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11

Biodiversity of Coleoptera

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More species of insect have been described than of any other life form, and beetles are the greatest proportion of these. Beetles are also the most diverse group of organisms on Earth. The estimated number of described species of beetles is between 300,000 and 450,000 (Nielsen and Mound 1999). Our tally of 386,755 described extant species (Table 11.1) is based on figures from Ślipiński et al. (2011), whose subtotals may contain rounding errors. Many described species are known only from one locality or even one specimen (Stork 1999a, Grove and Stork 2000). Beetles are so diverse, and most species so poorly known, that even enumerating the actual number of *described* species remains difficult, much less estimating the number of undescribed species.

Erwin (1982) first proposed an estimate of the total number of beetle species on the planet, based on field data rather than on catalog numbers. The technique used for his original estimate, possibly as many as 12 million species, was criticized, and revised estimates of 850,000 to 4 million species were proposed (Hammond 1995, Stork 1999b, Nielsen and Mound 1999). Some 70% to 95% of all beetle species, depending on the estimate, remain undescribed (Grove and Stork 2000).

The beetle fauna is not known equally well in all world regions. Yeates et al. (2003), for example, estimated that the known beetle diversity of Australia includes 23,000 species in 3265 genera and 121 families. This estimate of species is slightly lower than that reported for North America, a land mass of similar size: 25,160 species in 3526 genera and 129 families (Marske and Ivie 2003). While Marske and Ivie (2003) predicted that as many as 28,000 species could be in North America, including currently undescribed species, a realistic estimate of the true diversity of the little-studied Australian beetle fauna could be 80,000 to 100,000 (Yeates et al. 2003). Both continents are probably relatively well-studied compared with most tropical regions.

Studies of beetle communities in restricted areas such as oceanic islands (Peck 2005), large administrative units (Peck and Thomas 1998, Sikes 2004, Carlton and Bayless 2007), or specific habitat types (Hammond 1990, Chandler and Peck 1992, Carlton and Robison 1998, Anderson and Ashe 2000) can provide important data on biodiversity at finer scales. Comprehensive species lists from well-defined areas or habitat types are useful not only because they give insights about current ecosystem health and function,

Table 11.1 Extant families of Coleoptera, with the estimated number of described extant world genera and species.

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage		
Archostemata	—	Crowsoniellidae	1	1	0	0.00		
		Cupedidae	9	31	4	12.90		
		Micromalthidae	1	1	1	100.00		
		Ommatidae	2	6	1	16.67		
		Jurodidae	1	1	0	0.00		
Myxophaga	Lepiceroidea	Lepiceridae	1	2	0	0.00		
	Sphaeriuoidea	Torridincolidae	7	60	3	5.00		
		Hydroscaphidae	3	22	1	4.55		
Adephaga	—	Sphaeriusidae	1	20	10	50.00		
		Gyrinidae	12	1,000	47	4.70		
		Trachypachidae	1	6	4	66.67		
		Rhysodidae	40	350	3	0.86		
		Carabidae	1,500	40,000	1,660	4.15		
		Haliplidae	4	220	39	17.73		
		Meruidae	1	1	0	0.00		
		Noteridae	14	250	4	1.60		
		Amphizoidae	1	5	2	40.00		
		Aspidytidae	1	2	1	50.00		
		Hygrobiiidae	1	5	1	20.00		
		Dytiscidae	184	4,000	453	11.33		
		Polyphaga	Hydrophiloidea	Hydrophilidae	200	3,400	302	8.88
				Sphaeritidae	1	5	0	0.00
Synteliidae	1			7	0	0.00		
Histeridae	350			4,300	65	1.51		
Staphylinoidea	Hydraenidae		42	1,600	86	5.38		
	Ptiliidae		80	650	69	10.62		
	Agyrtidae		8	70	4	5.71		
	Leiodidae		342	3,700	209	5.65		
	Silphidae		15	200	77	38.50		
	Staphylinidae		3,500	56,000	2,078	3.71		
Scarabaeoidea	Pleocomidae		2	50	0	0.00		
	Geotrupidae		70	920	35	3.80		
	Belohinidae		1	1	0	0.00		
	Passalidae		64	800	1	0.13		
	Trogidae	5	300	14	4.67			

Table 11.1 (Continued)

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage
		Glaresidae	1	60	5	8.33
		Diphyllostomatidae	1	3	0	0.00
		Lucanidae	115	1,500	117	7.80
		Ochodaeidae	15	110	6	5.45
		Hybosoridae	74	570	5	0.87
		Glaphyridae	10	205	1	0.49
		Scarabaeidae	1,900	27,000	1,036	3.84
	Scirtoidea	Decliniidae	1	2	0	0.00
		Eucinetidae	11	53	7	13.21
		Clambidae	6	170	13	7.65
		Scirtidae	35	800	54	6.75
	Dascilloidea	Dascillidae	15	80	1	1.25
		Rhipiceridae	7	70	1	1.43
	Buprestoidea	Buprestidae*	470	14,700	268	1.82
	Byrrhoidea	Byrrhidae	38	430	33	7.67
		Elmidae	149	1,500	66	4.40
		Dryopidae	33	300	7	2.33
		Lutrochidae	1	11	0	0.00
		Limnichidae	37	390	3	0.77
		Heteroceridae	15	300	30	10.00
		Psephenidae	35	290	7	2.41
		Cneoglossidae	1	10	0	0.00
		Ptilodactylidae	34	500	10	2.00
		Podabrocephalidae	1	1	0	0.00
		Chelonariidae	3	250	0	0.00
		Eulichadidae	2	30	0	0.00
		Callirhipidae	9	150	0	0.00
	Elateroidea	Rhinorhipidae	1	1	0	0.00
		Artematopodidae	8	45	8	17.78
		Brachypsectridae	1	5	0	0.00
		Cerophytidae	3	21	1	4.76
		Eucnemidae	200	1,500	29	1.93
		Throscidae	5	150	27	18.00
		Elateridae	400	10,000	1,026	10.26
		Plastoceridae	1	2	0	0.00

(Continued)

Table 11.1 (Continued)

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage
		Drilidae	6	120	3	2.50
		Omalisidae	3	8	1	12.50
		Lycidae	160	4,600	50	1.09
		Telegeusidae	3	10	0	0.00
		Phengodidae	31	250	12	4.80
		Rhagophthalmidae	6	30	0	0.00
		Lampyridae	110	2,200	100	4.55
		Omethidae	8	33	0	0.00
		Cantharidae	160	5,100	201	3.94
	Derodontoidea	Derodontidae	4	30	12	40.00
		Nosodendridae	1	50	1	2.00
		Jacobsoniidae	3	20	0	0.00
	Bostrichoidea	Dermeestidae	50	1,200	44	3.67
		Endecatomiidae	1	4	0	0.00
		Bostrichidae	90	570	33	5.79
		Ptinidae	230	2,200	107	4.86
	Lymexyloidea	Lymexylidae	10	70	3	4.29
	Cleroidea	Phloiophilidae	1	1	1	100.00
		Trogossitidae	50	600	23	3.83
		Chaetosomatidae	4	12	0	0.00
		Metaxinidae	1	1	0	0.00
		Thanerocleridae	7	30	1	3.33
		Cleridae	200	3,400	64	1.88
		Acanthocnemidae	1	1	0	0.00
		Phycosecidae	1	4	0	0.00
		Prionoceridae	3	160	0	0.00
		Mauroniscidae	5	26	0	0.00
		Melyridae	300	6,000	142	2.37
	Cucujoidea	Boganiidae	5	11	0	0.00
		Byturidae	7	24	3	12.50
		Helotidae	5	107	0	0.00
		Protocucujidae	1	7	1	14.29
		Sphindidae	9	59	9	15.25
		Biphylidae	7	200	2	1.00
		Erotylidae	260	3,500	39	1.11

Table 11.1 (Continued)

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage
		Monotomidae	33	250	29	11.60
		Hobartiidae	2	6	1	16.67
		Cryptophagidae	60	600	111	18.50
		Agapythidae	1	1	1	100.00
		Priasilphidae	3	11	0	0.00
		Phloeostichidae	5	14	1	7.14
		Silvanidae	58	500	15	3.00
		Cucujidae	4	44	8	18.18
		Myraboliidae	1	13	0	0.00
		Cavognathidae	1	9	0	0.00
		Lamingtoniidae	1	3	0	0.00
		Passandridae	9	109	0	0.00
		Phalacridae	51	640	31	4.84
		Propalticidae	2	30	0	0.00
		Laemophloeidae	37	430	25	5.81
		Tasmosalpingidae	1	2	0	0.00
		Cyclaxyridae	1	2	0	0.00
		Kateretidae	14	95	15	15.79
		Nitidulidae	350	4,500	211	4.69
		Smicripidae	1	6	0	0.00
		Bothrideridae	38	400	3	0.75
		Cerylonidae	52	450	7	1.56
		Alexiidae	1	50	2	4.00
		Discolomatidae	16	400	0	0.00
		Endomychidae	130	1,800	13	0.72
		Coccinellidae	360	6,000	306	5.10
		Corylophidae	30	200	23	11.50
		Akalyptoischiidae	1	24	0	0.00
		Latridiidae	28	1,000	108	10.80
	Tenebrionoidea	Mycetophagidae	18	130	27	20.77
		Archeocrypticidae	10	60	0	0.00
		Pterogeniidae	7	26	0	0.00
		Ciidae	42	650	105	16.15
		Tetratomidae	13	150	12	8.00

(Continued)

Table 11.1 (Continued)

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage
		Melandryidae	60	420	63	15.00
		Mordellidae	100	1,500	130	8.67
		Ripiphoridae	38	400	4	1.00
		Zopheridae	190	1,700	74	4.35
		Ulodidae	14	30	1	3.33
		Promecheilidae	7	20	1	5.00
		Chalcodryidae	3	15	0	0.00
		Trachelostenidae	1	2	0	0.00
		Tenebrionidae	2,300	20,000	499	2.50
		Prostomidae	2	30	1	3.33
		Synchroidae	3	8	2	25.00
		Stenotrachelidae	7	19	6	31.58
		Oedemeridae	100	500	35	7.00
		Meloidae	120	3,000	80	2.67
		Mycteridae	29	160	2	1.25
		Boridae	3	4	2	50.00
		Trictenotomidae	2	13	0	0.00
		Pythidae	7	23	9	39.13
		Pyrochroidae	30	167	17	10.18
		Salpingidae	45	300	18	6.00
		Anthicidae	100	3,000	75	2.50
		Aderidae	50	900	4	0.44
		Scraptiidae	35	500	66	13.20
	Chrysomeloidea	Oxypeltidae	2	3	0	0.00
		Vesperidae	17	75	0	0.00
		Disteniidae	32	336	0	0.00
		Cerambycidae	5,232	30,079	703	2.34
		Megalopodidae	30	350	6	1.71
		Orsodacnidae	3	40	2	5.00
		Chrysomelidae	2,114	32,500	1,018	3.13
	Curculionoidea	Nemonychidae	20	70	12	17.14
		Anthribidae	372	3,900	50	1.28
		Belidae	38	375	4	1.07
		Caridae	4	6	1	16.67
		Attelabidae	150	2,500	54	2.16

Table 11.1 (Continued)

Suborder	Superfamily	Family	World genera	World species	World BINs**	World percentage coverage
		Brentidae	400	4,000	207	5.18
		Curculionidae [†]	4,600	51,000	2,430	4.76
Total			29,595	386,755	15,417	3.99

Family classification is based on Bouchard et al. (2011) (except where footnoted), with generic and species numbers from Ślipiński et al. (2011). Alternative classifications to Bouchard et al. (2011) and new additions at the rank of family are highlighted in the text (in the section “Overview of Extant Taxa”).

**Numbers of DNA barcoding index numbers (BINs) for each family are from the Barcode of Life Data System (BOLD: <http://www.boldsystems.org>) and are used to calculate the percent barcoding coverage by species. Based on data downloaded December, 2014.

*Includes Schizopodidae.

†Includes Dryophthoridae and Brachyceridae.

but also because they can be compared to lists generated at other periods to monitor changes over time (Howden and Howden 2001). Analysis of changes in species composition allows us to better understand human effects on ecosystems and provides evidence to guide land use and conservation decisions.

To explain the great diversity of beetles is difficult. One of the most important factors proposed was the development of the forewings into sclerotized elytra (Lawrence and Britton 1994). In most beetles, the elytra cover the membranous flight wings and the abdomen. In this way, the elytra are thought to protect beetles against environmental stresses and predation (Hammond 1979). In addition, the close historical association of some of the most diverse groups of beetles, such as weevils (Curculionoidea), longhorn beetles (Cerambycidae), and leaf beetles (Chrysomelidae), with flowering plants during their own period of diversification is thought to be one of the main reasons explaining the beetles' great diversification (Farrell 1998, Barraclough et al. 1998, McKenna et al. 2015a), but also see McKenna et al. (2015b).

Patterns of beetle diversity can illustrate factors that have led to the success of the group as a whole. Based on estimates for all 176 families (Table 11.1), more than 386,000 species of

extant beetles have been described and are considered valid. Most species (60%) are in six megadiverse families (Fig. 11.1), each with at least 20,000 described species (in decreasing order): Staphylinidae, Curculionidae, Carabidae, Chrysomelidae, Cerambycidae, and Scarabaeidae. The smaller families of Coleoptera account for 27% of the total species in the group, and include 139 families with one to 999 described species and 28 families with 1000 to 6000 described species. So, the success of beetles as a whole is driven not only by several extremely diverse lineages, but also by a high number of moderately diverse lineages. The patterns seen today indicate that beetles went through a massive adaptive radiation early in their evolutionary history, with many of the resulting lineages flourishing through hundreds of millions of years to the present. The adaptive radiation of angiosperms may have helped to drive the diversification of beetles, as four of the six megadiverse families of beetles are primarily angiosperm feeders (Curculionidae, Chrysomelidae, Scarabaeidae, and Cerambycidae). However, even non-phytophagous lineages of predators, scavengers, detritivores, and fungivores are also tremendously diverse.

Beetles occur in most terrestrial and freshwater habitats (Lawrence and Britton 1994),

and a few occupy marine environments (Doyen 1976, Moore and Legner 1976). Their body length ranges from 0.3–0.4 mm (Sörensson 1997, Polilov 2008, Grebennikov 2009) to more than 17 cm. Larvae of large beetles can weigh more than 140 g, and they are the heaviest insects known (Acorn 2006). The most common life-cycle type in beetles is holometaboly, whereby individuals emerge from eggs as larvae, develop through several instars, pupate, and eventually emerge as adults. Sexual reproduction is predominant, although parthenogenesis (i.e., production of viable, unfertilized eggs) also occurs. More specialized or unusual life cycles, which include the occurrence of active and inactive larval instars in parasitoid species, also are known in Coleoptera (Lawrence and Britton 1994).

Perhaps most people do not recognize that we live in the “age of beetles,” in which beetles are the most diverse order of organisms on Earth (The Coleopterists Society 2007). Beetles are important in most natural terrestrial and freshwater ecosystems, have a great effect on agriculture and forestry, and are useful model organisms for many types of science. A better understanding of beetle biodiversity will enhance our knowledge of the world and provide many practical applications. Coverage of all aspects of beetle biodiversity that affect science and society is not possible in one chapter. We have therefore chosen to cover each major taxonomic group of beetles and provide some examples to illustrate important aspects of beetle biodiversity.

11.1 Overview of Extant Taxa

A classification of world Coleoptera was published by Bouchard et al. (2011) and is used here to present data on extant beetle diversity (Table 11.1). A brief introduction to the major beetle groups is included below, with data on significant recent knowledge advances, based on new tools and data sets. Examples of beetles from the four coleopteran suborders are included in Fig. 11.2 and overall diversity patterns in Fig. 11.1.

A thorough review of the diversity, distribution, biology, and relationships of each extant beetle family was published in three recent authoritative books (Beutel and Leschen 2005a, Leschen et al. 2010, Leschen and Beutel 2014).

11.1.1 Suborders Archostemata and Myxophaga

The suborder Archostemata includes about 40 species of small to medium-sized beetles in five families (Ommatidae, Crowsoniellidae,

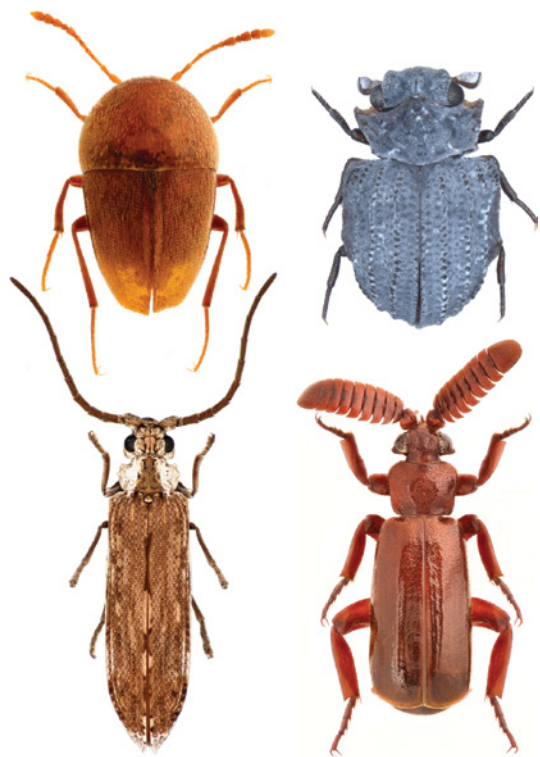


Figure 11.1 Examples of lesser-known representatives of the four suborders of Coleoptera (clockwise from top left): *Ptomaphagus hirtus* (Tellkamp) (Polyphaga) is found only in caves in Kentucky, USA; *Lepicerus inaequalis* Motschulsky (Myxophaga) lives in moist sand from Mexico to Venezuela; *Arthropterus wilsoni* (Westwood) (Adephaga) is associated with ants under bark and logs in southeastern Australia; and *Rhipsideigma raffrayi* (Fairmaire) (Archostemata) is found in rotten logs in the drier forests of Madagascar. (See color plate section for the color representation of this figure.)

