

# INSECT BIODIVERSITY IN THE PALEARCTIC REGION

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For more than 5 years, small dragonflies of apparently one species have occupied the tips of dry branches of a boxelder tree (*Acer negundo* L.) opposite B. A. Korotyaev's window on the first floor of his apartment building in Krasnodar, Russia. They appear in late July after the swifts migrate from the city. Although the traffic in the street is heavy, the dragonflies hunt all day in the polluted air. Liberally paraphrasing Kant's famous statement, two phenomena are most striking for biologists: the tremendous diversity of living organisms and the obvious, though often unapparent, organization of this diversity. To adequately describe insect biodiversity and its organization in the Palearctic Region is a major challenge.

The Palearctic Region is the world's largest biogeographic region and the best known with respect to its overall insect diversity. It also has the longest history of faunistic and biodiversity studies. Nevertheless, reliable estimates of the number of species are available for only some insect orders (Table 7.1). Existing Palearctic (e.g., Aukema and Rieger 1995–2006, Löbl and Smetana 2003–2007) and world catalogs (e.g., Hansen 1998, Heppner 1998, Woodley 2001) improve our understanding of insect biodiversity, but catalogs are unavailable for many groups, and the needed data can be provided only by experts. Some taxa have been treated or otherwise revised recently, while others have remained untouched for the last century or so, meaning that certain data are absent for some groups. In addition, some parts of the Palearctic, such as western and northern Europe, are better known than others, such as North Africa and China. However, exploration of the mountains of China in recent decades has resulted in discoveries of the species-rich alpine faunas of large coleopteran families such as the Carabidae (e.g., Zamotajlov and Sciaky 1996, Kataev and Liang 2005) and Tenebrionidae (e.g., Medvedev 2005a, 2006).

The great variety of views on subdivision of the Palearctic presents another difficulty in describing the region's insect diversity. We follow the main biogeographical units proposed by Emeljanov (1974), which are compatible with many of the existing schemes and are finding increasing support (Volkovitsh and Alexeev 1988, Krivokhatsky and Emeljanov 2000). We concentrate on general features and patterns of the entire insect fauna of the Palearctic Region, providing examples of taxa that are better known to us, mostly Coleoptera, or most typical of entities in various biogeographical units.

The Palearctic biota is an immense and irreplaceable source of organisms of the highest economic value for the entire world, particularly for the temperate regions, and includes cultivated plants and useful animals, their natural enemies (weeds, predators, and pathogens), and enemies of these enemies (the biological control agents). It is, however, experiencing increasing anthropogenic pressures, resulting in the disappearance of many species of plants and animals, as well as entire communities and landscapes.

## **GEOGRAPHIC POSITION, CLIMATE, AND ZONALITY**

The Palearctic Region (Fig. 7.1a) occupies cold, temperate, and subtropical regions of Eurasia and Africa north of the Sahara Desert, together with islands of the Arctic, Atlantic, and Pacific oceans – Azores, Canaries, Iceland, British Isles, and Cape Verde in the Atlantic, and Komandorski, Kurile, and Japan in the Pacific Ocean. The southern border of the Palearctic in Asia lies along the southern border of subtropical forests, leaving the southern part of China, Taiwan, and the Ryukyu Islands of Japan in the Oriental Region. The Himalayas are mostly attributed to the Palearctic, but distributional patterns of some (mostly phytophagous) insect groups suggest that the southern Himalayas could be considered Oriental. The southern border of the Palearctic in East Asia is nearly impossible to define, particularly in China, because the Chinese fauna is poorly known and the distributional patterns of various groups provide conflicting results. The southern border of the Palearctic generally is viewed as a wide band at the southern limits of subtropical forests between the Yantzu and Huanche rivers, where interchanges of the Palearctic and Oriental faunas occur.

The Palearctic, together with the Nearctic, forms a larger zoogeographic division, the Holarctic, which includes all nontropical areas of the northern hemisphere (Kryzhanovsky 1965, 2002, Takhtajan 1978, Lopatin 1989). Overall, the insect faunas of the Palearctic and Nearctic are more similar in the North and more unique in their southern parts (Kryzhanovsky 2002), where Afrotropical, Oriental, and Neotropical elements contribute significantly to the biodiversity. A few high-ranked groups of insects are endemic to the Holarctic: the only endemic order, the Grylloblattida (western North America, Japan, Russian Far East; with one species in the

**Table 7.1** Biodiversity of major insect groups in the Palearctic Region (for some insect orders, only selected fields could be filled; families of Diptera are not included).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Thysanura		22 (USSR)			A. L. Lobanov (personal communication)
Ephemeroptera		300 (USSR)			A. L. Lobanov (personal communication)
Odonata	Amphipterygidae	4	2		Steinmann 1997
Odonata	Calopterygidae	72			Steinmann 1997
Odonata	Euphaeidae	20			Steinmann 1997
Odonata	Chlorolestidae	9			Steinmann 1997
Odonata	Lestidae	19			Steinmann 1997
Odonata	Megapodagrionidae	3			Steinmann 1997
Odonata	Pseudolestidae	6	3		Steinmann 1997
Odonata	Coenagrionidae	78			Steinmann 1997
Odonata	Platycnemididae	17			Steinmann 1997
Odonata	Epiophlebiidae	2	1	Epiophlebiidae, Japan and Himalayas	Belyshev and Kharitonov 1981
Odonata	Petaluridae	1	1		Belyshev and Kharitonov 1981
Odonata	Gomphidae	38			Belyshev and Kharitonov 1981
Odonata	Cordulegasteridae	11			Belyshev and Kharitonov 1981
Odonata	Aeshnidae	27			Belyshev and Kharitonov 1981
Odonata	Corduliidae	24			Belyshev and Kharitonov 1981
Odonata	Libellulidae	96			Belyshev and Kharitonov 1981
Odonata	Macrodiplactidae	2			Belyshev and Kharitonov 1981
Blattaria		100 (USSR)	30		L. N. Anisyutkin (personal communication)
Mantodea		35 (USSR)			A. L. Lobanov (personal communication)
Isoptera		7 (USSR)			A. L. Lobanov (personal communication)
Grylloblattodea		3 (USSR)			A. L. Lobanov (personal communication)
Phasmatodea		8 (USSR)			A. L. Lobanov (personal communication)
Orthoptera		802 (USSR)			A. L. Lobanov (personal communication)
Orthoptera/ Ensifera		266 (USSR)			A. L. Lobanov (personal communication)
Orthoptera/ Caelifera		536 (USSR)			A. L. Lobanov (personal communication)

(continued)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Plecoptera		595	40	1	Zhiltzova 2003
Plecoptera	Scopuridae	5	1	Scopuridae	Zhiltzova 2003
Plecoptera	Taeniopterygidae	58	11		Zhiltzova 2003
Plecoptera	Nemouridae	281	8		Zhiltzova 2003
Plecoptera	Capniidae	100	13		Zhiltzova 2003
Plecoptera	Leuctridae	146	7		Zhiltzova 2003
Dermoptera		80	25		L. N. Anisyutkin (personal communication)
Embioptera		2 (USSR)			A. L. Lobanov (personal communication)
Zoraptera		2 (Tibet)			N. V. Golub and V. G. Kuznetsova (personal communication)
Psocoptera		352 (not including China)			N. V. Golub and V. G. Kuznetsova (personal communication)
Mallophaga		400 (USSR)			A. L. Lobanov (personal communication)
Anoplura		60 (USSR)			A. L. Lobanov (personal communication)
Thysanoptera		500 (USSR)			A. L. Lobanov (personal communication)
Sternorrhyncha/ Psyllina		520 (USSR)			A. L. Lobanov (personal communication)
Sternorrhyncha/ Aphidina		853 (Russia)			A. L. Lobanov (personal communication), A. V. Stekolshchikov (personal communication)
Sternorrhyncha/ Coccina	Aleyrodidae	49 (USSR)			A. L. Lobanov (personal communication)
Sternorrhyncha/ Coccina	Coccidae	~600 (USSR)			A. L. Lobanov (personal communication)
Auchenorrhyncha		>4000	718	Dorysarthriini, Ranissini, Colobocini, Almanini, Bocrini, Adenissini, Ommatidiotini, Durgulini, Adelungiini, Aphrodini, Stegelytrini, Grypotini, Fieberiellini	Nast 1972, A. F. Emeljanov (personal communication)
Hemiptera		8413	1489		

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Hemiptera	Aenictopecheidae	1	1		Aukema and Rieger 1995
Hemiptera	Enicocephalidae	15	6		Aukema and Rieger 1995, Schuh and Slater 1995
Hemiptera	Ceratocombidae	11	1		Aukema and Rieger 1995
Hemiptera	Dipsocoridae	14	1		Aukema and Rieger 1995, Schuh and Slater 1995
Hemiptera	Schizopteridae	9	6		Aukema and Rieger 1995, Schuh and Slater 1995
Hemiptera	Nepidae	21	5		Aukema and Rieger 1995
Hemiptera	Belostomatidae	14	5		Aukema and Rieger 1995
Hemiptera	Gelastocoridae	4	1		Aukema and Rieger 1995
Hemiptera	Ochteridae	3	1		Aukema and Rieger 1995
Hemiptera	Corixidae	143	15		Aukema and Rieger 1995
Hemiptera	Naucoridae	9	7		Aukema and Rieger 1995
Hemiptera	Aphelocheiridae	18	1		Aukema and Rieger 1995
Hemiptera	Notonectidae	50	4		Aukema and Rieger 1995
Hemiptera	Pleidae	6	2		Aukema and Rieger 1995
Hemiptera	Helotrephidae	6	5		Aukema and Rieger 1995
Hemiptera	Mesoveliidae	7	2		Aukema and Rieger 1995
Hemiptera	Hebriidae	24	4		Aukema and Rieger 1995
Hemiptera	Hydrometridae	14	1		Aukema and Rieger 1995
Hemiptera	Hermatobatidae	2	1		Aukema and Rieger 1995
Hemiptera	Veliidae	64	11		Aukema and Rieger 1995
Hemiptera	Gerridae	99	20		Aukema and Rieger 1995
Hemiptera	Aepophilidae	1	1	Aepophilidae	Aukema and Rieger 1995
Hemiptera	Saldidae	99	14		Aukema and Rieger 1995
Hemiptera	Leptopodidae	11	4		Aukema and Rieger 1995
Hemiptera	Omaniidae	2	2		Aukema and Rieger 1995
Hemiptera	Joppeicidae	1	1		Aukema and Rieger 1996
Hemiptera	Tingidae	473	61		Aukema and Rieger 1996
Hemiptera	Microphysidae	27	3		Aukema and Rieger 1996
Hemiptera	Nabidae	112	10		Aukema and Rieger 1996
Hemiptera	Anthocoridae	181	28		Aukema and Rieger 1996
Hemiptera	Cimicidae	15	5		Aukema and Rieger 1996
Hemiptera	Polycetenidae	3	2		Aukema and Rieger 1996
Hemiptera	Pachynomidae	2	1		Aukema and Rieger 1996
Hemiptera	Reduviidae	808	145		Aukema and Rieger 1996
Hemiptera	Miridae	2808	397		Aukema and Rieger 1999
Hemiptera	Aradidae	204	28		Aukema and Rieger 2001
Hemiptera	Lygaeidae	1001	225		Aukema and Rieger 2001
Hemiptera	Piesmatidae	19	2		Aukema and Rieger 2001
Hemiptera	Malcidae	25	2		Aukema and Rieger 2001
Hemiptera	Berytidae	54	13		Aukema and Rieger 2001
Hemiptera	Colobathristidae	7	2		Aukema and Rieger 2001
Hemiptera	Largidae	8	3		Aukema and Rieger 2001
Hemiptera	Pyrrhocoridae	43	13		Aukema and Rieger 2001
Hemiptera	Rhopalidae	69	14		Aukema and Rieger 2006

(continued)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Hemiptera	Stenocephalidae	18	1		Aukema and Rieger 2006
Hemiptera	Alydidae	69	26		Aukema and Rieger 2006
Hemiptera	Coreidae	306	84		Aukema and Rieger 2006
Hemiptera	Urostylididae	131	8		Aukema and Rieger 2006
Hemiptera	Thaumastellidae	1	1		Aukema and Rieger 2006
Hemiptera	Parastrachiidae	2	1		Aukema and Rieger 2006, Schuh and Slater 1995
Hemiptera	Cydnidae	167	37		Aukema and Rieger 2006
Hemiptera	Thyreocoridae	4	1		Aukema and Rieger 2006, Schuh and Slater, 1995
Hemiptera	Plataspidae	104	10		Aukema and Rieger, 2006
Hemiptera	Acanthosomatidae	107	9		Aukema and Rieger 2006
Hemiptera	Tessaratomidae	30	12		Aukema and Rieger 2006
Hemiptera	Dinidoridae	19	4		Aukema and Rieger 2006
Hemiptera	Pentatomidae	841	219		Aukema and Rieger 2006
Hemiptera	Incertae sedis	107			Aukema and Rieger 2006
Coleoptera		100,000			I. Löbl (personal communication), A. L. Lobanov (personal communication)
Coleoptera	Crowsoniellidae	1	1	Italy	Löbl and Smetana 2003
Coleoptera	Micromalthidae	1	1		Löbl and Smetana 2003
Coleoptera	Cupedidae	7	1		Löbl and Smetana 2003
Coleoptera	Jurodidae (= Sikhotealiniidae)	1	1	Russian Far East	Löbl and Smetana 2003
Coleoptera	Torridincolidae	1	1		Löbl and Smetana 2003
Coleoptera	Hydrosaphidae	9	1		Löbl and Smetana 2003
Coleoptera	Sphaeriusidae	8	1		Löbl and Smetana 2003
Coleoptera	Gyrinidae	102	7		Löbl and Smetana 2003
Coleoptera	Haliplidae	66	3		Löbl and Smetana 2003
Coleoptera	Trachypachidae	1	1		Löbl and Smetana 2003
Coleoptera	Noteridae	30	5		Löbl and Smetana 2003
Coleoptera	Amphizoidae	2	1		Löbl and Smetana 2003
Coleoptera	Hygrobiidae	2	1		Löbl and Smetana 2003
Coleoptera	Dytiscidae	901	67		Löbl and Smetana 2003
Coleoptera	Rhysodidae	24	5		Löbl and Smetana 2003
Coleoptera	Carabidae	11,333	579		Löbl and Smetana 2003
Coleoptera	Helophoridae	150	1		Löbl and Smetana 2004
Coleoptera	Epimetopidae	4	1		Löbl and Smetana 2004
Coleoptera	Georissidae	19	1		Löbl and Smetana 2004
Coleoptera	Hydrochidae	28	1		Löbl and Smetana 2004
Coleoptera	Spercheidae	5	1		Löbl and Smetana 2004
Coleoptera	Hydrophilidae	559	54		Löbl and Smetana 2004
Coleoptera	Sphaeritidae	3	1		Löbl and Smetana 2004
Coleoptera	Synteliidae	3	1		Löbl and Smetana 2004
Coleoptera	Histeridae	847	107		Löbl and Smetana 2004
Coleoptera	Hydraenidae	785	8		Löbl and Smetana 2004

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Coleoptera	Ptiliidae	188	21		Löbl and Smetana 2004
Coleoptera	Agyrtidae	45	8		Löbl and Smetana 2004
Coleoptera	Leiodidae	2172	245		Löbl and Smetana 2004
Coleoptera	Scydmaenidae	1005	26		Löbl and Smetana 2004
Coleoptera	Silphidae	117	15		Löbl and Smetana 2004
Coleoptera	Staphylinidae	15,307	903		Löbl and Smetana 2004
Coleoptera	Lucanidae	332	34		Löbl and Smetana 2006
Coleoptera	Passalidae	25	8		Löbl and Smetana 2006
Coleoptera	Trogidae	79	3		Löbl and Smetana 2006
Coleoptera	Glaresidae	24	1		Löbl and Smetana 2006
Coleoptera	Bolboceratidae	52	13		Löbl and Smetana 2006
Coleoptera	Geotrupidae	299	13		Löbl and Smetana 2006
Coleoptera	Ochodaeidae	26	2		Löbl and Smetana 2006
Coleoptera	Ceratocanthidae	4	2		Löbl and Smetana 2006
Coleoptera	Hybosoridae	16	7		Löbl and Smetana 2006
Coleoptera	Glaphyridae	158	5		Löbl and Smetana 2006
Coleoptera	Scarabaeidae	5787	404		Löbl and Smetana 2006
Coleoptera	Decliniidae	2	1	Russian Far East	Löbl and Smetana 2006
Coleoptera	Eucinetidae	18	7		Löbl and Smetana 2006
Coleoptera	Clambidae	43	3		Löbl and Smetana 2006
Coleoptera	Scirtidae	254	8		Löbl and Smetana 2006
Coleoptera	Dascillidae	40	8		Löbl and Smetana 2006
Coleoptera	Rhipiceridae	15	3		Löbl and Smetana 2006
Coleoptera	Buprestidae	2430	99	Paratassini, Kisanthobiini	Löbl and Smetana 2006, Bellamy 2003
Coleoptera	Byrrhidae	321	22		Löbl and Smetana 2006
Coleoptera	Elmidae	235	35		Löbl and Smetana 2006
Coleoptera	Dryopidae	64	11		Löbl and Smetana 2006
Coleoptera	Limnichidae	66	13		Löbl and Smetana 2006
Coleoptera	Heteroceridae	94	3		Löbl and Smetana 2006
Coleoptera	Psephenidae	92	16		Löbl and Smetana 2006
Coleoptera	Ptilodactylidae	47	9		Löbl and Smetana 2006
Coleoptera	Chelonariidae	11	2		Löbl and Smetana 2006
Coleoptera	Eulichadidae	11	1		Löbl and Smetana 2006
Coleoptera	Callirhipidae	16	3		Löbl and Smetana 2006
Coleoptera	Artematopidae	8	2		Löbl and Smetana 2007
Coleoptera	Cerophytidae	2	1		Löbl and Smetana 2007
Coleoptera	Eucnemidae	132	41		Löbl and Smetana 2007
Coleoptera	Throscidae	48	2		Löbl and Smetana 2007
Coleoptera	Elateridae	3661	233		Löbl and Smetana 2007
Coleoptera	Plastoceridae	1	1		Löbl and Smetana 2007
Coleoptera	Drilidae	44	6		Löbl and Smetana 2007
Coleoptera	Omalisidae	12	2	Europe	Löbl and Smetana 2007
Coleoptera	Lycidae	403	47		Löbl and Smetana 2007
Coleoptera	Phengodidae	27	5		Löbl and Smetana 2007
Coleoptera	Lampyridae	263	19		Löbl and Smetana 2007
Coleoptera	Omethidae	3	2		Löbl and Smetana 2007

(continued)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Coleoptera	Cantharidae	1981	62		Löbl and Smetana 2007
Coleoptera	Derodontidae	14	3		Löbl and Smetana 2007
Coleoptera	Nosodendridae	12	1		Löbl and Smetana 2007
Coleoptera	Dermestidae	520	25		Löbl and Smetana 2007
Coleoptera	Endecatomiidae	2	1		Löbl and Smetana 2007
Coleoptera	Bostrichidae	151	46		Löbl and Smetana 2007
Coleoptera	Ptinidae	717	99		Löbl and Smetana 2007
Coleoptera	Jacobsoniidae	3	2		Löbl and Smetana 2007
Coleoptera	Lymexylidae	15	8		Löbl and Smetana 2007
Coleoptera	Phloiophilidae	1	1	Europe	Löbl and Smetana 2007
Coleoptera	Trogossitidae	45	16		Löbl and Smetana 2007
Coleoptera	Thanerocleridae	7	3		Löbl and Smetana 2007
Coleoptera	Cleridae	311	62		Löbl and Smetana 2007
Coleoptera	Acanthocnemidae	1	1		Löbl and Smetana 2007
Coleoptera	Prionoceridae	41	3		Löbl and Smetana 2007
Coleoptera	Melyridae	59	9		Löbl and Smetana 2007
Coleoptera	Dasytidae	764	51		Löbl and Smetana 2007
Coleoptera	Malachiidae	1146	81		Löbl and Smetana 2007
Coleoptera	Sphindidae	14	3		Löbl and Smetana 2007
Coleoptera	Kateretidae	52	8		Löbl and Smetana 2007
Coleoptera	Nitidulidae	687	56		Löbl and Smetana 2007
Coleoptera	Monotomidae	72	11		Löbl and Smetana 2007
Coleoptera	Helotidae	55	1		Löbl and Smetana 2007
Coleoptera	Phloeostichidae	1	1		Löbl and Smetana 2007
Coleoptera	Silvanidae	94	21		Löbl and Smetana 2007
Coleoptera	Passandridae	16	3		Löbl and Smetana 2007
Coleoptera	Cucujidae	16	2		Löbl and Smetana 2007
Coleoptera	Laemophloeidae	82	17		Löbl and Smetana 2007
Coleoptera	Phalacridae	144	16		Löbl and Smetana 2007
Coleoptera	Cryptophagidae	336	30		Löbl and Smetana 2007
Coleoptera	Erotylidae	420	66		Löbl and Smetana 2007
Coleoptera	Byturidae	8	3		Löbl and Smetana 2007
Coleoptera	Biphyllidae	18	2		Löbl and Smetana 2007
Coleoptera	Bothrideridae	132	19		Löbl and Smetana 2007
Coleoptera	Cerylonidae	53	17		Löbl and Smetana 2007
Coleoptera	Alexiidae	42	1	West Palearctic	Löbl and Smetana 2007
Coleoptera	Discolomatidae	37	3		Löbl and Smetana 2007
Coleoptera	Endomychidae	282	56		Löbl and Smetana 2007
Coleoptera	Coccinellidae	1208	112	Lithophilinae (Mediterranean to Nepal and northern China)	Löbl and Smetana 2007
Coleoptera	Corylophidae	76	12		Löbl and Smetana 2007
Coleoptera	Latridiidae	268	18		Löbl and Smetana 2007
Coleoptera	Chrysomelidae	3500 (>2500 in USSR)			A. K. estimate, A. L. Lobanov (personal communication)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Coleoptera	Chrysomelidae, subfamily Bruchinae	> 120 (Russia)	15	Rhaebini (Israel to northern-central China); Kytorhinini (subendemic to central and eastern Palearctic, with one species in northwestern North America)	Egorov 1996a
Coleoptera	Cerambycidae	4500 (880 in USSR)			A. L. Lobanov (personal communication)
Coleoptera	Nemonychidae	7	3	Nemonychinae; Europe, NW Africa, Turkey (Anatolia), Armenia, Azerbaijan, Kazakhstan, Turkmenistan	Dieckmann 1974, Alonso-Zarazaga and Lyal 1999
Coleoptera	Urodontidae	> 50	2		Alonso-Zarazaga and Lyal 1999
Coleoptera	Anthribidae	118 (West Palearctic and Russian Far East); 170 (Japan)	68		Frieser 1981, Egorov 1996b, Alonso- Zarazaga and Lyal 1999
Coleoptera	Oxycorynidae	1	1		Alonso-Zarazaga and Lyal 1999
Coleoptera	Rhynchitidae	86 (Russia)	38		Legalov 2006
Coleoptera	Attelabidae	29 (Russia)	19		Legalov 2006
Coleoptera	Dryophthoridae	7 (Russia); (37 in Japan) (+ 9 – western and central Palearctic)	?29		Morimoto 1978, Alonso-Zarazaga and Lyal 1999, B. A. Korotyaev unpublished data
Coleoptera	Brachyceridae	48	3		Alonso-Zarazaga and Lyal 1999, 2002; Arzanov 2005
Coleoptera	Cryptolar yngidae	1	1		Alonso-Zarazaga and Lyal 1999
Coleoptera	Brentidae	31 (27 in Japan, 2 in Russian Far East)	?20 (16 in Japan)		Morimoto 1976, Alonso-Zarazaga and Lyal 1999

