading position, mainly owing to the great number of species of *Ceutorhynchus* which is, nevertheless, only one-fifth of its Palaearctic diversity. The second in the number of the endemic Nearctic species and the first in the number of the endemic genus-group taxa is the tribe Cnemogonini; it comprises there at least 10 endemic genera, including *Acanthoscelidius* Hustache with some 10 species. The tribe Phytobiini includes two endemic monotypical aquatic genera *Euhrychiopsis* Dietz and *Parenthis* LeC.

The most flourishing taxon in the fauna of the Indo-Malayan Region of the Palaeotropical Realm is the genus *Mecysmoderes* from the endemic monotypical tribe. The genus includes about a hundred described species, and this is no more than half the number of the species present in the collections. *Mecysmoderes* is distributed up to Sakhalin and the southern Kuril Islands in the north; it includes 10 species in Japan (Morimoto, 1994), only one of them being known from South Korea. A good example of the Indo-Malayan

fauna is the fauna of Sri Lanka where 12 mostly endemic species of *Mecysmoderes*, 2 species of the Indo-Malayan genus *Indohypurus* Kor., and 3 species of three Palaeotropical genera are known.

Tribe Egriini includes 3 genera in the Indo-Malayan Region, *Cyphosenus* Schze., *Ceutorhynchoides* Colonnelli, and *Hainokisaruzo* Yoshitake et Colonnelli, 2 of which include not less than 15 species. *Cyphosenus* is distributed from South Africa to North Korea, and 2 other genera are endemic to Asia, reaching South Korea or Japan in the north. Another large genus, *Augustinus* Kor. with an unclear systematic position, also comprising about 20 species, relates southern Asian and Afrotropical faunas. The majority of its species are distributed in East Asia from Jeju Island in South Korea to Malaysia, and 2 species are found in tropical Africa. In addition to the 3 genera listed in this paragraph, several others, including one to five species, are endemic to Southeast or South Asia; the systematic position of some of these genera is obscure. None of the genera from the Indo-Malayan Region manifests close affinity to the Neotropical taxa.

The overwhelming predominance of the tribes Ceutorhynchini and Egriini with a wide variety of the species is characteristic of southern and tropical Africa. Species of several genera of the tribe Hypurini also are numerous there; this tribe, in addition, is species-rich in the Saharo-Gobian Region of the Palaearctic. The small monotypical tribe Hypohypurini Colonnelli with the tropical Afro-Australian range includes 2 species in Madagascar and 1 species in Central Africa. The endemic African tribe Lioxyonychini occupying a widely isolated taxonomic position comprises at least 5 genera with over 15 species distributed from the South African Subregion to Ethiopia. In addition to these taxa, species of the genus *Ceutorhynchus* occur in southern and in some parts of tropical Africa; and species of the predominantly Palaearctic genus *Mogulones* occur in Ethiopia. The systematic position of a few small Afrotropical genera is unclear (Korotyaev, 2000).

In the Neotropical Realm, Ceutorhynchinae is represented by more than 20 genera of the single tribe Cnemogonini, subendemic to the New World and probably forming several rather widely separated lineages. This realm is the only one including no endemic species of the genus *Rhinoncus*; 1 species of this genus was introduced to Brazil from Australia. The affinities of the tribe Cnemogonini in the Old World are not found; the only Palaearctic species of this tribe, the Holarctic boreal *Auleutes epilobii* (Pk.), may have migrated to the Palaearctic relatively recently via the Bering Land Bridge and still occurs in Alaska, Kamchatka, and Magadan Province.

3. CHARACTERISTIC FEATURES OF THE COMPOSITION AND AFFINITIES OF THE HOLARCTIC FAUNA OF THE WEEVIL SUBFAMILY CEUTORHYNCHINAE

The faunas of the Palaearctic and Nearctic, united in the Holarctic Realm, have an important similarity which is classified as a homology (Geptner, 1936). It is manifested not only in the predominance of the genus *Ceutorhynchus* in the number of species in the Palaearctic and Nearctic faunas, but also in the presence of endemic and subendemic tribes, a subtribe, and genera, common and endemic to the two faunas. As one of the main distinctions between the Palaearctic and Nearctic faunas, occupation of the second position in them by different taxa may be mentioned. In the Palaearctic, these are the Ancient Mediterranean genera of the tribe Ceutorhynchini and two large tribes (also Ancient Mediterranean), the endemic Oxyonychini with more than 60 species in 20 genus-group taxa, and the subendemic Hypurini. In the Nearctic, the only highly diversified taxon besides the genus *Ceutorhynchus* is the tribe Cnemogonini, subendemic to the New World, while the Ceutorhynchini include, in addition to *Ceutorhynchus*, only 2 genera common with the Palaearctic, *Sirocalodes* Voss and *Nedyus* Schoenh., and 2 endemic genera *Allosirocalus* Colonnelli with ca 15 species on Scrophulariaceae, and mono- or oligotypical *Rileyonymus* Dietz.

The Nearctic fauna sharply differs in the absence of the tribe Coeliodini, the largest tribe of dendrophilous ceutorhynchines in the Palaearctic, including 3 species in the taiga zone on birches and alders, and over 30 species in the broadleaf forests, mostly on oaks. Its absence from the New World is especially noticeable considering a wide diversity of the genus *Curculio* L. represented in the U. S. A. and Mexico by 45 species (O'Brien, Wibmer, 1982), most of which also develop on oaks. In this distributional feature the tribe Coeliodini parallels the tribe Rhamphini of the subfamily Curculioninae, comprising several genera of leaf miners. Similarly to the tribe Coeliodini, Rhamphini are widely represented on oaks both in the Western and Eastern Palaearctic, but not in the Nearctic; however, in contrast to Coeliodini, the tribe Rhamphini includes

several Nearctic species on willows, alder, and birch. An important difference between the Palaearctic and Nearctic faunas is that they contain elements of different tropical faunas, the Afrotropical and Indo-Malayan faunas in the Eastern Hemisphere, and the Neotropical fauna in the Western Hemisphere.

The main host-plant taxa of the ceutorhynchines in southern parts of the Palaearctic and Nearctic are also different. In the southern Palaearctic forests, the greatest number of Ceutorhynchinae species develop on Fagaceae and Ericaceae, in the southwestern part of the subrealm also on Ulmaceae, Anacardiaceae, and Celastraceae; and in the southeastern part, on Styracaceae, Symplocaceae (see Yoshitake and Colonnelli, 2005) and Caprifoliaceae (see Yoshitake et al., 2006). The bulk of the desert fauna in the Palaearctic is formed by species of the endemic tribe Oxyonychini, developing on *Ephedra*, and subendemic tribe Hypurini, associated mainly with species of the family Chenopodiaceae and with *Lycium* L. (family Solanaceae); some characteristic species of *Ceutorhynchus* in North Africa live on plants of the family Capparaceae. In the southern Nearctic, the forest fauna is less enriched with the dendrophilous species as compared to the Palaearctic; their number is increased primarily by species of the predominantly Neotropical genera *Orchestomerus* Dietz and *Panophthalmus* Buchanan, developing on lianas of the family Vitaceae. A few known hosts of ceutorhynchines in the arid regions of North America belong to the families Onagraceae and Rubiaceae, which also harbor many species of the Cnemogonini in the forests of Central and South Americas. Only Brassicaceae and Fumariaceae are important constituents of the Ceutorhynchinae diet in the both parts of the Holarctic, supplemented by Polygonaceae in the central and northern zones of the realm.

The tribes and subtribes with Holarctic ranges are the monotypical tribe Mononychini, Tapinotini with c 2 monotypical genera in the Palaearctic and 1 oligotypical genus in North America, Scleropterini with 7 genera, and the subtribe Phytobiina (with 6 genera) of the worldwide distributed tribe Rhinoncini. These taxa include only a small part of species of the Holarctic fauna, and most of them have the majority of the genera and species in the Palaearctic. For example, the widely taxonomically isolated monotypical tribe Mononychini includes 1 Nearctic species, *Mononychus vulpeculus* (F.), widely distributed in the U. S. A. and Canada, and 9 species in the Palaearctic, evenly distributed between nemoral Europe (2 species), Western Mediterranean (1 species), Anatolia and eastern Transcaucasia (1 species), South Kazakhstan and plane Middle Asia (1 species), Hissaro-Darvaz Mountains (1 species), southern East Siberia and Mongolia (1 species), southern East Siberia and the Far East (1 species), and North China (1 species).