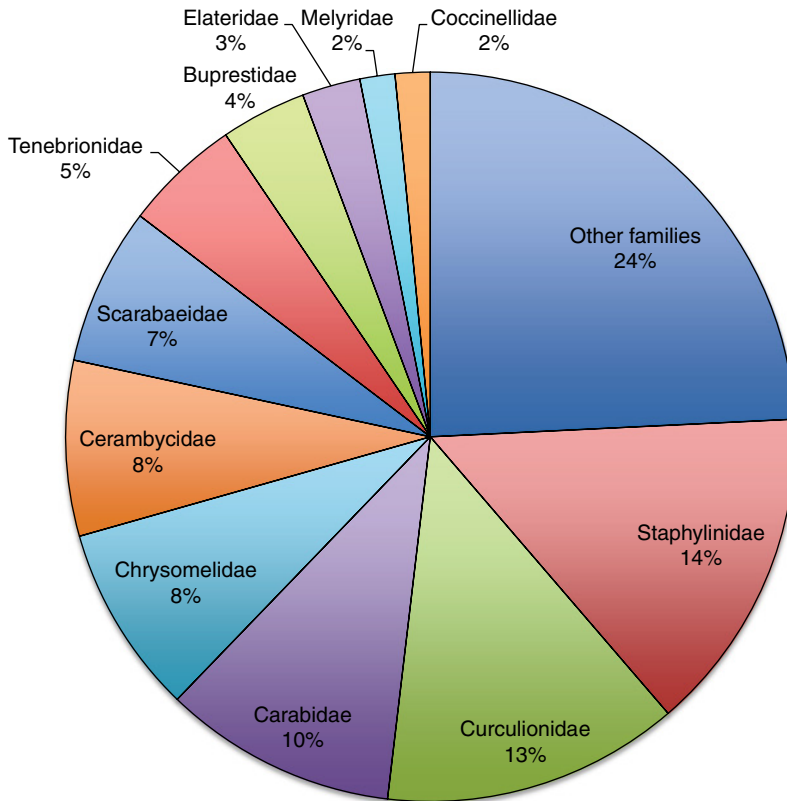


Figure 11.2 Diversity of Coleoptera families (from Table 11.1). The 11 largest beetle families (each with 6000 or more described species) are shown. The remaining 154 families (each with fewer than 6000 described species) are combined into “other families,” together representing 24% of the diversity.

Micromalthidae, Cupedidae, and Jurodidae). Hörnschemeyer (2005) provides a review of the morphology and biology of the families of Archostemata, from which most of the following is taken. Most larvae develop in fungus-infested wood, and the mouthparts of adults suggest that most species feed on plant pollen or sap, although the bionomics of members of two families (Crowsoniellidae and Jurodidae) are unknown. Ommatidae, which occur in Australia and southern South America, are thought to develop on subterranean dead wood. Cupedidae, with 31 species, comprise the largest and most widely distributed family, occurring on all continents except Europe and Antarctica; they generally feed on fungus-infested wood as larvae. The family Micromalthidae includes one species that has

been collected in many places throughout the world, but seems to be native to North America. The Crowsoniellidae are still known only from the original three specimens collected from soil beneath a chestnut tree in Italy, and extant Jurodidae are known only from a single specimen collected in the Far East of Russia. This is an unfortunate situation, as these two families are among the most enigmatic beetles, and fresh, DNA-quality specimens could shed light on early beetle evolution.

Myxophagans are small beetles (most less than 2.5 mm) that feed on algae or blue-green algae in freshwater and riparian habitats (Jäch 1998, Beutel 2005). The four myxophagan families include approximately 100 species worldwide. The family Torridincolidae, the largest in the

suborder with 60 species, is exceptional in occurring almost exclusively in fast-flowing streams, spray zones of waterfalls, or hygropetric habitats (Beutel and Vanin 2005). The Hydropsaphidae occur in many aquatic habitats, including hygropetric habitats and hot springs (Maier et al. 2010, Short et al. 2015). The Sphaeriusidae are more terrestrial than the previous families, but are usually found in close proximity to aquatic habitats (Beutel and Arce-Pérez 2005). The first possible larva of the poorest-known family, Lepiceridae, was only recently described from wet leaves and flood debris along the banks of a stream in Panama (Lawrence et al. 2013); adults occur in a similar habitat.

Direct effects of these two suborders on humans are minor. Examples of these include the rottenwood-feeding *Micromalthus debilis* (“telephone-pole beetle,” sole member of Micromalthidae), which was probably transported around the world via the timber trade (Philips 2001), and members of the family Cupedidae that live in structural timber (Neboiss 1968, 1984).

11.1.2 Suborder Adephaga

The Adephaga include more than 40,000 species (Ball and Bousquet 2000, Beutel and Ribera 2005). Phylogenetic evidence supports the division of this suborder into two clades, the terrestrial Geadephaga (containing one large family, the Carabidae) and the predominantly aquatic Hydradephaga (Maddison et al. 2009, McKenna et al. 2015a). Traditionally, the Geadephaga were divided into the three families, the Carabidae, Trachypachidae, and Rhysodidae (Table 11.1), but recent evidence from molecular data suggests that the latter two families are derived members of the Carabidae. Although numerous studies have used morphological and molecular data to infer the phylogeny of the Carabidae (Maddison et al. 1999, Ribera et al. 2005), relationships among the major lineages still remain largely unresolved. Molecular data have begun to clarify relationships among the eight hydradephagan families (Ribera et al. 2002, Balke et al. 2005, McKenna et al. 2015a), and relationships within the largest family,

the Dytiscidae, have been well studied (Ribera et al. 2008, Miller and Bergsten 2014). Two hydradephagan families, the Aspidytidae and Meruidae, were described from recently discovered beetles (Ribera et al. 2002, Spangler and Steiner 2005, respectively), highlighting the need for continued collecting (Beutel et al. 2006).

The Carabidae, commonly referred to as “ground beetles,” represent the most diverse family of Adephaga, with an estimated 40,000 known species (Erwin 1991). Most carabids are carnivores as larvae and adults, although several lineages are herbivores (e.g., Zabrinini and Harpalini), parasitoids (e.g., Brachinini and Lebiini), and specialists on myxomycetes (e.g., Rhysodinae) (Arndt et al. 2005). Among carnivorous carabids, some have evolved specialized diets, such as feeding on snails (Cychrini), millipedes (*Promecognathus*), and ants (many Paussinae). Numerous groups have evolved to occupy unique habitats, including caves (e.g., *Rhadine*, *Miquihuana*, *Dalyat*, and many Trechini), endogean habitats (Anillini), and ant nests (Pseudomorphini and many Paussinae).

Ground beetles are the most important adephagans in terms of anthropogenic interactions. A good understanding of species-level taxonomy, especially in northern temperate regions (Lindroth 1961–1969, 1974, 1985–1986), allows scientists to use species in this diverse group as tools to address many ecological and evolutionary questions. Studies of ground beetles have enhanced our understanding of the ecological effects of agricultural practices (Varchola and Dunn 1999, Freuler et al. 2001, Duan et al. 2006), forestry practices (Niemela et al. 1993, Magura et al. 2003), habitat fragmentation (Magagula 2003), fire management of natural habitats (Larsen and Work 2003), pollution (Freitag 1979), and other human activities. Ground beetles are also important for research on habitat conservation (Bouchard et al. 2006) and biogeography (Darlington 1943, Marshall and Liebherr 2000).

Because of their predatory habits, many carabid species are recognized as beneficial natural enemies of pestiferous insects (Lövei and Sunderland 1996, Kromp 1999). One of the

most famous uses of carabids in biocontrol is the introduction of the European *Calosoma sycophanta* into North America to help control invasive gypsy moths. Humans also have taken advantage of the toxic nature of some carabids. The Bushmen (San people) who inhabit the Kalahari apply secretions from larvae of *Lebistina* spp. to their arrow tips (Koch 1958) to increase their lethality.

Of the eight hydradephagan families, the Dytiscidae is by far the most species rich, with approximately 4000 described species. The rest of the families are much less diverse, with four families containing fewer than 10 species (Aspidytidae, Meruidae, Amphizoidae, and Hygrobiidae). Hydradephagans are predominantly associated with various freshwater habitats, although a few species of dytiscids are known from halobiontic environments such as saline lakes and estuaries (Balke 2005). Highly specialized groups inhabiting groundwater in aquifers have evolved in the Noteridae (*Phreatodytes*) and Dytiscidae (numerous genera of Hydroporinae and one species of Copelatinae). Stygobionts are known from every continent except Antarctica. The Australian fauna, which contains the highest species diversity, is remarkable in that it was completely unknown until the late 1990s (Watts and Humphreys 1999). Some dytiscids have lost the ability to swim and are restricted to deep, wet leaf litter in montane forests (Brancucci 1979, Brancucci and Monteith 1996). Most hydradephagans are predators or scavengers, although some species supplement their diet with plant material.

Hydradephagans have played a smaller role in human society than have the Carabidae. Adult mosquitoes often are infected with various human disease agents, and dytiscids can help to control these disease vectors at the larval stage (Dubitskii et al. 1975, Lopez et al. 1997, Bellini et al. 2000, Lundkvist et al. 2003). An unusual traditional practice using adephagan water beetles recently was reported from East Africa. There, young girls collect water beetles (Gyrinidae and Dytiscidae) and hold them to their nipples to stimulate a biting reflex from these beetles. The biting and the simultaneous

release of defensive secretions are locally believed to stimulate breast growth (Kutalek and Kassa 2005). Larger adult and larval dytiscids are also used as a source of food in numerous cultures (Ramos-Elorduy et al. 2009).

11.1.3 Suborder Polyphaga

11.1.3.1 Series Staphyliniformia

This series includes the superfamilies Hydrophiloidea *sensu lato* (Hydrophiloidea together with Histeroidea) and Staphylinioidea. Phylogenetic evidence is mounting that the superfamily Scarabaeoidea also should be included in this series (Hansen 1997, Beutel and Komarek 2004, Korte et al. 2004, Beutel and Leschen 2005b, Caterino et al. 2005, Hughes et al. 2006, McKenna et al. 2015a). However, it remains unclear whether the Scarabaeoidea are sister to the entire Staphyliniformia or derived within as sister to the Hydrophiloidea *sensu lato* (McKenna et al. 2015a, 2015b). We treat the Scarabaeiformia as a separate series to follow current classification schemes. The total number of described species of Staphyliniformia is about 90,000, or roughly a quarter of all beetles and considerably more than all Vertebrata combined. Unlike the high diversity of the Curculionoidea, which have co-diversified with angiosperm plants (McKenna et al. 2009), the high diversity of the Staphyliniformia seems to be a result of their repeated invasion of novel ecological niches from a generalized leaf litter-dwelling lifestyle (McKenna et al. 2015b).

The superfamily Hydrophiloidea unites the Hydrophilidae *sensu lato* (Helophorinae, Epimetopinae, Georissinae, Hydrochinae, and Spercheinae are here treated as subfamilies) with the histerid group of families: Histeridae, Sphaeritidae, and Synteliidae (Archangelsky et al. 2005). The Sphaeritidae and Synteliidae include fewer than 20 species each. These families are associated with decaying organic matter, and each includes one genus distributed in North America and Eurasia. The Histeridae (350 genera and 4300 species) and Hydrophilidae (200 genera and 3400 species) are two large, cosmopolitan

families that are most diverse in the tropics (Beutel and Leschen 2005a).

Hansen's (1991) work on hydrophiloid beetles, which includes taxonomic treatments down to the genus level, remains a good introduction to the family Hydrophilidae. A recent phylogeny and reclassification of the Hydrophilidae *sensu stricto* by Short and Fikáček (2013) features an identification key and ecological summaries of the higher taxa, and is a modern companion to the work by Hansen (1991). These beetles are primarily aquatic, occurring in a diversity of water-based microhabitats, including those associated with waterfalls and water-holding plants (Short and Fikáček 2013). Confirmed or suspected transitions to an entirely terrestrial lifestyle in leaf litter, decaying organic matter, flowers, moss, and dung are reported for most subfamilies, although the majority of terrestrial hydrophilids belong to the Sphaeridiinae (Short and Fikáček 2013). Adults are poor swimmers and normally crawl underwater, feeding mainly on plant material. Larger species prey on similar-sized organisms. Some hydrophilids are myrmecophilous, but this is far less widespread than in other beetle families (Parker 2016). Eggs are normally stored in variably shaped silk cases, which have a mast and can float; females of some Acidocerinae, Epimetopinae, and Spercheinae carry egg cases attached to their abdomens (Archangelsky et al. 2005). Larvae of most Hydrophilidae are aquatic, go through three instars, and are predators; pupation, however, takes place in moist soil (Archangelsky et al. 2005). Davis (1994) considered South African dung-inhabiting Hydrophilidae as potential biocontrol agents to be introduced against dung-breeding flies in Australia, based on their association with herbivore dung.

Unlike the Hydrophilidae, the Histeridae are strictly terrestrial and predatory in the adult stage, with only two larval instars (Kovarik and Caterino 2005). Fly maggots in dung, carcasses, or rotten vegetation are their most common prey. Adults of some species catch flies by hiding in crevasses in dung and seizing them with their mouthparts (Kovarik and Caterino 2005). Close

associations with social insects have evolved in most of the 12 histerid subfamilies, and two of these, the Hetaeriinae and Chlamydopsinae, are predominately myrmecophilous or termitophilous, with unusual morphology and strong host dependency and integration (Caterino and Dégallier 2007, Parker 2016). The chapter on Histeridae by Kovarik and Caterino (2005) is a good introduction to the systematics, distribution, and biology of the family. The Histeridae were used repeatedly as control agents against house flies (*Musca domestica*) (Kaufman et al. 2000) and other flies with dung-inhabiting larvae (Davis 1994). *Teretrius nigrescens*, a histerid beetle, was released as a biocontrol agent against the bostrichid beetle *Prostephanus truncatus* to protect maize stores in equatorial Africa, although success was only moderate (Holst and Meikle 2003).

The superfamily Staphylinoidea currently includes six families, and new morphological (Lawrence et al. 2011) and molecular (McKenna et al. 2015a) phylogenetic evidence suggests that the small family Jacobsoniidae (see Bostrichiformia) also might belong here. The Hydraenidae are consistently recovered as the sister group to the Ptiliidae, as is the Agyrtidae to Leiodidae, using diverse types of phylogenetic data (Beutel and Leschen 2005b; McKenna et al. 2015a, 2015b). The Scydmaeninae and Silphidae have been shown to be derived from within the large family Staphylinidae (Ballard et al. 1998; Grebennikov and Newton 2009; Bocák et al. 2014; McKenna 2015a, 2015b), although the latter is still classified as a separate family. A consensus on the relationships between these higher clades has not yet been achieved (McKenna et al. 2015a).

Five of these staphylinoid families are nearly worldwide in distribution, whereas the Agyrtidae are known only from northern temperate areas, except for one genus in New Zealand (Newton 1997). The family Hydraenidae comprises some 1600 described detritus-feeding species in 42 genera; however, true species richness is probably higher (Jäch et al. 2005). Most hydraenid species occur in freshwater habitats; some are terrestrial and either riparian or associated with wet leaf litter.

Their sister group, the Ptiliidae (featherwing beetles), are strictly terrestrial and mycophagous and include more than 650 described species in about 80 genera (Hall 2005). The Ptiliidae include the smallest known beetles, with most species less than 1.0 mm long (Sörensson 1997). The ptiliid *Scydosella musawasensis* is the smallest free-living insect, at a length of just 0.325 mm (Polilov 2015). Other remarkable features of some Ptiliidae include polymorphism in wing and eye development, association with social insects, obligate parthenogenesis, large egg size (approximately 50% of female body volume), and giant sperm (Hall 2005). The Agyrtidae represent a small family with about 70 species in eight genera that feed on decayed organic matter (Newton 1997). Their sister group, the Leiodidae, is a larger family with about 3700 species in about 342 genera (Newton 2005). Their food and habitat requirements vary, although most inhabit forests and feed on decaying organic matter or slime molds. Leiodids exhibit the only known case of true parasitism by beetles: *Platypsyllus castori* on beavers (Peck 2006). Some species of the cave-dwelling genera *Speonomus* and *Leptodirus* have unusual larval development with only one, non-feeding larval instar (Deleurance-Glaçon 1963). Several genera are closely associated with colonies of ants, termites, or stingless bees (Newton 2005). Newton's (1998, 2005) works on the Leiodidae are good introductions to the diversity of this family. The influence of the Agyrtidae, Hydraenidae, Leiodidae, and Ptiliidae on humans is unclear, although they might be important decomposers of organic matter in natural and agricultural ecosystems.

The Silphidae, also known as the large carrion beetles, include 200 species in 15 genera (Table 11.1), most of which are efficient decomposers of carrion, although some are predaceous or phytophagous (Sikes 2005). Species in the genus *Nicrophorus* (burying beetles) bury and actively guard small carrion to feed their larvae, with which they communicate via stridulation (Scott 1998). This system represents the most complex and well-studied instance of biparental care in Staphyliniformia (in the pre-

sent sense) and might be nearly 100 million years old (Cai et al. 2014).

The Staphylinidae, or rove beetles, include more than 56,000 described species in 3500 genera across 31 subfamilies, and rival the weevils (Curculionidae) in diversity. However, within Coleoptera, rove beetles are unrivaled in morphological, trophic, and ecological diversity. The Staphylinidae are predominantly predaceous, with widespread instances of mycophagy and saprophagy for entire subfamilies (Thayer 2005). Several groups are pollen feeders, algal grazers, or parasitoids, and the genus *Himalusa* even feeds on the tissues of higher plants (Klimaszewski et al. 2010). Predaceous staphylinids have evolved complex rapid prey-capture devices, including a protrusible labium (Betz 1998) and raptorial forelegs (Betz and Mumm 2001). Subsocial behavior in the form of larval provisioning and guarding occurs in multiple subfamilies (Ashe 1986, Wyatt 1986, Hanley and Goodrich 1995). Obligate associations with social insects have evolved more often in the Staphylinidae than in any other family of Coleoptera and the result is a remarkable array of morphological, chemical, and behavioral diversity, particularly in the subfamilies Aleocharinae and Pselaphinae (Parker 2016). A glowing larval staphylinid from Brazil might represent the only observation of bioluminescence in beetles outside the Elateriformia (Rosa 2010). Rove beetles are among the most commonly encountered beetles in nature, particularly in moist terrestrial habitats, and serve as indicators of human impact on natural ecosystems (Work et al. 2013). As predators, some control plant pests and nuisance arthropods, including flies (Hu and Frank 1995) and mites (Kishimoto and Adachi 2008). As larval parasitoids and adult predators of cyclorrhaphous flies, members of the genus *Aleochara* are especially well known for their biocontrol applications (Hemachandra et al. 2007). The chapter by Thayer (2005) is a thorough introduction to rove-beetle literature.