(continued)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Coleoptera	Apionidae	540	57	Ceratapiini; Exapiini (southwestern Palearctic); Metapiini (south of Western and Central Palearctic)	Wanat 1994, Alonso-Zarazaga 1990, Alonso-Zarazaga and Lyal 1999, Friedman and Freidberg 2007
Coleoptera	Nanophyidae	90	14	Corimaliini (subendemic to south of Western and Central Palearctic; also in Namibia and probably in India)	Alonso-Zarazaga 1989, Alonso-Zarazaga and Lyal 1999
Coleoptera	Raymondionymidae	>50	9		Alonso-Zarazaga and Lyal 1999
Coleoptera	Eirihinidae	96	34	Himasthlophallini (south of Russian Far East)	Alonso-Zarazaga and Lyal 1999, 2002
Coleoptera	Curculionidae excluding Scolytinae	?11,000		numerous examples	B. A. K. tentative estimate
Coleoptera	Curculionidae, subfamily Scolytinae	750	74		Wood and Bright 1992
Coleoptera	Platypodidae	35	3		Wood and Bright 1992
Neuroptera	Ascalaphidae	40			V. A. Krivokhatsky (personal communication)
Neuroptera	Berothidae	15			V. A. Krivokhatsky (personal communication)
Neuroptera	Chrysopidae	176			V. A. Krivokhatsky (personal communication)
Neuroptera	Coniopterygidae	50			V. A. Krivokhatsky (personal communication)
Neuroptera	Dilaridae	7			V. A. Krivokhatsky (personal communication)
Neuroptera	Hemerobiidae	80			V. A. Krivokhatsky (personal communication)
Neuroptera	Mantispidae	10			V. A. Krivokhatsky (personal communication)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Neuroptera	Myrmeleontidae	391		Pseudimarini (1 sp.), Gepini (31 spp.), Isoleontini (13 spp.)	V. A. Krivokhatsky (personal communication)
Neuroptera	Nemopteridae	10			V. A. Krivokhatsky (personal communication)
Neuroptera	Crocidae	20			V. A. Krivokhatsky (personal communication)
Neuroptera	Neurorthidae	5			V. A. Krivokhatsky (personal communication)
Neuroptera	Osmylidae	15			V. A. Krivokhatsky (personal communication)
Neuroptera	Sisyridae	5			V. A. Krivokhatsky (personal communication)
Raphidioptera	Inocelliidae	10			V. A. Krivokhatsky (personal communication)
Raphidioptera	Raphidiidae	100			V. A. Krivokhatsky (personal communication)
Megaloptera	Corydalidae	10			V. A. Krivokhatsky (personal communication)
Megaloptera	Sialidae	28			V. A. Krivokhatsky (personal communication)
Hymenoptera/ Symphyta		1384 (USSR)		Megalodontidae (45 spp.), Blasticotomidae (3–4 spp.)	A. L. Lobanov (personal communication)
Hymenoptera	Ichneumonidae	8712			Yu and Horstmann 1997
Hymenoptera	Braconidae	4500	250	Telengainae, Middle Asian deserts (Turkmenistan)	S. A. Belokobylsky (personal communication)
Hymenoptera	Aphidiidae	73 (Russian Far East)	24 (Russian Far East)		Davidian 2007
Hymenoptera	Cynipidae	>500	40		O. V. Kovalev (personal communication)

(continued)

Table 7.1 (continued).

Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Hymenoptera	Iballidae	7	2		O. V. Kovalev (personal communication)
Hymenoptera	Liopteridae	5	2		O. V. Kovalev (personal communication)
Hymenoptera	Figitidae	?150	15		O. V. Kovalev (personal communication)
Hymenoptera	Emarginidae	1	1		O. V. Kovalev (personal communication)
Hymenoptera	Charipidae	>100	4		O. V. Kovalev (personal communication)
Hymenoptera	Eucoilidae	>350	30		O. V. Kovalev (personal communication)
Hymenoptera	Eurytomidae/ Eurytominae	265	5		Zerova 1995
Hymenoptera	Eurytomidae/ Eudecatominae	9	1		Zerova 1995
Hymenoptera	Eurytomidae/ Rileyinae	2	2		Zerova 1995
Hymenoptera	Eurytomidae/ Buresiinae	1	1		Zerova 1995
Hymenoptera	Eurytomidae/ Harmolitinae	100	5		Zerova 1995
Hymenoptera	Torymidae/ Megastigminae	54			Grissell 1999
Hymenoptera	Torymidae/ Toryminae	334	30		Grissell 1995
Hymenoptera	Encyrtidae	1260	163		Trjapitzin 1989
Hymenoptera	Eupelmidae	130	16		Sharkov 1995
Hymenoptera	Eulophidae	318 (Russian Far East)	50 (Russian Far East)		Storozheva et al. 1995
Hymenoptera	Aphelinidae	60 (Russian Far East)	18 (Russian Far East)		Jasnosh 1995
Hymenoptera	Trichogrammatidae	150			Fursov 2007
Hymenoptera	Chrysididae	1236			Kimsey and Bohart 1990
Hymenoptera	Scoliidae	33 (USSR)	3		Lelej 1995a
Hymenoptera	Mutillidae	523	54		Lelej 2002
Hymenoptera	(Apoidea)	3840	112		Yu. A. Pesenko (personal communication)
Hymenoptera	Andrenidae		12		Yu. A. Pesenko (personal communication)
Hymenoptera	Halictidae		26		Yu. A. Pesenko (personal communication)
Hymenoptera	Halictidae/ Nomioidinae	35	1		Pesenko 1983
Hymenoptera	Melittidae		5	Protomelittini	Yu. A. Pesenko (personal communication)
Hymenoptera	Megachilidae		36	Pararhophini	Yu. A. Pesenko (personal communication)

**Table 7.1** (continued).

<b>Order/ Suborder</b>	<b>Family (Superfamily)</b>	<b>Number of Species</b>	<b>Number of Genera</b>	<b>Endemic Family-Group Taxa and their Ranges</b>	<b>Source</b>
Hymenoptera	Apidae			Ancylini	Yu. A. Pesenko (personal communication)
Hymenoptera	Formicidae	1200	80		Radchenko 1999
Hymenoptera	Pompilidae	285 (USSR)	47		Lelej 1995b
Hymenoptera	Sphecidae	1000 (USSR)	93		Nemkov et al. 1995
Hymenoptera	Vespidae	77 (Russian Far East)	17		Kurzenko 1995
Mecoptera		>42 (USSR)			A. L. Lobanov (personal communication)
Trichoptera		2530	215	Phrygano- psychidae (3 spp.); Thremmatidae (3 spp.; S Europe)	M. L. Chamorro-Lacayo (personal communication), Morse 2008
Lepidoptera		25,000		Catapterigidae (1 gen., 1 sp.) (Crimea) Crinopterygi- dae (1 gen., 1 sp.) (Hesperian Region) Axiidae (2 genn., 6 spp.) (Hesperian) Endromidae (Transpalearc- tic) Mirinidae (1 gen., 2 spp.) (Stenopean: Manchuria) Somabrachyi- dae (3 spp.; N Africa, Syria)	Heppler 1998, S. Yu. Sinev (personal communication)
Lepidoptera	(Microptergoidea)	78			Heppler 1998
Lepidoptera	(Eriocranioidea)	12			Heppler 1998
Lepidoptera	(Hepialoidea)	37			Heppler 1998
Lepidoptera	(Nepticuloidea)	493			Heppler 1998
Lepidoptera	(Incurvarioidea)	207			Heppler 1998
Lepidoptera	(Tineoidea)	1307			Heppler 1998
Lepidoptera	(Gelechioidea)	3843			Heppler 1998
Lepidoptera	(Copromorphaidea)	64			Heppler 1998
Lepidoptera	(Yponomeutoidea)	485			Heppler 1998
Lepidoptera	(Immoidea)	1			Heppler 1998
Lepidoptera	(Pyraloidea)	2936			Heppler 1998
Lepidoptera	(Pterophoroidea)	315			Heppler 1998
Lepidoptera	(Sesioidea)	382			Heppler 1998
Lepidoptera	(Zygaenoidea)	162			Heppler 1998
Lepidoptera	(Cossoidea)	210			Heppler 1998

(continued)

Table 7.1 (continued).

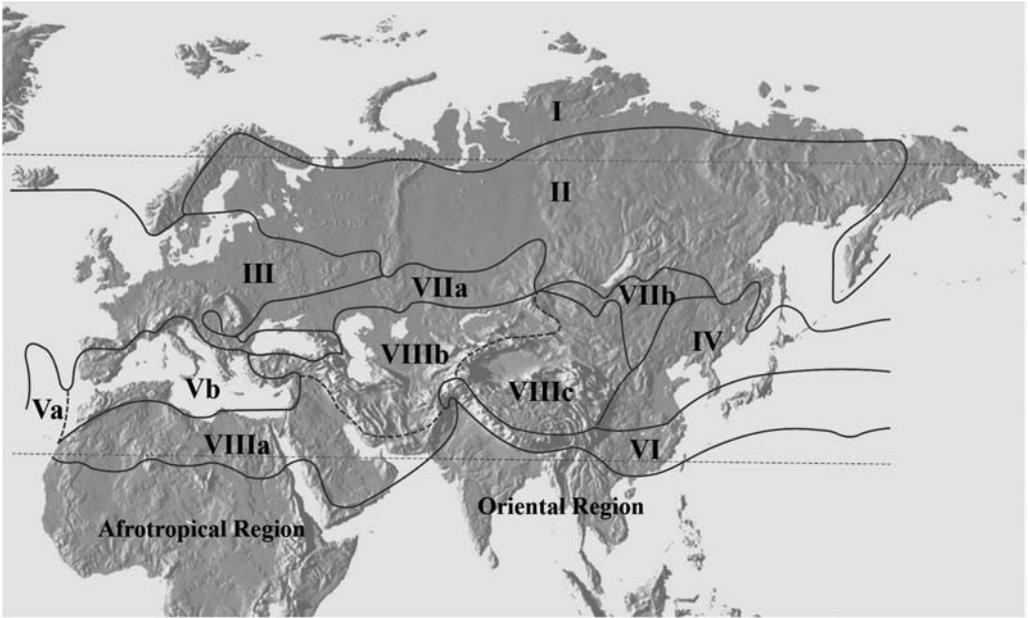
Order/ Suborder	Family (Superfamily)	Number of Species	Number of Genera	Endemic Family-Group Taxa and their Ranges	Source
Lepidoptera	(Tortricoidea)	1606			Heppner 1998
Lepidoptera	(Calluduloidea)	2			Heppner 1998
Lepidoptera	(Uranoidea)	18			Heppner 1998
Lepidoptera	(Geometroidea)	3545			Heppner 1998
Lepidoptera	(Papilionoidea)	1896			Heppner 1998
Lepidoptera	(Drepanoidea)	25			Heppner 1998
Lepidoptera	(Bombycoidea)	291			Heppner 1998
Lepidoptera	(Sphingoidea)	75			Heppner 1998
Lepidoptera	(Noctuoidea)	4475			Heppner 1998
Siphonaptera		900			S. G. Medvedev 1998
Diptera		40,291			Nartshuk 2003, Thompson 2006
<b>TOTAL</b>		<b>193,057</b>			

Altai Mountains and one in the Sayan Mountains, southern Siberia); and the beetle families Amphizoidae (mountain streams of North America, and north-western and eastern China) and Sphaeritidae (three species in the taiga of Eurasia, mountains of Sichuan, and northwestern North America). The range of the order Raphidioptera is limited almost entirely to the

Holarctic. Lindroth (1957) lists land and freshwater animal species common to Europe and North America. Despite its similarity to the Nearctic, however, the Palearctic is traditionally regarded as a separate region (Sclater 1858, Darlington 1963, Emeljanov 1974, Vtorov and Drozdov 1978, Krivokhatsky and Emeljanov 2000).

Fig. 7.1 (See figure on the following page.)

- (a) Main divisions of the Palearctic (after Emeljanov 1974, simplified).
- I. Arctic (Circumpolar Tundra) Region.
  - II. Taiga (Euro-Siberian) Region.
  - III. European (nemoral) Region.
  - IV. Stenopean (nemoral) Region.
  - V. Hesperian (evergreen forest) Region.
    - Va. Macaronesian Subregion.
    - Vb. Mediterranean Subregion.
  - VI. Orthrian (evergreen forest) Region.
  - VII. Scythian (Steppe) Region.
    - VIIa. West Scythian Subregion.
    - VIIb. East Scythian Subregion.
  - VIII. Sethian (Desert) Region.
    - VIIIa. Saharo-Arabian Subregion.
    - VIIIb. Irano-Turanian Subregion.
    - VIIIc. Central Asian Subregion.
- (b) NE Russia, Magadan Province, forest-tundra with flowering *Ledum decumbens* (Ericaceae) and a single bush of *Pinus pumila* on the right (Photo D. I. Berman).
- (c) NE Russia, Magadan Province, northern taiga (Photo D. I. Berman).
- (d) Russia, Smolensk District, Ugra River near Skotinino Village, mixed forest (Photo A. Konstantinov).
- (e) Russia, Caucasus (Photo M. Volkovitsh).



(a)



(b)



(c)



(d)



(e)

Insect biodiversity in the Palearctic is influenced by diverse climatic and other geographic conditions that exhibit a well-developed zonation. Temperature gradients are mainly responsible for the Arctic, Boreal, and Subtropical latitudinal belts. The following main zones are distributed from north to south in the western parts of the Palearctic: tundra, taiga, mixed and broadleaf (nemoral) forests, dry sclerophyll Mediterranean-type forests, wet subtropical forests, steppe, and deserts. Most mountain ranges demonstrate successive series of climatic altitudinal belts similar to lowland zonation. Atmospheric circulation and variations in precipitation yield the Atlantic, Continental, and Pacific longitudinal sectoral groups (Emeljanov 1974). The Atlantic sectoral group is characterized by two types of climate: Mediterranean with maximum precipitation in the winter, and boreal with maximum precipitation in the summer. The Pacific sectoral group has a monsoon climate with maximum precipitation during the summer. The boundary between the Atlantic and Pacific sectoral groups, though rather conventional, is usually drawn along the Yenisei River, Tien Shan mountains, and west of the Indus River in the south. The easternmost sectors of the Atlantic group and westernmost sectors of the Pacific group along this boundary where the oceanic influence is drastically weakened are characterized by lower precipitation and greater temperature fluctuations between summer and winter (continental and supercontinental climate); these sectors can be grouped as the Continental sectoral group. Continental climate is responsible for the taiga spreading southward and the steppe northward, squeezing out nemoral and subtropical zones in the Continental sectors (Emeljanov 1974). Continentality is one of the most important factors in Palearctic faunal differentiation, splitting subtropical and nemoral zones into two isolated fragments with rather different, though, in part, closely related insect faunas. In the easternmost Pacific sectors, high humidity is responsible for the lack of semidesert and desert

areas and the large meridional extension of mixed coniferous and broadleaf forests that are impoverished northward because of elimination of broadleaf elements and that gradually change to subtropical forests southward.

## GENERAL FEATURES OF INSECT BIODIVERSITY

More than 200,000 species of insects are known in the Palearctic Region – about one-fifth the total number of insect species in the world (Table 7.1). About half of all insects in the Palearctic are beetles. This estimate is far from final; hundreds of new species are described from the Palearctic every year. In recent years, parasitic Hymenoptera have been described most intensively, with 686 new species of Braconidae described from the Far East and neighboring areas in two volumes of the ‘Key to Insects of the Russian Far East’ by S. A. Belokobylsky and V. I. Tobias (1998, 2000), which include 2593 species. In the largest family of parasitic flies, the Tachinidae, more than 680 species are included in the key to the Far-Eastern fauna (Richter 2004), with 39 species and 9 genera described during the preparation of the key.

Most Palearctic species do not occur outside the region. In the Diptera (Fig. 7.2c), 37,123 species – 92% of the total 40,291 species – are Palearctic endemics (Thompson 2006). The percentage of endemic genera, and especially family-group taxa, is much less. Only four families of Diptera are endemic to the region (Nartshuk 1992): Eurygnathomyiidae, Phaeomyiidae, Risidae, and Stackelbergomyiidae. Of these, only the Risidae are generally accepted as a valid family; the others usually are treated as subfamilies or tribes (Sabrosky 1999).

One of the most obvious features of insect biodiversity in the Palearctic is its sharp increase from

**Fig. 7.2** (See figure on the following page.)

- A. *Calosoma sycophanta* (L.) (Coleoptera: Carabidae) (Turkey) (Photo A. Konstantinov).
- B. *Nemoptera sinuata* Olivier (Neuroptera: Nymphopteridae) (Turkey) (Photo M. Volkovitsh).
- C. *Eristalis tenax* (L.) (Diptera: Syrphidae) (Turkey) (Photo A. Konstantinov).
- D. *Cryptocephalus duplicatus* Suffrian (Coleoptera: Chrysomelidae) (Turkey) (Photo A. Konstantinov).
- E. *Poecilimon* sp. (Orthoptera: Tettigoniidae) (Turkey) (Photo M. Volkovitsh).
- F. *Capnodis carbonaria* (Klug) (Coleoptera: Buprestidae) (Turkey) (Photo M. Volkovitsh).
- G. *Cyphosoma euphraticum* (Laporte et Gory) (Coleoptera: Buprestidae) (southern Russia) (Photo M. Volkovitsh). (See color plate).



north to south, corresponding to the most fundamental pattern of life on earth (Willig et al. 2003). For example, the Orthoptera (Figs. 7.2e and 7.3e), Blattaria, Dermaptera, Mantodea, and Phasmatodea are represented by 72 species in the forest, 171 species in the steppe, and 221 species in the desert zone of the former USSR (Iablokov-Khnzorian 1961).

The insect fauna of the Palearctic is slightly depauperate at the order, family, and genus levels (compared to most other regions) but it has high species richness; that is, the number of higher taxa with only a single species in the Palearctic is relatively low and the relative number of species per higher taxon is large. In this regard, it is similar to island faunas characterized by a small number of introductions that were followed by extensive species-level radiations (Magnacca and Danforth 2006). The Palearctic and Oriental regions have about the same number of species of flea beetles (Chrysomelidae: Alticini) (about 3000, although the Oriental fauna is much less known), but differ sharply in generic diversity, with about 60 genera in the Palearctic and 220 in the Oriental. Most flea-beetle species richness in the Palearctic is concentrated in a few large, nearly cosmopolitan genera (e.g., *Aphthona*; see Konstantinov 1998).

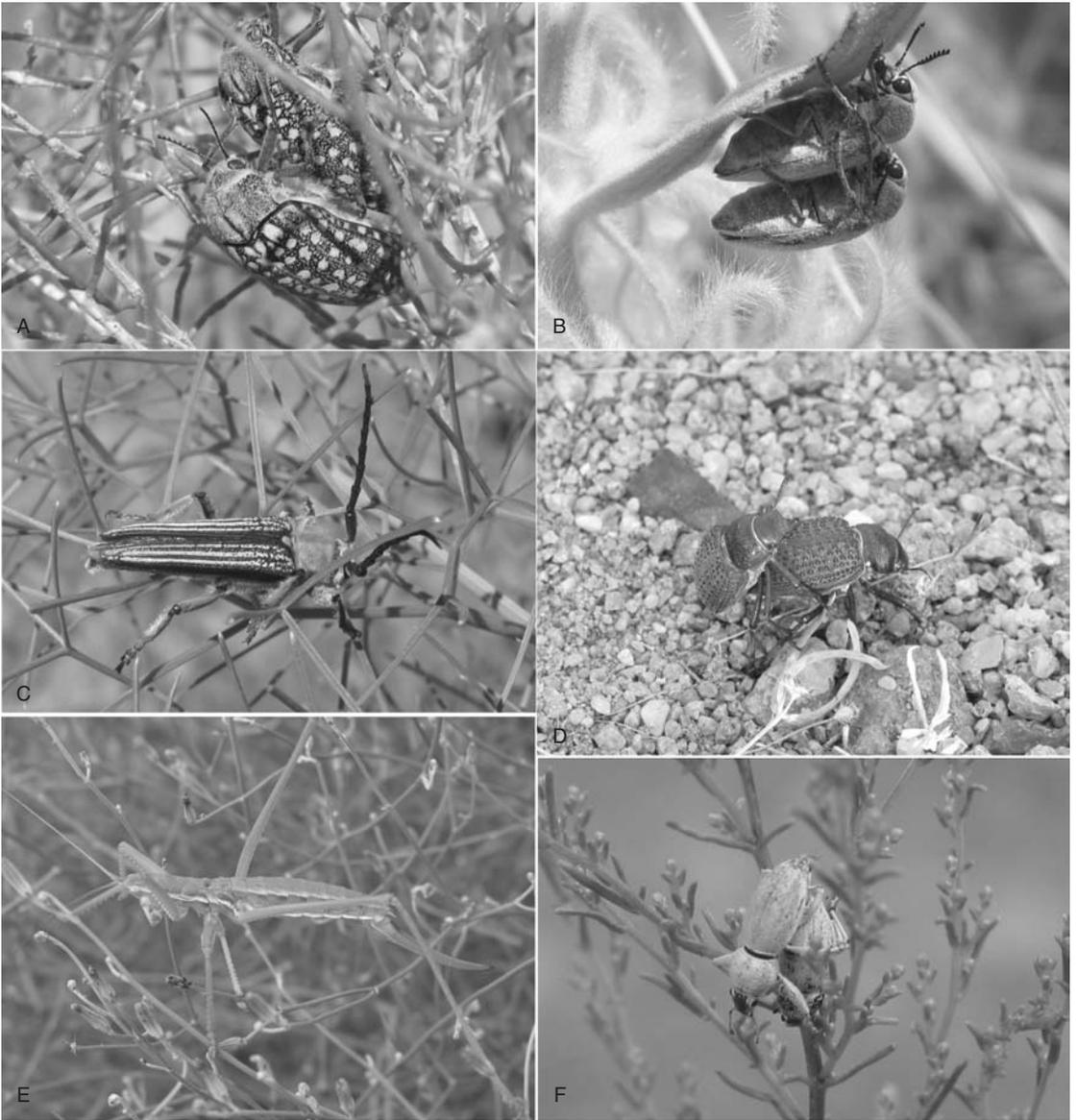
Historically, the Palearctic fauna is considered to have been derived from the ancient fauna of Laurasia, dramatically changed by the aridization of the Tertiary, but primarily by the Quaternary glaciation (Lopatin 1989), which includes the largest global glaciations of the upper Pliocene and Pleistocene. Also important were fluctuations of sea level, which led not only to changes in coast lines, but also to formation of a variety of land bridges between continents and various islands, and the Alpine orogenesis during which the largest mountain systems in Europe and Asia appeared (Kryzhanovsky 2002). These climatic and geomorphological changes might explain the appearance of a Tibetan scarab, *Aphodius holdereri* Reitter, in England (Coope 1973); disjunct distributions of *Helophorus lapponicus* Thompson (Coleoptera: Helophoridae) between its main range (Scandinavia to eastern Siberia) and relict populations in mountainous areas of Spain, Transcaucasia, and Israel/Lebanon (Angus 1983); and current restriction of the water beetle *Ochthebius figueroi* Garrido et al. (Coleoptera: Hydraenidae), known from Pleistocene deposits in England, to a small mountain area in northern Spain (Angus 1993).