The subendemic Holarctic tribe Scleropterini with 7 genera occurs outside the temperate belt only in the Ryukyus, in the south of the Korean Peninsula and China, including Taiwan, in Nepal and North Vietnam. It is represented in the Nearctic by 3 endemic species, of which 2, *Asperosoma echinatum* (Fall) and *Rutidosoma* (*Prorutidosoma*) *decipiens* (LeC.), belong to the endemic monotypical genus and subgenus, respectively. All 3 Nearctic species are members of the boreal and subboreal faunal complexes. In the Palaearctic, Scleropterini include 5 endemic genera, one of which, *Scleropterus* Schoenh., is represented in southern Siberia and the Far East, and also in China by several upland species. The genus *Rutidosoma* Steph. in addition to the Holarctic boreo-subboreal nominotypical subgenus with 2 or 3 species includes the mountain-forest European subgenus *Scleropteridius* Otto with 3 species, the monotypical Central Tien Shanian subalpine subgenus *Victorinus* Kor., and 2 endemic monotypical East Asian subgenera in the Stenopean and Orthrian regions. The subendemic Holarctic genus *Homorosoma* Friv. includes 9 species in the Palaearctic (1 in southeastern Europe, Kazakhstan, southern East Siberia and the Far East; 3 in the Far East, one of them distributed to the south as far as North Vietnam; and 5 endemic species in East China) and 1 in southern Canada and in the U. S. A.

Out of the 6 genera of the subendemic Holarctic subtribe Phytobiina only *Pelenomus* Thoms. includes 2 or 3 endemic species in tropical Asia, which are very closely related to the Siberian-American subboreal-subtropical *P. japonicus* (Roel.). All the other genera of the Phytobiina include subboreal or boreal species, constituting a considerable part of the high-latitude fauna of both the hemispheres; *Neophytobius* Wagn. has several endemic species in the Asian uplands. The genera of the subtribe Phytobiina are almost evenly distributed between the Palaearctic and Nearctic: *Pelenomus* and *Neophytobius* include in their faunas ca. 20 endemic and one common species, *Phytobius*, 1 common species; the subtribe also includes 1 endemic monotypical genus in the Palaearctic and 2 endemic monotypical genera in the Nearctic. Both the

genera with the Holarctic distribution are much more widely represented in the Palaearctic than in the Nearctic: *Pelenomus* includes 11 species in the former and 8 in the latter; *Neophytobius* has 8 or 9 species in the Palaearctic and only 1 species in western North America.

Separation of the tribe Tapinotini seems worthy; it comprises the monotypical Palaearctic genus *Tapeinotus* Schoenh. and a very dissimilar to it Nearctic *Acallodes* LeC. with 3 species; the monotypical *Tibetiellus* Kor. from the Tibet uplands is probably close to these genera. The species of *Tapeinotus* and *Acallodes* develop on *Lysimachia* L. (Primulaceae) and share a number of morphological features although they are strikingly different in appearance. All the 3 genera are typical of the temperate latitudes and uplands of the Northern Hemisphere.

Out of the 8 endemic Holarctic genera, only *Auleutes* Dietz is more widely represented in the Nearctic than in the Palaearctic. In the Nearctic, it includes 10 species, one of which, *A. epilobii* (Pk.), also occurs in the temperate and high latitudes of Eurasia. *Auleutes* belongs to the tribe Cnemogonini subendemic to the New World.

Other tribes include only a few genera with Holarctic ranges. These are the above-mentioned *Nedyus* Schoenh. with 1 transpalaearctic and 1 Nearctic species, both developing on nettle, and *Sirocalodes* Voss with approximately 20 species on Fumariaceae, of which only 4 are distributed in North America. In contrast to *Nedyus*, the genus *Sirocalodes* includes not only boreal, but also subboreal-subtropical and subtropical species, reaching central Mexico in North America, and Nepal and Taiwan, in Asia. Species from southern parts of the *Sirocalodes* range belong to characteristic endemic South Asian and Nearctic groups probably deserving the subgeneric rank, whereas species from the boreal belt constitute 2 vicarious pairs. The North American *S. sericans* (LeC.) and *S. siculus* (Dietz) are very close to the Eastern Siberian *S. marshakovi* Kor. and *S. notatus* (Bris.), correspondingly. It is noteworthy that the North American species from these pairs occur in the landscapes sharply different from the taiga where their Siberian counterparts occur.

Only a few species have Holarctic ranges. They are members of the boreal [*Auleutes epilobii* (Pk.)], taiga [*Ceutorhynchus querceti* (Gyll.)], and Circum-Polar [*Ceutorhynchus barkalovi*, *Prisistus olgae* (Kor.)]

faunal complexes, but there are also species with boreal-subboreal and even subboreal-subtropical ranges, for example, the aquatic *Phytobius leucogaster* (Marsh.) and near-water *Pelenomus japonicus* (Roel.). Several pairs of vicarious species have been found in the boreal complexes, and one pair is known in the meadow-steppe complex; it consists of the Eastern Siberian *Ceutorhynchus kolymensis* Kor., occurring in the steppefied meadows in the Upper Kolyma basin, and an undescribed species from Arizona which is very close to it.

As one can see, the portion of the family and genus groups taxa endemic to the Holarctic (and distributed in its both parts) is fairly large. All the Holarctic genera except *Sirocalodes* are distributed in the boreal and subboreal belts; endemic tribes and subtribes comprise aquatic, near-water, and woodland or predominantly mesophilic species. The number of species with Holarctic ranges is very small and is considerably smaller than the number of species incidentally or with a purpose introduced into North America from Eurasia. The latter number is steadily increasing due to both incidental invasions and acclimatization of species as biocontrol agents (Anderson and Korotyaev, 2004). Introduced species constitute 10% of the fauna of Canada and the U. S. A. Some of them, e.g., *Ceutorhynchus obstrictus* (Marsh.), *C. typhae* (Hbst.), *C. erysimi* (F.), and *Glocianus punctiger* (C. R. Sahlb.), are the commonest species in the North American collections.

The diversity of the Ceutorhynchinae fauna in North America gradually increases from the tundra and taiga zones [19 species in the Yukon Territory, Canada (Anderson, 1997); 75 species in Canada and Alaska (McNamara, 1991)] to the warm-temperate belt and reaches its maximum in the south of the nemoral zone and in the zone of the Mediterranean-type vegetation and prairies. Then the diversity drops in the coastal areas down to 17 species (only 2 *Ceutorhynchus*) in Florida (O'Brien and Wibmer, 1982; unpublished author's data) and 5 in southernmost California (unpublished author's data). The pattern of the ceutorhynchine faunal change at the southern border of the U. S. A. fits well the adopted scheme of the biogeographical division of America: Florida retains the Nearctic type of the fauna with the increasing role of the southern Nearctic elements (3 out of the 7 Nearctic species of the genus *Parauleutes* Colonnelli) and noticeable presence of the transzonal near-water and ruderal species; only the southernmost part of the pen-

insula (where no species of the *Ceutorhynchus*, *Pelenomus*, *Rhinoncus*, and *Perigaster* are found) the Neotropical *Perigasteromimus tetracanthus* (Champ.) and *Parauleutes inspersus* (Champ.) plus endemic monotypical *Pelenosomus* Dietz, close to Central American genera, occur. On the Pacific coast, the fauna retains the sharply depauperate Holarctic type down to Mexican border, where it is formed of 4 species of *Ceutorhynchus* and 1 species of the endemic Nearctic genus *Acanthoscelidius* Hust.