11.1.3.2 Series Scarabaeiformia

The series Scarabaeiformia, as currently classified, consists of 12 families (Pleocomidae,

Geotrupidae, Belohinidae, Passalidae, Trogidae, Glaresidae, Diphylostomatidae, Lucanidae, Ochodaeidae, Hybosoridae, Glaphyridae, and Scarabaeidae), 49 subfamilies, and 120 tribes (Smith 2006, Bouchard et al. 2011). Estimates of the number of described species in this group range from 31,000 to 35,000 (Jameson and Ratcliffe 2002, Scholtz and Grebennikov 2005). Gaston (1991) gave a conservative estimate that the actual number of species might be around 50,000 species. Scarab beetles are terrestrial, most with larvae inhabiting soil, detritus, or decaying wood. Scarab species can be found in most terrestrial habitats worldwide and are most diverse in tropical forests.

Several phylogenetic analyses for taxa in the series Scarabaeiformia have been published, based on morphological characters (Howden 1982, Browne and Scholtz 1995, Browne and Scholtz 1998, Browne and Scholtz 1999, Grebennikov and Scholtz 2004), and a preliminary phylogenetic analysis based on molecular characters is also available (Smith et al. 2006, Ahrens et al. 2014, McKenna et al. 2015b). The 12 families are well defined, but phylogenetic evidence for the relationships among many of these is weak or contradictory among studies. The Scarabaeidae are by far the most diverse family, containing an estimated 91% of the described species of the Scarabaeiformia (Ratcliffe et al. 2002). Two major clades occur in the family Scarabaeidae, the dung-beetle clade and the highly diverse phytophagous scarab clade (Smith et al. 2006, Tarasov and Génier 2015). Members of the phytophagous scarab clade primarily feed on angiosperm plant foliage, flowers, nectar, pollen, or fruit during their adult stage and roots, humus, detritus, or dead wood as larvae. The dung-beetle clade, in their shift to dung feeding, show the second most successful trophic adaptation in the evolution of scarab beetles, after angiosperm plant feeding, when looking at total biodiversity in the group (Smith et al. 2006, Ahrens et al. 2014, Tarasov and Génier 2015). Among the other major scarab lineages are the primarily dead-wood feeders (Lucanidae and Passalidae), carcass

feeders (Trogidae), fungivores (Geotrupidae), and detritivores (Hybosoridae).

Scarab beetles often have been used as a focal taxon for evolution, biodiversity, and conservation research. Dung beetles, in particular, have been used in ecological and biodiversity studies (Spector 2006). Dung beetles have been used to compare habitats (Nummelin and Hanski 1989, Jankielsohn et al. 2001, Estrada and Coates-Estrada 2002), to study diversity across landscapes and continents (Lobo and Davis 1999, Arellano and Halffter 2003, Lobo et al. 2006), as indicator taxa of ecosystem health (Halffter and Arellano 2002, Davis et al. 2004, Quintero and Roslin 2005, Scheffler 2005), and for many other purposes.

Scarab beetles are an extremely diverse, ubiquitous, and widely distributed group and, as such, affect humans. Hundreds of species of scarab beetles are nectar feeders and pollinators of diverse plant species. The benefits of dung removal and burial by dung beetles worldwide are well documented from the perspective of pastureland productivity, nutrient recycling, and health (Edwards and Aschenborn 1987, Mittal 1993, Tyndale-Biscoe 1994). In addition, dead-wood feeding and detritivorous scarabs have a major role in nutrient and carbon cycling; burrowing scarabs play a significant part in seed burial and germination for some plant species (Vulinec 2002, Chapman and Chapman 2003), and scarabs are a major food source for many predators. Many phytophagous species are pests of turfgrass, ornamental plants, and agriculture. Numerous invasive species damage plants and ecosystems (Potter and Held 2002, Jackson and Klein 2006) and might outcompete native species. Some scarab species cause human health problems as carriers of disease agents (Graczyk et al. 2005).

11.1.3.3 Series Elateriformia

This group of beetles contains four superfamilies (Dascilloidea, Buprestoidea, Byrrhoidea, and Elateroidea), 33 extant and two extinct families (Ślipiński et al. 2011), and at least 43,000 species (Table 11.1). Of these, about 30,000 species belong to the three largest families, the

Buprestidae, Elateridae, and Cantharidae. Elateriform beetles are found throughout the world and are most diverse in tropical regions. Chapters on Elateriformia in Beutel and Leschen (2005a), and Leschen et al. (2010) are good introductions to the classification and biology of the series and its superfamilies.

A recent DNA-based phylogenetic study (McKenna et al. 2015a) found a polyphyletic Elateriformia with weak support, including Nosodendridae but not Scirtoidea. In that study, the Dascilloidea, Byrrhoidea, and Elateroidea were monophyletic with weak support, and Buprestoidea was recovered as monophyletic with strong support. Kundera and Bocák (2011) found that Drilidae should be reduced to a tribe of Agrypninae in Elateridae. Kundera et al. (2014) confirmed the monophyly of Elateroidea; found new interrelationships between elateroid subfamilies; confirmed multiple origins of soft-bodiedness, neoteny, and bioluminescence; and reduced Telegeusidae to a subfamily of Omalidae. Kundera et al. (2016) altered the subfamily level classification of Elateridae. Douglas (2011) tested relationships in the Elateridae, using adult morphology, and attempted to homologize morphological characters for the family. The DNA-based phylogeny of Buprestoidea by Evans et al. (2014) supported the monophyly of the Buprestoidea and of its families, with multiple origins of larval leaf-mining behavior.

Although the major known economic effects of elateriform beetles are negative (e.g., Buprestidae as forest pests and Elateridae as agricultural pests), some are beneficial. Among these, several elaterids have been introduced for biological control (of Scarabaeidae: Bianchi 1937, Clausen 1978), and Elateridae have long been known as beneficial predators of wood-boring beetles (Craighead, 1950) and defoliators (Tostowaryk 1971). Many other predaceous larval and adult Elateridae, Cantharidae, and Lampyridae are expected to attack below-ground pests and terrestrial mollusks. Similarly, the role of elateroids and buprestoids as pollinators is probably undervalued (but see Peter and Johnson 2005).

Elateriform beetles could be good candidates for evolutionary and ecological research. Their diverse natural history includes seven apparent independent colonizations of aquatic habitats (Lawrence 1987). They have a wider diversity of larval feeding habits than for any other series. These include feeding on dry (e.g., Buprestidae) or submerged (e.g., Elmidae) dead wood, herbivory (including leaf mining and stem boring, e.g., Buprestidae, and moss feeding, e.g., Byrrhidae), fungivory (e.g., Elateridae, Luterek 1966), carnivory (as predators of invertebrates such as termites (Costa et al. 1992) and of vertebrates, such as sea turtle egg consumption by Elateridae (Donlan et al. 2004)), and ectoparasitoidism (e.g., of cicadas by Rhipiceridae). Their value to evolutionary and ecological research also includes their role as primary pollinators for at least one plant species (Peter and Johnson 2005), chemical defenses, mimicry, and multiple evolutionary origins of bioluminescence (Branham and Wenzel 2003, Sageami-Oba et al. 2007).

11.1.3.4 Series Derodontiformia

The Derodontiformia include three small, quite different-looking families of beetles, the Derodontidae, Jacobsoniidae, and Nosodendridae, with about 100 species in total. The series was only recently recognized as such, being split from the Bostrichiformia (Lawrence et al. 2010). Despite its low diversity, the group is distributed almost worldwide. The Derodontidae include about 30 species distributed in north and south temperate regions. The Jacobsoniidae, with about 20 species, occur predominantly in tropical regions, but also in New Zealand, and the Nosodendridae, with one genus (*Nosodendron*) and about 50 species, are distributed nearly worldwide. Habits and habitats of the group are disparate, cryptic, and often unusual; the Derodontidae are either (most genera) associated with fungi or (*Laricobius*) predaceous on Adelgidae (Hemiptera). The Jacobsoniidae are associated with dead wood, leaf litter, fungi, and bat guano, and the Nosodendridae are inhabitants of slime fluxes at tree wounds. Direct influence on human beings is minimal, but species of

Laricobius have shown great promise as a biological control agent of various devastating adelgid outbreaks (Lamb et al. 2006, Leschen 2011). More information on the bionomics of these families is in the respective chapters in Leschen et al. (2010).

In the recent broad-scale molecular phylogenetic analysis of Coleoptera by McKenna et al. (2015a), each of the three families was placed in a radically different part of the tree, rendering the series grossly polyphyletic. The Derodontidae were placed with the Scirtoidea, Jacobsoniidae with Staphylinoidea, and Nosodendridae alternatively at the base of Elateriformia or sister to Dascilloidea. Therefore, the future status of this series is in serious question.

11.1.3.5 Series Bostrichiformia

The Bostrichiformia include four low- to medium-diversity families. The Endecatomiidae contain only four species, whereas the Bostrichidae, Dermestidae, and Ptinidae contain between 500 and 2200 species each. The Endecatomiidae include only the genus *Endecatomus*, which is strictly Holarctic in distribution, and feed in fruiting bodies of bracket fungi (Lawrence 2010a). The family was relatively recently elevated to family status out of the Bostrichidae (Lawrence and Newton 1995).

The Bostrichidae are a worldwide group of about 570 species. The larvae of most members of the family are wood borers and several are major pests. The grain borers (*Prostephanus* and *Rhyzopertha*), powder-post beetles (*Lyctus* and *Trogoxylon*), and bamboo powder-post beetles (*Dinoderus*) are especially important economically (Ivie 2002). One species also damages books (Hoffman 1933). The Dermestidae, with more than 1200 species, are primarily scavengers of dried animal and plant material, including some of the most important pests of animal-based products, such as woolen carpets and clothes, furs, leather, and silk, whereas others are major pests of museum specimens. In addition, some carrion-feeding dermestids are useful in forensic entomology. Some dermestids, however, have disparate life histories, *Orphilus* feeding in dry, fungus-infested wood, and

Thaumaglossa feeding on mantid eggs (Lawrence and Ślipiński 2010). The family Ptinidae (until recently known as Anobiidae), which is most diverse in tropical and subtropical habitats, is by far the most diverse in the series with more than 2200 species. The larvae of the Ptinidae can be separated into two groups. The first group of species bore into plant materials such as bark, seeds, dry wood, and galls, whereas the other group feeds on dried animal and plant detritus (Howe 1959, Philips 2002). Some species are associated with vertebrate nests, whereas others breed in dung. Economically important species include the death watch beetle (*Anobium punctatum*), which damages furniture, woodwork, book bindings, and other cellulose products (Peters and Fitzgerald 1996, Philips 2002). Other species of Ptinidae including the ubiquitous cigarette beetle (*Lasioderma serricorne*) and drug-store beetle (*Stegobium paniceum*), are pests of stored products such as food commodities, wool, and products toxic to other insects, including spices, tobacco, and drugs (Howe 1959, Bousquet 1990).

11.1.3.6 Series Cucujiformia

The series Cucujiformia, as defined by Lawrence and Newton (1995), includes six superfamilies: Cleroidea, Lymexyloidea, Cucujoidea, Tenebrionoidea, Chrysomeloidea, and Curculionioidea. An additional superfamily, Coccinelloidea, was recently defined. The superfamily Lymexyloidea is the smallest, containing only the family Lymexylidae. Recent morphological and molecular phylogenetic studies (Lawrence et al. 2011, Bocák et al. 2014, Gunter et al. 2014, McKenna et al. 2015a) suggest that Lymexylidae have affinities to or should be combined with the Tenebrionoidea. Within the family, at least 60 mostly tropical species are organized in up to 12 genera (Paulus 2004). Adults of some species transmit spores of ambrosia fungi in specialized membranous cavities on their ovipositors (Wheeler 1986). Some adults (in the subfamily Atractocerinae) are longer than 60 mm and have shortened elytra resembling those of rove beetles (Staphylinidae). Some larval Lymexylidae burrow

into wood and cultivate ambrosia fungi, which is thought to be their only larval food source. This activity causes some damage to forestry in temperate areas, and in the tropics *Promelittomma insulare* is a pest of coconut palms (Brown 1954). The ship-timber worm *Lymexylon navale* was formerly a major pest of wooden ships (Lawrence 2010b).

The superfamily Cleroidea now includes 13 families and about 10,000 species, although some authors (Majer 1994, Kolibáč 2004, Bocáková et al. 2012) advocate splitting the largest family, Melyridae, into several smaller families. Additionally, Robertson et al. (2015), based on phylogenetic results, transferred the families Byturidae and Biphyllidae from Cucujoidea to Cleroidea. Byturidae (24 species) occur in the Holarctic region, Southeast Asia, and southern South America; one genus, *Byturus* (fruitworm beetle), can be a commercial pest of *Rubus* (Rosaceae) fruits. The Biphyllidae (200 species) occur throughout the world except in New Zealand; species seem to feed on cryptic fungi under bark of dead trees and in leaf litter. Most larvae of the Cleroidea seem to be predators or scavengers, whereas the adults are primarily predators or pollen feeders. The larvae of some species pursue and attack wood-boring insects inside their tunnels, benefitting forestry. The Acanthocnemidae have one extant species, *Acanthocnemus nigricans*, which is native to Australia and is attracted to fires and recently burnt wood (Lawrence and Leschen 2010). The Chaetosomatidae include three genera (Kolibáč 2004) and about 12 species in New Zealand and Madagascar; they are predatory (Lawrence et al. 1999). The Cleridae are perhaps the most conspicuous elements of the superfamily, with about 200 genera and 3400 described species, many of them brightly colored and diurnal. Most are predatory as adults and larvae, including some (e.g., *Thanasimus* spp.) that are important in controlling outbreaks of forest pests such as bark beetles (Curculionidae: Scolytinae) (Kolibáč 2010). Mauroniscidae are a small, rarely encountered family occurring in the New World; some feed in flowers, probably on pollen, but almost nothing further is known about the bionomics of

the group, which was recognized only recently as a family apart from the Melyridae (Majer 1994). The Melyridae (*sensu lato*, including Rhadalidae, Dasytidae, and Malachiidae *sensu* Majer 1994, Majer 2002, and Bocáková et al. 2012) have about 6000 species (Bocáková et al. 2012). They are an extremely diverse group of mostly soft-bodied beetles that frequent flowering plants as adults, feeding primarily on pollen. The Metaxinidae recently were established as a separate family (Kolibáč 2004) to accommodate one predatory, sooty-mold-inhabiting species from New Zealand, *Metaxina ornata*. There is just a single species in the family Phloiophilidae, *Phloiophilus edwardsii*, which is found in Europe; the larvae feed on fungi (Lawrence et al. 1999). The Phycosecidae include only the beach-dwelling genus *Phycosecis*, with four species endemic to Australia, New Caledonia, New Hebrides, and New Zealand (Leschen and Beutel 2010). The Prionoceridae have at least three genera in the Oriental and Afrotropical regions, and are pollen feeders as adults (Lawrence et al. 1999). The Thanerocleridae, with 30 species in seven mostly tropical genera, are known from all continents except Antarctica (Kolibáč 1992, Kolibáč 2004). The heterogeneous family Trogossitidae, which contains fewer than a thousand species, is the third largest in the Cleroidea, and has a similar nearly worldwide distribution (Kolibáč 2005).

The superfamily Cucujoidea has received a major reorganization in recent years (Robertson et al. 2015). Until recently, it included about 20,000 species in about 1500 genera in 35 families (Pakaluk et al. 1994), but now it includes only 25 families with about 915 genera and 10,950 species. Major recent changes include removal of the Byturidae and Biphyllidae to the Cleroidea (Robertson et al. 2015), carving of the Coccinelloidea out of the Cucujoidea (Robertson et al. 2015), splitting of the Cybocephalidae from the Nitidulidae (Cline et al. 2014), and combination of the Propalticidae with the Laemophloeidae (McElrath et al. 2015). The newly defined Cucujoidea consist of the following families (McElrath et al. 2015, Robertson et al. 2015):

Agapythidae, Boganiidae, Cavognathidae, Cryptophagidae, Cucujidae, Cybocephalidae, Cyclaxyridae, Erotylidae, Helotidae, Hobartiidae, Kateretidae, Laemophloeidae, Lamingtoniidae, Monotomidae, Myraboliidae, Nitidulidae, Passandridae, Phalacridae, Phloeostichidae, Priasilphidae, Protocucujidae, Silvanidae, Smicripidae, Sphindidae, and Tasmosalpingidae. The most diverse family in the group is the Nitidulidae, which boast an extraordinary range of habits and habitats, including fungus feeders, leaf miners, sap feeders, carrion feeders, pollen feeders, fruit feeders, seed predators, inquilines in ant and termite nests, and even an aquatic mosquito-feeding species (Jelínek et al. 2010). One species, the small hive beetle (*Aethina tumida*), is a pest of honeybee colonies and recently spread to the United States (1998), Canada (2002), and Australia (2002) from southern Africa (Hood 2004). Closely related to the Nitidulidae are the Kateretidae and Smicripidae, which feed in flowers; the latter family is restricted to the New World. The small family Cybocephalidae are important predators of sternorrhynchous Hemiptera, especially scale insects, and have been part of biocontrol programs. The Monotomidae are often found under bark or in decaying plant material; some are mycophagous, whereas others (e.g., *Rhizophagus*) are effective predators of destructive bark beetles (Curculionidae: Scolytinae). Most Laemophloeidae occur under bark, with a few possibly being predaceous on bark beetles, and some (especially *Cryptolestes* species) being important stored-product pests. The Passandridae are ectoparasitic as larvae on wood-inhabiting beetles and Hymenoptera. The Silvanidae contain many economically important pests of stored products, including species of *Oryzaephilus*, *Nausibius*, *Cathartus*, and *Ahasverus*, but are otherwise mostly found under bark of dead trees. Most cucujoid species are of little direct relevance to human economy because they are associated with decaying vegetation and fungi. The Boganiidae are pollen feeders associated with cycads and Myrtaceae, and occur only in Australia, New Caledonia, and South Africa (Escalona et al. 2015). The Cavognathidae are unique in exclusively inhabiting

bird nests; they occur in Australia, New Zealand, and South America. The Agapythidae and Cyclaxyridae are both sooty-mold-inhabiting beetles endemic to New Zealand. Most Cryptophagidae are associated with microfungi, and occur in a wide variety of habitats worldwide. Larvae of the small but widely distributed family Cucujidae can be predaceous. The Erotylidae are a large group of often colorful forms; most feed on either fungi (especially macrofungi) or plants, although a few are cycad feeders; some are even pests of stored grain. The Hobartiidae are fungus feeders that occur only in Australia and Chile. The Lamingtoniidae, Myraboliidae, and Tasmosalpingidae are all Australian endemic families, occurring on fungi or under bark. The Phalacridae occur worldwide; some are strongly associated with smut or rust fungi, whereas others (especially *Olibrus*) develop in flower heads. The Phloeostichidae are known from Australia, southern South America, and the Palearctic region. The Priasilphidae occur in south temperate regions and feed on microfungi in forested areas. The Protocucujidae occur in Australia and southern South America, and their bionomics are obscure. The Sphindidae are distributed worldwide and feed only on slime molds. The various cucujoid family chapters in Leschen et al. (2010), from which most of the previous information was taken, serve as entry points into detailed morphological and taxonomic treatments.