Insect biodiversity has a particular pattern in space and time. The distribution of specialized herbivores,

closely associated with specific plants and plant communities, often reveals a more distinct pattern than the distribution of insects with other food specializations. Changes in the Curculionoidea (Coleoptera) fauna along a 160-km transect that crosses six types of desert plant communities in the Transaltai Gobi Desert in Mongolia illustrate this pattern (Table 7.2). Two types of plant communities exist at the extremes of the profile – a northern steppified desert and a southern extra-arid desert. The numbers of weevil species at the extremes do not differ sharply (17 in the north and 11 in the south), but only one species, *Conorhynchus conirostris* (Gebler), occurs in all types of deserts. All ‘northern’ species (with ranges situated mostly north of the investigation site) gradually disappear southward, being substituted by ‘southern’ species in accordance with vegetational changes. The distribution of (mostly predatory) carabids and nonspecialized phyto- and detritophagous tenebrionid beetles mostly depends on climate, chemical and mechanical properties of soil, and vegetation density; it follows vegetational changes less closely, but exhibits similar patterns.

Different natural zones are characterized by the dominance of some higher taxa, particularly in the Arctic. The majority of the Arctic chrysomelid fauna is composed of 25 species of a single subfamily, the Chrysomelinae (with 12 species belonging to the genus *Chrysolina*; see Chernov et al. 1994), although a few boreal species of Cryptocephalinae and Galerucinae contribute to the Hypoarctic leaf-beetle fauna (Medvedev and Korotyaev 1980). The taxonomic pattern of the biogeographical regions has a historical background, but the zonal peculiarities of the faunas are largely due to specific requirements of the taxa. In the holometabolous insects, these requirements are related primarily to the environmental conditions appropriate for larval development. An example is illustrated by the chrysomelid fauna of the Transaltai Gobi Desert in Mongolia. Ten species of Chrysomelidae, out of the fourteen species found in the six types of desert plant communities (Korotyaev et al. 2005), belong to the tribes Cryptocephalini, Clytrini, and Cassidini. The case-bearing (Cryptocephalini) and sheltered (Clytrini) larvae apparently are better adapted to the xeric environment than are the ectophytic larvae of the Chrysomelinae and Galerucini or soil-inhabiting larvae of the Eumolpinae and some Alticini.

Another obvious feature of insect biodiversity in the Palearctic is its organization in time. Nearly



**Fig. 7.3**

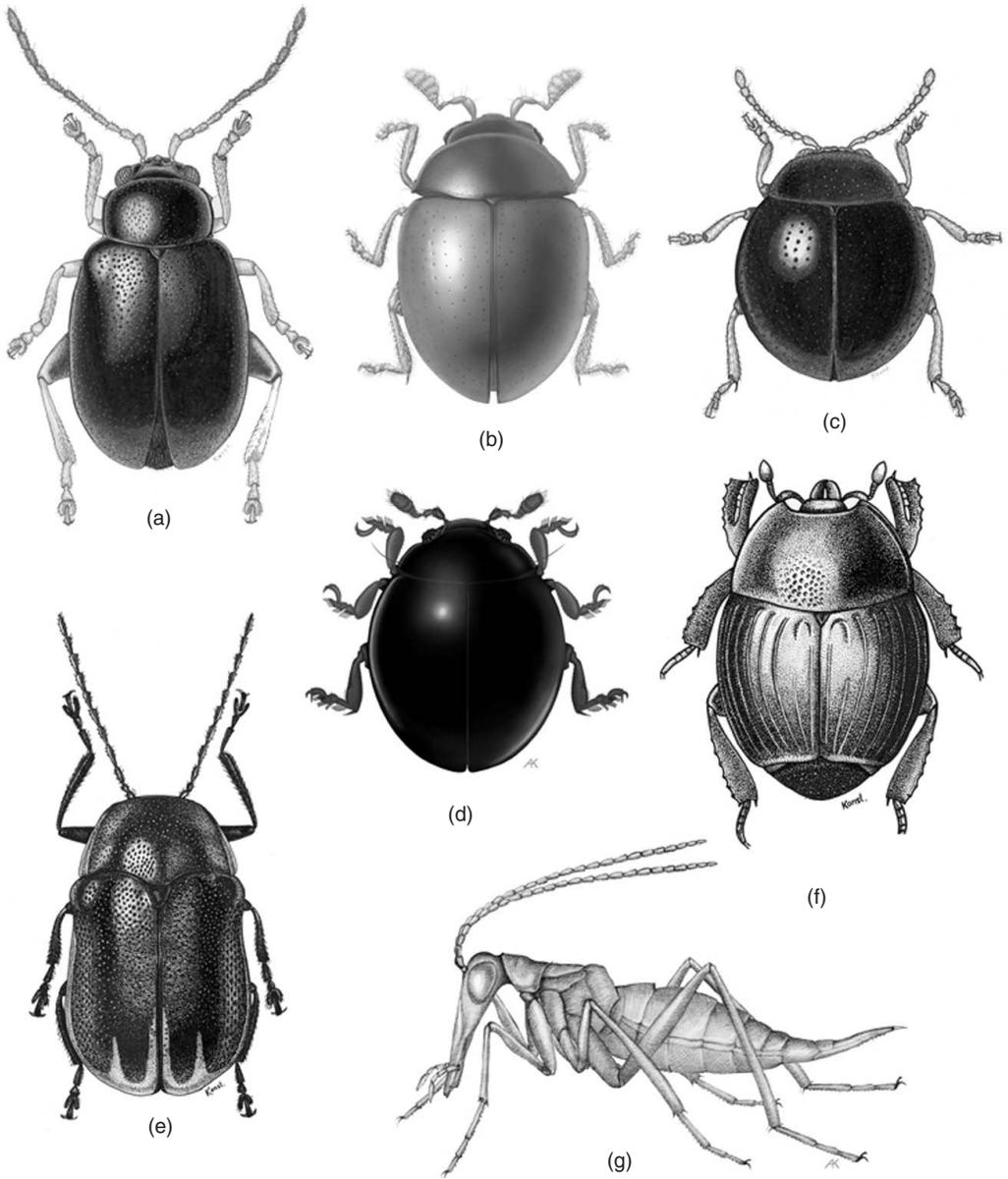
- A. *Julodis variolaris* (Pallas) (Coleoptera: Buprestidae) (Kazakhstan) (Photo M. Volkovitsh).
- B. *Julodella abeillei* (Théry) (Coleoptera: Buprestidae) (Turkey) (Photo M. Volkovitsh).
- C. *Mallosia armeniaca* Pic (Coleoptera: Cerambycidae) (Turkey) (Photo M. Volkovitsh).
- D. *Trigonoscelis schrencki* Gebler (Coleoptera: Tenebrionidae) (Kazakhstan) (Photo M. Volkovitsh).
- E. *Saga pedo* Pallas (Orthoptera: Tettigoniidae) (Kazakhstan) (Photo M. Volkovitsh).
- F. *Piazomias* sp. (Coleoptera: Curculionidae) (Kazakhstan) (Photo M. Volkovitsh). (See color plate).

**Table 7.2** Distribution of Curculionoidea across six types of desert plant communities in Transaltai Gobi, Mongolia. 6–1 = desert plant communities (from north to south): 6, *Anabasis brevifolia* steppeified desert; 5, *Reaumuria soongorica* + *Sympegma regelii* desert; 4, *Haloxylon ammodendron* desert; 3, *Reaumuria soongorica* + *Nitraria sphaerocarpa* desert; 2, extra-arid *Iljinia regelii* desert; 1, extra-arid *Ephedra przewalskii* + *Haloxylon ammodendron* (in dry temporary waterbeds) desert.

Steppe Species (+)	6	5	4	3	2	1	Desert Species (*)
	*		*				<i>Pseudorchestes furcipubens</i> (Reitter)
	*	*			*		<i>Deracanthus faldermanni</i> Faldermann
<i>Cionus zonovi</i> Korotyaev	+	*	*	*	*	*	<i>D. hololeucus</i> Faldermann
<i>Eremochorus inflatus</i> (Petri)	+	*	*			*	<i>Mongolocleonus gobiensis</i> (Voss)
<i>Macrotarrhus kiritshenkoi</i> Zaslavsky	+		*	*	*	*	<i>Pycnodactylus oryx</i> (Reitter)
<i>Philermus gracilitarsis</i> (Reitter)	+		*			*	<i>Stephanocleonus helenae</i> (Ter-Minassian)
<i>Pseudorchestes</i> sp.	+		*		*	*	<i>Elasmobaris alboguttata</i> (Brisout)
<i>Stephanocleonus paradoxus</i> (Fähræus)	+		*		*	*	<i>Perapion ?myochroum</i> (Schilsky)
<i>Fremuthiella vossi</i> (Ter-Minassian)	+	+	*		*	*	<i>P. centrasiaticum</i> (Bajtenov)
<i>Stephanocleonus potanini</i> Faust	+	+	*		*	*	<i>Anthypurinus kaszabi</i> (Bajtenov)
<i>S. inopinatus</i> (Ter-Minassian)	+	+	*				<i>Lixus incanescens</i> Boheman
<i>S. excisus</i> Reitter	+	+	*				<i>Sibinia</i> sp. pr. <i>beckeri</i> Desbrochers
<i>S. persimilis</i> Faust		+	*				<i>Cosmobaris scolopacea</i> (Germar)
<i>Gronops semenovi</i> Faust	+		+			*	<i>Oxyonyx kaszabi</i> Bajtenov
<i>Eremochorus mongolicus</i> (Motschulsky)	+	+	+			*	<i>Platygasteronyx humeridens</i> (Voss)
<i>Conorhynchus conirostris</i> (Gebler)	+	+	+	+	+	+	<i>P. macrosquamosus</i> Korotyaev
<b>Extrazonal consortium of <i>Reaumuria soongorica</i> (□)</b>							
<i>Corimalia reaumuriae</i> (Zherichin)	□	□		□			
<i>Coniatus zaslavskii</i> Korotyaev		□		□			
<i>C. minutus</i> Korotyaev	□	□		□			

all regions of the Palearctic are subjected to strong seasonal changes in temperature and precipitation. Long periods of fall and winter are characterized by minimum insect activity. Some of the most typical winter insects are representatives of the Holarctic family Boreidae, the snow scorpionflies. These small mecopterans of the genus *Boreus* (Fig. 7.4g) appear in the fall and winter and often hop and walk on the snow.

On the Russian Plain, maximum insect biodiversity of herbivores can be observed in late May and in June. The taxonomic aspect of any local fauna also changes with time. A number of species are active only in early spring, particularly those in southern, more xeric regions of the Palearctic. Good examples include many flightless black *Longitarsus* (Chrysomelidae) species that are associated with ephemeral plants,

**Fig. 7.4**

- A. *Aphthona nonstriata* Goeze (Coleoptera: Chrysomelidae).  
 B. *Clavicornaltica dali* Konstantinov and Duckett (Coleoptera: Chrysomelidae).  
 C. *Mniophila muscorum* Koch (Coleoptera: Chrysomelidae).  
 D. *Kiskeya baorucae* Konstantinov and Chamorro-Lacayo (Coleoptera: Chrysomelidae).  
 E. *Cryptocephalus ochroloma* Gebler (Coleoptera: Chrysomelidae).  
 F. *Margarinotus (Kurilister) kurbatovi* Tishechkin (Coleoptera: Histeridae).  
 G. *Boreus hyemalis* (L.) (Mecoptera: Boreidae).

and in their flightless features, are similar to alpine members of the genus (Konstantinov 2005). The maximum biodiversity of adult weevils in the steppe of the Northwestern Caucasus precedes the maximum local air temperature and precipitation, which might mean that the phenology of holometabolous herbivores is adjusted to the maximum supply of warmth and water for the feeding (larval) stage. Late maturation of the hemimetabolous insects (orthopterans, bugs, and leafhoppers) fits this speculation: the development of their larvae and nymphs proceeds in the warmest part of summer.

Several of the largest Palearctic genera of families of most species that are rich in woodlands of other biogeographic regions are confined to open landscapes in the Palearctic Region. The best illustration is the largest genus of the mostly xylophagous family Cerambycidae, the endemic *Dorcadion*, with all 300-plus species occurring in meso- to xerophilic grasslands. No genus of dendrobiont cerambycids has comparable diversity in the Palearctic. The leaf-mining tribe Rhamphini of the Curculioninae, with about 100 Palearctic species in some 10 genera on trees and bushes, has its largest subendemic genus in the region (with one species in Namibia). This subendemic genus, *Pseudorchestes*, has more than 35 described and dozens of yet undescribed species that develop on herbaceous plants and semi-shrubs of the Asteraceae. Among the predatory beetles, the lady-beetle genus *Tetrabrachys* (= *Lithophilus*) of the endemic subfamily Lithophilinae, with 51 species (Iablokoff-Khnzorian 1974), is the largest in the region. The vast majority of its species are confined to xeric areas of the southern Palearctic, mostly in the western half. The second largest genus in the region, *Hyperaspis*, with 45 species, also has most of its species distributed in the dry open landscapes. The great diversification of the open-landscape Hyperinae and Lixinae, compared with just a few typically woodland species of these large subfamilies of the Curculionidae, is also characteristic, as is the absence of dendrophilous Baridinae in the western and central Palearctic; the baridine fauna associated with herbs, however, is fairly species rich. The same tendency is also obvious in the Alticini (Chrysomelidae: Galerucinae), Cassidinae (Chrysomelidae), and the subfamily Ceutorhynchinae, tribes Cionini and Tychiini of the Curculioninae, and Sitonini of the Entiminae (Curculionidae). The faunal similarity with open landscapes of the Nearctic counterpart is rather low. The Nearctic has greater

representation of the predominantly tropical weevil families Anthribidae and Dryophthoridae and the subfamily Conoderinae of the Curculionidae, whereas the Hyperinae, Lixinae, Cyclominae, Rhythirini, *Tychius*, and many taxa of the Entiminae that dominate grassland communities in the Palearctic are absent or subordinate in the Nearctic.

## NOTES ON BIODIVERSITY OF SOME INSECT GROUPS IN THE PALEARCTIC

Most of the large orders have wide representation in the Palearctic. More than 100,000 species of beetles, for example, occur in the region. The other most species-rich orders are Diptera, Hymenoptera, and Lepidoptera. Higher taxa with different types of food specialization gain richness in the Palearctic, including its northern parts. Parasitic wasps, for example, are represented by a greater number of species than is the entire order Coleoptera in the British Isles (LaSalle and Gauld 1991, cited by Sugonyaev and Voinovich 2006). The less-specialized predatory, mycophagous, and phytophagous fungus gnats (Diptera: Mycetophilidae) and highly specialized phytophagous sawflies (Hymenoptera: Tenthredinidae) have enormous faunas, with 645 species in Karelia (Polevoi 2007) and about 800 species in Finland (A. G. Zinovjev, personal communication), respectively. Many higher taxa of noxious blood-sucking insects, such as the orders Siphonaptera and Phthiraptera and the dipteran families Culicidae, Ceratopogonidae, Simuliidae, Tabanidae, Gasterophilidae, Hypodermatidae, Oestridae, and Hippoboscidae, are widely represented in the Palearctic. Of the blood-sucking Diptera that transmit dangerous disease agents, only the Glossinidae with their infamous tse-tse are absent, and the Psychodidae are restricted to the southernmost regions of the Palearctic. The Palearctic Siphonaptera fauna, with 900 species, is the largest in the world, comprising 40% of the world species and genera, although only one monotypic subfamily, with 19 species, is endemic (Medvedev 1998). Scale insects (Sternorrhyncha: Coccinea), most conspicuous in the tropical forests, are less abundant and diversified in the Palearctic but are present in all climatic zones, including the Arctic. Entomophagous wasps of the superfamily Chalcidoidea, which are associated closely with scale insects, have developed a special strategy of host use in the high latitudes that differs

from the strategy used in the tropics (Sugonyaev and Voinovich 2006).

A few orders, largely contributing to the faunas of the adjacent tropical regions, and all belonging to the Orthopteroidea, are poorly represented in the Palearctic: Blattaria, Dermaptera, Isoptera, Mantodea, and Phasmatodea. Most higher taxa of Palearctic Orthoptera are widely distributed in the tropics, but a few subfamilies are mainly Palearctic (Deracanthinae, Glyphonotinae, Onconotinae, Pamphaginae, and Thrinchinae). Among tribes, the Chrysochraontini, Conophymatini, Drymadusini, Gampsocleidini, and Odonturini are endemic. Almost all the taxa in these groups have their centers of diversity and endemism in the southern Palearctic (Sergeev 1993).

For many large family-group taxa, the Palearctic contains a relatively small percentage of the world fauna. For example, the beetle family Buprestidae (Fig. 7.2f, g) comprises 2430 species in 99 genera in the Palearctic – approximately 17% of the species and 20.2% of the genera in the world (Bellamy 2003, Löbl and Smetana 2006). The large group of phytophagous flea beetles (Chrysomelidae, Alticini), with about 11,000 species and 600 genera worldwide, is represented in the Palearctic by about 2400 species and 64 genera. Yet only a few genera of the Alticini are endemic to the Palearctic; most of them are distributed in the mountains of southern Europe, the Caucasus, and the Mediterranean (Konstantinov and Vandenberg 1996). Many Oriental and some Afrotropical genera are represented by only a few species in the Palearctic at the eastern or southern borders of the region.

The subfamily Ceutorhynchinae of the Curculionidae – similar to the Alticini in many ecological features and range of body size – had 1316 described species as of 2003, and includes Palearctic representatives of 12 of 14 presently distinguished tribes (Colonnelli 2004), with only two Palearctic tribes (Lioxonychini and Hypohypurini) absent from the region. About half of the species of this worldwide subfamily and 102 of the total 167 genera occur in the Palearctic; 79 genera and 2 tribes are Palearctic endemics.

For many boreal and temperate groups, the Palearctic has the most species-rich fauna, compared with other zoogeographical regions. The Cecidomyiidae (Diptera), for example, have 3057 species in the Palearctic, compared with only 533 species in

the Neotropics (Gagne 2007). This trend is also true for aphids, which are mostly Holarctic; their complicated life cycle is possibly an adaptation to a temperate climate. Ichneumonidae (Hymenoptera) have a similar distribution of diversity. They are richer in the northern hemisphere, particularly in the Palearctic. The tribe Exenterini, for example, is distributed almost entirely in the Holarctic, with all genera represented in the Palearctic (Kasparyan 1990). Many species have wide transpalearctic ranges that are almost entirely confined to forest regions. Most (Kasparyan 1990) are parasites of various Tenthredinidae (Hymenoptera: Symphyta), which are also rich in species in the Palearctic. Taeger et al. (2006) counted 1386 species of Symphyta in Europe, 220 species in Norway, and 8 in Novaya Zemlya. For China, the estimate is 2600 species and 350 genera (Wei et al. 2006).

Aquatic and amphibiotic insect groups are also rich in the Palearctic. About one-third of the world's blood-sucking Simuliidae, all with aquatic larvae, are distributed in the Palearctic (Adler and Crosskey 2008). Chironomidae, with their predominantly aquatic larvae, also are species rich in the Palearctic, dominating the Arctic aquatic complexes and including the northernmost dipterans (also southernmost in the Antarctic: Nartshuk 2003). For Russia, the following species numbers are available for the largest insect orders (partly including the fauna of neighboring countries): Ephemeroptera – about 300 species (N. Ju. Kluge personal communication), Odonata – 148 species (Kharitonov 1997), Plecoptera – 225 species (Zhiltzova 2003), Megaloptera – 15 species (Vshivkova 2001), Trichoptera – 652 species (Ivanov 2007), Neuroptera – 11 species (Krivokhatsky 2001), Lepidoptera – 8 species (Lvovsky 2001), Coleoptera – about 700 species (Kirejtshuk 2001), and Hymenoptera – 24 species (Kozlov 2001). Plecoptera, with preference for cold water, are quite unique in the Palearctic (Zhiltzova 2003). In particular, the Euholognatha include a large number of taxa endemic to the Palearctic, including the Scopuridae, with a single genus of five species. The Taeniopterygidae and Capniidae contain large numbers of genera endemic to the Palearctic (6 of 13 worldwide and 7 of 17, respectively). Only one family, the Notonemouridae, with 69 species, is absent from the Palearctic, being distributed in the Neotropics, Australia, and Africa south of the Sahara (Zhiltzova 2003). The ranges of many Palearctic species are

relatively small, such as that of *Capnia kolymensis* Zhiltzova from the Kolyma River and several species of *Nemoura* from Iturup Island. The distributions of many species associated with cold water are restricted to mountain systems (Alps, Carpathians, Caucasus, Tien Shan). Their endemism at the species level reaches 60% (Zhiltzova 2003). Endemism of other aquatic insect groups, such as Trichoptera, is estimated at 36% (Zhiltzova 2003).