The Holarctic fauna rather gradually changes to the Neotropical fauna within Mexico. *Prima facies*, the presence of a group of small endemic genera and strengthening of the positions of the Neotropical fauna are more characteristic of the Mexican fauna than the retention of the Holarctic elements. No representatives of the Holarctic tribes Mononychini and Scleropterini are found in Mexico; of the almost worldwide distributed tribe Phytobiini with approximately 15 species from 6 genera in the U. S. A. and Canada, only *Pelenomus squamosus* (LeC.) has been found in northern Mexico. Out of the 3 Holarctic genera of the tribe Ceutorhynchini only *Ceutorhynchus* and *Sirocalodes* occur in Mexico; the former has only about 10 species in Mexico, of which 3 or 4 are endemic to the country, while *Sirocalodes* includes 1 species closely allied to *S. tescorum* (Fall) from the South-West of the U. S. A. No members of the largest Nearctic genus of the tribe Ceutorhynchini, *Allosirocalus* Colonnelli with ca. 15 species, about half of which are distributed in the southern U. S. A., are found in Mexico. Two largest subendemic (*Auleutes*) and endemic (*Acanthoscelidius* Hustache) Nearctic genera of the tribe Cnemogonini subendemic to the New World are known in Mexico from one record in the northernmost regions each. Small boreo-subboreal Nearctic genera *Perigaster* Dietz and *Cnemogonus* LeC. have not been found in Mexico at all, while the endemic genus *Euauleutes* Colonnelli comprises several common species, and the bulk of collections from forest landscapes consists of species of the Neotropical genera *Hypocoeliodes* Fst., *Borisauleutes* Colonnelli, *Orchestomerus* Dietz, and *Perigasteromimus* Colonnelli. The commonest species in the riparian landscapes are the Neotropical *Parauleutes inspersus* (Champ.) and *Perigasteromimus tetracanthus* (Champ.). A small Neotropical genus *Perigasteromimus* includes a very distinctive undescribed endemic Mexican species; one of the most advanced and species-rich genera in the Neotropical Realm, *Panophthalmus* Buchanan, includes 2 species in the Mexican fauna (Korotyaev, 2001).

4. A REVIEW OF HOLARCTIC SPECIES-GROUPS OF THE GENUS *CEUTORHYNCHUS*

4.1. The General Characteristic of the Genus *Ceutorhynchus*

The genus *Ceutorhynchus* Germ. is one of the largest in the family Curculionidae, with over 300 species known by the end of 2003 (Colonnelli, 2004). The majority of its species are distributed in the Holarctic. The range of this genus is also large; it includes the entire Holarctic Realm, and partly also the South African and Sudano-Zambezian subregions of the Afrotropical Region. The actual number of *Ceutorhynchus* species in tropical Africa is probably much greater than is presently known, as the families Brassicaceae, Resedaceae, and Capparaceae, on which weevils of this genus develop, are widely represented there. *Ceutorhynchus* comprises several times more species than any other genus of the subfamily Ceutorhynchinae. For example, it is twice as large as the genus *Mecysmoderes*, the largest in the Indo-Malayan Region and subendemic to it; in the Afrotropical Region and Neotropical Realm no genus with more than 50 species is known. About 70% species in the Palaearctic are concentrated in the western part of the region. The fauna of the central Palaearctic is much less diversified as compared to the Mediterranean, and only 80 species are distributed in the Eastern Palaearctic. The Nearctic representation of *Ceutorhynchus* is about one-fifth of the number of the Palaearctic species. A considerable part of the North American species belongs to endemic species-groups, but nearly a quarter of the fauna is closely related to the Palaearctic species.

No subgeneric subdivision of the genus *Ceutorhynchus* is adopted. After separation from this genus all the subgenera associated with plant families other than Brassicaceae and Resedaceae *Ceutorhynchus* looks a natural (mono- or paraphyletic) taxon. Synonymizing with *Ceutorhynchus* genus *Ceuthorhynchidius* Jacquelin du Val (= *Neosirocalus* Ner. et Wagn.), which included a number of well-defined groups with remote affinities counting over 30 species, the presence of several large groups of closely related species in *Ceutorhynchus*, and a wide morphological diversification in this genus imply the necessity of elaboration of its subgeneric classification. A yearly description of new, occasionally very characteristic species of *Ceutorhynchus* from different regions of the Old World and the New World makes a task of elaboration of the com-

prehensive classification in the close future very problematic; therefore, it seems reasonable to distinguish gradually as subgenera the most clearly defined groups of species. One of these is the Holarctic *C. cochleariae* (Gyll.) group dealt with below. In addition to this group, some others include representatives of both the Palaearctic and Nearctic faunas.

4.2. The Holarctic Species-groups of the Genus Ceutorhynchus

1. **C. assimilis** (Pk.) group. This group is one of the largest in the Palaearctic and comprises there over 20 species (Korotyaev, 1980); the North American *C. invisus* Fall and 2 its close allies from mountain regions in the arid South-West of the U. S. A. are related to them. An undescribed species very similar to, but clearly different from *C. invisus* was found recently in northeastern Yakutia. This finding shows that even in the northernmost Beringia different although closely related species usually occur in the Asian and American sectors, thus supporting the statement of Berman et al. (2001) concerning the separate existence and evolution of these two parts of the Beringian biota in the Pleistocene.

2. **C. rapae** Gyll. group includes the transpalaearctic polyzonal *C. rapae*, introduced to North America and widely established there as a pest of crucifer garden vegetables, and its close ally, endemic Northern American *C. subpubescens* LeC., also widespread in Canada and the U. S. A.

3. **C. puncticollis** Boh. group. An undescribed species from Arizona is very close to 4 very similar Palaearctic species of this group. This is the most xerophilic of the Holarctic species-groups of *Ceutorhynchus*. The finding of a member of this group in Arizona implies a possibility of the faunal exchange of the meadow-steppe species like *C. kolymensis* Kor. (a member of the *C. puncticollis* group) via the Bering Land Bridge in the Upper Pleistocene.

4. **C. seniculus** Ch. Bris. group. The northern Nearctic *C. omissus* Fall is closely related to *C. seniculus* from Mongolia and Siberia, isolated in the Palaearctic fauna.

5. **C. typhae** (Hbst.) group includes 3 very close Palaearctic and 2 Nearctic species. All of them are mesophilic; the Eastern Palaearctic *C. asiaticus* Kor. and western American *C. sparsus* Hatch are very similar ecologically, both developing on species of the genus *Barbarea* R. Br. (bittercress).

6. **C. semirufus** LeC. group includes 2 North American species and *C. sinicus* (Voss) from China, South Korea, and Japan. The two Nearctic species are much more similar to each other than any of them to *C. sinicus*, but the latter is very similar bionomically to *C. semirufus*, both developing on small-sized *Cardamine* in open wet habitats (often at roadsides).

7. **C. zimmermannii** Gyll. group includes, in addition to this North American species, *C. piceolatus* Ch. Bris., distributed from European Russia to Yakutia and Mongolia. Both the species belong to the ruderal complex and occur from the mountain-taiga regions of Siberia to Caspian semideserts (*C. piceolatus*), and from southern Canada to the sparse pine forests of Florida and Mexico (*C. zimmermannii*).

8. **C. buniadis** Pen. group, in addition to this Eastern European species and the Eastern Siberian *C. matisi* Kor., includes an undescribed species from northern California which, similarly to *C. matisi*, occurs in moist habitats; it is found on *Barbarea*.

9. **C. barkalovi** Kor. group is formed of the only species with a Circum-Polar distribution.

10. **C. pervicax** Wse. group includes several closely allied species in the Palaearctic, to which belong, in particular, the Western Palaearctic *C. pervicax* and Palaearchearctic [= Southeastern Palaearctic] *C. nitidulus* Fst., associated primarily with near-water crucifers of the genus *Cardamine*, and the widely distributed in North America *C. americanus* Buchanan, also mesophilic and mesohygrophilic.

11. **C. cochleariae** (Gyll.) group in the number of species included is the second-largest after the *C. assimilis* group, but differs from that group in the almost even distribution between the Palaearctic and Nearctic. It consists of a number of well-defined assemblages of species, which are classified as subgroups in the text below.