The superfamily Coccinelloidea, newly erected by Robertson et al. (2015), contains the group of families previously referred to as the “Cerylonid Series” of Cucujoidea. Before Robertson et al. (2015), it contained nine families, but these were fractured into 15 families in that publication: Akalyptoischiidae, Alexiidae, Anamorphidae, Bothrideridae, Cerylonidae, Coccinellidae, Corylophidae, Discolomatidae, Endomychidae, Eupsilobiidae, Euxestidae, Latridiidae, Murmidiidae, Mycetaeidae, and Teredidae. Most of the families are relatively small, but one family, the Coccinellidae, dominates in terms of diversity, with about 6000 species in 350 genera worldwide (Ślipiński and Tomaszewska 2010). Coccinellidae have a

marked impact on human activities, with most species being predators, which can be useful for control of a variety of plant pests, mostly sternorrhynchous Hemiptera, with a few feeding on spider mites. *Harmonia axyridis*, the widely introduced multicolored Asian lady beetle, ecologically displaces native coccinellids, and is a nuisance pest entering human houses in search of hibernation places, and contaminating wine grapes (Pervez and Omkar 2006). Still other species (in the subfamily Epilachninae) are plant feeders as larvae and adults, and eat mostly squashes, beans, and nightshades, on which they can be serious pests. Most of the other families are primarily obscure, cryptic fungus or slime-mold feeders, including the recently elevated (from Latridiidae) family Akalyptoischidae (Lord et al. 2010), which occurs only in western North America; the family Alexiidae, which occurs only in the western Palearctic; the families Anamorphidae, Cerylonidae, Corylophidae, Euxestidae, and Latridiidae, each of which occur worldwide; the family Discolomatidae, which occurs pantropically; the small family Mycetidae, which has been introduced around the world and can be a pest of moldy stored products (Tomaszewska 2010); the family Murmidiidae, with a similar cosmopolitan distribution and habitat to the Mycetidae (Ślipiński and Lawrence 2010); the Bothrideridae, which include specialized parasitoids of coleopteran and hymenopteran wood-boring insects (Ślipiński et al. 2010); the Eupsilobiidae, which are poorly known, but can occur in association with ants (Tomaszewska 2010); and the Teredidae, a widely distributed group generally of fungus feeders and commensals in bark beetle tunnels (Ślipiński et al. 2010).

The superfamily Tenebrionoidea includes 28 families (Table 11.1), 19 of which are minor, each with only 5 to 500 described species (Archeocrypticidae, Boridae, Melandryidae, Mycetophagidae, Mycteridae, Promecheilidae, Prostomidae, Pterogeniidae, Pyrochroidae, Pythidae, Ripiphoridae, Salpingidae, Scaptiidae, Stenotrachelidae, Synchronidae, Tetratomidae,

Trachelostenidae, Trictenotomidae, and Ulodidae). The small family Trachelostenidae has recently been downgraded to a tribe within Tenebrionidae by Matthews and Lawrence (2015). The relationships and diversification patterns of beetles in this morphologically challenging superfamily have benefited from analyses of molecular data sets (Gunter et al. 2014; Kergoat et al. 2014a, 2014b). Typical feeding habitats include under dead tree bark or in fungi, decaying wood, and litter. Larvae of the Ripiphoridae are unusual beetle endoparasites of immature insects (bees, wasps, and cockroaches). The Mycetophagidae include minor stored-product pests (perhaps feeding on fungus-infested commodities) and a known vector of disease agents (Bousquet 1990, Hald et al. 1998). One *Hemipeplus* (Mycteridae) species is a pest of palms (Lepesme 1947, Zelazny and Pacumbaba 1982).

The families Aderidae, Anthicidae, Ciidae, Meloidae, Mordellidae, Oedemeridae, and Zopheridae are moderately diverse within the Tenebrionoidea, each with 550 to 3000 described species. A large proportion of these beetles develop in dead wood, fungi, and leaf litter and are uncommonly encountered by people (Leschen et al. 2010). *Nacertes melanura* (Oedemeridae) is a pest of wooden marine structures and archeological timber (Pitman et al. 1993, 2003). Beetles of the families Meloidae and Oedemeridae produce antipredator secretions called cantharidins that can harm humans or kill domesticated animals. A few species in the family Anthicidae prey on the eggs and small larvae of pests and are useful biological control agents (McCutcheon 2002).

By far the most diverse tenebrionoid family is the Tenebrionidae, with nearly 20,000 described species. This family is expected to include many undescribed species, especially in tropical regions. Recent studies of tropical groups have greatly increased the number of known species (Bouchard 2002). Different groups of Tenebrionidae have evolved remarkable adaptations to survive in some of the most extreme habitats in the world. The production of glycerol-like compounds in adults of *Upis ceramboides* enables their survival under

tree bark during prolonged freezing periods to -50°C (Miller 1978, Lundheim and Zachariassen 1993). Conversely, unusual morphological and behavioral adaptations in other tenebrionids enable them to survive in the hottest deserts (Cloudsley-Thompson 1964, McClain et al. 1985, Zachariassen 1991). Detailed studies of these adaptations might yield important applications for humans. Tenebrionids are a major faunal component of most deserts and have a significant role in food webs (Crawford et al. 1993). Shifts in the abundance and range of xerophiles, versus moist-forest species, have been used as indicators of climate change (Geisthardt 2003). Several pest tenebrionid species have been transported across the world for centuries with stored products (Andres 1931, Chaddick and Leek 1972). These beetles cause billions of dollars in direct and indirect losses to stored products every year. One major pest, *Tribolium castaneum*, is among the most-studied insects. Similar to adephagans, many tenebrionids produce antipredator secretions containing a combination of repulsive agents (e.g., quinones and phenols), wetting agents, and spreading agents (e.g., hydrocarbons) or other compounds with unknown purposes (Hurst et al. 1964, Tschinkel 1975). These repulsive secretions also have antibacterial or antifungal properties (Blum 1981). Some endangered Tenebrionidae species, especially flightless species, require habitat conservation to avoid extinction.

The superfamily Chrysomeloidea is a group of seven beetle families (Beutel and Leschen 2005a) with more than 50,000 species arranged in the cerambyciform (Cerambycidae, Disteniidae, Oxypeltidae, and Vesperidae) and chrysomeliform (Chrysomelidae, Megalopodidae, and Orsodacnidae) lineages. Because they are almost exclusively phytophagous, many are economically important as plant pests or biological agents against weeds. The families Cerambycidae (long-horn beetles) and Chrysomelidae (leaf beetles) are by far the largest in this superfamily and include more than 30,000 and 32,000 species, respectively (Table 11.1). Reid (2014) recently reviewed phylogenetic analyses of the chrysomeliform lineage, and Reid (2000) provided a key to

subfamilies based on adults and larvae. Švácha et al. (1997) provided the most recent phylogenetic hypothesis of the cerambyciform lineage based on larvae. Although most species in the Cerambycidae are winged and have arboreal habits, specialized adaptations to ground-dwelling habits are known in the flightless genus *Dorcadion* and related genera (Plavilstshikov 1958). The remaining five families combined include fewer than 1000 species. The Disteniidae have more than 300 species occurring in all major biotic regions, except Australia, Europe, and New Zealand (Lawrence et al. 1999, Švácha and Lawrence 2014b). The Oxypeltidae include three large and brightly colored South American species in two genera (Lawrence et al. 1999). The Vesperidae have nearly 80 species in the warmer regions, among which the soil-dwelling larvae of *Philus antennatus* are notorious pests of pine plantations in China (Švácha and Lawrence 2014a). The pantropical Megalopodidae include some 350 species, and the Orsodacnidae have approximately 40 species in three genera in the Nearctic, Neotropical, and Palearctic regions (Clark and Riley 2002, Lawrence and Ślipiński 2014).

The classification of the herbivorous superfamily Curculionoidea has been, and continues to be, in a state of flux, based on recent works (Bouchard et al. 2011, Löbl and Smetana 2011, Löbl and Smetana 2013, Leschen and Beutel 2014). This superfamily currently contains six smaller families with fewer than 4500 described species each (Attelabidae, Anthribidae, Belidae, Brentidae, Caridae, and Nemonychidae), as well as the second most diverse family of beetles, the Curculionidae (Table 11.1). Most species in this superfamily have the mouth on a distinctive cylindrical extension of the head. This rostrum is used to prepare cavities in plant tissues for egg deposition. The evolution of the rostrum is thought to be a reason for the weevils' success because it allows them to exploit plant tissues that other beetles cannot access (Anderson 1995).

Members of the six smaller families of Curculionoidea generally are associated with plants that predate flowering plants (e.g., conifers,

cycads, and ferns) (Farrell 1998). These weevils are also important pollinators for their host plants (Kevan and Baker 1983). The anthribid *Araecerus fasciculatus* (coffee-bean weevil) feeds on dried plant materials and has become a serious pest of stored products such as coffee and cocoa beans (Childers and Woodruff 1980, Bousquet 1990). Some species of the subfamily Apioninae (Brentidae) are specific to one or several host plants and have been introduced in new regions as biological tools to control invasive weeds (O'Brien 1995).

The family Curculionidae is one of the most diverse groups of organisms, with more than 50,000 species described and thousands more to be formally described. Their close association with flowering plants is a main factor explaining their great diversity. Curculionids feed on plants of any terrestrial or freshwater habitat, and on any plant tissue, from roots to seeds (Anderson 2002). Because of these characteristics, curculionids are important economically. Some species are pests of agriculture and forestry, including about half of the species of important plant pests; others feed on stored-plant commodities. Curculionids have been used to control populations of invasive plants (O'Brien 1995). The subfamilies Scolytinae and Platypodinae (considered separate families until recently) are specialized in exploiting woody plants (Anderson 2002). Most either feed on the phloem of the inner bark of their hosts or on symbiotic ambrosia fungi that they cultivate in the wood. About 100 species in these two subfamilies are major forestry pests.

11.2 Overview of Fossil Taxa

The first beetle-like fossils originated in the Early Permian (approximately 280 mya); however, the true Coleoptera appeared in the Triassic (approximately 230 mya) (Grimaldi and Engel 2005, Lawrence and Ślipiński 2013). A large amount of data on fossil Coleoptera has been published and significant new discoveries (i.e., description of new taxa up to the rank of

family) are published on a regular basis (Kukalová-Peck and Beutel 2012; Bai et al. 2012, 2013; Kirejtshuk and Nel 2013; Kirejtshuk and Azar 2013; Kirejtshuk et al. 2016). The four suborders of extant Coleoptera (Archostemata, Myxophaga, Adephaga, and Polyphaga) and 63% of extant beetle families are known from the fossil record (Smith and Marcot 2015). Ślipiński et al. (2011) reported a total of 230 genera and 600 fossil species of beetles, and Smith and Marcot (2015) established a database of 5553 beetle fossil occurrences from 221 localities. A list of beetle families only represented by fossils is given in Table 11.2.

11.3 Societal Benefits and Risks

11.3.1 Beetles of Economic Importance

11.3.1.1 Negative Effects of Beetles

Agriculture Beetles have a major effect on the world's agriculture. Hundreds of species of beetles, including many in the families Chrysomelidae, Curculionidae, Elateridae, and Scarabaeidae, feed on crops and ornamental plants as adults and larvae (Campbell et al. 1989). At least one species probably attacks each cultivated seed-plant species around the world. One of the best-studied pests is the boll weevil (*Anthonomus grandis grandis*), which harms cotton. This species is native to tropical and subtropical America, but has been established in the United States since the late 1800s (Burke et al. 1986). In the past 100 years, yield losses and control costs against this species have been estimated at more than US\$22 billion (Kaplan 2003). A boll weevil eradication program that started in 1983 (Dickerson et al. 2001), coordinated by the US Department of Agriculture and state agencies, has resulted in the eradication of the weevil from more than 80% of the cotton-production area in the United States.

Blister beetles can contaminate animal feed. These meloid beetles are sometimes abundant in hay fields and possess antipredator cantharidin

Table 11.2 Coleoptera families represented by extinct taxa only, with number of described genera and species (from Ślipiński et al. 2011).

Suborder	Superfamily	Family	World genera	World species	
Protocoleoptera	Tshekardocoleoidea	Tshekardocoleidae	13	18	
		Labradorocoleidae	1	1	
		Oborocoleidae	2	2	
	Permocupedoidea	Permocupedidae	11	30	
		Taldycupedidae	6	18	
		Ademosynidae	12	29	
		Permosynidae	3	14	
Archostemata	—	Triadocupedidae	8	16	
		Magnocoleidae	1	1	
		Obrienidae	5	7	
Myxophaga	Asiocoleoidea	Asiocoleidae	1	1	
		Tricoleidae	3	6	
	Rhombocoleoidea	Rhombocoleidae	5	10	
	Schizophoroidea	Schizophoridae	20	36	
		Catiniidae	5	6	
		Schizocoleidae	4	30	
Adephaga	—	Tritarsusidae	1	1	
		Triaplidae	1	2	
		Colymbotethidae	2	2	
		Parahygrobiidae	1	1	
		Coptoclavidae	14	32	
		Liadytidae	2	6	
		Liadytidae	2	6	
Polyphaga	Scarabaeoidea	Coprinisphaeridae	4	9	
		Pallichnidae	2	3	
	Scirtoidea	Elodophthalmidae	1	2	
		Mesocinetidae	4	7	
		Elateroidea	Praelateriidae	2	2
	Elateroidea	Berendtimiridae	1	1	
		Lasiosynidae	4	7	
		Cleroidea	Parandrexidae	3	5
		Cucujoidea	Sinisolvanidae	1	1
	Curculionioidea	Ulyanidae	2	3	
Total			145	309	

Taxa are ordered following the classification of Bouchard et al. (2011). New family-group additions published since 2011 are highlighted in the text (in “Overview of Fossil Taxa”).

compounds. Cattle, emu, goats, horses, and sheep have become ill or died after consuming alfalfa contaminated by dead blister beetles (Capinera et al. 1985). The incidence of this condition, termed cantharidiasis, has increased recently due to the common practice of hay conditioning, which crushes the beetles inside the hay and incorporates them into the bales (Capinera et al. 1985, Blodgett et al. 1992).

Beetles are important vectors of pathogens to crops and livestock (Harris 1981). One species, the striped cucumber beetle (*Acalymma vittatum*), is a specialist herbivore of the cucumber family Cucurbitaceae. The association of these beetles with the wilt-inducing plant bacterium *Erwinia tracheiphila* often leads to major losses (Garcia-Salazar et al. 2000). Management of bacterial wilt relies heavily on vector management (Ellers-Kirk and Fleisher 2006) through field and laboratory studies of the bionomics of the striped cucumber beetle and the effects of varying agricultural practices. The lesser mealworm beetle (*Alphitobius diaperinus*) commonly colonizes poultry houses, feeding on shed feathers, droppings, and spilled poultry meal, as well as on dead, dying, or newly born chicks (Harris 1966, Kumar 1988, Watson et al. 2001). Although the beetles have a minor beneficial effect in consuming chicken mites and house fly maggots, the benefits are more than offset by their role in the transmission of disease-causing bacteria and fungi such as *Campylobacter*, *Metarhizium*, and *Salmonella* (Davies and Wray 1995, Alves et al. 2004, Strother et al. 2005).

Hinton (1945) stated that the Coleoptera was the most important order of insects attacking stored products. More than 600 species of beetles are associated with stored products around the world. Although many of these eat the stored products, others feed on associated fungi or animals (Bousquet 1990). Some of the most problematic groups of beetles in stored products are the Dermestidae, Chrysomelidae, Curculionidae, and Tenebrionidae. The red flour beetle (*Tribolium castaneum*), a frequently

encountered pest of stored products, can feed on many products in the larval and adult stages. Because of its economic importance and ease of rearing, the red flour beetle is used extensively as a tool in genetics research.

Museum Collections Museums assemble millions of specimens for research and public displays. Beetles, especially the family Dermestidae, threaten the world's museum collections. Species of *Anthrenus*, *Dermestes*, and *Thyrodrias* commonly attack and destroy preserved animals such as pinned insects and preserved pelts and skins, as well as cultural artifacts that incorporate feathers, fur, hair, leather, wool, and other animal derivatives (Armes 1988, Campbell et al. 1989). The control of museum beetle pests is becoming increasingly difficult because pesticides and fumigants used in the past can cause health problems for museum workers. Museum-pest research is now focusing largely on preventive conservation (Goldberg 1996).