The Palearctic is sometimes among a few places on Earth where a rare group of flies is distributed. The family Canthyloscelidae, for example, has a single genus (*Hyperoscelis*) with three species in the Palearctic and two other genera with four species in southern South America and four species in New Zealand (Nartshuk 1992). Among the widely distributed families of flies, the following are known from the Palearctic but are absent in the Nearctic: Camillidae, Cryptochetidae, Megamerinidae, and Xenasteiidae of the Acalyptratae, and Eugeniidae and Villeneuveiellidae of the Calyptratae. Almost all are widely distributed in the Oriental or Afrotropical Regions. The Nearctic has seven families of flies not known from the Palearctic. The recently established family Xenasteiidae in the Palearctic occurs in the Mediterranean and on the islands of the Indian and Pacific oceans. The Apioceridae are known from all regions except the Palearctic (Nartshuk 1992).

Many endemic Palearctic higher taxa have relatives in either the Nearctic or the temperate areas of the Southern Hemisphere. But the weevil subfamily Orobittidinae, in addition to the oligotypic Palearctic genus *Orobittis* associated with *Viola* plants, includes the genus *Parorobittis* (Fig. 7.5c), with a few species (hosts unknown) in tropical South America (Korotyaev et al. 2000) where Violaceae are represented by more than 300 species (Smith et al. 2004).

Small insect families contribute considerably to the insect biodiversity of the Palearctic Region. *Panorpa* species, the scorpionflies (Mecoptera), although neither speciose nor abundant, are common in mixed and nemoral European forests, and the oligotypic Sialidae (Megaloptera) comprise a conspicuous component of the European riparian landscape. A relatively small beetle family, the Trogossitidae, includes the worldwide synanthropic *Tenebrioides mauritanicus* L., which is injurious to stored products. *Ostoma ferrugineum* (L.) and a few species of the genera *Peltis* and *Thymalus* frequently are found under bark in all types of Palearctic forests except the northernmost

taiga. Larvae of one of the two European representatives of the beetle family Byturidae in some years destroy a considerable part of the raspberry harvest. The European *Dascillus cervinus* (L.) and the Caucasian *D. elongatus* Faldermann of the small family Dascillidae are abundant under the forest canopy for short periods of their adult lives. Their Eastern Palearctic ally, *Macropogon pubescens* Motschulsky, is one of the few common beetles around bushes of *Pinus pumila* Regel in the hills of the middle Kolyma basin (North-east Asia), which has a markedly impoverished insect fauna. *Mycterus curculionoides* (F.) of the small family Mycteridae often dominates assemblages of medium-sized beetles in the mid-summer dry grasslands of the Western Palearctic.

Two myco-detritophagous families of small beetles, Cryptophagidae and Latridiidae, include several hundred brown beetles, all rather uniform in appearance, occurring almost everywhere except the northern tundra. They are especially abundant in wet riparian litter. These families, as well as the predominantly mesohygrophilous and rather uniform Helodiidae (= Cyphonidae), illustrate a tendency that the least conspicuous taxa often have the greatest species richness. Many staphylinid beetles fit this trend, including those that live in the open (some *Stenus*) and the cryptobionts (e.g., small Aleocharinae). The largest genus of the Alticini in the Palearctic, *Longitarsus*, with 221 species in the region (29 species only on Mount Hermon in Israel; Chikatunov and Pavliček 2005), is not particularly diverse morphologically. One of the largest genera of weevils in the Palearctic, *Ceutorhynchus*, with about 300 species, is also morphologically less diverse, compared with the showy Oriental *Mecysmoderes* from the same subfamily.

## BIODIVERSITY OF INSECT HERBIVORES

Among the herbivores, the greatest species richness is achieved by insects with rhizophagous, soil-inhabiting larvae. These groups include the weevil subfamily Entiminae (Fig. 7.3f) with about 14,000 known species (3500 in the Palearctic), the tribe Alticini of the Chrysomelidae with about 11,000 species worldwide and ca 3000 species in the Palearctic, and the noctuid moths with 27,000 species (5500 in the Palearctic). Of the Entiminae, the largest genus is the Palearctic

*Otiorhynchus s.l.*, with about 1000 species; all are wingless and many have restricted ranges in the mountains of southern Europe, Anatolia, and Middle and Central Asia<sup>1</sup>. The high number of species probably relates little to trophic specializations because many species are apparently polyphagous, which is probably true most of the subfamily Entiminae. Winglessness likely facilitates geographic isolation. *Otiorhynchus* also includes a great number of parthenogenetic forms that are genetically isolated, with their own ranges and ecological associations. Many other mostly wingless genera of the Entiminae include parthenogenetic forms, which probably enables rapid range extensions. The vast territory of the Russian Plain with its short post-glaciation history has faunas of the genera *Otiorhynchus* (18 species) and *Trachyphloeus* (9 species) that consist exclusively of parthenogenetic forms whose known bisexual ancestors, when present, have narrow ranges in the neighboring or rather distant mountain systems. Most of the parthenogenetic forms occur in the temperate and boreal forests and in the steppe zone, whereas no endemic parthenogenetic forms are known from the tundra, and only a few live in the desert zone (Korotyaev 1992). The relict bisexual forms often are localized in the mountains, whereas their parthenogenetic derivatives are in the plains.

The wingless species of *Otiorhynchus* contradict speculation that a limited number of species can be produced within a single genus, presuming that only a certain number of combinations of morphological characters co-occur to give rise to viable forms, whereas many other combinations, being maladaptive, are

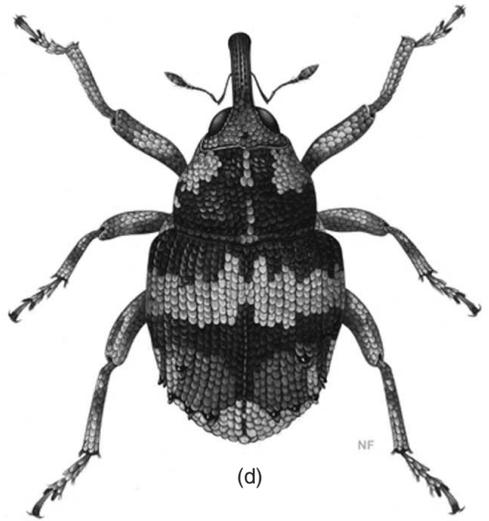
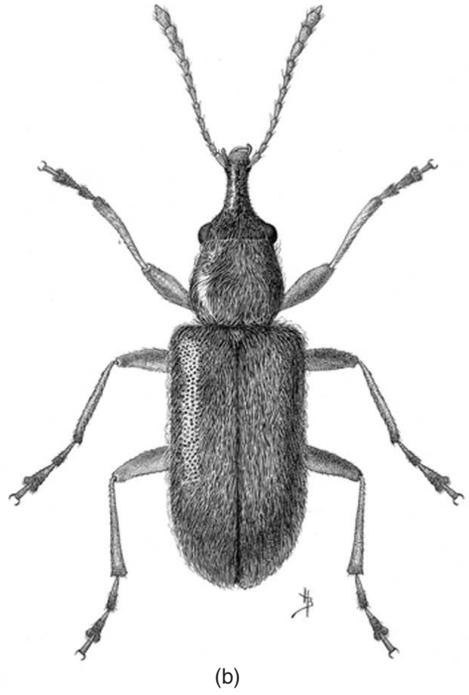
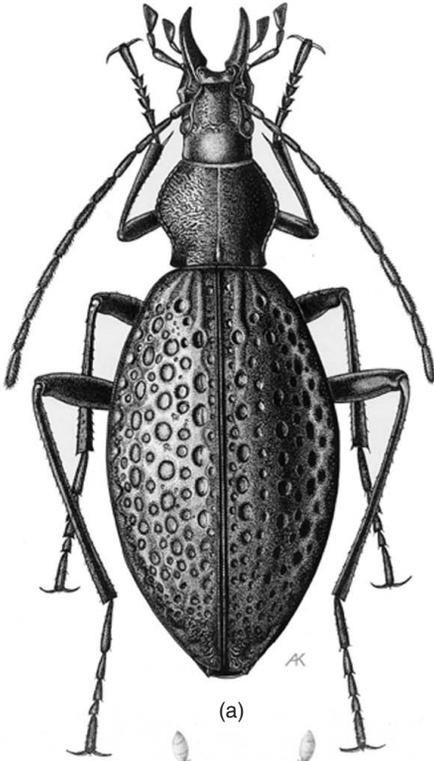
selected against. This idea might apply to planktonic forms (Zarenkov 1976) but is wrong for terrestrial beetles. *Otiorhynchus* in the broad sense has a great number of species that differ only in the proportions of their antennal funicle, sexually dimorphic characters, vestiture, and coloration. Considering that every new taxon potentially could produce a further set of descendants with innumerable combinations of old and new characters, one can hardly imagine reasonable limitations for the diversity of species that could evolve in *Otiorhynchus* and other apterous beetles. Parthenogenesis increases this diversity, but here a limitation does exist: parthenogenetic forms of weevils do not have more than six haploid chromosome sets; hexaploids are terminal products of parthenogenesis.

The diversity of a taxon of specialized herbivores is often proportional to the number of species in the host-plant taxon (although this statement is more hypothetical than verified), but sometimes it is not. Even when it is, many species of the higher host taxon have no insect consortia of their own, whereas a single or a few species harbor many herbivores. This situation is true for *Ephedra* in Mongolia: 10 species of the weevil tribe Oxyonychini (Coleoptera: Curculionidae) (Fig. 7.5d) known from this country (Korotyaev 1982 and unpublished data) live on *Ephedra sinica* Stapf and *E. przewalskii* Stapf, whereas no species of Oxyonychini is apparently associated with 6 (Grubov 1982) other Mongolian species of *Ephedra*. Similarly, 14 species of Oxyonychini (half the species with known hosts) are associated with *Ephedra major* Host (= *E. procera* Fisch. and Mey.) in the Western Palearctic (Colonnelli 2004), which is probably the host plant with one of the greatest numbers of weevils specialized on a single species in the Palearctic Region. Often, only a few, or no, herbivores can be found in localities or regions with a wide variety of potential hosts, while relatively poor habitats or countries can harbor greater insect biodiversity. For example, in Ul'yanovsk Province in the middle Volga area of Russia, 9 species of the weevil genus *Tychius* are found on 9 species of *Astragalus* (Fabaceae) (Isaev 2001), whereas in Mongolia, with

<sup>1</sup>Middle Asia is a climatic/natural region distinct from Central Asia (Korotyaev et al. 2005, Medvedev 2005b). It includes the Asian republics of the former USSR and neighboring parts of Afghanistan and Iran. The region is characterized by warm winters and maximum rainfall in spring and autumn. Central Asia is a climatic region that includes Mongolia and a large area of northwestern China. It is characterized by an extreme continental climate with harsh winters and maximum rainfall in late summer. The term Middle Asia is used in the Russian literature, but in the English-language literature Middle Asia is incorporated in Central Asia.

**Fig. 7.5** (See figure on the following page.)

- A. *Carabus lopatini* Morawitz (Coleoptera: Carabidae).
- B. *Cimberis attelaboides* (F.) (Coleoptera: Nemonychidae).
- C. *Pararobitis gibbus* Korotyaev, O'Brien and Konstantinov (Coleoptera: Curculionidae).
- D. *Theodorinus* sp. (Coleoptera: Curculionidae).



68 species (Sanchir 1982) of *Astragalus*, only 4 or 5 species of *Tychius* are known to be associated with this host genus.

The number of specialized and occasional arthropod feeders on a particular plant species can be quite high. For example, 175 species are reported on *Lepidium draba* L. (Brassicaceae), with the majority being insects (Cripps et al. 2006).

For the entire superfamily Curculionoidea, excluding scolytines, the plant species to beetle species ratio is 6:1 in the Caucasus and Mongolia. In continental Northeast Asia, in the northern taiga and tundra zones of Magadan Province and Chukchi Autonomous District, this ratio is about 12:1 (13:1 in the impoverished biota of the Kamchatka Peninsula and the Koryak Plateau north of it), and about 30:1 in the Arctic Wrangel Island (B. A. Korotyaev unpublished data). In local steppe areas, the ratio is about 2.5:1 (Korotyaev 2000 – isolated steppe site; Korotyaev, unpublished data – Taman' Peninsula).

The diversity of beetle herbivores is unevenly distributed among higher plant taxa. Grasses and sedges that dominate the vegetation over vast territories in the Palearctic usually possess poor insect consortia, consisting mostly of planthoppers (Auchenorrhyncha), although the genus *Carex* has the greatest number of insect herbivores among herbaceous plants (75; Emeljanov 1967). Most Palearctic insects with chewing mouthparts, such as weevils and leaf beetles, avoid monocots. Among the Palearctic Chrysomelidae, a few genera of flea beetles (e.g., *Chaetocnema* and *Psylliodes*) include a relatively large number of species that feed on monocots. Most other chrysomelids associated with monocots in the Palearctic belong to a few primitive subfamilies, such as the predominantly temperate, aquatic Donaciinae with 62 species in the former USSR (Lopatin et al. 2004). A few Palearctic species of the large, mostly tropical tribe Hispini are associated with grasses. In Belarus, 64 of 351 species of leaf beetles feed on Poaceae and Cyperaceae (Lopatin and Nesterova 2005). Two small genera of stem-mining cerambycids (*Theophilea* and *Calamobius*) and the two largest Palearctic genera with rhizophagous larvae (*Dorcadion* and *Eodorcadion*) are associated with Poaceae. Among weevils, most of the monocot feeders belong to specific family- and genus-group taxa with predominantly extratropical distributions (family Eirrhinidae; subfamily Bagoinae, tribe Mononychini, and genera *Prisistus* and *Oprohinus* of the Ceutorhynchinae; and genus *Limnobaris* of the

Baridinae, Curculionidae) and tropical distributions (families Brachyceridae and Dryophthoridae; *Apsis albolineatus* (F.) of the Curculionidae; Myrorhinini). Buprestids of the small but morphologically specialized genera *Cylindromorphus* and *Paracylindromorphus* are associated with grasses, sedges, and reed (*Phragmites australis* (Cav.) Trin. ex Steudel). Several species of *Aphanisticus* develop on *Juncus* (Juncaceae), and larvae of the highly specialized genus *Cyphosoma* (Chrysochroinae: Dicerini) (Fig. 7.2g) develop in tubers of *Bolboschoenus* (Ascherson) Palla (Cyperaceae). Orthopterans – ‘hexapod horses’ with powerful mandibles – are the only insects with chewing mouthparts that are abundant on grasses, although not all of them feed on monocots.

The majority of Palearctic phytophagous insects are associated with seed plants (Spermatopsida). Conifers (Pinophyta) have less diverse insect assemblages than do angiosperms (Magnoliophyta). For example, of 351 species of leaf beetles (Chrysomelidae) in Belarus, only 4 feed on conifers: the monophagous *Cryptocephalus pini* L. (Cryptocephalinae), oligophagous *Calomicrus pinicola* Duftschmidt (Galerucinae), and polyphagous *Cryptocephalus quadripustulatus* Gyllenhal (Cryptocephalinae) and *Luperus longicornis* F. (Galerucinae) (Lopatin and Nesterova 2005). Even at the northern border of taiga in Northeast Asia, only 8 of 130 species of Curculionoidea (excluding Scolytinae) are associated with conifers. Yet, a vast number of wood-borers are associated with conifers, primarily beetles of the families Anobiidae (including Ptininae), Bostrichidae, Buprestidae, Cerambycidae, and Scolytinae of the Curculionidae, all of which possess many species, even in northern taiga, and regularly cause damage to forests and plantations. Lepidoptera developing on foliage also include serious forest pests, and a few Symphyta (Hymenoptera) attack both strobiles and wood. In total, 202 species of strictly oligophagous insects are associated with 5 genera of conifers in the former USSR, according to Emeljanov (1967): *Pinus* (82 species), *Picea* (50), *Larix* (25), *Juniperus* (23), and *Abies* (22). *Ephedra* (Ephedraceae) is unique in having an entire fauna of the endemic weevil tribe Oxyonychini, with 20 genera and about 60 species. Most of the few xylophagous buprestids and longhorn beetles that develop on *Ephedra* also are specific to this genus. Some planthoppers and apparently less mobile Sternorrhyncha also are specialized on this plant. Small predatory coccinellids of the genus *Pharoscytmus* in southern Mongolia occur

only on *Ephedra* (B. A. Korotyaev unpublished data), and *Pharoscyminus auricomus* Savoiskaya is associated mainly with these plants in sand deserts of Middle Asia (Savoiskaya 1984). Leaf beetles and weevils do not commonly feed on both conifers and angiosperms, but some large and widely distributed weevil genera (e.g., *Anthonomus*, *Hyllobius*, and *Cossonus*) include species that develop on either conifers or angiosperms.

Ferns and mosses have relatively small numbers of phytophagous insects in the Palearctic. Among leaf beetles, fern feeding is known only in the far south of the region, in the Himalayas where many species of the genus *Manobia* (Alticini) use a variety of ferns. In the New World, fern-feeding flea beetles are assigned to a Caribbean genus (*Normaltica*), with one species in the Dominican Republic and one in Puerto Rico and the genus *Leptophysa*, about 18 species of which are distributed in Central and South America and in the Caribbean. *Leptophysa* species are remarkably similar to those of *Manobia*. Among the Buprestidae, larvae of the mainly Oriental genus *Endelus* (Agrilinae) feed on ferns. Some European *Otiorrhynchus* weevils feed on ferns. Mosses are less populated by flea beetles in the northern Palearctic than in the south. The only known moss-living flea beetle in the northern Palearctic is *Mniophila muscorum* Koch (Fig. 7.4c). In the Himalayas, the mountains of Yunnan, and farther south in Asia, most of the moss-living flea beetles belong to the same genera as the leaf-litter flea beetles (e.g., *Benedictus*, *Clavicornaltica* (Fig. 7.4b), *Paraminota*, and *Paraminotella*) (Konstantinov and Duckett 2005), except for *Ivalia* and *Phaelota*, which live in mosses in southern India, but are not found in leaf litter or mosses in the Palearctic (Duckett et al. 2006, Konstantinov and Chamorro-Lacayo 2006). In the New World, the only moss-living flea beetles belong to the genus *Kiskeya* (Fig. 7.4d), with two species known from two neighboring mountain systems in the Dominican part of the Caribbean island Hispaniola (Konstantinov and Chamorro-Lacayo 2006). All moss-feeding flea beetles share a similar habitus. They are among the smallest flea beetles and have round bodies, relatively robust appendages, and somewhat clavate antennae. The Holarctic flea-beetle genus *Hippuriphila* is unique in its host choice. All four species of the genus feed on *Equisetum* (Equisetopsida) (Konstantinov and Vandenberg 1996). No other leaf beetle in the Palearctic feeds on plants of this taxon, but a few species of *Bagous* weevils and all four species of the Holarctic genus *Grypus* of erirhinid weevils also are associated with *Equisetum*.

It is unknown why some plant groups have diverse phytophagous assemblages while others do not. Some plant taxa that are diverse and significant in plant communities have a low diversity of insect consumers. Two plant genera have similar representation in the Mongolian vegetation but differ sharply in the diversity of their weevil consortia. Thirty species of *Allium* are found in Mongolia. Many of them dominate plant communities and are major sources of food for grazing animals, but only a single weevil of the specialized ceutorhynchine genus *Oprohinus* is associated with them. The wormwood genus *Artemisia* has 65 species in Mongolia (Leonova 1982) and dominates many types of plant communities. These plants have diverse phytophagous assemblages of more than 100 species of Auchenorrhyncha and Coleoptera (Buprestidae, Chrysomelidae, and Curculionidae). Some plants that dominate certain communities have species-rich phytophagous consortia, such as oaks (*Quercus*) among trees, *Artemisia* among herbs and semishrubs, and sedges (*Carex*) among herbs (Emeljanov 1967). Many highly specialized herbivores are associated with plants that have a high level of mechanical and chemical defenses, including many *Euphorbia*-eating *Apthona* (Chrysomelidae) (Fig. 7.4a), *Perotis cuprata* (Klug) (Buprestidae), and *Oberea* (Cerambycidae); *Apthona nonstriata* Goeze and *Mononychus punctumalbum* (Herbst) (Curculionidae) on *Iris pseudacorus* L.; *Nastus* and *Lixus* species (Curculionidae) on *Heracleum* species; and a few Buprestidae, *Lema decempunctata* (Gebler), several Alticini in the genera *Psylliodes* and *Epitrix*, two species in two genera of Cassidini (Chrysomelidae), and *Neoplatygaster venustus* (Faust) (Curculionidae: Ceutorhynchinae) on various Solanaceae. Some chrysomelids and weevils specialize almost exclusively on plants that contain toxic secondary compounds, combining unrelated taxa in their host ranges. For example, *Psylliodes* species feed on Brassicaceae, Cannabaceae, Cardueae, and Poaceae, as well as on Solanaceae; and of the four Far-Eastern Russian *Lema* species (Coleoptera: Chrysomelidae), two develop on monocots, one on Solanaceae, and one on Cardueae (Medvedev 1992). An analysis of host specialization of 321 species of flea beetles (Chrysomelidae) in the European part of the former USSR and the Caucasus shows that plant families most popular as hosts for flea beetles are among the most speciose in the flora. The most species-rich families of plants on the Russian Plain are the Asteraceae, Poaceae, Rosaceae,

Fabaceae, Cyperaceae, Lamiaceae, Scrophulariaceae, and Brassicaceae (Alexeev and Gubanov 1980). The plant families most popular for flea beetles are the Brassicaceae, Lamiaceae, Asteraceae, Boraginaceae, Scrophulariaceae, Euphorbiaceae, and Poaceae; for the buprestid tribe Acmaeoderini, they are the Fabaceae, Fagaceae, Anacardiaceae, Apiaceae, Rosaceae, Asteraceae, and Moraceae (Volkovitsh and Lobanov 1997); and for the weevil subfamily Ceutorhynchinae (in the entire Palearctic), they are the Brassicaceae, Ephedraceae, Lamiaceae, Boraginaceae, Asteraceae, Fagaceae, and Liliaceae.