4.3. Review of the Ceutorhynchus cochleariae Species-group

The main distinguishing character of the *C. cochleariae* group is an unusual secondary sex character: the females have mucro on the middle tibia; females from some populations of *C. japonicus* Korotyaev, 2004 have mucro also on hind tibia. Of all the species of the *C. cochleariae* group, only females of the North American *C. anthonomoides* Dietz have middle tibia non-mucronate, but in females of closely allied species

the mucro is present. The aedeagus in most species is similar: poorly sclerotized, subparallel-sided or weakly widening apically, with a wide, almost straight or, occasionally, weakly emarginate apical margin. In addition, the group is characterized by the following combination of features.

Body small, 1.3–2.8 mm long, usually with moderately convex dorsum, rather wide, noticeably shiny in the majority of species. Vestiture usually sparse, fine and uniform, except for *C. querceti* (Gyll.) subgroup where it is finely speckled and composed of recumbent white and dark scales; dorsal side in *C. pusillus* LeC. densely covered with white scales and subrecumbent yellow hairs, and in *C.* sp. pr. *pusillus* intervals of elytra with almost regular rows of rather long erect hairs. Rostrum rather thick in the *C. cochleariae* subgroup and relatively slender in *C. pusillus* and *C.* sp. pr. *pusillus*, moderately to rather long, evenly curved, matte, occasionally with weak median carina in basal half. Antennae rather long; club spindle-shaped, short or moderately elongate, rarely (in *C. squamatus* LeC.) rather strongly elongate. Pronotum moderately transverse, with convex disc, obtuse lateral tubercles and shallow median sulcus. Apical margin very weakly raised, usually with shallow emargination medially. Elytral striae rather wide and deep; intervals usually weakly convex, shining; in the Caucasian *C. filirostris* Rtt. intervals moderately or strongly convex and bearing 1 row of well-visible granules. Legs moderately long and thick, femora unarmed, claws small, weakly diverging. simple or with fine basal tooth. Anal sternite of male with moderately deep fovea in apical part; in species of the *C. querceti* subgroup anal sternite deeply foveate also in female and pygidium in both sexes varyingly strongly raised along midline and bearing comb of yellow hairs. Dorsal surface always with more or less distinct white scutellar spot, sides of pronotum in some species also densely covered with white scales and thus contrasting with darker disc. Legs and antennae in some species red or brown; in species of *C. querceti* subgroup large part of elytra often also reddish brown.

All Palaearctic members of this group are mesophilic and occur usually in forest habitats, often near water. Plants of several genera have been recorded as hosts for *C. cochleariae*. *C. querceti* occurs in Europe and in the largest part of Siberia only on *Rorippa islandica* Oel., but lives in great numbers on *Draba sibirica* L. in southern Tuva in the absence of *R. islandica*, and is common on *Rorippa palustris* (L.)

Besser in Magadan Province. *C. filirostris* in the Caucasus occurs in the forests on *Alliaria petiolata* M. B., *Dentaria quinquefolia* M. B., *Cardamine uliginosa* M. B., occasionally also on *Erysimum aureum* M. B. Hosts of the Far Eastern species are unknown. A series of *C. dauricus* Kor. was collected in South Korea at the forest margin, near rice fields, and by the river, but special examination of several species of crucifers in that locality, including more than one species of *Cardamine*, provided no additional specimen.

The *C. cochleariae* group includes a number of varyingly distinct subgroups.

The **C. querceti** subgroup includes *C. querceti*, the only Holarctic member of the *C. cochleariae* group, which is common in the north of the forest zone and in the south of the tundra zone of Eurasia and North America and reaches Mexico City along the high mountains of western U. S. A.; very similar to it *C. neglectus* Bl. from central and eastern Canada and the U. S. A.; and an undescribed species closely related to *C. neglectus* from northwestern North America spread as far as Fairbanks in the north. A separate position in this subgroup is occupied by *C. hamiltoni* Dietz, developing on *Cakile* Mill. on the Atlantic coast of North America in southern Canada and in New England. This boreo-subboreal forest subgroup without endemic species in the nemoral, steppe, and desert zones is widely distributed in the tundra zone of both the hemispheres and has formed a distinctive species in very specific oceanic coastal environment.

The **C. cochleariae** subgroup in addition to its central species distributed in the broadleaf and mixed forests of Europe and Siberia as far as Lake Baikal in the east includes 3 clearly distinct from *C. cochleariae* and closely allied species from the forests of the Caucasus and Northeast Turkey, 4 southern Far Eastern species clearly separated from each other and from their European allies, and *C. erwini* Kor. et O'Brien from the middle part of California. Apart from *C. cochleariae*, these are almost exclusively nemoral species; only *C. dauricus*, common in Primorskii Territory of Russia and in South Korea, is distributed westward as far as eastern Mongolia. Most species of this subgroup are associated with cardamines and are also found on other woodland crucifers *Alliaria petiolata* and on species of *Dentaria* L. An undescribed species from Northeast Turkey is monophagous on *Pachyphragma macrophyllum* (Hoffm.) N. Busch, a Tertiary relict endemic to the Euxine Province. This

group is also characterized by distribution within one subzone, that of the broadleaf forests, the presence of one species with a wide Euro-Siberian range, and the Holarctic range of the entire subgroup. The existence of 3 centers of endemism is worth of mentioning: those in eastern Pontian area, in mid-latitude part of the Far East, and in middle California.

The Nearctic *C. anthonomoides* Dietz subgroup is close to the preceding one. Its central species is associated with *Dentaria* in the broadleaf forests of the central-eastern U. S. A. A closely related undescribed species occurs in the forests of Texas and Louisiana and also has been collected from *Dentaria*. Another undescribed species has been reared from *Selenia aurea* in Texas, and *C. carteri* Broun occurs in the prairies of the U. S. A. and southwestern Canada; the latter species is very distinct from the woodland members of this subgroup but clearly continues the lineage of *C. anthonomoides*—*C.* sp. pr. *anthonomoides* (from Texas and Louisiana). A separate position in this subgroup is occupied by *C. squamatus* LeC., the host plant of which is unknown. Within this subgroup, a transition may be seen from habitation on mesophilic and near-water crucifers, probably from the genera *Cardamine* and *Dentaria*, apparently initial for this subgroup and for the Palaearctic *C. cochleariae* subgroup, to life in the prairies.

Another endemic Nearctic subgroup, the *C. pusillus* LeC. subgroup, has adapted to the arid landscapes and comprises 2 common species from the western U. S. A. *C. pusillus* occurs in the prairies and semidesert regions from Oregon to southern California, feeding on several ruderal species of crucifers. An undescribed species closely related to *C. pusillus* is endemic to the coastal regions of southern California and apparently also belongs to the ruderal complex, as it has been collected on the introduced Mediterranean *Brassica nigra* Koch, densely covering the slopes of the hills along the Pacific coast. These 2 species retain the secondary sex characters typical of the group and are closest to the *C. querceti* subgroup in the structure of the tarsal claws and coloration of the body, but have acquired a number of strongly expressed xeromorphic features in the vestiture and proportions of the body. The dorsum in both the species is flattened, elytral outline is more angular than in the woodland species, the sides of the pronotum and elytra with varyingly wide rufous margin, tarsi narrow and long, vestiture of dorsal surface rather long, dense, and, in addition, more or less strongly raised; dorsum of *C. pusillus* is

densely covered with light scales. In contrast to the preceding subgroup, no species relating this subgroup to the mesophilic allies is present, or has been found in the recent fauna.

The *C. cochleariae* species-group exemplifies wide possibilities of an even low-rank taxon in adaptation to different landscapes in several natural zones, including those so contrasting as the tundra and Sonoran deserts. This group also shows the conventional character of the taxonomic categories above the species rank: it has a complicated structure and possesses a range including an entire zoogeographical realm, which is usually typical of the tribes, and its members occur in a wide range of landscapes of the cold, temperate, and subtropical belts of the Northern Hemisphere.