Forestry Many species of Coleoptera are highly relevant to humans through their activity as forest pests. The assemblage of forest pests varies among countries. Up to 45% of the annual wood volume grown in Sweden was estimated to be lost to two bark beetles: *Tomicus piniperda* and *Ips typographus* (Eidmann 1992). *Dendroctonus frontalis*, feeding on loblolly pine (*Pinus taeda*), killed about 40,000 trees with a value exceeding \$10 million in the southeastern United States in 18 months (Strom et al. 2004). These and many other species together cause tree mortality levels similar to those caused by fire or commercial harvest.

Weevils of the subfamilies Scolytinae and Platypodinae (Curculionidae), with 5812 and 1463 species, respectively (Wood and Bright 1992), are the most infamous forest pests. Phloem-feeding, tree-killing bark beetles constitute most of the diversity of the Scolytinae. Female bark beetles normally burrow in phloem and lay eggs, from which larvae hatch and construct further feeding burrows. Phloem of dying or freshly killed trees is the typical environment

for bark beetles. Many bark beetles use chemical signals (pheromones) to schedule a synergistic attack by many individuals on one tree, thus overcoming its resistance, killing it, and making it suitable for beetle reproduction (Paine et al. 1997). Other species overcome tree defenses with the aid of pathogenic fungi (Farrell et al. 2001).

One notorious phloem feeder is, however, not a scolytine weevil, but rather the emerald ash borer, *Agrilus planipennis*, a jewel beetle (Buprestidae). This species, native temperate east Asia, recently was accidentally introduced to and became established in North America. The larvae feed on phloem of ash trees (*Fraxinus* spp.) and cause widespread decline and mortality of the trees. The species was first detected in July 2002 in Detroit (Michigan, USA) and Windsor (Ontario, Canada). The cumulative death toll of ash trees is estimated to be as high as 15 million, many of which are high-value urban trees (Poland and McCullough 2006). The genus *Agrilus* is among the most species-rich genera of all organisms, with 2767 species (Bellamy 2003), and many pose a risk of introduction and loss of forest ecosystems around the world.

Phloem-feeding scolytine beetles are among the species most easily introduced accidentally to new regions, primarily through dunnage and wood packaging used in international trade. Island countries such as New Zealand are particularly vulnerable to introductions because of their isolated and mostly endemic native biota. Some 103 species of scolytine weevils were intercepted at New Zealand's borders between 1950 and 2000 (Brockerhoff et al. 2006), including high-risk species such as *Dendroctonus ponderosae* and *I. typographus*. The mainland Eurasian species *Dendroctonus micans* was first recorded in Wales in 1982 and then spread throughout the United Kingdom (Gilbert et al. 2003). The North American species *Dendroctonus valens* was introduced to China in 2001 and currently infests more than 0.5 million hectares of pine forest (Cognato et al. 2005). The pine shoot beetle (*T. piniperda*) is a Palearctic bark beetle that was recently introduced to North America.

Since its discovery in Ohio in 1992, this beetle has become established in Ontario and Quebec and in 13 states in the northcentral and northeastern United States (Morgan et al. 2004). Haack (2006) reviewed the history of bark- and wood-boring beetles introduced to the United States over the past 20 years and concluded that two exotic Buprestidae, five Cerambycidae, and 18 Scolytinae species have been introduced and are expanding their ranges in North America.

Although most forestry-important Coleoptera species are phloem feeders, many beetles also tunnel through sapwood, weakening or killing the host tree. Ambrosia weevils of the Scolytinae and Platypodinae have evolved a type of agriculture, cultivating ambrosia fungi in their burrows (Farrell et al. 2001). The Asian longhorn beetle *Anoplophora glabripennis* emerged recently as a top-profile beetle in the news in North America and Western Europe. In the early 1990s, this species hitchhiked with international trade and infested urban forests in the United States and Canada, rapidly killing eudicot trees of many species. This prompted government agencies to cut down thousands of trees in Massachusetts, New Jersey, New York, Ohio, and Toronto in an ongoing effort to eradicate the species. The genus *Anoplophora* has some 35 other species in Northwest Asia, which were revised by Lingafelter and Hoebeke (2002). Their study indicates that other *Anoplophora* species also could become introduced pests overseas.

Forestry in the southern hemisphere is based mainly on the hardwood *Eucalyptus* trees, which also have an associated complex of beetle pests. The Christmas beetle *Anoplognathus chloropyrus* (Scarabaeinae) and the leaf beetles *Paropsis atomaria*, *Paropsis charybdis*, and some other taxonomically poorly known paropsines (Chrysomelinae) are significant defoliators of commercially grown eucalypts in Queensland, Australia (Johns et al. 2004, Nahrung 2004).

Many highly destructive fungal forest pathogens are transmitted by beetles. Black-stain root disease of conifers in western North America, for example, is caused by the ophiostomatoid fungus *Leptographium wageneri*. Spores of this

species were detected in 37% of bark beetles in California, with individual beetles carrying zero to more than 100,000 spores (Schweigkofler et al. 2005). The mountain pine beetle (*D. ponderosae*) and its mutualistically associated blue-stain fungi (*Grossmannia* spp.) have benefitted from unusually high winter temperatures, which have lowered larval mortality in recent years. These factors created the largest beetle epidemic in Canada's history, primarily killing lodgepole pines (*Pinus contorta* var. *latifolia*) in British Columbia (Kim et al. 2005). This phenomenon of beetle–fungus mutualistic association is not restricted to bark and ambrosia beetles, but has evolved independently in a few other beetle taxa.

An understanding of the biodiversity of tree-associated beetles is relevant to the world forest industry. Only a few groups, such as the European and North American bark and ambrosia beetles, are adequately known taxonomically. Elsewhere, most tree-living beetle species remain inadequately known.

A list of Coleoptera species of high economic importance was compiled from various sources and is presented in Table 11.3.

11.3.1.2 Positive Effects of Beetles

Biological Control of Weeds Plant-feeding beetles, primarily of the families Curculionidae and Chrysomelidae, have been used successfully to control the spread of invasive alien plant species throughout the world. Weed seeds have been transported accidentally throughout the world for centuries, and the trend is increasing with global trade (Mason et al. 2002). Once established in a new area, weeds often spread quickly, primarily because of the absence of insect herbivores associated with them. Biological control of weeds, or the introduction and manipulation of natural enemies to reduce the spread of invasive weeds, is often used as a pesticide-free control method. Careful studies of the biology of beetles in the weed's country of origin and destination country are necessary for safe and effective control (O'Brien 1995, Rea 1997, Lindgren et al. 2002).

Recent success stories include control of houndstongue (*Cynoglossum officinale*) using a weevil (De Clerck-Floate et al. 2005) and control of purple loosestrife (*Lythrum salicaria*) using two species of leaf beetles (Lindgren et al. 2002).

Dung Removal One cow can produce more than 9000 kg of solid waste every year (Fincher 1981). The accumulation of dung from agriculture pollutes waterways, reduces pasture quality, and creates microhabitats for the development of flies and other pests. Dung beetles (Scarabaeidae and Geotrupidae) promote manure decomposition by burying it in the ground for larval food. They annually avert economic losses to the United States of \$0.38 billion by accelerating burial of livestock feces (Losey and Vaughan 2006). Dung beetles have been imported into countries, such as Australia, where native species did not remove an increase of livestock dung (Hughes et al. 1975). They also provide a vital ecosystem service in urban environments, where they use dog dung, thereby reducing stream pollution and improving nutrient-poor soils (Wallace 2005).

Pollination Beetles, along with other insect groups, are crucially important in the pollination of cultivated and wild plants. Pollination by beetles is often referred to as cantharophily. The Coleoptera are considered to be the most primitive pollinators (Kevan and Baker 1983). Beetles have been associated with flowering plants over millions of years, leading in some cases to the evolution of specialized structures in the host-plant flowers and in their beetle pollinators (Barth 1985, Fenster et al. 2004). Thirty-four families of flowering plants contain at least one primarily beetle-pollinated species (Bernhardt 2000). In some cloud forests, more than 45% of palms and herbs are beetle-pollinated (Seres and Ramirez 1995). A decline in native and non-native pollinators worldwide was attributed to pesticide use, habitat loss, plant biodiversity loss, and poor agricultural practices (Allen-Wardell et al. 1998). If this trend continues, we

Table 11.3 Pest Coleoptera species of high economic concern, based on current CABl, USDA-APHIS, Japan-MAFF, NAFIS, CFIA, and EPPO (A1 and A2) lists.

Superfamily	Family	Subfamily	Genus	Species	Author and year			
[Adephaga]	Carabidae	Carabinae	<i>Zabrus</i>	<i>tenebrioides</i>	(Goeze, 1777)			
Scarabaeoidea	Scarabaeidae	Cetoniinae	<i>Cheirolasia</i>	<i>burkei</i>	(Westwood, 1843)			
			<i>Chiloloba</i>	<i>acuta</i>	(Wiedemann, 1823)			
			<i>Pachnoda</i>	<i>marginata peregrina</i>	Kolbe, 1906			
			<i>Protaetia</i>	<i>interrupta</i>	(Olivier, 1789)			
				<i>auripes</i>	(Hope, 1831)			
				<i>bipunctata</i>	(Kraatz, 1889)			
				<i>celebica</i>	(Wallace, 1867)			
				<i>cretica</i>	(Kraatz, 1880)			
				<i>cuprea</i>	(Fabricius, 1775)			
				<i>himalayana</i>	Mikišić, 1987			
				<i>milani</i>	Antoine and Pavicevic, 1994			
				<i>nox</i>	Janson, 1881			
				<i>speciosa</i>	(Adams, 1817)			
			Dynastinae	Dynastinae		<i>Smaragdesthes</i>	<i>speciosissimus</i>	(Scopoli, 1786)
						<i>Diloboderus</i>	<i>africana</i>	(Drury, 1773)
						<i>Golofo</i>	<i>abderus</i>	(Sturm, 1826)
						<i>Heterorhynchus</i>	<i>eacus</i>	Burmeister, 1847
						<i>Oryctes</i>	<i>arator</i>	(Fabricius, 1775)
							<i>agamemnon</i>	Burmeister, 1847
	<i>boas</i>	(Fabricius, 1775)						
	<i>monoceros</i>	(Olivier, 1789)						
	<i>rhinoceros</i>	(Linnaeus, 1758)						
	<i>uninodis</i>	Prell, 1912						
	<i>Podischnus</i>	<i>woodlarkiana</i>	(Montrouzier, 1855)					
	<i>Xylotrupes</i>	<i>agenor</i>	(Olivier, 1789)					
		<i>gideon</i>	(Linnaeus, 1767)					

Melolonthinae	<i>Amphimallon</i>	<i>majale</i>	(Razoumowsky, 1789)
		<i>solstitiale</i>	(Linnaeus, 1758)
	<i>Costelytra</i>	<i>zealandica</i>	(White, 1844)
	<i>Holotrichia</i>	<i>disparilis</i>	Arrow, 1916
		<i>mindanaona</i>	Brenske, 1893
		<i>serrata</i>	(Fabricius, 1787)
	<i>Leucopholis</i>	<i>irrorata</i>	(Chevrolat, 1841)
		<i>lepidophora</i>	Blanchard, 1851
	<i>Maladera</i>	<i>castanea</i>	(Arrow, 1913)
	<i>Melolontha</i>	<i>hippocastani</i>	Fabricius, 1801
		<i>melolontha</i>	(Linnaeus, 1758)
	<i>Phyllophaga</i>	<i>smithi</i>	(Arrow, 1912)
		spp.	—
Rutelinae	<i>Adoretus</i>	<i>sinicus</i>	Burmeister, 1855
		spp.	—
		<i>versutus</i>	Harold, 1869
	<i>Anomala</i>	<i>sulcatula</i>	Burmeister, 1844
	<i>Exomala</i>	<i>orientalis</i>	(Waterhouse, 1875)
	<i>Popillia</i>	<i>japonica</i>	Newman, 1838
		spp.	—
Buprestoidea		<i>anxius</i>	Gory, 1841
Buprestidae	<i>Agrilus</i>	<i>biguttatus</i>	(Fabricius, 1777)
		<i>hyperici</i>	(Creutzer, 1799)
		<i>auroguttatus</i>	Schaeffer 1905
		<i>planipennis</i>	Fairmaire, 1888
		<i>sulcicollis</i>	Lacordaire, 1835
Buprestinae	<i>Chrysobothris</i>	<i>femorata</i>	(Olivier, 1790)
	<i>Melanophila</i>	<i>fulvoguttata</i>	(Harris, 1829)
Chrysochroinae	<i>Sphenoptera</i>	<i>gossypii</i>	Cotes, 1891

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
Elateroidea	Elateridae	Agrypninae	<i>Conoderus</i>	<i>rufangulus</i>	(Eschscholtz, 1829)
		Dendrometrinae	<i>Limonius</i>	<i>californicus</i>	(Mannerheim, 1843)
		Elaterinae	<i>Agriotes</i>	<i>lineatus</i> <i>sputator</i> <i>ustulatus</i> <i>communis</i>	(Linnaeus, 1767) (Linnaeus, 1758) (Schaller, 1783) (Gyllenhal, 1817)
Bostrichoidea	Dermestidae	Megatominae	<i>Melanotus</i>	<i>granarium</i>	Everts, 1898
		Bostrichinae	<i>Amphicerus</i>	<i>cornutus</i>	(Pallas, 1772)
			<i>Heterobostrychus</i>	<i>aequalis</i>	(Waterhouse, 1844)
Lymexyloidea	Lymexyloidea	Dinoderinae	<i>Sinoxylon</i>	<i>unidentatum</i>	(Fabricius, 1801)
		Melittomatinae	<i>Prostephanus</i>	<i>truncatus</i>	(Horn, 1878)
		—	<i>Melittomma</i>	<i>insulare</i>	Fairmaire, 1893
Cucujoidea	Laemophloeidae	—	<i>Cryptolestes</i>	<i>capensis</i>	(Waldl, 1834)
			<i>Carpophilus</i>	<i>obsoletus</i>	Erichson, 1843
			<i>Meligethes</i>	<i>aeneus</i>	(Fabricius, 1775)
Nitidulidae	Nitidulinae		<i>Aethina</i>	<i>tumida</i>	Murray, 1867
			<i>Stelidota</i>	<i>geminata</i>	(Say, 1825)
			<i>Chilocorus</i>	<i>kuwanae</i>	Silvestris, 1909
Coccinellidae	Coccinellinae		<i>Chnootriba</i>	<i>similis</i>	(Thunberg, 1871)
			<i>Coleomegilla</i>	<i>maculata</i>	Timberlake, 1943
			<i>Epilachna</i>	<i>borealis</i> <i>chrysomelina</i> <i>varivestis</i>	(Fabricius, 1775) (Fabricius, 1775) Mulsant, 1850
			<i>Harmonia</i>	<i>axyridis</i>	(Pallas, 1773)
			<i>Henosepilachna</i>	<i>elaterii</i> <i>vigintioctopunctata</i>	(Rossi, 1794) (Fabricius, 1775)

Chrysomeloidea	Cerambycidae	Cerambycinae	<i>Sasajiscymnus</i>	<i>tsugae</i>	(Sasaji and McClure, 1997)
			<i>Stethorus</i>	<i>punctum</i>	(LeConte, 1852)
			<i>Aeolesthes</i>	<i>sarta</i>	(Solsky, 1871)
			<i>Aromia</i>	<i>bungii</i>	(Faldermann, 1835)
			<i>Callidiellum</i>	<i>rufipenne</i>	(Motschulsky, 1862)
				<i>vilosulum</i>	(Fairmaire, 1900)
			<i>Cerambyx</i>	<i>cerdo</i>	Linnaeus, 1758
			<i>Chloridolum</i>	<i>alcemene</i>	Thomson, 1865
				<i>thomsoni</i>	(Pascoe, 1859)
			<i>Chlorophorus</i>	<i>annularis</i>	(Fabricius, 1787)
				<i>strobilicola</i>	Champion, 1919
			<i>Cordylomera</i>	<i>torrida</i>	(Fabricius, 1775)
			<i>Enaphalodes</i>	<i>rufulus</i>	(Haldeman, 1847)
			<i>Eurypagus</i>	<i>lundi</i>	(Fabricius, 1793)
			<i>Hesperophanes</i>	<i>campestris</i>	(Faldermann, 1835)
			<i>Hylotrupes</i>	<i>bajulus</i>	(Linnaeus, 1758)
			<i>Oemona</i>	<i>hirta</i>	(Fabricius, 1775)
			<i>Phoracantha</i>	<i>recurva</i>	Newman, 1840
				<i>semipunctata</i>	(Fabricius, 1775)
			<i>Placosternus</i>	<i>difficilis</i>	(Chevrolat, 1862)
			<i>Plagionotus</i>	<i>arcuatus</i>	(Linnaeus, 1758)
			<i>Stromatium</i>	<i>barbatum</i>	(Fabricius, 1775)
			<i>Trichoferus</i>	<i>campestris</i>	(Faldermann, 1835)
			<i>Xylotrechus</i>	<i>altaicus</i>	(Gebler, 1836)
				<i>chinensis</i>	(Chevrolat, 1852)
				<i>colonus</i>	(Fabricius, 1775)
				<i>namanganensis</i>	Heyden, 1885
				<i>pyrrhoderus</i>	Bates, 1873
				<i>quadripes</i>	Chevrolat, 1863

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
				<i>rufilius</i>	Bates, 1884
				spp.	—
			<i>Xystrocera</i>	<i>globosa</i>	(Olivier, 1795)
		Lamiinae	<i>Anoplophora</i>	<i>chinensis</i>	(Forster, 1771)
				<i>glabripennis</i>	(Motschulsky, 1854)
				spp.	—
			<i>Anthores</i>	<i>leuconotus</i>	Pascoe, 1869
			<i>Apomecyna</i>	<i>binubila</i>	Pascoe, 1858
			<i>Apriona</i>	<i>cinerea</i>	(Chevrolat, 1852)
				<i>germari</i>	(Hope, 1831)
				<i>japonica</i>	(Thomson, 1878)
			<i>Batocera</i>	<i>rufomaculata</i>	(De Geer, 1775)
			<i>Bixadus</i>	<i>sierricola</i>	(White, 1858)
			<i>Dectes</i>	<i>texanus</i>	LeConte, 1862
			<i>Desmiphora</i>	<i>hirticollis</i>	(Olivier, 1795)
			<i>Lagocheirus</i>	<i>araneiformis</i>	(Linnaeus, 1767)
			<i>Monochamus</i>	<i>alternatus</i>	Hope, 1842
				<i>carolinensis</i>	(Olivier, 1792)
				<i>galloprovincialis</i>	(Olivier, 1795)
				<i>saltuarius</i>	(Gebler, 1830)
				<i>sartor</i>	(Fabricius, 1787)
				<i>scutellatus</i>	(Say, 1824)
				spp.	—
			<i>sutor</i>		(Linnaeus, 1758)
				<i>urussovi</i>	(Fischer von Waldheim, 1805)
			<i>Oberea</i>	<i>linearis</i>	(Linnaeus, 1761)
				<i>oculata</i>	(Linnaeus, 1758)