Among plant families, the Brassicaceae are common and numerous in the Palearctic and Nearctic, but their weevil consortia in the two regions are quite different. Nearly half of the Palearctic fauna of the weevil subfamily Baridinae – about 60 species in 6 endemic genera – is associated with crucifers, whereas crucifer-eating Baridinae are lacking in the Nearctic. Another weevil subfamily, the Ceutorhynchinae, is much less species rich in the Nearctic than in the Palearctic, with about 80 species of a single genus *Ceutorhynchus*, as opposed to more than 220 species of *Ceutorhynchus* and 6 species of 3 other small genera in the Palearctic. This subfamily includes members of at least 11 Holarctic species groups, totaling about 25–30% of the Nearctic fauna. The Brassicaceae are unique in having at least 450 species of specialized beetles in the Palearctic (Cerambycidae, Chrysomelidae, Urodontidae, and Curculionidae: Baridinae, Ceutorhynchinae, and Lixinae) that feed on its many species. About 60 species of flea beetles feed on the Brassicaceae in France (Doguet 1994).

The plant family Asteraceae has a diverse fauna of phytophagous beetles. About 65 species of flea beetles, for example, feed on various asteraceans in France (Doguet 1994), and 67 species of the leaf beetles feed on Asteraceae in Belarus (Lopatin and Nesterova 2005). Asteraceae-feeding Baridinae (Curculionidae) are present in both the Palearctic and Nearctic, but they belong to different genera or even tribes, as do the Baridinae living on hygrophilous monocots.

Oak consortia probably are richest in the Palearctic (Emeljanov 1967). Some weevil genera (e.g., *Curculio*) of these consortia are equally represented in the Nearctic, but some, such as several genera of the tribe Rhamphini (Curculioninae) and genus *Coeliodes* (Ceutorhynchinae), are lacking in the Nearctic.

Some insects demonstrate major differences in their host choice in the Palearctic and other biogeographical

regions. Flea beetles in the Palearctic, for example, feed mostly on herbs and grasses, with just a few species on woody plants. In the Oriental Region, flea beetles feed mostly on bushes and trees. Thus, in the Palearctic, they occur mostly in open spaces such as meadows and swamps, whereas in the Oriental Region, they are rich in species in forest communities.

## BOUNDARIES AND INSECT BIODIVERSITY

The boundaries between faunal complexes of any rank (e.g., biogeographical realms or assemblages of insects in two adjacent localities) and the distributional limits for particular species typically run across physical gradients. Although the literature on this matter is voluminous (Darlington 1963), we add several new Palearctic examples.

The boundary between the western and eastern parts of the Palearctic for most groups of plants and animals is situated between the Altai Mountains and Lake Baikal; for some taxa, it coincides approximately with the Yenisei River. Two typical Arctic *Chrysolina* species (Chrysomelidae), *Ch. cavigera* Sahlberg and *Ch. subsulcata* Mannerheim, have not been found west of the Yenisei River (Chernov et al. 1994). At the source of the Yenisei, at Kyzyl City in Tuva, where the width of the river barely exceeds 100 m, the fauna differs considerably between the left (western) bank and the right (eastern; in Tuva, northern) bank. *Chrysolina jakovlevi* Weise occurs mostly north of Tuva in southern Krasnoyarsk Territory and Khakasia. In Tuva, it inhabits only stony slopes in a narrow strip of desert steppe on the right bank of the Yenisei (Medvedev and Korotyaev 1976). *Chrysolina tuvensis* L. Medvedev is known only from the desert steppe on the right bank near Kyzyl, and *Ch. sajanica* Jacobson occurs in the dry steppe on the southernmost West Sayans piedmont. The wingless *Chrysolina urjanichaica* Jacobson, an endemic of the right-bank steppe and the interfluvial area of the Ka-Khem and Bii-Khem rivers (Korotyaev 2001b), is substituted on the left bank by a similar and closely related species, *Ch. convexicollis* Jacobson, distributed throughout the rest of Tuva and in adjacent northwestern Mongolia. A wingless weevil, *Eremochorus zaslavskii* Korotyaev, endemic to the right bank, substitutes there for the widely distributed *E. simuatocollis* (Faust). These examples

demonstrate the isolating role that a relatively narrow river can play. Rivers and their valleys also play a role as distribution pathways. Land insects with both relatively limited and large ranges tend to penetrate farther north or south along valleys of major rivers in the Palearctic.

Another boundary exists along the Ural Mountains and lower course of the Volga River. Isaev (1994) found several species of beetles with eastern distributions reaching the right bank of the Volga in Ul'yanovsk Province, including a steppe weevil, *Ceutorhynchus potanini* Korotyaev, distributed in Siberia from the Western Sayan Mountains to central Yakutia, as well as in Mongolia.

Mountain systems represent obvious borders between faunas. The Carpathians limit distribution to the east for a number of beetle species including carabids (*Carabus auronitens* F. and *C. variolosus* F.) and a chafer (*Hoplia praticola* Duftschmidt). A number of southeastern European species do not reach farther west than the Carpathians (Arnoldi 1958).

Climate might explain why some distributional limits do not coincide with obvious physical boundaries. The southern boundaries of the ranges of several Euro-Siberian weevils, such as *Phyllobius thalassinus* Gyllenhal (Entiminae), *Ceutorhynchus pervicax* Weise, *C. cochleariae* Gyllenhal, and *Trichosirocalus barnevillei* (Grenier) (Ceutorhynchinae), run along the southern slope of the West Sayan Range, but not in the northern foothills of this range, presently impassable for these weevils. The distribution of these species to the south is apparently not limited by the high mountain ranges, but rather by the aridity. *Trichosirocalus barnevillei* is present in the Yenisei flood land below and south of the forest margin, which is a typical distribution for woodland species outside forest massifs.

Two common Euro-Siberian weevils have the southern margins of their ranges on northern slopes of different mountain chains in Tuva. *Hemitrichapion reflexum* (Gyllenhal) is found only on the southernmost ridge of the West Sayan, the Uyukskii Range, whereas *Brachysomus echinatus* (Bonsdorff) is found only on the northern slope of the Eastern Tannu-Ola Range. One is a steppe species, the other is a forest species. Their distributions in Tuva fit the rule formulated by the well-known plant geographer O. E. Agakhaniantz (1987): migrants occupy slopes facing the direction of the country from which they came. Yet the preceding examples of species with the southern boundaries of their ranges

running along the southern slope of West Sayan do not follow this rule.

## LOCAL BIODIVERSITY

High local biodiversity is illustrated by five closely related endemic species of the weevil genus *Ptochus* in a small area of Dagestan (Caucasus) (Ismailova 2006). Three species are located along the river, about 30 km apart, and two on the opposite sides of the mountains facing the river. All species are flightless, similar externally, and feed on the same species of *Artemisia*. A similar pattern of local biodiversity is known for some Middle Asian *Prosodes* (Coleoptera: Tenebrionidae). The high level of biodiversity often is maintained by reproductive isolation associated with complicated structure of the genitalia (Medvedev 1990).

Local biodiversity of some insect groups is increased by separation of periods of insect activity, either daily or seasonal. A well-known example is the scarabaeid genus *Chioneosoma* in southern Kazakhstan. Six sympatric species of the genus, in addition to having different habitat associations, have sequential flight periods, with most adults flying in different plant layers. Of the two species that co-occur in the Muyunkum Sands and exhibit no clear differences in flight habits, one flies before sunset and the other half an hour after the flight of the first species ceases (Nikolajev 1988). These differences enhance reproductive isolation of species with similar larval habits. Seasonal differentiation of phytophagous insect assemblages follows changes in vegetational aspects: ephemeral plants possess specific insect consortia often formed by particular insect taxa, occasionally using a specific habit such as gall inducement (Kaplin 1981).

Supposedly nonspecialized feeders also can exhibit high species diversity, such as predatory carabids, coprophagous scarabs, and detritophagous tenebrionids, of which many include genera with more than 500 species (e.g., *Carabus*, Fig. 7.5a). Local biodiversity of parasitoids can be higher than that of herbivores. For example, about 80 species of ichneumonids were collected on one excursion to the Kamchatka Peninsula (D. R. Kasparyan personal communication), whereas the entire weevil fauna of the Peninsula comprises about 50 species (Korotyaev 1976). Yet in farther southern regions, phytophagous insects are locally rich. On the plains of the Northwestern Caucasus, for example, one excursion in May yielded 39 species of the

weevil subfamily Ceutorhynchinae. The entire superfamily Curculionoidea is represented by 551 species in Berlin (Winkelmann 1991). Wanat (1999) reported 480 species of Curculionoidea (excluding Platypodidae and Scolytinae) in the Białowieża Primeval Forest (eastern Poland), probably the largest broadleaf forest in Europe.

## INSECT BIODIVERSITY AND HABITATS

Plant communities (habitats) in the Palearctic are classified as zonal, azonal, or extrazonal (Chernov 1975, Walter and Breckle 1985). Zonal communities are situated on 'the flat elevated areas with deep soil which are neither too porous to water, like sand, nor retain too much water, like clay. . . . There must be no influence from ground water' (Walter and Breckle 1985). The particular regional climate has its full effect on such areas, called euclimatopes or 'plakor' in Russian. Azonal vegetation appears when the groundwater table is so high that the whole area is covered with bogs or when vegetation is on sand or alluvial soil. Extrazonal vegetation is zonal vegetation outside its climatic area, for example, steppe meadows in forest zones.

The distribution of insects among these types of communities has some regularity. Zonal communities are not particularly rich in the northern Palearctic, but increase in richness southward (Chernov 1966). They usually are formed of species whose ranges are associated with a particular zone. Ranges tend to be relatively large in northern zonal communities and small in southern communities. Most southern zones (e.g., steppe) have some endemics (e.g., the chrysomelid *Aphthona sarmatica* Ogloblin), whereas azonal communities in the North have a larger number of species with wider ranges.

Insects with larger ranges tend to occur in nonspecific habitats, either intra- or extrazonal. In Mongolia, for example, leaf beetles with transpalearctic ranges commonly occur in ruderal and agricultural habitats, whereas species with smaller, Central Asian ranges occur in deserts or saline habitats specific to Mongolia (Medvedev 1982), where many widespread species also occur in high populations (Korotyaev et al. 1983). Ranges of many taiga insects also can be quite large, covering the entire taiga.

The azonal riparian landscape has a high proportion of insect biodiversity in most of the natural zones, including the tundra (Chernov 1966), taiga (Ivlev

et al. 1968), northern part of the Stenopean forests (Egorov et al. 1996), steppes (Medvedev and Korotyaev 1976), and deserts (Korotyaev et al. 1983), with the proportion of the riparian species in the total fauna increasing northward within the taiga zone.

Azonal, mainly riparian, communities also include species endemic to certain zones. The weevil genus *Dorytomus*, for example, is one of the largest genera of riparian beetle complexes, with 63 species in the Palearctic. Most of its members occur in floodland habitats. In the oceanic sectors, they are distributed across several zones, so that in the Russian Far East, the fauna of the taiga zone is largely the same as that in the nemoral Stenopean forests. Yet in the desert and lower mountain zones of Middle Asia, most *Dorytomus* species are endemic; for example, all four species in southern Tajikistan are endemic to Middle Asia (Nasreddinov 1975). The entire riparian landscape in the desert zone, with its specific type of forests called 'tugai', has characteristic insect complexes that include water beetles and bugs, many amphibionts, xylobionts, and herbivorous insects. Leaf-beetle communities of tugai are highly specific (Lopatin 1977). Most genera endemic to Middle Asia and southern Kazakhstan occur there (e.g., *Atomyria*, *Jaxartiolus*, and *Parnops*). Lopatin (1977) suggested that the tugai leaf-beetle fauna is closely related to the Mediterranean fauna, differing from it in having a number of northern elements (e.g., *Donacia*, *Gastrophysa*, and *Phaedon*), which migrated to Middle Asia around the Pleistocene.

Many insect communities are hidden in the substrate and less conspicuous than the large and beautiful butterflies, dragonflies, acridids, and bees, or the nasty horse flies and mosquitoes. They, nonetheless, play diverse roles, such as preying on injurious and beneficial animals and decomposing dead organisms. Beetles, with their hard bodies, dominate most types of these hidden assemblages except those where rapid larval development in semi-liquid substrates (e.g., dung and carrion) gives an advantage to flies, although there, too, many beetles hunt fly larvae. Dozens of insect species constitute different kinds of coprobiont, necrobiont, and various dendrobiont (mostly under-bark) communities. Several large beetle families are specialized for these sorts of habitats. Most Silphidae (carrion beetles) consume large and medium-sized carrion; Catopinae (Leiodidae) feed on small dead bodies; Trogidae, probably *Necrobia* (Cleridae), and *Dermestes* (Dermestidae) feed on dry skin remnants of vertebrates. Several beetle families are specialized fungivores, including most of

the Ciidae, Erotylidae, Endomychidae, many Tenebrionidae (e.g., *Bolitophagus reticulatus* L.), the subfamily Dorcatominae of the Ptinidae, and some Nitidulidae (e.g., *Cyllodes ater* (Herbst) and *Pocadius* species). Beetle consortia of a particular tree fungus in the southern taiga of the Urals and Western Siberia comprise dozens of species. For example, 54 species in 16 families occur on *Daedaleopsis confragosa* (Bolton: Fr.) Schrot (Basidiomycetes) (Krasutskii 2007). In the nemoral zone, especially in the Far East, fungal beetle consortia are more diversified and include representatives of exotic Oriental genera. On Kunashir Island, large erotylids of several species are visible for 20 m in thin forest, where they sit on the stroma of large tree fungi. Leiodidae are far more speciose and abundant in the mild and humid oceanic climate, especially in autumn. *Agathidium laevigatum* Erichson is present even on Bering Island (Lafer 1989).

Diversified insect communities exist under bark and in forest leaf litter. These communities are dominated by beetles, but several families of flies also contribute to the overall diversity, as do many parasitic Hymenoptera and several families of bugs, the strongly flattened Aradidae being the most characteristic. A considerable part of these communities consists of scolytines, their predators and parasites, and consumers of the fungi and debris in their tunnels. One of the largest genera of beetles in these complexes is *Epuraea* (Nitidulidae), with more than 100 species in the former USSR (Kirejtshuk 1992).

Coprophagous assemblages are particularly diverse, depending on season, landscape, and type and age of the excrement. These assemblages include many well-known scarabs such as *Copris*, *Scarabaeus*, and *Sisyphus*, as well as countless species of the largest beetle genera *Aphodius* and *Onthophagus*. Up to 13 species of *Aphodius*, plus two species of *Onthophagus*, can be found in just a few neighboring deposits of dung in Leningrad Province, northwestern Russia (O. N. Kabakov, personal communication). In addition to the Scarabaeidae, some Hydrophilidae are common in dung. Numerous coprophagous insects are hunted by fly larvae and predatory beetles of the families Histeridae (Fig. 7.4f) and Staphylinidae.

Animal nests also possess variably specific insect communities where many flies, beetles, bugs, fleas, and lice predominate. Zhantiev (1976) gives extensive data on the occurrence of dermestids in insect and mammal nests, as well as in tree hollows. Nests and colonies of social insects host species-rich communities;

200 species of beetles, for example, occur in bumblebee nests. Myrmecophilous insects include many species with characteristic structural adaptations to life in ant nests, including bare, glabrous, uniformly brown bodies with tufts of setae for tactile or chemical communication with the hosts. The largest genus is probably *Thorictus* of the Dermestidae, which, because of its aberrant habitus, was long kept in a separate family. The termitophilous *Eremoxenus chan* Semenov-Tian-Shansky of Middle Asia and the myrmecophilous *Amorphocephalus coronatus* Germar of the Mediterranean region are the few Palearctic members of a group of commensal Brentidae.

Even in urban environments, insects form species-rich communities. Occasionally, some predatory and saprophagous species irritate humans. In the Academy Archive in St. Petersburg in the mid-1990s, increased activity of larval dermestids (*Attagenus smirnovi* Zhantiev) caused anxiety among the staff. Inspection of the volumes of the Academy Sessions protocols with M. V. Lomonosov's autographs revealed an invasion by *Lasioderma* (Ptinidae), whose remains were then eaten by larvae of the harmless *Attagenus smirnovi*. During the reconstruction of the Stroganov Palace at Nevski Prospect in St. Petersburg in the late 1980s, a dozen beetle species were found in the 40-cm thick larch beams in the attic, including dermestids and wood-borers. Forty-two species of dermestids were listed by Zhantiev (1976) as harmful to stored products in the former USSR. Although some introduced species can be harmful, the majority of the most destructive species of dermestids in every natural zone belong to the local fauna (Zhantiev 1976).

The urban fauna of phytophagous insects is also rich and increasing; 799 species of insects, for example, are known from the city of Moscow (Russia). This fauna is dominated by exposed and partly hidden phyllophagous forms (328 species), followed by exposed and partly hidden Rhynchota (Auchenorrhyncha, Sternorrhyncha, and Heteroptera; 143 species), leaf miners (124), gall inducers (122), and wood-borers (110, mainly scolytines) (Belov 2007).

A specialized insect assemblage, including beetles and flies of three families, occurs along the seashore. The most widely distributed coleopterous group in this assemblage is the tenebrionid tribe Phaleriini, which lives on sandy beaches. A characteristic feature of these fast, small, and medium-sized beetles is their sand-colored integument, with dorsomedial infuscation. Small hydrophilids of the genus *Cercyon*

and various Staphylinidae and Histeridae occur under decaying algae. On the Pacific shore, several similar species of the endemic genus *Lyrosoma* of Silphidae are abundant at the shoreline, especially on the Kurile and Komandorski islands. A member of the weevil subfamily Molytinae, *Sthereus ptinoides* (Germar), with a boreal amphipacific distribution, lives on driftwood. In southern Japan, the peculiar weevil genus *Otibazo*, with uncertain affinities, is confined to seashores. The characteristic plant genus *Cakile* (Brassicaceae) occupies the outermost sandy strip of beach where the salt spray reaches. It has a complex of two weevil species in the northern Atlantic basin: *Ceutorhynchus cakilis* Hansen in Europe and *C. hamiltoni* Dietz in North America. These two weevils belong to different species groups, illustrating a tendency of the Ceutorhynchinae (and other weevil taxa) to exploit marginal habitats with pioneer plant communities. In Europe, several nonspecialized crucifer feeders of the Curculionidae occur on *Cakile maritima* Scopoli and *C. euxina* Pobed. A tribe of supralittoral weevils, the Aphelini, is distributed along the Pacific Coast from northern California to the temperate Far East, as well as in Australia.

In Japan and the southernmost portion of the Russian Far East, *Isonycholips gotoi* Chûjo and Voss, another representative of the Aphelini, lives among grasses on dry coastal sand dunes. An additional coastal insect assemblage exists here, including large weevils of the tribe Tanymecini and *Craspedonotus tibialis* Schaum of the fossorial ground-beetle tribe Broscini. In the Atlantic sector, the genus *Onycholips* (two species in northwestern Africa), the fossorial broad-nosed weevil *Philopedon plagiatius* (Schaller) in the tribe Cneorhinini, and several species of the tribe Brachyderini live on sand dunes along the Baltic coast. *Philopedon plagiatius* is parthenogenetic and apparently introduced to inland seashores. Carabids of the genera *Brosicus* and *Scarites* and tiger beetles (*Cicindela*) are common on sandy beaches. Coastal rocks in the northern Pacific have a highly specific beetle, *Aegialites stejnegeri* Linell, of the monotypic subfamily Aegialitinae (Salpingidae), which lives in cracks and seabird nests (Nikitsky 1992).

## INSECT BIODIVERSITY AND PALEARCTIC MOUNTAINS

The Palearctic has a number of mountain systems, including the Alps, Carpathians, Caucasus, Pamirs,

Tien Shan, Urals (dividing the continents of Europe and Asia), Altai, Sayan, Tibet, and northern Himalaya. The majority of Palearctic Mountains belonging to the Alp–Himalayan mountain ‘belt’ are relatively young, except the Urals. The mountain systems are situated in different parts of the Palearctic, with different climatic and other geographic conditions. Their patterns of insect biodiversity, however, share a number of features.

Insect biodiversity in the Palearctic mountains changes with climate along altitudinal gradients (Walter and Breckle 1985). Generally, from the piedmont to the mountain tops, the following altitudinal belts are recognized: colline–montane (lower and upper), alpine (lower and upper), and nival (Walter and Breckle 1985). Although these altitudinal belts do not correspond precisely to the zones from south to north, insect biodiversity usually decreases from the bottom to the top of the mountains, as it does from south to north in the Palearctic. The degree of endemism, however, increases from bottom to top. An important reason for high biodiversity of mountain-insect faunas is that many groups in the plains find refugia in corresponding mountain belts when climatic conditions change and zones fluctuate. For example, many species widely distributed in the Arctic and Boreal regions occur in the upper mountain belts in southern Europe; this kind of distribution is called arcto-alpine or boreo-montane, depending on the specific features of the range. During the glacial age, these insects moved southward following the glaciers, and found refugia in the high mountains when the climate became warmer and the ice shield retreated. Many mesophilous groups find appropriate environments in mountains during aridization in adjacent plains, accounting for the considerable number of so-called paleoendemics usually represented by one or a few species in remote mountain systems. Examples include carabid beetles of the genus *Brosicosoma* scattered along the entire Alp–Himalayan mountain belt (Kryzhanovskiy 2002), or the monotypic cerambycid genus *Morimonella* recently described from the Caucasus. The capacity of the mountain systems to accumulate great numbers of endemic species is facilitated by the broad diversity of habitats plus the apparently effective distributional barriers. Wingless species are among the most speciose mountain taxa; they are usually classified as neoendemics. For example, the Caucasian fauna of the largest weevil genus, *Otiorhynchus s.l.*, is provisionally

estimated at 250 species (Savitskii and Davidian 2007); 50 small, blind, wingless, forest litter and, partly, endogean species of the carabid tribe Trechini are recorded from the Caucasus, mostly from its western part (Belousov 1998). On the other hand, meridionally oriented mountain chains allow the possibility of deep penetration of some typically Palearctic insect groups into the Oriental Region and vice versa.