As one can see, at least 25 species (about a quarter of the fauna) of the genus *Ceutorhynchus* in North America belong to species-groups common with the Palaearctic fauna. Representatives of the Holarctic groups are present in the fauna of all the natural zones of North America. One of the two species of *Ceutorhynchus* common for the Palaearctic and Nearctic, *C. barkalovi*, occurs in the tundra zone, the other, *C. querceti*, is a polyzonal mesohygrophilous species distributed from the tundra of Alaska and northern Canada to the highlands of the southwestern U. S. A. and northern Mexico. Other species from the Holarctic groups are to a varying degree similar to their allies from the neighboring continent but clearly distinct. This implies effective exchange by species between Eurasia and North America in the Tertiary and, probably, lower Quaternary time, and yet an independent existence of the two faunas even at high latitudes during most of the Pleistocene (Berman et al., 2001).

5. CHARACTERISTICS OF THE PALAEARCTIC FAUNA OF THE SUBFAMILY CEUTORHYNCHINAE

Twelve out of the 14 tribes of the subfamily Ceutorhynchinae accepted in the modern classification (Colonnelli, 2004: Oxyonychini, Coeliodini and Tapinotini E. Colonnelli amalgamates with other tribes) are represented in the Palaearctic, only two Palaeotropical tribes Lioxyonychini and Hypohypurini are missing. 102 out of the 167 genera of the world fauna are distributed in this region [some genera accepted by Colonnelli (2004) are treated here as subgenera], with over half of the 1316 species of Ceutorhynchinae known by the end of 2003 (Colonnelli, 2004). Seventy-eight genera are endemic to the Palaearctic,

eight genera (*Auleutes*, *Mononychus*, *Nedyus*, *Neophytobius*, *Pelenomus*, *Prisistus*, *Rutidosoma*, and *Sirocalodes*) are represented also in the Nearctic fauna, one (*Homorosoma*), in the Nearctic and in the Indo-Malayan Region of the Palaeotropics, six (*Ceutorhynchoides*, *Hainokisaruzo*, *Cyphauleutes*, *Dieckmannius*, *Mecysmoderes* and *Phytobiomorphus*), in the Indo-Malayan Region, two (*Micrelus* and *Neoplatygaster*), in the Afrotropical Region, five (*Augustinus*, *Hypurus*, *Pericartius*, *Phytobius*, and *Cyphosenus*), in the Palaeotropical Realm, and the largest genus *Ceutorhynchus*, in the Nearctic and in the Afrotropical Region (mainly in the South African Subregion). The genus *Rhinoncus* has an almost worldwide distribution, out of its 36 species 23 belong to the Palaearctic fauna and most of them are endemic to it. The greatest numbers of species in the Palaearctic after the widespread genus *Ceutorhynchus* (300) include the endemic genera *Mogulones* (67), *Thamiocolus* (40), and *Coeliodes* (34 species) (Colonnelli, 2004).

Characteristic features of the Palaearctic fauna are strong prevalence of the Western Palaearctic over the eastern part of the region in the generic and species diversity and the dominance of the fauna of open landscapes over the forest faunas. Local and common species diversity in the Korean Peninsula (58 species) constitutes one-quarter to one-third of the diversity in the European regions of approximately the same size and with similar landscapes (Korotyaev and Hong, 2004). For example, 125 Ceutorhynchinae species are recorded for Greece (Colonnelli, 2004) which has a territory smaller by one-third than that of the Korean Peninsula. The fauna of Tuva with its sharply continental climate and the territory 3/4 as large as that of the Korean Peninsula is somewhat more species-rich (67 species) than the Korean fauna.

A specific feature of the Western Palaearctic fauna is the association of the majority of the species with herbaceous plants from the families that played an important role in the Tertiary Ancient Mediterranean flora: Brassicaceae, Boraginaceae and Lamiaceae. All the largest endemic and subendemic genera of the ceutorhynchine fauna of the southeastern Palaearctic are associated with genera or families of trees and shrubs most widely represented in extratropical regions of East Asia. For example, 10 species of the genus *Mecysmoderes*, the most species-rich in the Indo-Malayan and East Asian regions, have been recorded in Japan from *Rhododendron* L. (Morimoto, 1994) with 650 out of the 850 known species occur-

ring in China (Wielgorskaya, 1995). Host plants of the ceutorhynchine genus *Wagnerinus* Kor. with 16 species (Yoshitake et al., 2006) belong to 2 genera of the family Caprifoliaceae mainly distributed in the boreal and temperate belts of the Northern Hemisphere and the most diversified in East Asia (Wielgorskaya, 1995): East Asian genus *Weigela* Thunb. and genus *Abelia* R. Br. which, in addition to the Turano-Orthrian-Stenopean part of the range also occurs in Mexico. Species of two closely allied genera *Ceutorhynchoides* Colonnelli and *Hainokisaruzo* Yoshitake et Colonnelli, occurring in the warm-temperate and cold-temperate forests, are associated with trees and shrubs of the families Styracaceae and Symplocaceae (see Yoshitake and Colonnelli, 2005) which are grouped together in many classifications (Takhtajan, 1987). It is noteworthy that the genus *Ceutorhynchoides* is distributed mostly in the East Asian Region where Styracaceae also have their greatest diversity, while most species of the genus *Hainokisaruzo* are known from the Indo-Malayan Region, where the family Symplocaceae is widely represented (Takhtajan, 1987).

A new characteristic feature found in the composition of the highland faunas of the extratropical Asia is the presence of a complex of endemic species of the genera *Ceutorhynchus*, *Neophytobius* and *Scleropterus* in the upper mountain belt of Tien Shan, Himalayas, Tibet, Altai-Sayan Mountains, and Sredinnyi Khrebet in Kamchatka. Ceutorhynchinae is the only taxon of the division Phanerognatha of the Curculionidae nearly reaching, together with broadnosed weevils, the upper distributional limit of the seed plants in Asian highlands. Outside the Palaearctic, alpine representatives of this subfamily are known only in North America, where several *Ceutorhynchus* species occur at elevations above 3000 m. High-latitude species of Ceutorhynchinae are also known only in the Northern Hemisphere, and most of them belong to the genus *Ceutorhynchus*.

It would be of some interest to compare, on the material of the Ceutorhynchinae, two schemes of the zoogeographical subdivision of the Palaearctic in the part where they are conflicting, i.e., in the approach to the longitudinal and latitudinal separation of the nemoral and subtropical forest faunas, and also in clarifying the zoogeographical attribution of the fauna of Anatolia (Asia Minor).

The scheme of zoogeographical subdivision proposed by Emeljanov (1974) reflects regularities of the

Distribution of the genus-group taxa of the subfamily Ceutorhynchinae over four regions of the Palaearctic

Genus (subgenus)	Region			
	European	Stenopean	Hesperian	Orthrian
Mononychus	+	+	+	−
Eubrychius	+	−	+	−
Phytobius	+	+	+	+
Pelenomus	+	+	+	+
Rhinoncus	+	+	+	+
Marmaropus	+	−	−	−
Amalus	+	+	+	−
Homorosoma	+	+	+	+
Rhinoncomimus	−	+	−	+
Brachiodontus	+	−	−	−
Rutidosoma s. str.	+	+	−	−
Rutidosoma (*Scleropteridius*)	+	−	−	−
Rutidosoma (*Heorutidosoma*)	−	+	−	−
Rutidosoma (subgen.?)	−	−	−	+
Scleropteroides	−	+	−	+
Scleropterus	+	+	+	+
Wagnerinus	−	+	−	+
Tapeinotus	+	+	+	−
Amalorrhynchus	+	+	+	−
Drupenatus	+	−	+	−
Poophagus	+	−	−	−
Ceutorhynchus	+	+	+	+
Oprohinus	+	−	+	−
Calosirus	+	?+	+	?+
Sirocalodes	+	+	+	+
Ranunculiphilus s. str.	+	+	+	−
Ranunculiphilus (*Austroceuto-rhynchus*)	+	−	+	−
Prisistus	+	+	+	+
Cardipennis	−	+	−	+
Ethelcus	+	−	+	−
Stenocarus	+	−	+	−
Neoglocianus	+	−	+	−
Glocianus	+	+	+	−
Hesperorrhynchus	−	−	+	−
Phrydiuchus	+	−	+	−
Parethelcus	+	−	+	−
Dieckmannius	−	−	−	+
Bohemanius	−	−	+	−
Hadroplontus	+	+	+	−
Ectamnogaster	−	−	+	−

Table (Contd.)