	<i>Psacotheca</i>	<i>hilaris</i>	(Pascoe, 1857)
	<i>Saperda</i>	<i>calcarata</i>	Say, 1824
		<i>candida</i>	Fabricius, 1787
		<i>carcharias</i>	(Linnaeus)
		<i>perforata</i>	(Pallas, 1773)
	<i>Steirastoma</i>	<i>breve</i>	(Sulzer, 1776)
Lepturinae	<i>Encyclops</i>	<i>caerulea</i>	(Say, 1826)
Prioninae	<i>Prionus</i>	<i>californicus</i>	Motschulsky, 1845
		<i>laticollis</i>	(Drury, 1773)
Spondylidinae	<i>Arhopalus</i>	<i>ferus</i>	(Mulsant, 1839)
	<i>Tetropium</i>	<i>castaneum</i>	(Linnaeus, 1758)
		<i>fuscum</i>	(Fabricius, 1787)
		<i>gracilicorne</i>	Reitter, 1889
		<i>obtectus</i>	(Say, 1831)
Chrysomelidae	<i>Acanthoscelides</i>	<i>lentis</i>	Frölich, 1799
Bruchinae	<i>Bruchus</i>	<i>analis</i>	(Fabricius, 1781)
	<i>Callosobruchus</i>	<i>rhodesianus</i>	(Pic, 1902)
		<i>serratus</i>	(Olivier, 1790)
Cassidinae	<i>Caryedon</i>	<i>longissima</i>	(Gestro, 1885)
	<i>Brontispa</i>	<i>elaeidis</i>	Maulik, 1920
	<i>Coelaenomenodera</i>	<i>armigera</i>	(Olivier, 1808)
	<i>Dicladispa</i>	<i>gestroi</i>	(Chapuis, 1877)
		<i>dorsalis</i>	(Thunberg, 1805)
	<i>Promecotheca</i>	<i>cumingii</i>	Baly, 1858
	<i>Trichispa</i>	<i>sericea</i>	(Guérin-Méneville, 1844)
Chrysomelinae	<i>Gonioctena</i>	<i>fornicata</i>	Brüggemann, 1873
	<i>Leptinotarsa</i>	<i>decemlineata</i>	(Say, 1824)
	<i>Mesoplatys</i>	<i>cincta</i>	(Olivier, 1790)
	<i>Microtheca</i>	<i>ochroloma</i>	Stål 1860

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
			<i>Phaedon</i>	<i>brassicae</i>	Baly, 1874
		Criocerinae	<i>Criocerus</i>	<i>asparagi</i>	(Linnaeus, 1758)
				<i>duodecimpunctata</i>	(Linnaeus, 1758)
			<i>Liliocerus</i>	<i>lili</i>	(Scopoli, 1763)
			<i>Oulema</i>	<i>melanopus</i>	(Linnaeus, 1758)
		Eumolpinae	<i>Typophorus</i>	<i>nigritus</i>	(Fabricius, 1801)
		Galerucinae	<i>Acalymma</i>	<i>vittatum</i>	(Fabricius, 1775)
			<i>Alocypha</i>	<i>bimaculata</i>	(Jacoby, 1903)
			<i>Autacophora</i>	<i>foveicollis</i>	(Lucas, 1849)
				<i>indica</i>	(Gmelin, 1790)
			<i>Cerotoma</i>	<i>trifurcata</i>	(Forster, 1771)
			<i>Chaetocnema</i>	<i>basalis</i>	(Baly, 1877)
				<i>corfinis</i>	Crotch, 1873
				<i>pulicaria</i>	Melsheimer, 1847
			<i>Diabrotica</i>	<i>balteata</i>	LeConte, 1865
				<i>barberi</i>	Smith and Lawrence, 1967
				<i>speciosa</i>	(Germar, 1824)
				<i>undecimpunctata</i>	Mannerheim, 1843
				<i>virgifera virgifera</i>	LeConte, 1868
			<i>Epitrix</i>	<i>ucumeris</i>	(Harris, 1851)
				<i>asciata</i>	latchley, 1918
				<i>imilaris</i>	entner, 1944
				<i>ubcrinita</i>	(LeConte, 1857)
				<i>uberis</i>	entner, 1944
			<i>Exosoma</i>	<i>lusitanicum</i>	(Linnaeus, 1767)
			<i>Luperomorpha</i>	<i>xanthodera</i>	(Fairmaire, 1888)
			<i>Madurasia</i>	<i>obscura</i>	Jacoby, 1896
			<i>Medythia</i>	<i>quaterna</i>	(Fairmaire, 1880)

Curculionioidea	Attelabidae	Rhynchitinae	<i>Ootheca</i>	<i>bennigseni</i>	Weise, 1900
	Brentidae	Apioninae	<i>Phylotreta</i>	<i>mutabilis</i>	(Sahlberg, 1829)
		Brentinae	<i>Pyrrhalta</i>	<i>chotanica</i>	Duvivier, 1892
	Brachyceridae	Rhynchitinae	<i>Caenorhinus</i>	<i>cruciferae</i>	(Goeze, 1777)
			<i>Ischnopterapion</i>	<i>striolata</i>	(Illiger, 1803)
			<i>Arrhenodes</i>	<i>viburni</i>	(Paykull, 1799)
			<i>Cylas</i>	<i>marginellus</i>	(Faust, 1898)
			<i>Brachycerus</i>	<i>virens</i>	(Herbst, 1797)
			<i>Lissorhoptrus</i>	<i>minutus</i>	(Drury, 1773)
			<i>Rhinostomus</i>	<i>brunneus</i>	(Olivier, 1790)
<i>Cosmopolites</i>			<i>formicarius</i>	(Fabricius, 1798)	
Dryophthoridae	Rhynchophorinae	<i>Diocalandra</i>	<i>puncticollis</i>	Boheman, 1833	
		<i>Metamasius</i>	spp.	—	
		<i>Odoiporus</i>	<i>oryzophilus</i>	Kuschel, 1952	
		<i>Rhabdoscelus</i>	<i>barbirostris</i>	(Fabricius, 1775)	
		<i>Rhynchophorus</i>	<i>sordidus</i>	(Germar, 1824)	
		<i>Scyphophorus</i>	<i>frumenti</i>	(Fabricius, 1801)	
		<i>Sphenophorus</i>	<i>taitense</i>	(Guérin-Méneville, 1834)	
		<i>Tennoshoita</i>	<i>hemipterus</i>	(Linnaeus, 1758)	
		<i>Tryphetus</i>	spp.	—	
		<i>Copturus</i>	<i>longicollis</i>	(Olivier, 1807)	
Curculionidae	Cossoninae	<i>Tryphetus</i>	<i>obscurus</i>	(Boisduval, 1835)	
		<i>Caulophilus</i>	<i>ferrugineus</i>	(Olivier, 1791)	
Curculionidae	Cossoninae	<i>Tryphetus</i>	<i>palmarum</i>	(Linnaeus, 1758)	
		<i>Copturus</i>	<i>acupunctatus</i>	Gyllenhal, 1838	
		<i>Caulophilus</i>	<i>venatus</i>	(Say, 1832)	
		<i>Caulophilus</i>	<i>nigroplagiata</i>	(Quedenfeldt, 1888)	
		<i>Caulophilus</i>	<i>incarnatus</i>	(Gyllenhal, 1838)	
		<i>Caulophilus</i>	<i>aguacatae</i>	Kissing, 1957	
		<i>Caulophilus</i>	<i>oryzae</i>	(Gyllenhal, 1838)	
		<i>Caulophilus</i>	<i>oryzae</i>	(Gyllenhal, 1838)	
		<i>Caulophilus</i>	<i>oryzae</i>	(Gyllenhal, 1838)	
		<i>Caulophilus</i>	<i>oryzae</i>	(Gyllenhal, 1838)	

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year		
Cryptorhynchinae			<i>Cryptorhynchus</i>	<i>mangiferae</i>	(Fabricius, 1775)		
			<i>Elytroteinus</i>	<i>subtruncatus</i>	(Fairmaire, 1881)		
			<i>Eusepea</i>	<i>postfasciatus</i>	(Fairmaire, 1849)		
			<i>Mitrasethus</i>	<i>baridioides</i>	Redtenbacher, 1868		
			<i>Sternochetus</i>	<i>mangiferae</i>	(Fabricius, 1775)		
				<i>frigidus</i>	(Fabricius, 1787)		
				<i>bisignifer</i>	Schenking and Marshall, 1934		
				<i>eugeni</i>	Cano, 1894		
				<i>grandis</i>	Boheman, 1843		
				<i>pomorum</i>	(Linnaeus, 1758)		
Curculioninae				<i>quadrigibbus</i>	Say, 1831		
				<i>signatus</i>	Say, 1832		
			<i>Curculio</i>	<i>caryae</i>	(Horn, 1873)		
				<i>elephas</i>	(Gyllenhal, 1836)		
				<i>nucum</i>	Linnaeus, 1758		
				<i>alni</i>	(Linnaeus, 1758)		
				<i>gibberus</i>	Boisduval, 1835		
				<i>scutellatus</i>	Gyllenhal, 1833		
				<i>costirostris</i>	Schönherr, 1826		
				<i>subcinctus</i>	Boheman, 1842		
Cyclominae				<i>bonariensis</i>	(Kuschel, 1955)		
				<i>oregonensis</i>	(LeConte, 1857)		
				<i>asellus</i>	(Olivier, 1807)		
				<i>abbreviatus</i>	(Linnaeus, 1758)		
				<i>famelicus</i>	(Olivier, 1790)		
				<i>splengleri</i>	(Linnaeus, 1767)		
				<i>chilensis</i>	(Boheman, 1842)		
Entiminae			<i>Blosyrus</i>				
			<i>Diaprepes</i>				

<i>Hypomeces</i>	<i>squamosus</i>	(Fabricius, 1792)
<i>Naupactus</i>	<i>leucoloma</i>	(Boheman, 1840)
	<i>xanthographus</i>	(Germar, 1824)
<i>Otiorynchus</i>	<i>armadillo</i>	(Rossi, 1792)
	<i>corruptor</i>	(Host, 1789)
	<i>cribricollis</i>	Gyllenhal, 1834
	<i>dieckmanni</i>	Mangano, 1979
	<i>ligustici</i>	(Linnaeus, 1758)
	<i>meridionalis</i>	Gyllenhal, 1834
	<i>pseudonotus</i>	Apfelbeck, 1897
	<i>singularis</i>	(Linnaeus, 1767)
	<i>sulcatus</i>	(Fabricius, 1755)
	<i>ovatus</i>	(Linnaeus, 1758)
	<i>rugosostriatus</i>	(Goeze, 1777)
<i>Pantomorus</i>	<i>cervinus</i>	(Boheman, 1840)
<i>Phlyctinus</i>	<i>callosus</i>	Schoenherr, 1826
<i>Premnotrypes</i>	<i>latithorax</i>	(Pierce, 1914)
	<i>suturicallus</i>	Kuschel, 1956
	<i>vorax</i>	(Hustache, 1933)
<i>Pseudocnecorhinus</i>	<i>bifasciatus</i>	(Roelofs, 1880)
<i>Sitona</i>	<i>cylindricollis</i>	(Fähræus, 1840)
	<i>discoideus</i>	Gyllenhal, 1834
	<i>hispidulus</i>	(Fabricius, 1777)
	<i>humeralis</i>	Stephens, 1831
<i>Tanymecus</i>	<i>dilaticollis</i>	Gyllenhal, 1834
<i>Hypera</i>	<i>postica</i>	(Gyllenhal, 1813)
<i>Bothynoderes</i>	<i>punctiventris</i>	(Germar, 1824)
<i>Hypolixus</i>	<i>truncatulus</i>	(Fabricius, 1798)
<i>Lixus</i>	<i>juncii</i>	Boheman, 1835

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
		Mesoptiliinae	<i>Pissodes</i>	<i>castaneus</i>	(De Geer, 1775)
				<i>harcyniae</i>	(Herbst, 1795)
				<i>nemorensis</i>	Germar, 1824
				<i>strobi</i>	(Peck, 1817)
				<i>terminalis</i>	Hopping, 1920
		Molytinae	<i>Alicidodes</i>	<i>dentipes</i>	(Olivier, 1790)
			<i>Conotrachelus</i>	<i>aguacatae</i>	Barber, 1924
				<i>nenuphar</i>	(Herbst, 1797)
				<i>perseae</i>	Barber, 1919
				spp.	—
			<i>Heilipus</i>	<i>lauri</i>	Boheman, 1845
			<i>Hylobius</i>	<i>abietis</i>	(Linnaeus, 1758)
				<i>transversovittatus</i>	(Goeze, 1777)
		Platypodinae	<i>Crossotarsus</i>	<i>externedentatus</i>	(Fairmaire, 1850)
				<i>squamulatus</i>	Chapuis, 1865
			<i>Diapus</i>	<i>minutissimus</i>	Schedl, 1969
				<i>pusillimus</i>	Chapuis, 1865
				<i>quinquespinatus</i>	Chapuis, 1865
			<i>Dinoplatypus</i>	<i>agnatus</i>	(Schedl, 1969)
				<i>biuncus</i>	(Blandford, 1896)
				<i>cavus</i>	(Strohmeyer, 1913)
				<i>chevrolati</i>	(Chapuis, 1865)
				<i>cupulatus</i>	(Schedl, 1941)
				<i>cupulatus</i>	(Chapuis, 1865)
				<i>forficula</i>	(Chapuis, 1865)
				<i>luniger</i>	(Motschulsky, 1863)
				<i>pallidus</i>	(Chapuis, 1865)

	<i>pseudocupulatus</i>	(Schedl, 1935)
	<i>uncatus</i>	(Browne, 1980)
<i>Euplatypus</i>	<i>compositus</i>	(Say, 1824)
	<i>hintzi</i>	(Schaufuss, 1897)
	<i>parallelus</i>	(Fabricius, 1801)
<i>Genyocerus</i>	<i>borneensis</i>	(Browne, 1980)
	<i>diaphanus</i>	(Schedl, 1939)
	<i>pendleburyi</i>	(Schedl, 1936)
	<i>spinatus</i>	(Browne, 1980)
	<i>mutatus</i>	(Chapuis, 1865)
<i>Megaplatypus</i>	<i>quadridentatus</i>	(Olivier, 1795)
<i>Oxoplatypus</i>	<i>apicalis</i>	(White, 1846)
<i>Platypus</i>	<i>curtus</i>	Chapuis, 1865
	<i>cylindrus</i>	(Fabricius 1792)
	<i>excedens</i>	Chapuis, 1865
	<i>geminatus</i>	Chapuis, 1865
	<i>jansoni</i>	Chapuis, 1865
	<i>koryoensis</i>	(Murayama, 1930)
	<i>parallelus</i>	(Fabricius, 1801)
	<i>porcellus</i>	Schedl, 1942
	<i>pseudocurtus</i>	Schedl, 1935
	<i>quercivorus</i>	(Murayama, 1925)
	<i>subdepressus</i>	(Schedl, 1935)
	<i>westwoodi</i>	Chapuis, 1865
	<i>solidus</i>	(Walker, 1859)
<i>Treptoplatypus</i>	<i>punctatissimus</i>	(Eichhoff, 1880)
<i>Ancipitius</i>	<i>maiche</i>	Stark, 1936
<i>Anisandrus</i>		
Scolytinae		

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
			<i>Arixyleborus</i>	<i>dispar</i>	(Fabricius, 1792)
				<i>canaliculatus</i>	(Eggers, 1923)
				<i>granifer</i>	(Eichhoff, 1878)
				<i>granulifer</i>	(Eggers, 1923)
				<i>hirsutulus</i>	Schedl, 1969
				<i>imitator</i>	(Eggers, 1927)
				<i>mediosectus</i>	(Eggers, 1923)
				<i>rugosipes</i>	Hopkins, 1903
			<i>Cnestus</i>	<i>mutilatus</i>	(Blandford, 1894)
			<i>Cocotrypes</i>	<i>subcribrosus</i>	(Blandford, 1896)
			<i>Cryphalus</i>	<i>latus</i>	Eggers, 1929
			<i>Cryptoxyleborus</i>	<i>subnaevus</i>	Schedl, 1937
			<i>Crypturgus</i>	<i>cinereus</i>	(Herbst, 1794)
			<i>Cyclorhipidion</i>	<i>sexspinatum</i>	(Schedl, 1935)
			<i>Dendroctonus</i>	<i>adjunctus</i>	Blandford, 1897
				<i>armandi</i>	(Tsai and Li, 1959)
				<i>brevicomis</i>	LeConte, 1876
				<i>frontalis</i>	Zimmerman, 1868
				<i>micans</i>	(Kugelann, 1794)
				<i>ponderosae</i>	Hopkins, 1902
				<i>pseudotsugae</i>	Hopkins, 1905
				<i>rufipennis</i>	(Kirby, 1837)
				<i>valens</i>	LeConte, 1857
			<i>Dolargus</i>	<i>pumilus</i>	(Mannerheim, 1843)
			<i>Dryocoetes</i>	<i>confusus</i>	Swaine, 1912
				<i>affaber</i>	(Mannerheim, 1852)
			<i>Eccoptyterus</i>	<i>spinosisus</i>	(Olivier, 1795)