Alpine insect communities of Middle Asia are relatively poor, but highly endemic. For example, of approximately 800 leaf beetles in Middle Asia, 175 occur in the alpine belt, of which 150 are endemics (Lopatin 1996). Among them are *Oreomela*, with more than 80 species in the alpine regions of the Tien Shan, Himalayas, Altai, and southwestern ridges of China between 2400 and 4300 m, and *Xenomela*, all 11 species of which are known from the Tien Shan between 1300 and 3000 m (Lopatin and Nesterova 2004). This unusually high level of endemism might be explained by the specific alpine environment and high degree of isolation. Alpine biodiversity further increases because many species with larger ranges are represented by specialized morphs in the mountains that might not have species status, but differ genetically. However, insect groups that are most abundant and species rich elsewhere are not always species rich in the alpine belt. For example, the most speciose leaf-beetle groups in the Palearctic are the Galerucinae *sensu lato*, followed by the Chrysomelinae and Cryptocephalinae (Fig. 7.4e). In the alpine belt of Middle Asia and northwestern China, the most speciose are the Chrysomelinae followed by the Galerucinae, Eumolpinae, and Cryptocephalinae (Lopatin 1996).

In Yakutia, thousands of male hover flies (Syrphidae) sometimes hover over mountain peaks, while females feed on flowers at the bottoms and on the slopes of the mountains. In the late afternoon, with the flow of warm air, females fly to the mountaintops where copulation occurs. A similar kind of behavior ('hilltopping') is known for butterflies and flies in the families Sarcophagidae, Tabanidae, and Tachinidae (Barkalov and Nielsen 2007).

Mountain forest belts usually have higher species biodiversity than does the alpine belt. Mid-altitude forests in the Caucasus and Transcaucasia include a number of endemics, many of which are flightless. Examples include *Psylliodes valida* Weise and *Aphthona testaceicornis* Weise (Chrysomelidae) in the forests of the Northwestern Caucasus and *Altica breviscula* Weise (Chrysomelidae) in the narrow strip of mountain forest

in Talysh (Azerbaijan). Specialized herbivores (e.g., weevils) are most species rich in the piedmont forest belt in Abkhazia (Caucasus) (Zarkua 1977).

The high-altitude fauna of the Palearctic is also unique, compared with the neighboring Oriental Region. Palearctic montane flea-beetle communities (in the Caucasus, Crimea, and Middle and Central Asia) consist of species from rich, cosmopolitan genera such as *Longitarsus* and *Psylliodes*. In the Oriental Region (southern Himalayas, Western Ghats), however, species occurring at high altitudes belong to genera with limited ranges, and many are confined to the Himalayas or do not occur outside the Oriental Region.

A characteristic feature of the Palearctic highland fauna are weevils of the subfamily Ceutorhynchinae at the upper margin of insect distribution. Several species of *Ceutorhynchus*, *Neophytobius*, *Scleropterus*, and others reach highest altitudes in the upper mountain zone in the Altai, Sayan Mountains, Tien Shan, Sredinnyi Kamchatka Range, Tibet, and Himalayas. Another characteristic feature of the Palearctic alpine fauna of weevils is the concentration of bisexual forms of species that reproduce parthenogenetically at lower elevations (Korotyaev 1992).

The alpine belt in the largest part of the Continental sector lacks the multicolored, tallgrass meadows typical of the European mountains, or if they are present, they are poorly developed. Typical of the Sayan Mountains and ranges to the south and southwest are mountain tundra, shortgrass subalpine meadows with large orange–yellow flowers of *Trollius asiaticus* L. (Ranunculaceae), alpine steppe, and an endemic alpine type of vegetation – dense, mesophilous, meadow-like grasslands dominated by *Cobresia* species (Cyperaceae), from which no specific weevils or leaf beetles are known. Edelweisses (*Leontopodium*, Asteraceae) are common in the West Sayan and other mountains of Tuva, descending in places to the mid-forest belt and occurring in pastures. Intense collecting in Tuva on edelweisses by B. A. Korotyaev in 1969–1972 revealed no herbivores, although Bajtenov (1977) described the weevil *Pseudostyphlus leontopodi* from Altai. The alpine weevil fauna of this mountain country is poor but characteristic, formed largely of representatives of several genera of Apionidae, *Notaris* and *Tournotaris* of the Eirrhinidae, *Lepyryus*, several genera of Hyperinae, *Dactylotus globosus* (Gebler), a few *Sitona* species, and the Ceutorhynchinae (Curculionidae). Endemic to this area are many wingless Carabidae, including

*Carabus*, *Nebria*, and *Trechus* in the highlands; the montane subgenus *Aeneobyrrhus* of *Byrrhus*, with five species, and one of the three species of the Holarctic genus *Byrrhobolus* (Byrrhidae); and several oligotypic genera and considerable species of Chrysomelidae. The predominantly montane butterfly genus *Parnassius* (Papilionidae) is represented by several species. The multizonal *Aporia crataegi* L. (Pieridae) often occurs in great numbers. In the tangle of mountain ridges of West Altai, at the boundary of Kazakhstan and Russia, a heterogeneous butterfly fauna with 176 species exists, including several pairs of closely related Western and Eastern Palearctic species, as well as representatives of the Middle Asian fauna (Lukhtanov et al. 2007).

Wide variation in altitude is characteristic of the steppes of Mongolia, adjacent Tuva, and the Russian Altai. Steppes occupy plains and bottoms of variably sized depressions, but also south-facing mountain slopes in the forest zone and the highest mountain reaches, usually with southern exposure, adjacent to and alternating with other subalpine and alpine habitats, such as isolated *Larix* stands, subalpine meadows, and mountain tundra. The latter type of steppe, with its characteristic flora, is referred to by botanists as 'alpine steppe'. Insects of alpine steppe include a few characteristic species, along with several common mountain-steppe insects. Among beetles, this kind of distribution is found in *Stephanocleonus* (Curculionidae: Lixinae), *Crosita*, and *Chrysolina* (Chrysomelidae: Chrysomelinae).

Mountain steppe consists of several altitudinal types that are less clearly separated than the alpine steppe from the rest of the steppes. In the most elevated southwestern part of Tuva, adjacent to the Altai, a few subendemic species of weevils and chrysomelids, mostly of the same genera that constitute the bulk of the alpine steppe fauna, occur only in the highest areas of the steppe, usually on stony slopes, but not in the alpine steppe.

A diverse and characteristic fauna is associated with mountain areas that have climates intermediate between that of steppe and desert, and vegetation with shrubs (mostly *Caragana* and *Atraphaxis*) and perennial wormwoods (Medvedev 1990). One of the largest weevil genera subendemic to Central Asia, *Alatavia* (Entiminae) with 13 species, is distributed there, with only three species in central and eastern Mongolia occurring in the plains, which in this area are about 1000 m or more above sea level.

Many insects in the mountains developed common features viewed as adaptations to high-altitude life. A high percentage of alpine insects are flightless (e.g., more than 80% of chrysomelid beetles in the genus *Oreomela*). Mountain beetles, such as *Psylliodes valida* Weise (Chrysomelidae) and *Geotrupes inermis* Ménétrié (Geotrupidae), have a more swollen prothorax than do their lowland relatives. Many alpine beetles have a high level of melanization of the integument, similar to that found in Arctic insects. Their elytra, often covered with ridges, are convex, forming a subelytral cavity that functions as a temperature and humidity buffer for the poorly sclerotized abdominal tergites. Most alpine insects live close to the ground or under rocks and plants, even if their closest relatives occupy other habitats (Lopatin 1971). Numerous alpine leaf beetles are viviparous or oviviviparous (*Oreomela* species; Lopatin 1996), as are some Arctic leaf beetles. Because of the short warm season, the life cycle of some insects exceeds 2 years, and overwintering can occur at various life stages (Lopatin 1996).

## INSECT BIODIVERSITY IN MAJOR BIOGEOGRAPHICAL DIVISIONS OF THE PALEARCTIC

Various ideas exist on the subdivision of the Palearctic, beginning in 1876 with that of Wallace (Semenov-Tian-Shansky 1936, Lopatin 1989). We follow the subdivision proposed by Emeljanov (1974), which is based on climatic and other physical geographic conditions most closely reflected by vegetational cover and which largely follows subdivisions proposed by botanists (Lavrenko 1950). Emeljanov (1974) recognized the following eight regions: Circumpolar, Euro-Siberian taiga (boreal), European and Stenopean nemoral, Hesperian (Mediterranean and Macaronesian) and Orthrian evergreen forest (subtropical), Scythian steppe, and Sethian (Saharo-Gobian) desert regions.

### Arctic (Circumpolar Tundra) Region

The northernmost part of the Palearctic Region is the Arctic (Fig. 7.1a: I, b). It includes the coldest regions of the Palearctic and its southern border corresponds approximately with the 12°C isotherm of the warmest month (July) (Chernov 2002). In European Russia, the

southern border runs along the southern border of the tundra and forest–tundra (Lopatin 1989). Here, we consider the Arctic in the broad sense, including the Hypoarctic (= Subarctic) as its southern subzone.

Altogether, about 3300 species of insects live in the Arctic (including the American Arctic), representing 0.6% of total insect diversity. Relative species richness of insects in the Arctic is about 15%, compared with 50% for the World (Chernov 2002). Of 25 insect orders, 16 occur in the Arctic. Of the 1800 genera of carabid beetles, 22 occur in the Arctic (Chernov et al. 2000, 2001). Beetles constitute 13% of the Arctic insect fauna, and flies 60% (about 90% in more northern regions) (Chernov 1995). The most common beetles in the Arctic are the Carabidae, Staphylinidae, and Chrysomelidae. The Curculionidae are less common but are represented by a relatively large number of species. Of the remaining large families of Coleoptera, in addition to the entirely aquatic Dytiscidae, the Coccinellidae and Elateridae are most conspicuous in the southern part of the tundra, but they are represented by only a few species. The biodiversity of phytophagous insects decreases more strongly than that of predatory insects from south to north. For example, even an outdated list of Carabidae of Magadan Province and Chukchi Autonomous District (Budarin 1985) includes 161 species, whereas an updated list of Apionidae, Erirhinidae, and Curculionidae of the same area has slightly more than 100 names (B. A. Korotyaev, unpublished data). In the Northwestern Caucasus, with its wide range of mountain belts, the Carabidae (576 species; Zamotajlov 1992) are slightly less species rich than the fauna of listed weevil families (B. A. Korotyaev, unpublished data). Predatory beetles constitute about 70% of the total beetle fauna in the Arctic, whereas in temperate areas they make up about 25% (Chernov et al. 1994).

A characteristic feature of the Asian Arctic is the wide distribution of steppe-plant communities of several types, including the cryophytic steppe and the tundra-steppe, which are especially developed in Northeast Asia. Many insects occur in these Arctic steppes. Some are endemic, many are distributed outside the tundra zone in the southern Siberian and Mongolian steppes and in the mountains of Eastern Middle Asia, and some also occur in dry areas of North America (Berman et al. 2002).

Insect communities of Wrangel Island, north of the Chukchi Peninsula, described in detail by Khruleva (1987), are dominated by Diptera (76 species),

Coleoptera (67), Lepidoptera (54), and Hymenoptera (at least 46). Aquatic insects are well represented by the Ephemeroptera, Plecoptera, and Trichoptera, and the aquatic Diptera are dominated by the Tipulidae and Chironomidae. Among other groups, relatively large forms with well-developed flight predominate. The Lepidoptera include two species of Pieridae (*Colias*), two of Lycaenidae (two genera), seven of Nymphalidae (all *Boloria*), five of Satyridae (three *Erebia* and two *Oeneis*), two of Geometridae, two of Lymantriidae, ten of Noctuidae (six genera), seven of Arctiidae (six genera), and one of Pterophoridae. Of the Hymenoptera, the entire superfamily Apoidea is represented by three species of *Bombus* only (Khruleva 1987, O. A. Khruleva, personal communication).

The absence in the Arctic of a few taxa that are abundant and diverse from the southern boundary of the Palearctic to the taiga zone is noteworthy. These taxa include the Orthoptera, beetles of the family Tenebrionidae, ants (represented by a single species in the riparian shrub tundra; Chernov 1966), and predatory Hymenoptera (e.g., Sphecoidea and Vespoidea).

### Forest regions

Forests occupy most of the Palearctic. They are classified into five regions: the taiga, stretching across Eurasia in the boreal climatic zone; the nemoral European and Stenopean regions in the temperate zone; and the subtropical Hesperian and Orthrian regions. The contiguous regions of the different climatic zones are more similar to each other, in many respects, than to their zonal counterparts. Along the same lines, the affinities of the insect faunas of the Hesperian and Orthrian regions are overshadowed by the similarities they have with their respective neighboring regions. As a result, biogeographic attribution of some large areas often becomes problematic. Anatolia, for example, is classified by Emeljanov (1974) as the zone intermediate between the Mediterranean Subregion of the Hesperian Region and the Saharo-Gobian Desert Region, but it is often considered an area with predominantly steppe-type vegetation that is attributed to the boreal biota by Kryzhanovskiy (2002). The Anatolian insect fauna includes some taxa typical of each of the three regions but lacks others no less characteristic of them. It also has many endemic species and genera. Anatolia apparently has accumulated natural complexes typical of several climatic zones in a much narrower range of altitudes,

compared with the Himalayas where all vegetational types from tropical forests to boreal deserts and nival communities exist.

Insect biodiversity in the forests of the Palearctic is great, compared with that of the Arctic, due mostly to a relatively warm, humid climate that allows a variety of plant communities to thrive. Numerous plant species provide environments for many phytophagous insects, even those not directly associated with woody plants. The number of species of flea beetles, for example, increases from a few in the Arctic to 83 in the taiga, 131 in mixed forests, and 163 in broadleaf forests of the Russian Plain (Konstantinov 1991). Iablokov-Khnzorian (1961) gives a figure of 580 species of beetles in 35 families, feeding on various Pinaceae in the Palearctic. Most species belong to the Scolytinae (Curculionidae) (177), Cerambycidae (108; Fig. 7.3c), other Curculionidae (76), Buprestidae (59), and Anobiidae (37). A good portion of the species (121) is known from Europe and the Mediterranean (84).

The Palearctic fauna of weevils in the genus *Magdalis*, with 57 species associated exclusively with woody plants (Barrios 1986), is distributed across all forest zones. Only three (the largest) of the ten Palearctic subgenera of *Magdalis* are represented in taiga and none of them are endemic to it, whereas seven subgenera occur only in the temperate and subtropical zones. The northern boundary of the range of *Magdalis* is formed by species of the nominotypical subgenus that develop on *Pinus silvestris* L. in Europe and on *P. pumila* Regel in Northeast Asia where this characteristic shrub forms the northern forest margin. The southern boundary also is formed by species of *Magdalis s. str.*, most of which are associated with *Pinus* species (13 of 16 species with known hosts), whereas one species is associated with *Picea*, *Abies*, and *Cedrus*, and two nonspecific feeders develop on *Larix*. No specialized *Magdalis* (or scolytines; M. Yu. Mandelshtam, personal communication) are known from *Pinus sibirica* Du Tour (Barrios 1986), the most valuable Siberian conifer. In the taiga, only *Betula*, *Sorbus*, and *Prunus* among deciduous trees are used by *Magdalis*, whereas *Quercus*, *Ulmus*, *Populus*, and several Rosaceae are hosts of all southern species except those of the nominotypical subgenus.

Of the variety of deciduous trees, the Salicaceae have the most diversified coleopterous fauna in the northern forests (Ivliev et al. 1968, Korotyaev 1976, Medvedev and Korotyaev 1980), whereas *Quercus* has the greatest number of specialized phytophagous insects in the entire Palearctic (Emeljanov 1967).

*Dorytomus* is the most species-rich genus of weevils in the south of the Russian Far East (the northernmost part of the Stenopean Region). Most weevils, including phyllo- and carpophagous and wood-boring species, differentiate *Salix* from *Populus*, and many distinguish *Populus tremula* L. from other *Populus* species, but some polyphagous species, such as *Saperda populnea* (L.), *Lamia textor* (F.) (Cerambycidae), and *Cryptorhynchus lapathi* (L.) (Curculionidae: Cryptorhynchinae), feed on *Salix* and *Populus*. Among the willows, narrow-leaved riparian species (*Salix viminalis* L. and similar species in Europe, and *S. udensis* Trautv. and C. A. Mey. and *S. schwerinii* E. Wolf in the Far East) possess the largest consortia of weevils and chrysomelids. The broad-leaved *S. caprea* L. in Europe has a considerable number of specialized feeders. The family Salicaceae includes a Far-Eastern monotypic genus (*Chosenia*), in addition to *Populus* and *Salix*. Little is known of the phytophagous consortium of this tall tree in the south of its range in Korea, Japan, northeastern China, and the Russian Far East. In Northeast Russia (Magadan Province and Kamchatka Territory), two species of the genus *Dorytomus* (probably developing in catkins) and a leaf-miner *Rhamphus choseniae* Korotyaev (all Curculionidae) are monophagous on *Chosenia arbutifolia* (Pall.) A. Skvorts. All three are distributed southward at least to Primorskii Territory in Russia. No specialized chrysomelids or cerambycids are known on *Chosenia*; several species from poplars and willows are recorded as occasional feeders.

Highly diversified riparian assemblages of phytophagous insects associated with the Salicaceae are endemic to the Holarctic Region. A large gravel area along the Ma River in the low mountains of Thanh Hoa Province in North Vietnam was investigated by B. A. Korotyaev in 1988. This area is dominated by bushes of *Drypetes salicifolia* Gagnep., which look similar to willows but belong to the family Euphorbiaceae, widely represented in the tropics. The bushes harbor no coleopteran genus typical of the Palearctic riparian shrub.

Temperate and subtropical forest faunas of many insect groups are more diversified in the Far East than in the Western Palearctic, which is separated from the woodland Afrotropical biota by the wide desert zone. Coleoptera are represented in the Stenopean Region by many families unknown from the European Region, such as the Cupedidae of the Archostemata; the

aquatic Aspidytidae recently described (Ribera et al. 2002) from South Africa and found in China (Shaanxi: *Aspidytes wrasei* Balke, Ribera, and Beutel); and the Helotidae, Inopeplidae, Ischaliidae, Monommidae, Othniidae, Pilipalpidae, Synteliidae, Trictenotomidae, and Zopheridae of the Polyphaga (Lehr 1992). Many subfamilies and tribes of the largest phytophagous families can be added to this list, such as the Megalopodinae and Chlamysini of the Chrysomelidae, and more than 20 tribes of the Curculionoidea.

Many large weevil taxa with predominantly tropical (Oriental or Palearctic) distributions gradually decrease in representation in the eastern forest faunas through the subtropical Orthrian and temperate nemoral Stenopean regions, and some do not reach the boreal taiga region. This trend is demonstrated at the family level by the Anthribidae, Brentidae, and Dryophthoridae (Table 7.1) and by the Palearctic tribe Mecysolobini of the Curculionidae (Molytinae), with far more than 150 species (more than 40 in Vietnam), including 7 in Japan (Morimoto 1962), 4 in Korea (all shared with Japan and Russia), and 2 in the south of the Russian Far East. At the generic level, the northern impoverishment of the fauna is best exemplified by the second largest genus of the weevil subfamily Ceutorhynchinae, *Mecysmoderes*, with more than 100 species in East and Southeast Asia (more than 40 in Vietnam alone), more than 10 in Japan, only 2 in South Korea, and 1 in the Sakhalin and Kunashir islands of the Russian Far East.

On the contrary, large boreal and temperate genera decrease in species numbers southward and reach tropical countries, if at all, as single representatives in the northernmost mountain systems; examples include *Carabus* and *Chrysolina* in Vietnam. The Holarctic weevil genus *Dorytomus* includes 19 species in boreal Northeast Asia, 28 species in the southern (Stenopean) part of the Russian Far East, 10 species in Japan, and 7 in Korea, mostly in the central and south-central Stenopean part of the peninsula (Hong et al. 2001).

## Taiga

The taiga (Fig. 7.1a: II, c) is the largest ecozone in the world, stretching from the Atlantic to the Pacific Ocean in the Palearctic. Together with its Nearctic counterpart, it occupies 13% of the earth's landmass (Schultz 1995). Despite its large size, it is relatively uniform floristically. Sochava (1953) recognized three main

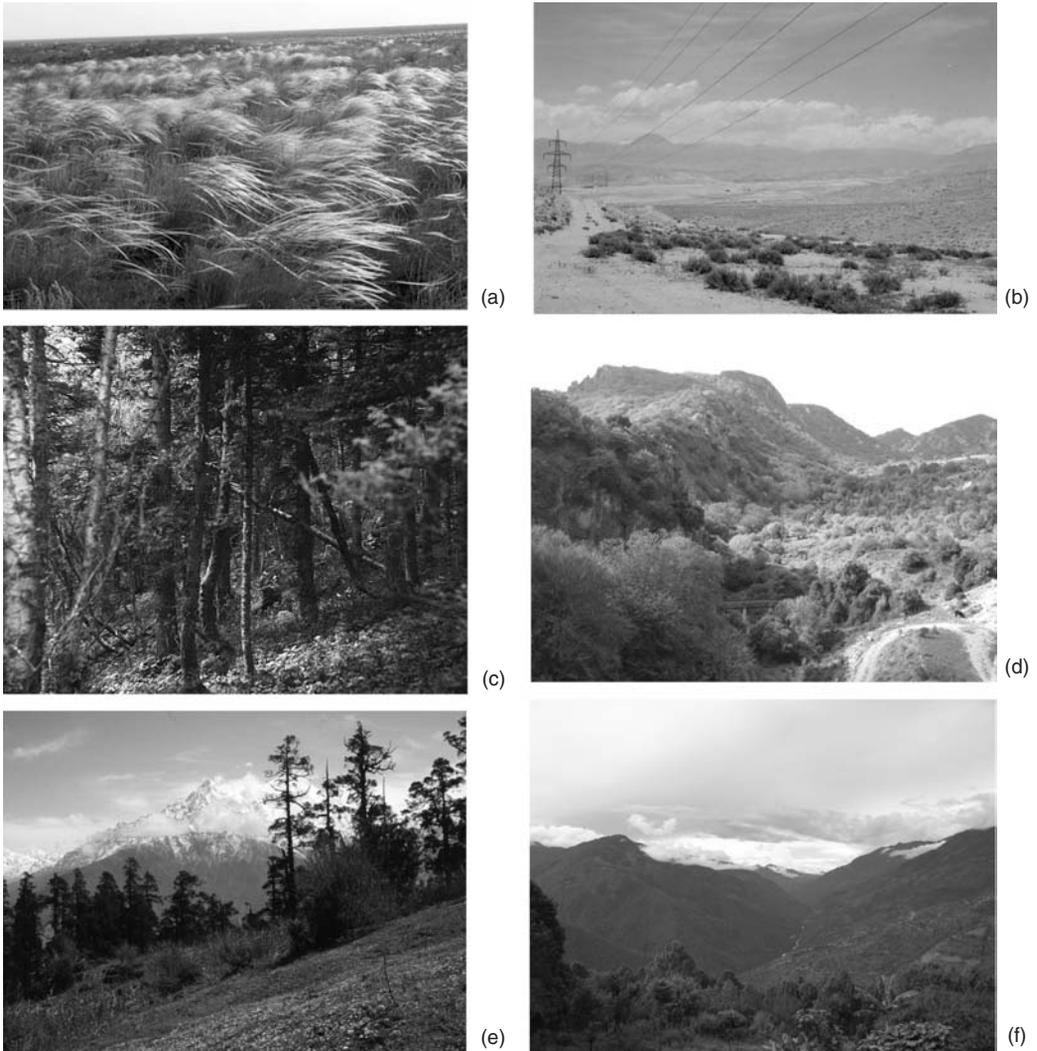
types of taiga in the former USSR: dark coniferous forests dominated mostly by spruces (*Picea* spp.) and firs (*Abies* spp.); pine forests with *Pinus silvestris*; and larch forests formed in different areas by three species of *Larix*. One of the characteristic features of the taiga is the small number of lianas. *Clematis* (Ranunculaceae) is the only common representative, with an oligotypic, specialized genus of flea beetles (*Argopus*) feeding on it.