Genus (subgenus)	Region			
	European	Stenopean	Hesperian	Orthrian
Coeliastes	+	–	+	–
Nedyus	+	+	+	–
Datonychidius	–	–	+	–
Datonychus	+	+	+	–
Thamiocolus	+	+	+	–
Sinocolus	–	+	–	–
Mogulones	+	+	+	–
Mogulonoides	+	–	?+	–
Boragosirocalus	–	–	+	–
Microplontus	+	+	+	–
Indicoplontus	–	–	–	?+
Trichosirocalus	+	–	+	–
Micrelus	+	–	+	–
Zacladus s. str.	+	+.	+	–
Zacladus (*Scythocladus*)	+	–	+	–
Zacladus (*Angarocladus*)	–	+	–	–
Zacladus (*Amurocladus*)	–	+	–	–
Eucoeliodes	+	–	+	–
Paracoeliodes	–	–	+	–
Coeliodes (*Brevicoeliodes*)	–	–	–	+
Coeliodes s. str.	+	+	+	+
Coeliodes (*Coeliodinus*)	+	+	–	–
Trichocoeliodes	–	+	–	+
Conocoeliodes	–	–	–	+
Pseudocoeliodes	–	?–	+	–
Barioxyonyx	–	–	+	–
Phoeniconyx	–	–	+	–
Neoxyonyx	–	–	+	–
Pseudoxyonyx (*Aferonyx*)	–	–	+	–
Pseudoxyonyx s. str.	–	–	+	–
Theodorinus (*Atlantonyx*)	–	–	+	–
Theodorinus s. str.	–	–	+	–
Mesoxyonyx	–	–	+	–
Protoxyonyx	–	–	+	–
Paroxyonyx	–	–	+	–
Perioxyonyx	–	–	+	–
Platypteronyx	–	–	+	–
Mecysmoderes s. str.	–	–	–	+
Mecysmoderes (*Coelioderes*)	–	+	–	+
Mecysmoderes (*Coeliosomus*)	–	–	–	+
Mecysmoderes (*Belonnotus*)	–	–	–	+

Table (Contd.)

Genus (subgenus)	Region			
	European	Stenopean	Hesperian	Orthrian
Mecysmoderes subgenn. div.	–	–	–	+
Augustinus	–	–	–	+
Cyphauleutes	–	+	–	+
Sinauleutes	–	+	–	+
Phytobiomorphus	–	+	–	+
Auleutes	+	+	–	–
Cyphosenus	–	+	–	+
Ceutorhynchoides	–	+	–	+
Hainokisaruzo	–	–	–	+
Anthypurinus	–	–	+	–
Aphytobius	+	–	+	–
Hypurus	–	–	+	+
Oreorrhynchaeus	+	–	–	–
Pseudophytobius	–	–	+	–
Total of the genus-group taxa	47	41	61	32
Proportion of the endemic taxa	11 %	5–7 %	26 %	12 %

differentiation of the abiotic environment (first of all climate) and is not based on the specific features of taxa distribution, but rather on the general conditions that are believed to have produced the recent distribution, and, therefore, provides a general framework for specifying the distributions of particular animal taxa.

Kryzhanovskii (2002), based on the distribution of the insect faunas, have united nemoral and subtropical biotas of the Eastern Palaearctic in the East Asian Region, while attributing the subtropical and nemoral biotas of the Western Palaearctic to different regions, the Ancient Mediterranean and Boreal, respectively.

Analysis of the arealogical data on the Ceutorhynchinae shows that distribution of even a relatively large group of specialized phytophagous insects does not necessarily show in fine details the specific features of the physico-geographical and biotic differentiation of the environment and provides sustainable reasons for demarcation of the zoogeographical entities. In addition to specific distributional features of particular taxa, the problem is complicated by the conflicting estimations of the measure of the closeness between the faunas provided by different methods (e.g., comparison of the proportion of endemism and the coefficient of similarity of the generic composition).

The closeness of the European and Stenopean nemoral regions is reflected by disjunctive ranges of several species [*Pelenomus waltoni* (Boh.), *Rhinoncus bosnicus* Schze., *Homorosoma validirostre* (Gyll.), *Tapeinotus sellatus* (F.), *Amalorrhynchus melanarius* (Steph.), and *Thamiocolus kraatzi* (Ch. Bris.)] and considerable similarity of generic composition of their faunas: the Jaccard coefficient for these faunas is 42% (for the faunas of the Stenopean and Orthrian regions, 40%). Yet species with disjunctive amphipalaearctic ranges constitute only 1% of the faunas, and there are no pairs of the vicarious species in many genera, including largest ones except for *Ceutorhynchus*.

The European and Stenopean faunas also have no pairs of closely allied genera. With great reserve only, the monotypical genus *Sinocolus* Kor. from temperate East China (Harbin) and oligotypical *Trachelanthus* Kor. with one species in alpine Transcaucasia and Northeast Turkey and the other one in Kopet Dagh, both developing on plants of the predominantly nemoral genus *Lamium* L. (Lamiaceae), may be considered as an example of such a pair.

It is characteristic that there is absolute prevalence of the European fauna over the Stenopean one in the representation of the largest ceutorhynchine genera except *Coeliodes*: *Ceutorhynchus* (over 100 species in

the European Region and 25, in the Stenopean: Colonnelli, 2004; Korotyaev and Hong, 2004; unpublished author's data), *Mogulones* (33 and 2 species), and *Thamiocolus* (14 and 5 species, respectively). The genus *Mogulones*, in particular, is represented in the fauna of the Korean Peninsula by 2 wingless species, one of which (*M. koreanus* Kor.) is close to a group of European species, and the other (*M. kwoni* Kor. et Hong) has an appearance so modified in connection with the loss of wings that its generic placement is uncertain. Out of the 5 species of the genus *Thamiocolus* in the Stenopean fauna, *Th. kraatzi*, *Th. virgatus* (Gyll.) and *Th. nubeculosus* (Gyll.) are also present in Europe, *Th. kerzhneri* Kor. is a desert-steppe Central Asian element, and only *Th. fausti* (Ch. Bris.) is endemic to the Far East. It belongs to the nemoral complex and does not demonstrate any clear relationships with any congener, being similar to *Th. viduatus* (Gyll.), which occupies a similarly isolated position in the European fauna. None of the largest genera of the European fauna, associated with herbaceous plants, has formed in the Far East diversity comparable with the Western Palaearctic one.

The tribe Coeliodini, the members of which are associated with arboreal and shrubby vegetation, is the only one represented in the European and Stenopean faunas by close numbers of species (11 and 8 respectively) of one genus (*Coeliodes*). These species, however, constitute no vicarious pairs. In addition to *Coeliodes*, the tribe includes 2 monotypical genera in the Hesperian Region and at least 3 mono- or oligotypical genera in the Orthrian Region, the subtropical genera from different regions forming no close pairs. The *Coeliodes* fauna in both the subtropical regions is more species-rich than in the neighboring nemoral regions, e.g., 10 species are known from Taiwan (Colonnelli, 2004). It is noteworthy that the range of the genus *Coeliodes* does not extend (in the west) or only slightly extends (in the east) to the tropical regions south of the Palaearctic in spite of a great diversity of oaks, the main hosts of *Coeliodes* species, in tropical Asia.