<i>Eiwallacea</i>	<i>formicatus</i>	Eichhoff, 1868
	<i>destruens</i>	(Blandford, 1896)
<i>Gnathotrichus</i>	<i>sulcatus</i>	(LeConte, 1868)
	<i>retusus</i>	(LeConte, 1868)
<i>Hylastes</i>	<i>ater</i>	(Paykull, 1800)
<i>Hylesinus</i>	<i>varius</i>	(Fabricius, 1775)
	<i>aculeatus</i>	Say, 1826
<i>Hylurgopinus</i>	<i>rufipes</i>	(Eichhoff, 1868)
<i>Hylurgops</i>	<i>palliatu</i>	(Gyllenhal, 1813)
	<i>rugipennis</i>	(Mannerheim, 1843)
<i>Hylurgus</i>	<i>ligniperda</i>	(Fabricius, 1787)
<i>Hypothenemus</i>	<i>hampei</i>	(Ferrari, 1867)
<i>Ips</i>	<i>amitinus</i>	(Eichhoff, 1872)
	<i>calligraphus</i>	(Germet, 1824)
	<i>cenbrae</i>	(Heer, 1836)
	<i>confusus</i>	(LeConte, 1876)
	<i>duplicatus</i>	(Sahlberg, 1836)
	<i>grandicollis</i>	(Eichhoff, 1868)
	<i>hauseri</i>	(Reitter, 1894)
	<i>lecontei</i>	Swaine, 1924
	<i>paraconfusus</i>	Lanier, 1970
	<i>pini</i>	(Say, 1826)
	<i>plastographus</i>	(LeConte, 1868)
	<i>sexdentatus</i>	Börner 1766)
	<i>subelongatus</i>	(Motschulsky, 1860)
	<i>typographus</i>	(Linnaeus, 1758)
	<i>montanus</i>	(Eichhoff, 1881)
	<i>perturbatus</i>	(Eichhoff, 1869)

(Continued)

Table 11.3 (Continued)

Superfamily	Family	Subfamily	Genus	Species	Author and year
			<i>Monarthrum</i>	<i>tridens</i>	(Mannerheim, 1852)
				<i>fasciatum</i>	(Say, 1826)
				<i>mali</i>	(Fitch, 1855)
			<i>Orthotomicus</i>	<i>erosus</i>	(Wollaston, 1857)
				<i>caelatus</i>	(Eichhoff, 1868)
				<i>latidens</i>	(LeConte, 1874)
			<i>Pagiocerus</i>	<i>frontalis</i>	(Fabricius, 1801)
			<i>Phloeosinus</i>	<i>cupressi</i>	Hopkins, 1903
				<i>punctatus</i>	LeConte, 1876
				<i>sequoiae</i>	Hopkins, 1903
			<i>Phloeotribus</i>	<i>liminaris</i>	(Harris, 1852)
				<i>scarabaeoides</i>	(Bernard, 1788)
			<i>Pityoborus</i>	<i>cornatus</i>	(Zimmermann, 1868)
			<i>Pityogenes</i>	<i>chalcographus</i>	(Linnaeus, 1760)
			<i>Pityophthorus</i>	<i>juglandis</i>	Blackman, 1928
			<i>Polygraphus</i>	<i>proximus</i>	Blandford, 1894
				<i>occidentalis</i>	Schedl, 1954
				<i>rufipennis</i>	(Kirby, 1837)
			<i>Pseudips</i>	<i>concinus</i>	(Mannerheim, 1852)
			<i>Pseudohylesinus</i>	<i>granulatus</i>	(LeConte, 1868)
			<i>Pseudopityophthorus</i>	<i>minutissimus</i>	(Zimmermann, 1868)
				<i>pruinosis</i>	(Eichhoff, 1878)
			<i>Scolytus</i>	<i>intricatus</i>	(Ratzeberg, 1837)
				<i>morawitzi</i>	(Semenov, 1902)
				<i>multistriatus</i>	(Marshall, 1802)
				<i>ratzeburgi</i>	(Janson, 1856)

	<i>rugulosus</i>	(Müller, 1818)
	<i>schevyrevi</i>	Semanov, 1902
	<i>scolytus</i>	(Fabricius, 1775)
	<i>ventralis</i>	LeConte, 1868
<i>Tomicus</i>	<i>destruens</i>	(Wollaston, 1865)
	<i>minor</i>	(Hartig, 1834)
	<i>piniperda</i>	(Linnaeus, 1758)
	<i>agnatum</i>	(Eggers, 1923)
<i>Truncaudum</i>	<i>domesticum</i>	(Linnaeus, 1758)
<i>Trypodendron</i>	<i>dispar</i>	(Fabricius, 1792)
<i>Xyleborus</i>	<i>ferrugineus</i>	(Fabricius, 1801)
	<i>fornicatus</i>	Eichhoff, 1868
	<i>glabratus</i>	Eichhoff, 1877
	<i>perforans</i>	(Wollaston, 1857)
	spp.	—
	<i>costatomorphus</i>	Schedl, 1950
	<i>monographus</i>	(Fabricius, 1792)
<i>Xylosandrus</i>	<i>compactus</i>	(Eichhoff, 1876)
	<i>crassiusculus</i>	(Motschulsky, 1866)
	<i>germanus</i>	(Blandford, 1894)
	<i>morigerus</i>	(Blandford, 1894)
<i>Xyloterinus</i>	<i>politus</i>	(Say, 1826)
<i>Xyloterus</i>	<i>lineatus</i>	(Olivier, 1795)

Subfamilies, genera and species are listed in alphabetical order within each family. All families except Carabidae belong to the suborder Polyphaga; the classification follows Table 11.1.

can expect threats to our food supply and global biodiversity (Allen-Wardell et al. 1998).

11.3.2 Beetles of Cultural Importance

Beetles have cultural significance to societies around the world. The most ubiquitous of these cultural practices is the use of beetles as a food and the traditions around that use. Beetles are recognized by most indigenous societies as good food. Onore (1997) found that at least 30 species of beetles were eaten in Ecuador, including many large and common beetles found near settlements in the Ecuadorian highlands. Smith and Paucar (2000) provide a detailed account of the traditions surrounding the eating of the scarab beetle *Platycoelia lutescens*. Based on these accounts, the practice of entomophagy seems to be widespread and important to Ecuadorian society, especially among the poor. Ecuadorians are generally familiar with how and when to collect and prepare these beetles for food (Smith and Paucar 2000). In another example, Utsunomiya and Masumoto (1999) found striking similarities between beetle consumption practices in northern Thailand and Ecuador. In northern Thailand, approximately 100 different species of beetles are eaten, with 89% of respondents listing “taste” as the answer to the question of why insects are eaten. Cultural traditions surrounding beetle consumption are not restricted to Ecuador and Thailand. They also have been observed in many other world cultures. However, these traditions might be in decline because of apparent disdain for eating insects in cultures of European origin, and competition with vertebrate-based agricultural production.

Perhaps the best-known use of beetles in mythology and religion is the sacred scarab of the ancient Egyptians. The scarab beetle symbol was used prominently over approximately 3000 years, from the First Dynasty (5000 years ago) (Cambefort 1994) to the conquest of Egypt by the Roman Empire. Ancient Egyptians likened the rolling of dung balls by dung beetles to the sun rolling across the sky each day. Because the sun was thought to be reborn each day, scarab beetles became powerful symbols of resurrection and

eternal life, which were prominent aspects of ancient Egyptian mythology. Through 3000 years of ancient Egyptian cultural development, an elaborate mythology developed around scarab beetles, including the incorporation of scarab pupation (likened to mummification) and other aspects of their natural history and life cycle into mythological stories. Cambefort (1994) gives a detailed review of all facets of the use of scarab beetles by ancient Egyptians. Kritsky (1991) and Cambefort (1994) reported that the carvings and symbols of Buprestidae and Elateridae also held meaning to the ancient Egyptians. They hypothesized that buprestids symbolized the Egyptian myth of rebirth, perhaps due to the emergence of adult beetles from the trunks of living trees.

In many countries, keeping personal beetle collections and live beetles are popular hobbies, especially in Europe, Japan, and North America. Beetles are a major component of the multimillion dollar insect trade. This trade is conducted by mail and Internet or at annual insect fairs in cities including Los Angeles, Paris, Prague, and Tokyo. Keeping live beetles is popular in Japan, where an industry provides not only live beetles, but the required food and paraphernalia for keeping them alive. Evidence for the popularity of this pastime in Japan can be seen on the website www.youtube.com, which features numerous Japanese videos of live beetles.

11.3.3 Beetles of Medical and Legal Importance

11.3.3.1 Medical Entomology

Blistering of human skin (dermatosis) can be caused by beetles of the families Meloidae, Oedemeridae, and Staphylinidae (*Paederus* and *Paederidus*) (Frank and Kanamitsu 1987, Nicholls et al. 1990). Dermatitis occurs when a beetle's hemolymph is released onto the skin after it is crushed or touched accidentally. The vesicant chemical compound in the body fluids of the Meloidae and Oedemeridae is cantharidin, whereas pederin is the vesicant in beetles of the genera *Paederus* and *Paederidus* (Mackie et al. 1945, Nichols et al. 1990, Piel et al. 2005). These

chemicals are generally used by the beetles against predators (Pinto and Bologna 2002).

Pederin belongs to a group of complex compounds found only in these staphylinid genera and a few marine sponges (Piel et al. 2004a). This compound is found only in females of some species and is thought to be produced by symbiotic bacteria (Kellner 2001). Research on the biosynthesis and mode of action of pederin has increased since the discovery that related compounds have potent antitumor properties (Piel et al. 2004a, b). Pederin inhibits protein biosynthesis in tumor cells, and the isolation of pederin-producing genes in these symbiotic bacteria might lead to the development of anticancer drugs (Piel et al. 2005).

Canthariasis is a term used to describe the infection of human internal organs by beetles. The most common type of canthariasis occurs when people accidentally or voluntarily ingest beetles. Accidental ingestions generally occur when people eat foods contaminated by stored-product pests. Adults, larvae, and cast skins can be ingested in this manner, resulting in irritation of the digestive system or allergic responses. The inadvertent ingestion of larder beetle larvae (*Dermestes lardarius*, Dermestidae), which are covered by long, narrow, and barbed setae, can cause diarrhea, abdominal pain, and perianal itch (Goddard 2000).

Deliberate ingestion of beetles for medicinal purposes also has also been reported. Cantharidin is a well-known insect-derived medicinal compound from the families Meloidae and Oedemeridae. The insect referred to as Spanish fly (*Lytta vesicatoria*) is a European meloid beetle. Dried, crushed beetles containing cantharidin have been ingested as a vesicant to treat ailments and as an aphrodisiac for millennia (Karras et al. 1996). Cantharidin can be toxic to humans, causing significant illness (Sandorini 2001). Ingestion of live darkling beetles (*Ullomoides dermestoides*) for similar purposes was reported from Southeast Asia (Sandroni 2001). The practice of ingesting uncooked beetles for food or medicine is risky because some are intermediate hosts for tapeworm and nematode parasites of vertebrates (Mackie et al. 1945, Lethbridge 1971, Halffter and

Matthews 1966), possibly including humans (Chu et al. 1977).

One type of canthariasis, called scarabiasis, refers to the short-term infestation of the human gut by adult dung beetles (Scarabaeidae). This condition usually affects preschool children in the tropics. The infestation begins when dung beetles fly into dwellings with sleeping children. Adult dung beetles, usually shorter than 1 cm, follow the smell of feces and are thought to enter the anus and feed internally (Arrow 1931, Halffter and Matthews 1966). Adult beetles are often seen flying away from newly passed stool (Rajapakse 1981). Other types of canthariasis involve the infrequent cutaneous, nasal, ocular, and urinary infections of humans caused by beetle eggs, larvae, or adults (Mackie et al. 1945).

Several families of elateroid beetles produce light, using a biochemical reaction (Lloyd 1983, Viviani 2002). Light is produced when enzymes called luciferases catalyze the oxidization of luciferin compounds. Beetles principally use this cold light, called bioluminescence, for sexual communication, although other possible functions, including aposematic signals, attraction of prey, and defense, are possible (Lloyd 1983, Underwood et al. 1997). Studies of firefly (Lampyridae) light production have resulted in the development of several medical applications, based on the use of luciferases and their associated genes. These applications range from monitoring the progress of infections such as HIV (Contag et al. 1997) to visualizing living cells in human embryonic development (Greer and Szalay 2002). Luciferases have played a significant role in the development of more efficient drugs for many diseases (Viviani 2002).

11.3.3.2 Forensic Entomology

The major contribution of insects in criminal cases involving homicide is to estimate the limits of the postmortem interval (time between death and discovery of the body). Flies are dominant on human corpses, although several groups of beetles are also often present, either preying on other arthropods or feeding on the body itself (Smith 1986, Catts and Haskell 1990).

The postmortem interval is usually estimated from experimental studies using pigs or other vertebrates, and then applied to human corpses in criminal cases (Tabor et al. 2004, Arnaldos et al. 2005). The period of development of the beetles and the succession of species that colonize carcasses in various stages of decomposition provide data for estimating the postmortem interval (Franc et al. 1989, Moura et al. 1997, Carvalho et al. 2000, Turchetto and Vanin 2004). The succession of beetle species tends to follow a rough pattern from an initial fresh stage of decomposition through bloated and active decay stages to a final dry stage. The Dermestidae (skin beetles) and Cleridae (bone beetles) are among the most common beetles on corpses and have provided important postmortem information, especially for finds of dry skeletal remains (de Souza and Linhares 1997, Kulshresta and Satpathy 2001).

Although most experimental postmortem-interval studies use bodies on the ground surface, some research has examined buried or submerged bodies (Smith 1986). A few beetles (e.g., Histeridae, Silphidae, and Staphylinidae) are associated with buried bodies (Payne et al. 1968, VanLaerhoven and Anderson 1999, Bourel et al. 2004). Molecular and toxicological analyses show that necrophagous beetles also could be informative for criminal cases involving badly decomposed bodies (DiZinno et al. 2002), movement of bodies (Benecke 1998), and bodies with toxic substances (e.g., drugs, heavy metals, and poisons) (Bourel et al. 2001, Gagliano-Candela and Aventaggiato 2001).

11.3.4 Beetles as Research Tools

Beetles are used widely as research tools in biophysics and related disciplines. Because they are the most diverse animal order, beetles possess great potential for bioengineering studies. Geometry and mechanics of elytral opening and closing are studied by aeronautic and astronautic engineers (Frantsevich et al. 2005). Whirligig beetles (Gyrinidae), roughly 1 cm in length, swim on

the water surface at 55 cm per second and are capable of making 12 horizontal rotations per second (Fish and Nicastrò 2003), which would be a dream performance for any human-made autonomous device. Aquatic larvae of *Hydrobius fuscipes* (Hydrophilidae) demonstrate how simple side-to-side body swimming movements allow a novel kind of limbless skating on the lower surface of the water, with tracheal gills acting as anchors (Brackenbury 1999). Walking mechanics in *Pachnoda marginata* (Scarabaeidae) involve friction forces between the tarsal claw systems and walking substrates (Dai et al. 2002). Specialized insect adhesive devices, such as the arolium, euplantulae, pulvilli, and tarsal hairs (Gorb 2001), inspire engineers to develop novel adhesive surfaces. Legs of the leaf beetle *Gratiana spadicæa* (Chrysomelidae) attach to leaf surfaces by matching tarsal claw aperture with that of pointed rays of the host-plant trichomes (Medeiros and Moreira 2002). Wide, bilobed tarsi of rove beetles in the genus *Stenus* (Staphylinidae) allow the beetles to run well on solid surfaces or water (Betz 2002).

The high diversity of beetles makes them useful tools for physiological research. Studies of muscle function in arthropods, using the beetle *Cotinis mutabilis* (Scarabaeidae), suggest that asynchronous flight muscles can provide greater power output than can synchronous muscles for operation at the high-contraction frequencies of insect flight (Josephson et al. 2001). Some dung-rolling scarab beetles (*Scarabaeus* species) possess a strong sensitivity to polarized light, a sense lacking in humans. The crepuscular beetle *Scarabaeus zambesianus* rolls dung balls away from the dung pile to avoid competition, navigating by polarized skylight sensed by specialized ommatidia of the dorsal rims of its eyes (Dacke et al. 2003). Biophysical and behavioral studies of bioluminescent insects, including click beetles (Elateridae) and fireflies (Lampyridae), provide insights into the evolution of color vision (Stolz 2003, Booth et al. 2004). Discoveries of the abilities of tiger and scarab beetles (Carabidae: Cicindelinae and Scarabaeidae) to use paired membranous ears to detect airborne sounds

(Forrest et al. 1997) shed light on the evolution of this sense in the Animalia.

Many phytophagous beetles rely on aggregation pheromones to coordinate behaviors. Bark beetles use pheromones to coordinate attacks on host trees (Raffa and Berryman 1983). The discovery of the first pheromone for the Colorado potato beetle, *Leptinotarsa decemlineata*, is unusual because it is the first male-produced pheromone known in the Chrysomelidae (Dickens et al. 2002). In longhorn beetles (Cerambycidae), males use sex pheromones to attract females or aggregate (Lacey et al. 2004).

Beetles are particularly important research tools for biochemistry and DNA research. *Tribolium castaneum*, the red flour beetle (Tenebrionidae), commonly consumes stored grains worldwide. Like the famous fruit fly, *Drosophila melanogaster*, it is used widely in genetics and developmental biology research, and was the first beetle species whose complete genome sequence was published. Its genome consists of about 200 million nucleotides arranged in a haploid set of 10 chromosomes. For comparison, the human genome has about 15 times more nucleotides and a haploid set of 23 chromosomes. *Tribolium castaneum* was the first animal reported to produce inhibitors of prostaglandin synthetase, which were purified from the beetle's defensive secretions (Howard et al. 1986). These substances are used widely in aspirin-like anti-inflammatory drugs. This beetle is also intensively studied as a model for understanding the mechanisms of insect resistance to insecticides.

Using beetles as research tools sheds light on bizarre aspects of evolution, some of which are unique. For example, *Micromalthus debilis*, the sole North American member of the family Micromalthidae, possesses one of the most bizarre life cycles in the Metazoa. This species combines both thelytokous and viviparous larviform diploid females and rare haploid males, which eat and kill their own mothers from inside (Pollock and Normark 2002). The second known case of haplodiploid sex determination in beetles is that of

some scolytine weevils including *Ozopemon* from Southeast Asia, which is also the only beetle genus with neotenic and strangely modified larviform males (once thought to be Histeridae) (Jordal et al. 2002). The huge diversity of ecological relationships with other organisms makes beetles ideal for researching the origins of sociality (Scott 1998), parasitism (Weber et al. 2006), symbiosis (Kellner 2003), and phoresy (Bologna and Pinto 2001).