Many insects in the taiga are associated with the most common conifers and occur in abundance, sometimes becoming serious pests. Among the lepidopteran pests are *Lymantria monacha* (L.) (Lymantriidae), *Dendrolimus pini* L. (Lasiocampidae), and *Dioryctria abietella* Denis and Schiffermüller (Pyralidae). Common pests also include many scolytines (e.g., *Ips*, *Pityogenes*, and *Polygraphus*). The Scolytinae have a fairly large number of species in the taiga, mostly associated with conifers. In northern Europe, both *Pinus silvestris* and *Picea abies* (L.) Karsten have multispecies assemblages of scolytines (up to 15 species on a single tree; M. Yu. Mandelshtam, personal communication), and in Siberia and the Far East, *Larix* species are heavily attacked, although by few species. Birches, constituting a considerable part of the northern forests, harbor a few species, and alder still fewer. Xylophagous Cerambycidae are not species rich in the taiga but include several species that damage conifers and rather regularly exhibit outbreaks.

Coleoptera constitute a considerable part of the taiga insect fauna, and are dominated by the Staphylinidae, Carabidae, and Curculionidae. Ermakov (2003) listed 592 beetle species in 64 families collected in the northern Urals in 1998–2001, from the plains to the highest point at 1492 m.

Characteristically, many taiga insects have enormous ranges stretching across the Palearctic and have a tendency to become invasive if introduced to the Nearctic. For example, the core of the buprestid fauna (Coleoptera) of the Euro-Siberian taiga is formed mainly of transpalearctic species, such as *Dicerca furcata* (Thunberg) (Chrysochroinae), *Buprestis rustica* (L.), and *Anthaxia quadripunctata* (L.). Two of the most common buprestids are associated with the coniferous genus *Larix*: *Buprestis strigosa* Gebler and *Phaenops guttulatus* (Gebler).

Some high-level forest taxa constituting a considerable part of the nemoral and subtropical faunas are absent from the taiga. Singing cicadas (Auchenorrhyncha: Cicadidae) are one of the most noticeable examples during the day, and crickets

**Fig. 7.6**

- (A) Russia, Astrakhan Province, near Lake Baskunchak, steppe (Photo M. Volkovitsh).  
 (B) Armenia, Vedi Desert (Photo A. Konstantinov).  
 (C) Russia, Sakhalin Island, mixed forest (Photo A. Konstantinov).  
 (D) Italy, Sicily, mountain nemoral forest with *Fagus* (Photo M. Volkovitsh).  
 (E) Nepal, Lantang District, mountain forest (3200 m) (Photo A. Konstantinov).  
 (F) Bhutan, Shemgang District (2900 m) (Photo A. Konstantinov).

(Orthoptera: Grylloidea), glow-worms, and fireflies (Coleoptera: Lampyridae) at night. Among the weevils, no Brentidae or Platypodidae are present. Among the Chrysomeloidea, the Chlamysini, Lamprosomini, and Megalopodinae are not represented in the taiga.

### Nemoral European and Stenopean Forests

These forests account for 10% of the earth's landmass (Schultz 1995) (Figs. 7.1a: III, IV, d: 7.6c). The Palearctic nemoral zone, with aborigine vegetation

dominated by coniferous–broadleaf (or mixed) and broadleaf forests, consists of two currently isolated parts, the European and Stenopean regions (Emeljanov 1974). The fragmentation of the nemoral zone followed an increase of continentality that probably occurred in the Pliocene (Sinitsyn 1965) when the northern tundra and taiga zones expanded southward and the steppe and desert zones drifted northward. An occurrence of numerous closely related vicarious species of buprestids, carabids, cerambycids, histerids, and other insects in both European and Stenopean regions supports this hypothesis (Volkovitsh and Alexeev 1988, Kryzhanovsky 2002). For example, a number of pairs of closely related vicarious species of Buprestidae are in the European and Stenopean nemoral regions, including *Lamprodila rutilans* (F.) – *L. amurensis* (Obenberger), *Eurythyrea aurata* (Pallas) – *E. eoa* Semenov, and *Chrysobothris affinis* (F.) – *Ch. pulchripes* Fairmaire.

In European forests, the most species-rich weevil taxa are associated with the woodland landscape – herbage both under the canopy and, especially, in the openings, forest litter and decaying plant tissues – rather than with the trees themselves. Representative genera include *Acalles* and its allies (Cryptorhynchinae), *Dichotrachelus* (Cyclominae), *Otiorynchus* (Entiminae), *Plinthus*, and several smaller genera of Plinthini (Molytinae), none of them being represented in the Stenopean Region. On the contrary, major taxa of the Curculionidae with larval development in the leaves, fruits, or wood of woody plants, have poorer representation in the European forests, compared with the Stenopean forests. Examples include the leaf-mining tribe Rhamphini of the Curculioninae (7 genera with 51 species in Japan; Morimoto 1984; and 5 genera with 27 species in Europe; Lohse 1983), the genus *Curculio* in the broad sense (13 species in the south of the Russian Far East, 50 in Japan (Egorov et al. 1996), and 11 in Central (nemoral) Europe). Of the main forest-inhabiting higher taxa, only the tribes Anthonomini of the Curculioninae, Magdalini of the Mesoptiliinae, and Pisodini of the Molytinae are almost equally represented in the European and Stenopean regions. The Western and Eastern Palearctic members of the largest weevil subfamily, Entiminae, with soil-inhabiting larvae, are represented almost exclusively by endemic genera (and subgenera in a few trans- or amphipalaearctic genera), except for a small number of widely distributed species. Many other insects associated with trees also are

more species rich in the Stenopean Region than in the European Region. For example, the nitidulid genera *Epuraea*, mostly occurring under bark, and *Meligethes*, associated exclusively with herbaceous woodland plants, are represented in the fauna of the southern Russian Far East by 47 and 20 species, respectively, out of approximately 100 in the former USSR (Kirejtshuk 1992).

Among ancient faunal elements worthy of mention as endemic to the Stenopean Region is the beetle *Sikhotealinia zhiltzovae* Lafer, originally (Lafer 1996) placed in the separate monotypic family Sikhotealiniidae, but later (Kirejtshuk 2000) transferred to the Mesozoic family Jurodidae Ponomarenko (suborder Archostemata), which was thought to be extinct. Other examples include *Declinia relictata* Nikitsky et al. (1993) a species of the recently described coleopteran family Decliniidae; a relict longhorn beetle, *Callipogon (Eoxenus) relictus* Semenov, with Neotropical affinities; the aquatic beetle *Aspidytes wrasei*; and representatives of the coleopteran family Synteliidae (Histeroidea) known only in this part of the Palearctic.

### Hesperian and Orthrian evergreen forests

These forests (Figs. 7.1a: V, VI; 7.6d, e, f) originated from a single region of sclerophyll vegetation that existed at the edge of Arcto-Tertiary and Tropical–Tertiary forests until the end of the Neogene along the Tethys Ocean (Axelrod 1975a). Aridization changed the dominant plant communities from evergreen laurophyllous forests to sclerophyll forests and chaparral-macchia. Insect relicts of the laurophyllous forests currently occur in some semi-arid areas of the Palearctic such as the Canary Islands, Himalayas, and southern China. As a result of Pleistocene glaciation, boreal elements are also present in the Hesperian and Orthrian evergreen forests, mostly at high elevations in various mountain systems.

The Macaronesian Subregion of the Hesperian Region includes islands of Madeira, the Canaries, Azores, and Cape Verde, with typical oceanic climates. The insect fauna of the islands is less rich than the continental fauna. It contains many endemics and includes Mediterranean and Afrotropical elements. For example, the fauna of the Canary Islands, the largest of the region, contains 230 species of ground beetles, of which 140 are endemics; of 83 genera, 14 are endemic to the Canaries and 2 are shared with Madeira. The

buprestid fauna of the Canaries includes 20 species in 9 genera, of which 12 species are endemics. The Canary fauna of buprestids is less diverse compared with the 189 species and 29 genera in Spain, and 224 species and 31 genera in Morocco.

The Mediterranean insect fauna is species rich and highly endemic. Oosterbroek (1994) suggested that the Mediterranean region in a broad sense (including Anatolia, Armenia, and Hirkanian) together with the Far East is the most species rich in the Palearctic. The insect fauna of the Mediterranean proper constitutes about 75% of the Western Palearctic fauna (Balletto and Casale 1991). For example, for the flea-beetle genus *Longitarsus*, with about 500 valid species in the world and 221 in the Palearctic, 158 occur in the Mediterranean (in the narrow sense) and about 10% of them are endemics. Of 461 species of Neuroptera in the Mediterranean (in the broad sense), 230 are endemics; of 677 species of Rhopalocera (Lepidoptera), 416 are endemics; and of 498 species of Tipulidae (Diptera), 361 are endemics (Oosterbroek 1994). The most species-rich areas of the Mediterranean are the Balkans and Asia Minor (Oosterbroek 1994). Widespread temperate European and Palearctic species contribute significantly to the overall biodiversity of the region. The Mediterranean biota, however, has been impoverished by human influences over a long period of time, which have completely transformed the region (Mooney 1988).

The Orthrian Region includes the Himalayas (lower and middle altitudinal belts of the southern slope of the Central and Eastern Himalayas up to 2000–3000 m, belonging to the Oriental Region or to territories transitional between the Palearctic and Oriental Regions; Emeljanov 1974) and parts of China, Japan, and southernmost Korea. Because Pleistocene glaciation did not cover the eastern part of its territory, the region contains a large number of floristic and faunistic relicts (Axelrod 1975b). The insect fauna of the Orthrian Region is rich and has many Oriental elements. For example, the leaf-beetle fauna of the small Himalayan country of Nepal contains 797 species, which is nearly half the number of species in the entire fauna of the former USSR (Medvedev and Sprecher-Uebersax 1999) and more than twice that in Mongolia (Medvedev 1982). The most primitive dragonfly family, Epiophlebiidae, occurs in the Orthrian Region (Himalayas and Japan) (Kryzhanovskiy 2002).

Faunal connections between the Mediterranean Subregion of the Hesperian Region and the Orthrian Region are of interest. Species of a few buprestid genera are split almost evenly between these zoogeographical entities. *Polyctesis* has two species in the Mediterranean Subregion and two in the Orthrian Region. *Ptosima* has one species in the Mediterranean Subregion and two in the Orthrian Region. Eastern Mediterranean and Irano-Turanian faunal elements are common in the West Orthrian Subregion, but disappear in the eastern portion of the region. Species of the predominantly Western Palearctic and Afrotropical buprestid genera *Julodis* (Fig. 7.3a) and *Julodella* (Fig. 7.3b) occur in the West Orthrian Subregion. The West Orthrian Subregion is also the western limit for Oriental genera such as *Microacmaeodera*, and the northern limit of distribution for the Paletropical genera *Sternocera* and *Coroebina*. From west to east in the Orthrian Region, the influence of the Oriental fauna increases significantly. In Yunnan, for example, about half of the buprestid fauna is Oriental. An influence of the Holarctic and Stenopean groups increases in the East Orthrian Subregion, as illustrated by a few buprestid genera and subgenera: *Nipponobuprestis* (six species in southern China and Japan) and *Sapaia* (Yunnan and North Vietnam) (Volkovitsh and Alexeev 1988, Kuban et al. 2006).

### Scythian (Steppe) Region

The steppe (Figs. 7.1a: VII; 7.6a) stretches from the Hungarian lowland to eastern Siberia, Mongolia, and northern China, with the southern border along the Black Sea, Crimean and Caucasian mountains, and the deserts of Kazakhstan and Middle Asia. The steppe is characterized by the following climatic conditions: well-developed to extreme continentality (Mongolian steppes differ by more than 100°C between the winter minimum and summer maximum), limited and uneven precipitation, and strong winds. Genuine steppe landscape nearly lacks forests, with only some gallery forests situated along the rivers, small isolated forests in depressions (ovragi, balki), and forest belts in the mountains.

The steppe landscape (the steppe proper, prairies, and pampas), occupying only 8% of the land, provides 80% of the cereals and meat and other cattle products (Mordkovich et al. 1997); 66% of the steppes are located in Eurasia. Due to its fertile soils

and favorable climate, the steppe has been severely transformed by agriculture. Some remnants of steppe occur in southern Ukraine and the south of European Russia, but in the northern Caucasus, steppe communities are almost entirely gone, except for some fragments on slopes unsuitable for agriculture (Korotyaev 2000); the same is true for the nearly completely cultivated northern Kazakhstan steppes ('Tselina' = virgin soil). Large steppe areas still exist in Tuva and Mongolia.

The steppe is usually subdivided into the West Scythian and East Scythian subregions (Emeljanov 1974), with the boundary in the area between the Altai Mountains and Yenisei River; subregions are further subdivided into provinces and subprovinces. The boundary between the Western and Eastern Palearctic steppe faunas is quite sharp. In the close territories of southeastern West Siberia and in Tuva, the weevil faunas are nearly equal, consisting of 320 species (Krivets 1999) and 311 species, respectively (B. A. Korotyaev, unpublished data), including 1 and at least 35 species, respectively, of *Stephanocleonus* (Coleoptera: Curculionidae).

Strong and frequent winds might be largely responsible for insects with well-developed flight skills or flightless forms having an advantage in the steppe. Flightlessness is particularly common for ground-dwelling beetles. Among them, the cerambycid genus *Dorcadion*, with many species, is characteristic of the western and central parts of the Steppe Region, whereas the eastern part is populated by its close relative *Eodorcadion*. Species of *Dorcadion* are active in the spring, and those of *Eodorcadion* in the middle of the summer, according to the maximum precipitation in the respective regions. Many steppe carabids are also flightless, including the most conspicuous, viz., *Callisthenes* and some *Calosoma* (Fig. 7.2a). Flightless insects are especially common in dry variants of the steppe with sparse vegetation, for example, in Tuva and Mongolia, where the predominance of medium-sized and large wingless orthopterans and beetles is impressive. Some large weevil genera, including almost exclusively fully winged species, are represented in the Palearctic steppe by wingless species. Examples include a wingless species of *Pseudorchestes*, which is a minute leaf miner on semidesert wormwoods (*Artemisia pauciflora* Web. ex Stechm.) in Kazakhstan and Mongolia, and the entire subgenus *Anthonomidius* of the worldwide *Anthonomus*, with four species on *Potentilla*.

A characteristic feature of steppe vegetation is the prevalence of the underground biomass over the above-ground biomass, leading Paczoski (1917) to call the steppe 'the forest upside down'. The proportion of weevils with soil-inhabiting larvae in the Ciscaucasian steppe (20%), nonetheless, is less than that in the six types of the Transaltai Gobi desert communities (40–57%) and at the southern boundary of the adjacent mountain steppes (54%), and equals that in the desert solonchaks and oases (Korotyaev 2000).

A variety of beetles, from carnivores to phytophages, is rich in the steppe. Medvedev (1950) gave an excellent review of the steppe fauna, which is especially detailed for the western steppes. He considered that 5300 species of beetles occur in the steppes from Moldova to Transbaikalia; however, only half of them occur in the true steppe landscape. Weevils (Curculionidae in a broad sense, excepting Scolytinae) are the most species-rich group of beetles in the steppes of the former USSR (763 species), followed by ground beetles (Carabidae, 752 species), rove beetles (Staphylinidae, 657), leaf beetles (Chrysomelidae, 500), and scarabs (Scarabaeoidea, 288) (Medvedev 1950, cited by Iablokov-Khinzorian 1961).

Many groups of saprophagous (copro-, detrito-, and proper saprophagous) beetles are well represented in the steppe. The largest beetle genera, *Aphodius* and *Onthophagus*, dominate the dung-beetle assemblages throughout the steppe zone. Some species of *Aphodius* are associated with burrows of typical steppe rodents, the susliks (ground squirrels) and marmots. Regional faunas of *Aphodius* include as many as 150 species in Kazakhstan and Middle Asia (Nikolajev 1988) and about 50 mostly steppe species in Mongolia (Puntsagdulam 1994). The Mongolian steppe fauna of coprophagous scarabaeids is more diversified (59, 32, and 35 species in the forest steppe, genuine steppe, and desert steppe, respectively) than the desert fauna (seven species) (Puntsagdulam 1994).

The most conspicuous detrito- and phytodetritophagous group of beetles in the steppe is the family Tenebrionidae, of which the most common is *Opatrum sabulosum* (L.). A few species of the genus *Pedinus* also are typical of the Eastern European steppe (*P. femoralis* (L.) being the most common and widely distributed), but missing from the steppes of Kazakhstan, Siberia, and Mongolia, whose fauna is dominated by the genera *Anatolica*, *Penthicus*, *Melanesthes*, *Scythis*, and *Blaps* with 42, 25, 13, 12, and 10 species, respectively, in Mongolia and Tuva (Medvedev 1990).

These genera, except *Blaps*, are poorly represented in the European steppes where no genus of Tenebrionidae has gained a particular diversity. For example, on the Taman' Peninsula, with its predominantly steppe landscape, each of the 12 genera of tenebrionid beetles is represented by only one species (B. A. Korotyaev, unpublished data).

Among pollinators, several medium-sized, hairy, and brightly colored scarabaeoid beetles of the family Glaphyridae, with thin, short elytra (*Amphicomma* and *Glaphyrus*) – apparently mimicking bumblebees – are specific to the western steppe but lacking in the Siberian and Mongolian steppe. Two related families, the Malachiidae and Dasytidae, are common on flowers throughout the steppe zone. Alleculids are conspicuous only in the western steppes.

Steppe herbivores are numerous and specific. Two orders, the Lepidoptera and Coleoptera, are apparently most species rich in the steppe. In the Karadagh Nature Reserve in the Crimean steppe, 1516 species of Lepidoptera have been found (Budashkin 1991); 796 species are recorded from the largely dry-woodland Abrau Peninsula in the Black Sea, and 300 species from the almost forestless Taman' Peninsula (Shchurov 2004). In the steppes of the Northwestern Caucasus near Novoaaleksandrovsk, 169 species of weevils dominate the herbivorous insect assemblage, with the second largest group, the Chrysomelidae, barely reaching half the weevil total, and other beetle families (Buprestidae and Cerambycidae) being represented by 6 or 7 species. The Auchenorrhyncha (planthoppers and leafhoppers) and Orthoptera have no more than 20 and 6 species, respectively, in that area (Korotyaev 2000, 2001a, unpublished data).

Most steppe-specific buprestids are representatives of *Sphenoptera* (subgenera *Chilostetha* and *Sphenoptera* s. str.), which are mainly root borers; *Agrilus* (subgenus *Xeragrilus*), associated mainly with *Artemisia*; and endemic Palearctic *Cylindromorphus* that feed on Cyperaceae and Poaceae. Leaf-mining species of the genus *Trachys* are common on Lamiaceae plants in the western steppes, whereas representatives of another leaf-mining genus, *Habroloma*, are associated mainly with *Erodium* (Geraniaceae).

The tribe Dorcadionini, with soil-inhabiting larvae, is the most characteristic group of cerambycid beetles in the steppe. The three cerambycid genera with the greatest numbers of species in the Caucasus – *Dorcadion* (43), *Phytoecia* (40), and *Agapanthia* (16) – comprise more than a quarter of

the entire fauna (343 species) of this extensively wooded mountain system. They are associated with herbaceous vegetation, and most (31 of 43 species of *Dorcadion* recorded from the Caucasus; Danilevskii and Mirosnikov 1985) live in the steppes.

Leaf beetles have a number of groups specific to the steppe. No fewer than 50 species of several subgenera of *Chrysolina* occur in the steppe and some large subgenera (e.g., *Pezocrozita*) are subendemic. All species of *Chrysolina* are associated with herbs and semishrubs (mostly *Artemisia* species), and are especially conspicuous and diversified in the steppes of southern Siberia and Mongolia. Many of the central Palearctic steppe *Chrysolina* are wingless, but two tribes of actively flying leaf beetles, the Clytrini and Cryptocephalini (Fig. 7.2d), with no flightless species in the Palearctic, codominate, with *Chrysolina*, the steppe chrysomelid assemblages. In the Cryptocephalini, *Cryptocephalus* is apparently the most species-rich genus of leaf beetles in the steppe and includes many common species on *Artemisia*, *Atraphaxis*, and *Caragana*, the most characteristic steppe semishrubs and shrubs.

The steppe flea-beetle (Alticini) fauna is the most species rich among the flatland flea-beetle faunas of the European part of the former USSR, with 198 species (Konstantinov 1991). This fauna also has the lowest percentage of species with transpalearctic ranges (16.2%) (Konstantinov 1991).