Data on the high level of the differences between the ceutorhynchine faunas of the European and Stenopean regions agree with the Borkin's (1984) conclusion on the faunogenesis of amphibians. Similarly to the latter, complexes of the most closely allied species are distributed only in one of the two regions, i.e., only a few cases of vicariation between the European and Stenopean faunas are known. Some species of the Stenopean or East Asian faunas are closer to representatives of the Nearctic nemoral fauna (e.g., *Ceutorhynchus sinicus* to *C. semirufus*) than to European species, or approximately equally separated from both (see about the position of *Ceutorhynchus erwini* in the *C. cochleariae* group, and *C. americanus* in the *C. pervicax* group).

Endemic genus-group taxa constitute 11% of the European fauna. Genus *Brachiodontus* Schze. and subgenus *Scleropteridius* Otto from the subendemic Holarctic tribe Scleropterini and genus *Oreorrhynchaeus* Otto from the Ancient Mediterranean and Palaeotropical tribe Hypurini include 3–6 wingless species in the faunas of the mountain systems (predominantly the Alps). Monotypical genera *Marmaropus* Schoenh. (Phytobiini) and *Mogulonoides* Colonnelli (Ceutorhynchini) occur in the plain regions of the southern part of the Central and Eastern European forest zone. *Marmaropus* sharply differs from all species of the worldwide distributed genus *Rhinoncus* and is likely to be a palaeoendemic of the European Region. *Mogulonoides*, on the contrary, may rather be treated as a relatively young derivate of the Mediterranean species-group of the genus *Mogulones* which was formerly considered a distinct genus.

The monotypical genus *Eucoeliodes* Smrecz. (Coeliodini) subendemic to the European Region is standing separately among the Palaearctic Ceutorhynchinae but has clear relationships in the South African fauna. The range of its only species, *E. mirabilis* (A. Villa et J. B. Villa), covers the central part of the northern Mediterranean and may be attributed to the Hesperian or European regions for nearly equal reasons.

The closeness between the faunas of the Hesperian and Orthrian regions is meager, the Jaccard similarity coefficient of amounting only 11%. No genus with predominantly subtropical distribution is known, which would be common for the two faunas except for *Hypurus* Rey, the only species of which may have followed its host (*Portulaca oleracea* L.), in the subtropical belt of the both Northern and Southern hemispheres. Neither is any reliable example of the disjunctive or vicarious distribution of species in the Hesperian and Orthrian regions available. Only one pair of close genera relates these faunas, *Parethelcus* Wagn. with one European nemoral (*P. pollinarius* Forst.) and one Hesperian species (*P. nesicola* Colonnelli), and the subtropical Orthrian genus *Dieckmannius* Colon-

nelli with three species. It is noteworthy that the closest relative of the Macaronesian endemic, *P. nesicola*, is distributed in nemoral Europe and not in the Orthrian Region.

European and Hesperian faunas are closest among the four faunas in question, the Jaccard similarity coefficient amounting 57%. Although the number of the vicarious pairs of species in these two regions is small even in the largest genera, the bulk of the species diversity of many large genera is shared by the European and Hesperian faunas. There are many instances of the substitution of the nemoral European species by different, although closely allied species in the Western and Eastern Mediterranean.

Mononychus punctumalbum Hbst.—*M. superciliaris* Boh. (Mediterranean)

Ceutorhynchus sergii Kor. (Transcaucasia, Northeast Turkey)—*C. duvali* Ch. Bris. (northern Mediterranean)

Ceutorhynchus pyrrhorhynchus (Marsh.)—*C. canariensis* Hr. Lindberg (Macaronesia), *C. linealbatus* (Schze.) (Middle East)

Oprohinus consputus (Germ.)—*O. picipennis* (Schze.) (Western Mediterranean), *O. libanoticus* (Schze.) (Eastern Mediterranean)

Calosirus terminatus (Hbst.)—*C. orientalis* (Hust.) (Eastern Mediterranean)

Sirocalodes mixtus (Muls. et Rey)—*S. nigroterminatus* (Woll.) (Macaronesia)

Neoglocianus maculaalba (Hbst.)—*N. gethsemaniensis* (Pic) (Western Mediterranean), *N. smyrnensis* (Schze.) (Eastern Mediterranean), *N. transcaucasicus* (Kor.) (Transcaucasia, Anatolia, Iran, Afghanistan)

Glocianus brevicollis (Schze.)—*G. incisus* (Schze.) (Mediterranean)

Glocianus distinctus (Ch. Bris.)—*G. granulithorax* (Schze.) (Western Mediterranean)

Parethelcus pollinarius (Forster)—*P. nesicola* Colonnelli (Macaronesia)

Coeliastes lamii (F.)—*C. nitidus* Colonnelli (Eastern Mediterranean)

Datonychus melanostictus (Marsh.)—*D. maurus* (Schze.) (Western Mediterranean)

Thamiocolus pubicollis (Gyll.)—*Th. lodosi* Kor. (Eastern Mediterranean)

Mogulones crucifer (Pall.)—*M. cingulatus* (Schze.) (Mediterranean)

Microplontus fairmeirii (Ch. Bris.)—*M. riedeli* Kor. (Northeast Turkey)

Trichosirocalus barnevillei (Grenier)—*T. bellus* (Rtt.) (Eastern Mediterranean)

Micrelus ericae (Gyll.)—*M. ferrugatus* (Perris) (Western Mediterranean)

Species of the monotypical genus, *Drupenatus sisymbrii* (F.), and monotypical subgenus, *Ranunculiphilus* (*Austroceutorhynchus*) *italicus* (Ch. Bris.), are distributed in both the regions, while the range of *Eucoeliodes mirabili*s occupies a rather narrow stripe at the border of the Eastern European Mediterranean with the South of the nemoral Central Europe.

Fifteen genera are endemic to the Hesperian Region. In addition to 7 genera of the tribe Oxyonychini and 3 genera of the tribe Hypurini, these are *Datonychidius* Kor. with 2 species in the Eastern Mediterranean, and monotypical *Bohemanius* Schze., *Ectamnogaster* Schze. (all Ceutorhynchini) and *Paracoeliodes* Colonnelli (Coeliodini) in the Western Mediterranean; *Hesperorrhynchus* Peyer. (Ceutorhynchini) with 5 species (Colonnelli, 2004) is endemic to the Macaronesian Subregion. In contrast to the Orthrian Region, rich in genera and species common with the Indo-Malayan fauna, the Hesperian Region is subject only to a slight influence of the tropical fauna; the only representative of the Ethiopian-Cape fauna, *Micrelus ?arabicus* Colonnelli, has been found in the south of Israel.

Similarity between the Stenopean and Orthrian ceutorhynchine faunas (40%) is less than that between the European and Hesperian faunas. The first two faunas are much less known than the latter two, but as the Stenopean fauna is investigated in more detail than the Orthrian fauna, one can anticipate rather a decrease than an increase of this figure in the subsequent studies. The Stenopean and Orthrian faunas are characterized by the presence of common genera and species with predominantly Indo-Malayan of Palaeotropical ranges, as well as common taxa endemic or subendemic to these two regions. The first group is constituted by the genera *Mecysmoderes* Schoenh., *Cyphosenus* Schze., *Cyphauleutes* Kor., *Phytobiomorphus* Wagn., the second one, by *Wagnerinus* Kor., *Scleropteroides* Colonnelli, *Ceutorhynchoides* Colonnelli, *Trichocoeliodes* Colonnelli, *Conocoeliodes* Kor.,

Sinauleutes Kor., *Cardipennis* Kor., *Dieckmannius* Colonnelli, and *Rhinoncomimus* Wagn., and subgenera *Heorhynchus* Kor. (genus *Ceutorhynchus*) and *Brevicoeliodes* Kor. (genus *Coeliodes* Schoenh.). Two genera, common to the Orthrian Region and Indo-Malalyan Region (*Hainokisaruzo* Yoshitake et Colonnelli) or Palaeotropical Realm (*Augustinus* Kor.) but missing from the Stenopean Region, are among those most species-rich in the Indo-Malayan Region and include several endemic species in the East Orthrian Subregion each. There are much more genera (19) represented in the Stenopean Region but absent from the Orthrian Region (Korotyaev and Hong, 2004). Only 1 genus (*Sinocolus* Kor.) and 1 subgenus [*Amurocladus* (Kor.), genus *Zacladus* Reitt.], both of them monotypical, are endemic or subendemic to the Stenopean Region. The monotypical subgenus *Heorutidosoma* Kor. et Hong of the genus *Rutidosoma* Steph. is conventionally considered endemic to this region as well. All endemic and subendemic Stenopean genus-group taxa are allied (with varying degree of closeness) to representatives of the temperate Holarctic fauna.

Endemics of the East Asian Region are more heterogeneous, but the majority of them are also related to the temperate Holarctic fauna. Out of the 11 above-listed genus-group taxa, only genus *Ceutorhynchoides* with 6 species (Yoshitake and Colonnelli, 2005) is closely related to one of the most species-rich in the Indo-Malayan Region genus *Hainokisaruzo*. The systematic position of the genera *Wagnerinus* and *Sinauleutes* is obscure. Genus *Cardipennis* cannot be related to any other in the Palaearctic fauna; in a unique secondary sex character (all tibiae in male non-mucronate) it is similar to the Nearctic *Allosirocalus* which also has no closer relationships. The rest of East Asian endemics belong to the Holarctic tribes Scleropterini and Coeliodini or are close to the Palaearctic genera and subgenera of the tribe Ceutorhynchini (genus *Dieckmannius* and subgenus *Heorhynchus* of *Ceutorhynchus*). In contrast to the genus and subgenus endemic and subendemic to the Stenopean Region, each including only a single very rare species, 8 out of the 11 East Asian endemics and the subendemic genus *Homorosoma* each comprise several species many of them being the commonest weevils in the Far East, for example, *Scleropteroides hypocrita* (Hust.) and *Homorosoma asper* (Roel.), species of the genera *Cardipennis* and *Rhinoncomimus*, and also *Ceutorhynchus ibukianus* Hust.

The boundary between the ceutorhynchine faunas of the nemoral Stenopean Region and the subtropical Orthrian Region is apparently sharper than the boundary between the fauna of the Orthrian Region and Indo-Malayan Region of the Palaeotropical Realm. The proportion of the endemic genus-group taxa in the Stenopean Region (5%) is only one-half or one-third of their proportion in the European (10%) or Orthrian regions (12%), or in the Stenopean and Orthrian regions combined (14–16%).

The fauna of Anatolia is characterized first of all by the presence of several groups of endemic and subendemic species predominantly with Hesperian relationships or ranges. Of these groups, the most characteristic are 5 species of the genus *Thamiocolus*, 4 species of the genus *Boragosirocalus* Dieckm., and 2 species of *Coeliastes* Wse. (tribe Ceutorhynchini), 2 species of *Barioxyonyx* Hust. and 2, of *Theodorinus* Kor. (tribe Oxyonychini). In Central and Eastern Anatolia the two latter genera each include an endemic species in the landscapes of the Mediterranean type. Of special importance is the presence of 24 species (Colonnelli, 2004), or over one-third of the genus *Mogulones* with the main center of diversity in the Mediterranean, and especially the presence of seven (two of them endemic) species of the almost exclusively Mediterranean group of species with large denticles on the elytra. Out of the two largest genera of the Saharo-Gobian Oxyonychini fauna, *Paroxyonyx* Hust. in the Saharo-Arabian Subregion and *Oxyonyx* Fst. in the Irano-Turanian and Gobian subregions, only *Oxyonyx* is represented in Anatolia by a single species, *O. brisouti* Fst. This species is widely distributed in Kazakhstan, Middle Asia, and Mongolia; in Turkey its distribution is restricted to isolated mountain depressions of the Araks basin with the vegetation rather of the mountain xerophytic than desert type. The only Anatolian representative of the tribe Hypurini, *Anthypurinus loginovae* Kor., with the largest part of the range in the Transcaucasia and in the south of Middle Asia (Korotyaev, 2005), also occurs in the desert part of the Araks valley. In the Armenian and Azerbaijan parts of the Araks valley, several other Turanian and endemic (*Anthypurinus verae* Kor.) species of the tribes Oxyonychini and Hypurini, and also Southern Turanian *Glocianus bituberculatus* (Fst.) occur, although they are not found so far in the adjacent regions of Northeast Turkey. Thus, desert elements concentrate mostly in the Araks basin in the peripheral northeastern part of Anatolia adjacent to Eastern Transcaucasia

and possessing biota predominantly of the Irano-Turanian type. The inner regions of the Anatolian Plateau are deprived of the typical desert taxa; their northern part is mainly concentrated in steppe (including desert-steppe), and middle and southern parts, Mediterranean xerophilic complexes. A typical example of this distributional pattern is provided by a small genus *Coeliastes*: it is represented in the northern half of Turkey by the endemic *C. rustemi* Kor. et al., common on a ruderal labiate, *Wiedemannia multifida* (L.) Benth., also endemic to this area, while in southern Turkey the Eastern Mediterranean *C. nitidus* Colonnelli occurs (Korotyaev et al., 2002). A similar distribution is demonstrated by two genera of the tribe Cyphicerini of the subfamily Entiminae, typical of the arid landscapes of the central Palaearctic. Species of the predominantly steppe genus *Ptochus* Boh. occur, and in places are common, on wormwoods in Eastern Anatolia as far south as Cappadocia and Lake Tuz, while in the southern part of the plateau in sparse oak forests, and also on the Mediterranean coast species of the genus *Myllocerus* Schoenh. are common. In the Palaearctic, the latter genus has its maximum species richness in the subtropical evergreen-forest landscapes. This substitution proceeds against the background of retaining co-dominance in the oak canopy by typically Hesperian weevils from other entimine tribes, *Rhinoscythropus serripes* Desbr. (tribe Phyllobiini) and species of the *Polydrusus* Germ. subgenus *Conocetus* Desbr. (tribe Polydrusini), up to Erzurum Province in the north. A peculiar appearance of the Anatolian fauna is created by the endemic and subendemic species dominating insect complexes in a number of the communities. The core of this characteristic assemblage is formed of the moderately thermo- and xerophilic species living in open landscapes and sparse forests of the Mediterranean type.

As evidenced from the above data, Anatolia may rather be considered a zone of contact of the northeastern part of the Hesperian Evergreen Forest Region with the southwestern extremity of the Scythian (Steppe) Region at the northern boundary of the Saharo-Gobian Desert Region, with its peculiar fauna rich in endemic species, than an area with a fauna intermediate between those of the Mediterranean and desert types. Similarly to what one can see in Mexico, the zone of contact of two large zoogeographical entities is characterized not merely by a gradual substitution of taxa of one of the faunas by the taxa from its neighbor, but by the existence of a characteristic endemic fauna in the varyingly large border zone. This type of the faunal change is known in classical zoogeography (Geptner, 1936).

CONCLUSION

The nearly worldwide distribution, considerable generic and species diversity of the faunas of the majority of the zoogeographical realms and their highly specific composition, together with biological features of the subfamily Ceutorhynchinae, demonstrate its considerable evolutional success. The evolutional possibilities of ceutorhynchines are well illustrated by the distribution of the *Ceutorhynchus cochleariae* (Gyll.) species-group, a low-rank taxon which has adapted to landscapes of all Holarctic natural zones from the Hypoarctic tundra to the wet warm-temperate forests of Japan and dry subtropics of southern California. In spite of its adjacency to the powerful centers of tropical biotas, the core of the Holarctic Ceutorhynchinae fauna in both the hemispheres is formed of the endemic and subendemic genera, which are especially abundant in the Palaearctic. This region possesses the most diversified at the genus and species levels fauna consisting of the predominantly endemic and subendemic genera (in the Mediterranean and Saharo-Gobian regions, also of the highly diversified tribe Oxyonychini) up to its southern border. The existence of characteristic transitional faunas in the zones of contact of the Holarctic fauna with the faunas of the tropical regions in East Asia and Mexico is shown. These transitional faunas include a considerable number of endemic taxa of the genus and species groups. A conspicuous feature of the Palaearctic ceutorhynchine fauna is a rather numerous complex of the upland and high-latitude species.

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