In the Bruchinae, the monotypic tribe Kytorhinini includes about a dozen species associated mostly with *Caragana* (Fabaceae) and distributed from southeastern European Russia to Nepal and the Far East. The genera *Bruchidius*, *Bruchus*, and *Spermophagus* are represented in the steppe by a few species, including some endemics. A Nearctic species, *Acanthoscelides pallidipennis* (Motschulsky), has been introduced together with its American host, *Amorpha fruticosa* L. (Fabaceae), and is now the second most common (after *Spermophagus sericeus* Geoffroy) bruchine in the North Caucasian steppe, having reached China in the east.

The largest phytophagous group, the Curculionidea, is species rich in the steppes. Of the 11 families represented in the steppe, only the Apionidae and Curculionidae are represented by more than 10 species, but most of the families, except the Nanophyidae and Dryophthoridae, include at least one endemic or subendemic steppe species. The Nemonychidae (Fig. 7.5b) and Brachyceridae occur only in the southeastern European steppes. The Anthribidae and Rhynchitidae are represented by one endemic species each in the

Continental sector on *Caragana* (Fabaceae) and *Spiraea* (Rosaceae), respectively. The Urodontidae include 10 species of the Palearctic genus *Bruchela* in the steppe, of which *B. orientalis* (Strejček) is trans-zonal, *B. exigua* Motschulsky is endemic to extreme south-eastern Europe, and *B. kaszabi* (Strejček) is endemic to southern Mongolia; all are associated with xerophilic Brassicaceae. The Erihrinidae include the riparian endemic trans-zonal *Lepidonotaris petax* (Sahlberg) and East Scythian *Notaris dauricus* Faust. The Attelabidae are represented in eastern Mongolia and Transbaikalia by a few Stenopean species, mostly on *Ulmus pumila* L.

The Apionidae are common throughout the entire steppe zone from its southernmost parts to the cold (= cryophytic) steppes and tundra-steppe of the Siberian Arctic zone. They comprise 10% of the entire Curculionoidea fauna (340 species) of the steppe on Taman' Peninsula (Korotyaev 2004 and unpublished data), and 12% of the 169 species in the steppe of Stavropol Territory in the Northwestern Caucasus (Korotyaev 2000, 2001b, unpublished data). In Siberia and Mongolia, with their poorer steppe flora and extreme continental climate, the Apionidae constitute a smaller part of the steppe-weevil fauna (about 3% in the steppe zone of Tuva, with somewhat over 220 species).

The Curculionidae is the most species-rich family in the entire steppe zone, although only a few estimates are available. Of the two investigated steppe areas in the plains of the Northwestern Caucasus, one is the Taman' Peninsula (Korotyaev 2004), with a variety of habitats. The other steppe area is a fragment of the steppe with a territory of about 2 hectares, completely isolated from the closest sites of native vegetation by fields and orchards (Korotyaev 2000). Both lists of the Curculionoidea are dominated by the Ceutorhynchinae, Entiminae, and Curculioninae, followed by the Apionidae. Aside from the steppes of China, where no specific studies have been conducted, the rest of the Eurasian steppe-weevil fauna is characterized by dominance of four subfamilies, the Ceutorhynchinae, Entiminae, Curculioninae, and Lixinae. The first three of these subfamilies are most species rich in Europe and Anatolia, while the Lixinae overwhelmingly dominate in Mongolia and adjacent parts of eastern Siberia.

The xylophagous Curculionoidea are poorly represented in the steppe. Scolytines are represented mostly by thamnobionts and dendrobionts that develop on steppe bushes such as *Prunus spinosa* L. One scolytid genus, *Thamnurgus*, is herbivorous. One of its species,

*Th. russicus* Alexeev, is endemic to the meadow-steppe subzone of European Russia, developing on *Delphinium cuneatum* Stev. (Ranunculaceae; Alexeev 1957), and another species, *Th. caucasicus* Reitter, is common on *Carduus* (Asteraceae) in the North Caucasian steppes.

### Sethian (Desert) Region

Palearctic deserts form a great belt stretching from Northern Africa to Northwestern China and Western India (Figs. 7.1a: VIII; 7.6b). Depending on the climatic conditions, soil composition, and vegetation, three large subregions usually are distinguished in Palearctic deserts: Saharo-Arabian, Irano-Turanian, and Central Asian (Lavrenko 1950, Emeljanov 1974, Kryzhanovsky 2002). Geographic position and climate partly determine the similarities and distinctions among the insect faunas of all subregions. The Saharo-Arabian Subregion includes a great number of taxa of Afrotropical (Ethiopian) origin. The Irano-Turanian Subregion shares many taxa with the Mediterranean Subregion, particularly with the East Mediterranean Province of the Hesperian Region, while its North Turanian Province has many features of the Central Asian Subregion.

The flatland desert insect fauna is xerophilic and relatively poor, other than some desert-specific groups adapted to xeric conditions. Of approximately 800 species of leaf beetles in Central and Middle Asia, 233 species occur in deserts (Lopatin 1999). Among them, the Cryptocephalinae are the most numerous, followed by the Alticini and Eumolpinae.

Some insect groups are poorly represented or absent in flatland deserts. These groups include grasshoppers (Orthoptera: Ensifera), earwigs (Dermaptera), aphids (Aphidina), some brown lacewings (Hemerobiidae), ground beetles (Carabidae, excluding specialized groups), Megaloptera, Raphidioptera, and Mecoptera. Other insect groups are abundant in the deserts, including some groups of Blattaria, Mantodea, Isoptera, Orthoptera (particularly some groups of locusts: Catantopinae, Oedipodinae, and Pamphaginae), Rhynchota (particularly Psyllina, Auchenorrhyncha, and Heteroptera), and Neuroptera (Ascalaphidae, Mantispidae, Myrmeleontidae, and Nemopteridae (Fig. 7.2b)). The desert fauna has a large percentage of endemic taxa (Kryzhanovsky 1965). In the Orthoptera, the family Acrididae contains a number of endemic tribes (Dericorythini, Diexini, Egnatiini, Iranellini, and

**Table 7.3** Distribution of Tenebrionidae across six types of desert plant communities in Transaltai Gobi, Mongolia. 6–1 = desert plant communities (from north to south): 6, *Anabasis brevifolia* steppeified desert; 5, *Reaumuria soongorica* + *Sympegma regelii* desert; 4, *Haloxylon ammodendron* desert; 3, *Reaumuria soongorica* + *Nitraria sphaerocarpa* desert; 2, extra-arid *Iljinia regelii* desert; 1, extra-arid *Ephedra przewalskii* + *Haloxylon ammodendron* (in dry, temporary waterbeds) desert.

Steppe Species (+)	6	5	4	3	2	1	Desert Species (*)
						*	<i>Dilamus mongolicus</i> Kaszab
						*	<i>Penthicus lenczyi</i> Kaszab
					*		<i>Psammoestes dilatatus</i> Reitter
<i>Blaps miliaria</i> Fischer de Waldheim	+		*				<i>Blaps kiritshenkoi</i> Semenov and Bogačev
<i>Melanesthes heydeni</i> Cziki	+	+	*	*			<i>Melanesthes czikii</i> Kaszab
<i>Platyope mongolica</i> Faldermann	+	+		*	*	*	<i>Sternoplax mongolica</i> Reitter
<i>Monatrum prescottii</i> Faldermann	+	+	+	*	*		<i>Anatolica mucronata</i> Reitter
<i>Blaps femoralis medusula</i> Kaszab	+	+	+	*	*	*	<i>A. polita borealis</i> Kaszab
<i>Eustenomacidius mongolicus</i> (Kaszab)	+	+	+	*	*	*	<i>Blaps kashgarensis gobiensis</i> Frivaldski
<i>Anatolica cechinia</i> Bogdanov-Kat'kov	+	+	+	*	*	*	<i>Trigonoscelis sublaevigata granicollis</i> Kaszab
<i>A. sternalis gobiensis</i> Kaszab	+	+	+	*	*	*	<i>Cyphosthete mongolica</i> Kaszab
<i>Eumilada punctifera amaroides</i> Reichardt	+	+	+	*	*	*	<i>Anatolica amoenula</i> Reitter
<i>Epitrichia intermedia</i> Kaszab	+	+	+	*			<i>Anemia dentipes</i> Ballion
<i>Microdera kraatzii</i> Reitter	+	+	+	+	+	+	<i>Cyphogenia intermedia</i> A. Bogačev
	*	*	*	*		*	<i>Pterocomma reitteri</i> Frivaldski

Uvaroviini), mostly in the subfamily Catantopinae, which is common in both the Sahara and Gobi Subregions (Sergeev 1993). Endemics constitute almost 70% of the leaf beetles (Lopatin 1999). Insect biodiversity sharply increases in the mountains, with altitude belts inhabited by mesophilous groups, particularly in the Irano-Turanian Subregion (Kryzhanovsky 2002).

The borders between steppes and deserts in the Palearctic generally are not sharp and usually are represented by an intermediate subzone of semideserts now typically attributed to the steppe zone as the desert steppe. Faunal changes along climatic and vegetational gradients are well-organized phenomena, which is illustrated with examples of three family-group taxa of the Coleoptera in the Transaltai Gobi. Gradual changes were studied in species assemblages of the

superfamily Curculionoidea (Table 7.2), Chrysomelidae (except Bruchinae), and Tenebrionidae (Table 7.3) across six types of zonal plant communities, from steppeified deserts (sites 6 and 5) in the north of the 160-km long soil and vegetation profile to extra-arid deserts with only one (site 2) or two species of plants (site 1). The general pattern is a subsequent substitution of species with the greatest portions of their ranges in the mountain steppe or desert steppe north of site 6 by species distributed in true deserts.

The Tenebrionidae differ from the herbivorous taxa in the broader overlapping of the steppe and desert complexes along the profile, such that the number of tenebrionid species is greater than the number of weevils at most sites, although the total number of weevils in the profile is 1.3 times that of

tenebrionids. Also distinguishing the Tenebrionidae from the herbivorous beetles is their much larger portion of zonal desert species in the total Transaltai Gobi fauna (see Table 7.3): 59% for the tenebrionids, compared with 37% for the Curculionoidea and 31% for the Chrysomelidae (excluding Bruchinae). A drop in biodiversity occurs at site 6 close to the Dzhinst Mountains, with developed steppe communities, relative to the more distant site 5, and the highest diversity is found at the sandy *Haloxylon* desert (site 4).

Two special faunistic surveys of Coleoptera have been conducted in different parts of the Palearctic deserts. The first was by a French Scientific Mission (Peyerimhoff 1931) along an 800-km route in the Central Sahara, including the Hoggar Plateau, in February–May 1928, and the second was a part of the investigation on insects in the main plant communities of the Transaltai Gobi in July–early October 1981 and in the summer of 1982 by the Joint Soviet–Mongolian Biological Expedition (Korotyaev et al. 1983). Although the periods and organization of the collecting differed significantly, the results (Table 7.4) are essentially similar. Differences in the family sets from the two surveys are of two kinds. The absence of several aquatic families in the Transaltai Gobi is due to the small number and small size of natural water bodies, whereas a rather large river and several freshwater streams were investigated in the Sahara. The other important difference is the presence of the two predominantly tropical families in the Sahara, the Bostrichidae and Brentidae, which can be explained by the location of the area at the southern border of the Palearctic. The presence of a few families (e.g., Alleculidae, Cantharidae, Leiodidae, Nitidulidae, Oedemeridae, and Pselaphidae) with one or two species in only one of the two faunas is probably accidental, resulting mainly from the difference in collecting periods.

Several features are common to the Saharan and Gobian coleopteran faunas and characteristic of the desert Palearctic fauna in general. These are the leading positions of the Curculionidae and Tenebrionidae and the relatively wide representation of other large families such as the Buprestidae, Carabidae, Chrysomelidae, Scarabaeidae, and Staphylinidae, but not the Cerambycidae. Also noteworthy is the absence of the Silphidae from the desert faunas, in sharp contrast to the Mongolian steppes where large black beetles of *Nicrophorus argutor* B. Jakovlev are common around dense colonies of pikas and susliks. The Scolytinae also are absent, although a desert species, *Thamnurgus pegani*

Eggers, occurs in Middle Asia on *Peganum harmala* L. (Peganaceae) in Turkmenistan. Relatives of this species are known from Euphorbiaceae in tropical Africa and the Mediterranean.

To survive in extreme conditions of deserts, insects have developed a number of specialized behavioral, ecological, morphological, and physiological adaptations. A specific sand-desert morphobiological form has arisen in several beetle families (e.g. Dermestidae; Zhantiev 1976). The set of hypertrophied adaptive characters can mask the affinities to such an extent that a desert dermestid, *Thylodrias contractus* Motschulsky, has been described repeatedly in several families (R. D. Zhantiev, personal communication). Adaptive rearrangements of various body structures are manifested by desert Braconidae (Hymenoptera). In addition to depigmentation of the integument and enlargement of the eyes, in connection with nocturnal activity, the braconid wasps exhibit a smoothening of the body sculpture for reflection of light and heat, shortening of the wings with basal shifting of the cells associated with strong winds in open landscapes, and elongation of the labiomaxillary complex for feeding on flowers of desert plants (Tobias 1968).

## ACKNOWLEDGMENTS

This work would not have been possible without help and advice from our friends and colleagues – experts on various insect groups – especially those at the Zoological Institute in St. Petersburg (Russia): L. N. Anisyutkin (Blattaria, Dermaptera), S. A. Belokobylsky (Hymenoptera: Braconidae), A. F. Emeljanov (Auchenorrhyncha, zoogeography), N. V. Golub (Zoraptera, Psocoptera), A. V. Gorokhov (Orthoptera), D. R. Kasparyan (Hymenoptera: Ichneumonidae), the late I. M. Kerzhner (Heteroptera) A. G. Kirejtshuk (Coleoptera), O. V. Kovalev (Hymenoptera: Cynipoidea), V. A. Krivokhatsky (Neuropteroidea), V. G. Kuznetsova (Zoraptera, Psocoptera), A. L. Lobanov (Coleoptera, database), M. Yu. Mandelshtam (Scolytinae), A. Yu. Matov (Lepidoptera, Noctuidae), G. S. Medvedev (Coleoptera: Tenebrionidae), E. P. Nartshuk (Diptera), the late Yu. A. Pesenko (Hymenoptera: Apoidea), V. A. Richter (Diptera: Tachinidae), S. Yu. Sinev (Lepidoptera), A. V. Stekolshchikov (Sternorrhyncha: Aphidina), and from many other institutions: M. L. Chamorro-Lacayo (Trichoptera, Department of Entomology, University

**Table 7.4** Number of species of Coleoptera in the Transaltai Gobi and Central Sahara.

Family	Transaltai Gobi	Central Sahara
Carabidae	43	36
Haliplidae	–	1
Dytiscidae	4	19
Gyrinidae	–	2
Georissidae	–	1
Hydrophilidae (including Helophoridae)	5	13 (including Helophoridae and Hydraenidae)
Hydraenidae	3	?
Histeridae	15	11
Leiodidae	1	–
Staphylinidae	30	43
Pselaphidae	–	2
Scarabaeidae <i>sensu lato</i>	15 ( <i>Aphodius</i> – 6, <i>Onthophagus</i> – 1)	30
Dryopidae	–	4
Heteroceridae	–	2
Buprestidae	16 ( <i>Anthaxia</i> – 1, <i>Acmaeoderella</i> – 1, <i>Sphenoptera</i> – 7, <i>Agrilus</i> – 3, <i>Paracylindromorphus</i> – 1)	20 ( <i>Anthaxia</i> – 4, <i>Acmaeodera</i> – 4, <i>Sphenoptera</i> – 2, <i>Agrilus</i> – 1, <i>Cylindromorphus</i> – 1)
Elateridae	9 ( <i>Aeoloides</i> – 1, <i>Aeloderma</i> – 1, <i>Zorochrus</i> – 1, <i>Agriotes</i> – 1, <i>Cardiophorus</i> – 2)	8 ( <i>Drasterius</i> – 2, <i>Zorochrus</i> – 1, <i>Agriotes</i> – 1, <i>Cardiophorus</i> – 1)
Cantharidae	1	–
Dermestidae	12 ( <i>Dermestes</i> – 4, <i>Attagenus</i> – 6–7, <i>Anthrenus</i> – 2)	11 ( <i>Dermestes</i> – 1, <i>Attagenus</i> – 5, <i>Anthrenus</i> – 1)
Bostrichidae	–	8
Anobiidae	2 ( <i>Xyletinus</i> )	1 ( <i>Theca</i> )
Stylopidae	1	–
Cleridae	3 ( <i>Emmepus arundinis</i> Motsch., <i>Necrobia rufipes</i> DeG., <i>Opetiopalpus sabulosus</i> Motsch.)	4 ( <i>Emmepus</i> sp., <i>Necrobia rufipes</i> )
Dasytidae	–	5
Melyridae	3	5
Nitidulidae	–	1
Cybocephalidae	2	3
Phalacridae	4	2
Cucujidae	3 ( <i>Airaphilus</i> – 1)	2 ( <i>Airaphilus</i> – 1)
Helodidae	–	1
Cryptophagidae	3 ( <i>Cryptophagus</i> – 2)	1 ( <i>Cryptophagus</i> )
Coccinellidae	27 ( <i>Hyperaspis</i> – 1, <i>Coccinella</i> – 5, <i>Scymnus</i> s. l. – 6, <i>Pharoscymnus</i> – 2)	11 ( <i>Hyperaspis</i> – 1, <i>Coccinella</i> – 1, <i>Scymnus</i> s. l. – 4, <i>Pharoscymnus</i> – 2)
Mordellidae	4 ( <i>Mordellistena</i> – 3, <i>Pentaria</i> – 1)	3 ( <i>Mordellistena</i> – 1, <i>Pentaria</i> – 2)
Rhipiphoridae	1 ( <i>Macrosiagon medvedevi</i> lablokov-Khnzorian)	1 ( <i>Macrosiagon</i> )
Oedemeridae	1 ( <i>Homomorpha cruciata</i> Sem.)	–
Anthicidae	15 ( <i>Steropes latifrons</i> Sumakov, <i>Notoxus</i> – 2, <i>Anthicus</i> s. l. – 11, <i>Formicomus</i> sp. – 1)	19 ( <i>Notoxus</i> – 2, <i>Anthicus</i> s. l. – 14)
Meloidae	3	23
Alleculidae	–	1
Tenebrionidae	42	70

(continued)

Table 7.4 (continued).

Family	Transaltai Gobi	Central Sahara
Scarptiidae	1 ( <i>Scraptia</i> sp.)	1 ( <i>Scraptia straminea</i> Peyer.)
Cerambycidae	4 ( <i>Chlorophorus ubsanurensis</i> Tsherep., <i>Ch. obliteratus</i> Ganglb., <i>Asias mongolicus</i> Ganglb., <i>Eodorcadion kozlovi</i> Suv.)	6
Chrysomelidae	51 [incl. Bruchinae (6): <i>Rhaebus</i> – 1, <i>Spermophagus</i> – 2, <i>Bruchidius</i> – 3]	23 [incl. Bruchinae (2): <i>Caryoborus</i> – 1, <i>Bruchidius</i> – 1]
Urodontidae	1	5
Brentidae	–	1
Apionidae	15	13
Curculionidae	73	39

of Minnesota, Minneapolis, MN, USA), O. N. Kabakov (St. Petersburg, Russia), N. Ju. Kluge (Ephemeroptera, Department of Entomology, St. Petersburg University, Russia), A. S. Lelej (Hymenoptera: Mutillidae, Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia), S. W. Lingafelter, M. Pogue, J. Prena, F. C. Thompson, N. E. Woodley (Systematic Entomology Laboratory, USDA, Washington DC, USA), W. Steiner (Department of Entomology, Smithsonian Institution, Washington DC, USA), I. Löbl (Genève, Switzerland), I. K. Lopatin (Department of Zoology, Byelorussian State University, Minsk, Belarus), R. D. Zhantiev (Department of Entomology, Moscow State University, Moscow, Russia), and A. G. Zinovjev (Hymenoptera: Tenthredinidae, Boston, MA, USA).

We thank V. I. Dorofeyev (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg) for identification of some plants referred to in the text; D. I. Berman and Yu. M. Marusik (Institute of the Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences, Magadan), O. A. Khruleva (Institute of the Ecology and Evolution, Russian Academy of Sciences, Moscow), and S. A. Kuzmina (Paleontological Institute, Russian Academy of Sciences, Moscow) for useful advice and the many-year supply of interesting material collected in their studies in the North; D. I. Berman for excellent photographs of the northern landscapes; O. Merkl (Hungarian Natural History Museum, Budapest) for help at the Budapest Museum and consultations and excursions with B. A. Korotyaev to several unique landscapes in Hungary; L. Gültekin (Atatürk University, Erzurum, Turkey) for organizing collecting trips to Turkey and the fruitful long-term collaboration;

N. A. Florenskaya (St. Petersburg, Russia) for the habitus illustration of *Theodorinus* sp.; E. Roberts (Systematic Entomology Laboratory, USDA, Washington DC, USA) for the habitus illustration of *Clavicornaltica dali*; and H. Bradford (Systematic Entomology Laboratory, USDA, Washington DC, USA, archives) for the habitus illustration of *Cimberis attelaboides*. The work was performed with the use of the collection of the Zoological Institute, Russian Academy of Sciences (UFC ZIN no. 2–2.20), contract No. 02.452.11.7031 with Rosnauka (2006-RI-26.0/001/070).

We greatly appreciate the advice and constructive suggestions of our friends and colleagues who read this manuscript at various stages of completion: V. Grebennikov (Entomology, Canadian Food Inspection Agency, Ottawa), V. Gusarov (Department of Zoology, Natural History Museum, University of Oslo, Oslo, Norway), S. W. Lingafelter, R. Ochoa, A. Norrbom (Systematic Entomology Laboratory, Washington DC, USA), and A. K. Tishechkin (Department of Entomology, Louisiana State University, Baton Rouge, Louisiana, USA). We thank A. S. Lelej for help with the literature. We are particularly thankful to P. H. Adler and R. Footitt for editing this manuscript and their numerous and valuable suggestions.

This study was supported in part by the Collaborative Linkage Grant No. 981318 of the NATO Life Science and Technology Program. The work of MGV and BAK was partly supported also by the Russian Foundation for Basic Research, Grant nos. 07-04-00482-a, 07-04-10146-k, and 04-04-81026-Bel2004a. BAK's collecting in the steppes of the Northwestern Caucasus in 2007, which provided additional observations and material for this chapter, was supported by a grant from the Systematics Research Fund (London).

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