Beetle groups with well-resolved phylogenies also allow biogeographical and paleogeographical reconstructions. Most commonly, these reconstructions are achieved using DNA data for species with weak dispersal capacities, such as flightless *Scarabaeus* dung beetles (Scarabaeidae), which show grades of colonization of the Namib Desert during the Miocene (Sole et al. 2005). Phylogenetic trees inferred from *Nesotes* darkling beetle (Tenebrionidae) mitochondrial DNA (mtDNA) suggested how the genus colonized the Canary Islands (Rees et al. 2001). The well-resolved phylogeny of endemic Iberian diving beetles (Dytiscidae) indicated that their speciation was induced by repeated fragmentation of populations during glacial and interglacial periods (Ribera and Vogler 2004). Patterns of insect colonization of Pacific islands were deduced based on the distribution and phylogeny of Colymbetinae diving beetles (Dytiscidae) on New Caledonia and Fiji (Balke et al. 2007). Analysis of fossil and subfossil chitinous remains of beetles in Quaternary sediments (1.8 mya–present) provides quantitative estimates of ancient temperatures and precipitation levels (Porch and Elias 2000). All these studies capitalized on the diversity and relative abundance of beetles to focus on more inclusive natural phenomena.

Fireflies (Lampyridae) are central to bioluminescence research (McElroy and DeLuca 1983, Viviani 2002). In addition to its medical applications, bioluminescence research has yielded several other commercial applications. For example, luciferases are routinely used as environmental biosensors to monitor levels of pollutants such as agrochemicals, lead, and mercury (Naylor 1999).

11.3.4.1 DNA Barcoding of Beetles – A North American Case Study

Beetles represent one of the taxonomically better-known major orders of North American insects. Diversity estimates are available from Bousquet et al. (2013) for Canada and from Arnett and Thomas (2000), Arnett et al. (2002), and Marske and Ivie (2003) for North America as a whole. A concerted effort was recently initiated to document the diversity of beetles in North America using DNA barcodes. Here, we examine its progress, expand on some findings, and discuss remaining gaps in barcoding coverage.

The Canadian National Collection of Insects, Arachnids, and Nematodes (CNC; Ottawa, Ontario, Canada) has recently (2010–14) collaborated with the International Barcode of Life Project (University of Guelph, Ontario, Canada) to build a barcode-sequence library for the beetles of Canada. Secondarily, many beetle taxa have been barcoded from the United States to increase North American coverage. This effort was central to increasing the number of North American beetle species with high-quality barcode data (> 500 base pairs of the cytochrome oxidase subunit I gene (COI)) in the Barcode of Life Data System (BOLD: <http://www.boldsystems.org>) from 1613 to 6905.

The barcoding diversity and coverage were examined using the barcoding index number (BIN) system in BOLD detailed by Ratnasingham and Hebert (2013). BINs can approximate species diversity well, but are discordant with current taxonomy in roughly 10% of cases (Ratnasingham and Hebert 2013). According to Ratnasingham and Hebert (2013), these limitations are due to four main factors: taxonomic error, sequence contamination, problems with the BIN calculation methodology, and lack of COI-sequence variation due to introgression or their evolutionarily young age. In our observations, misidentification of specimens is also a confounding factor when working with the BOLD data, as samples come from multiple sources and are not all identified by experts. For this study, barcodes were only considered if they

met the 500 base-pair threshold for quality, following Ratnasingham and Hebert (2013).

The barcoding coverage for the beetles of Canada and North America is summarized in Table 11.4, Fig. 11.3, and Fig. 11.4. The number of BINs divided by the number of known species approximates barcoding coverage well, with a few caveats. First, the number of known species is only an approximation for most North American families, as there are still many gaps in basic taxonomic knowledge of these groups. The number of known species is less than the actual number of species for most families because many North American families have not undergone thorough taxonomic revisions and many beetle species remain undescribed. In addition, the number of BINs contains a degree of error for the reasons mentioned above, and overestimates or underestimates the actual number of species sampled roughly 10% of the time. Beyond this, barcoding sampling of North American beetles is still in its early stages and lacks coverage of much of the observed variation in described species.

Our results show that 49.7% of described Canadian beetle species and 27.4% of North American beetle species have been barcoded in BOLD. The percentage is significantly higher for Canada, reflecting the specific efforts there and the lower diversity at northern latitudes. Our general observations of the coverage are what one might expect: easily collected taxa (abundant, easily observed, and with a wide distribution) are well represented, whereas difficult to collect taxa (rare, cryptic habits, and with limited distribution) are poorly represented. The former is exemplified by the Silphidae and Geotrupidae (76.7% and 78.6% North American coverage, respectively), as these families are relatively well known and have low diversity in North America, and most species are fairly widespread, readily observed and collected, and easily attracted to traps. The latter is exemplified by the Histeridae and Ripiphoridae (3.9% and 5.9% North American coverage, respectively), as these families are also reasonably well known taxonomically but have

Table 11.4 Estimated number of Coleoptera species for North America and Canada, with the associated number of DNA-barcoding BINs and the calculated percent regional barcoding coverage.

Suborder	Superfamily	Family	North America species	North America BINs	North America percentage coverage	Canada species	Canada BINs	Canada percentage coverage
Archostemata	—	Cupedidae	4	4	100.00	3	3	100.00
		Micromalthidae	1	1	100.00	1	0	0.00
Myxophaga	Sphaeriusoidea	Hydroscaphidae	1	0	0.00	0	0	0.00
		Sphaeriusidae	3	1	33.33	0	0	0.00
Adephaga	—	Gyrinidae	56	33	58.93	34	25	73.53
		Trachypachidae	4	2	50.00	2	2	100.00
		Rhyssodidae	8	3	37.5	2	1	50.00
		Carabidae	2,402	929	38.68	989	581	58.75
		Halplidae	67	15	22.39	34	10	29.41
		Noteridae	14	1	7.14	2	1	50.00
		Amphizoidea	3	2	66.67	3	2	66.67
		Dytiscidae	513	196	38.21	284	162	57.04
		Hydrophilidae	258	124	48.06	151	79	52.32
		Sphaeritidae	1	0	0.00	1	0	0.00
Polyphaga	Hydrophiloidea	Histeridae	435	17	3.91	136	8	5.88
		Hydraenidae	67	5	7.46	27	4	14.81
		Ptiliidae	117	30	25.64	49	29	59.18
		Agyrtidae	11	2	18.18	8	1	12.50
		Letodidae	324	87	26.85	182	71	39.01
		Silphidae	30	23	76.67	26	18	69.23
		Staphylinidae	4,370	939	21.49	1,682	736	43.76
		Pleocomidae	27	0	0.00	0	0	0.00
		Geotrupidae	28	22	78.57	12	8	66.67
		Passalidae	4	1	25.00	1	0	0.00

(Continued)

Table 11.4 (Continued)

Suborder	Superfamily	Family	North America species	North America BINs	North America percentage coverage	Canada species	Canada BINs	Canada percentage coverage
		Trogidae	43	11	25.58	15	4	26.67
		Glareidae	25	4	16.00	2	0	0.00
		Diphylostomatidae	3	0	0.00	0	0	0.00
		Lucanidae	26	10	38.46	14	8	57.14
		Ochodaeidae	35	6	17.14	4	1	25.00
		Hybosoridae	5	4	80.00	1	1	100.00
		Glaphyridae	8	1	12.50	1	0	0.00
		Scarabaeidae	1,700	586	34.47	221	143	64.71
	Scirtoidea	Eucinetidae	11	6	54.55	7	6	85.71
		Clambidae	12	3	25.00	7	3	42.86
		Scirtidae	50	34	68.00	25	31	124.00
	Dascilloidea	Dascillidae	5	0	0.00	0	0	0.00
		Rhipiceridae	5	1	20.00	1	0	0.00
	Buprestoidea	Schizopodidae	7	0	0.00	0	0	0.00
		Buprestidae	762	171	22.44	177	91	51.41
	Byrrhoidea	Byrrhidae	35	21	60.00	26	18	69.23
		Elmidae	99	25	25.25	32	7	21.88
		Dryopidae	13	0	0.00	6	0	0.00
		Lutrochidae	3	0	0.00	1	0	0.00
		Limnichidae	28	0	0.00	3	0	0.00
		Heteroceridae	34	16	47.06	28	8	28.57
		Psephenidae	16	6	37.50	4	2	50.00
		Ptilodactylidae	19	10	52.63	4	6	150.00
		Chelonariidae	1	0	0.00	0	0	0.00
		Eulichadidae	1	0	0.00	0	0	0.00

	Callirhipidae	1	0	0.00	0	0	0.00
Elateroidea	Artematopodidae	8	8	100.00	5	5	100.00
	Brachysectridae	1	0	0.00	0	0	0.00
	Cerophytidae	2	0	0.00	0	0	0.00
	Eucnemidae	85	17	20.00	38	14	36.84
	Throscidae	20	21	105.00	8	17	212.50
	Elaterridae	965	436	45.18	386	238	61.66
	Lycidae	76	37	48.68	29	24	82.76
	Telegeusidae	3	0	0.00	0	0	0.00
	Phengodidae	23	9	39.13	1	2	200.00
	Lampyridae	124	48	38.71	32	24	75.00
	Omethidae	10	0	0.00	0	0	0.00
	Cantharidae	473	116	24.52	154	92	59.74
Derodontoidea	Derodontidae	9	5	55.56	8	4	50.00
	Nosodendridae	4	0	0.00	2	0	0.00
	Jacobsoniidae	1	0	0.00	0	0	0.00
Bostrichoidea	Dermestidae	117	29	24.79	49	24	48.98
	Endecatomiidae	2	0	0.00	1	0	0.00
	Bostrichidae	75	20	26.67	24	7	29.17
	Ptinidae	471	48	10.19	98	31	31.63
Lymexyloidea	Lymexyloidae	2	1	50.00	1	1	100.00
Cleroidea	Trogossitidae	59	11	18.64	22	2	9.09
	Cleridae	243	44	18.11	52	22	42.31
	Melyridae	520	85	16.35	53	23	43.40
Cucujoidea	Byturidae	2	1	50.00	1	1	100.00
	Sphindidae	9	5	55.56	6	4	66.67
	Biphyllidae	3	0	0.00	1	0	0.00
	Erotylidae	82	28	34.15	28	14	50.00
	Monotomidae	55	11	20.00	27	8	29.63

(Continued)

Table 11.4 (Continued)

Suborder	Superfamily	Family	North America species	North America BINs	North America percentage coverage	Canada species	Canada BINs	Canada percentage coverage
		Cryptophagidae	145	50	34.48	73	46	63.01
		Silvanidae	32	6	18.75	16	5	31.25
		Cucujidae	8	5	62.50	8	5	62.50
		Passandridae	3	0	0.00	1	0	0.00
		Phalacridae	122	14	11.48	8	10	125.00
		Laemophloeidae	52	5	9.62	13	3	23.08
		Kateretidae	11	4	36.36	8	3	37.50
		Nitidulidae	173	72	41.62	101	57	56.44
		Smicripidae	2	0	0.00	0	0	0.00
		Bothriideridae	18	0	0.00	4	0	0.00
		Cerylonidae	19	3	15.79	8	3	37.50
		Endomychidae	45	8	17.78	16	6	37.50
		Coccinellidae	481	147	30.56	161	109	67.70
		Corylophidae	61	13	21.31	16	13	81.25
		Latridiidae	140	67	47.86	64	58	90.63
Tenebrionoidea		Mycetophagidae	26	11	42.31	16	8	50.00
		Archeocrypticidae	1	0	0.00	0	0	0.00
		Ciidae	84	15	17.86	29	10	34.48
		Tetratomidae	26	7	26.92	20	6	30.00
		Melandryidae	50	27	54.00	43	26	60.47
		Mordellidae	189	96	50.79	75	59	78.67
		Rhiphoridae	51	3	5.88	11	2	18.18
		Zopheridae	36	11	30.56	19	4	21.05
		Tenebrionidae	1,184	350	29.56	141	69	48.94

Prostomidae	1	0	0.00	1	0	0.00
Synchroidae	2	2	100.00	2	2	100.00
Stenotrachelidae	10	6	60.00	9	5	55.56
Oedemeridae	87	6	6.90	13	4	30.77
Meloidae	424	55	12.97	47	25	53.19
Mycteridae	12	1	8.33	4	1	25.00
Boridae	2	1	50.00	2	1	50.00
Pythidae	7	7	100.00	6	6	100.00
Pyrochroidae	50	13	26.00	22	13	59.09
Salpingidae	20	5	25.00	15	4	26.67
Anthicidae	229	61	26.64	65	27	41.54
Aderidae	48	2	4.17	10	1	10.00
Scrautiidae	49	39	79.59	22	36	163.64
Cerambycidae	958	301	31.42	368	198	53.80
Megalopodidae	9	3	33.33	7	3	42.86
Orsodacnidae	4	1	25.00	1	1	100.00
Chrysomelidae	1,869	487	26.06	598	266	44.48
Nemonychidae	15	8	53.33	8	6	75.00
Anthrribidae	88	22	25.00	20	13	65.00
Belidae	2	0	0.00	0	0	0.00
Attelabidae	51	25	49.02	14	13	92.86
Brentidae	152	87	57.24	49	50	102.04
Dryophthoridae	84	17	20.24	27	7	25.93
Brachyceridae	41	25	60.98	19	11	57.89
Curculionidae	2,794	474	16.96	823	274	33.29
Total	25,106	6,894	27.46	8,237	4,096	49.73

Numbers originate from Arnett and Thomas (2000), Arnett et al. (2002), and Marske and Ivie (2003) for North American species; Bousquet et al. (2013) for Canadian species; and the Barcode of Life Data System (BOLD: <http://www.boldsystems.org>) for North American and Canadian barcoding index numbers (BINs).

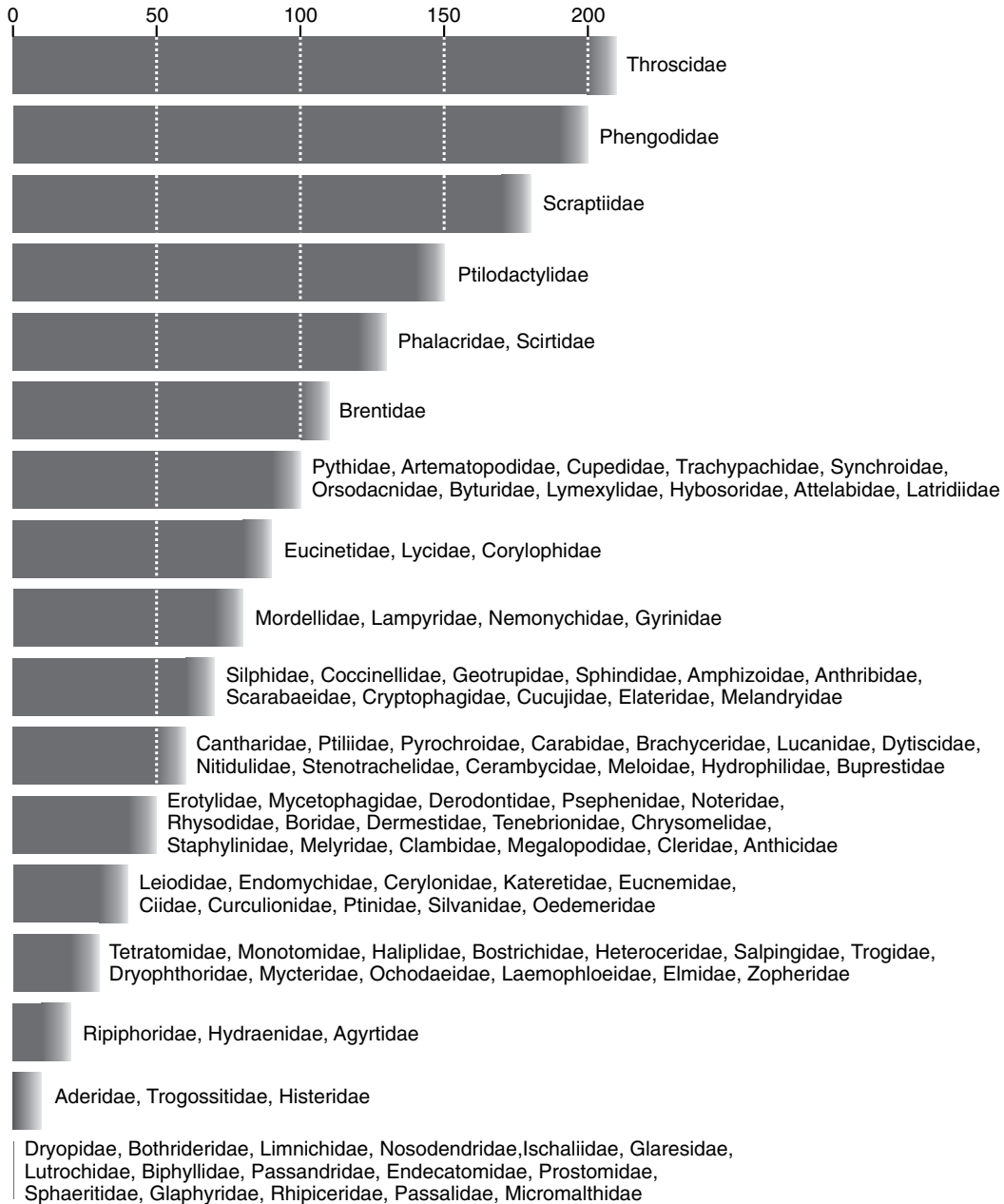


Figure 11.3 Percentage (aggregated in 10% increments) of Canadian Coleoptera species included in the Barcode of Life Data System (BOLD: <http://www.boldsystems.org>). Percentage coverage is the number of barcoding index numbers (BINs) for a family divided by the number of known species (from Table 11.4). Percentage coverage values of more than 100% indicate poorly known groups in need of further taxonomic and survey research.

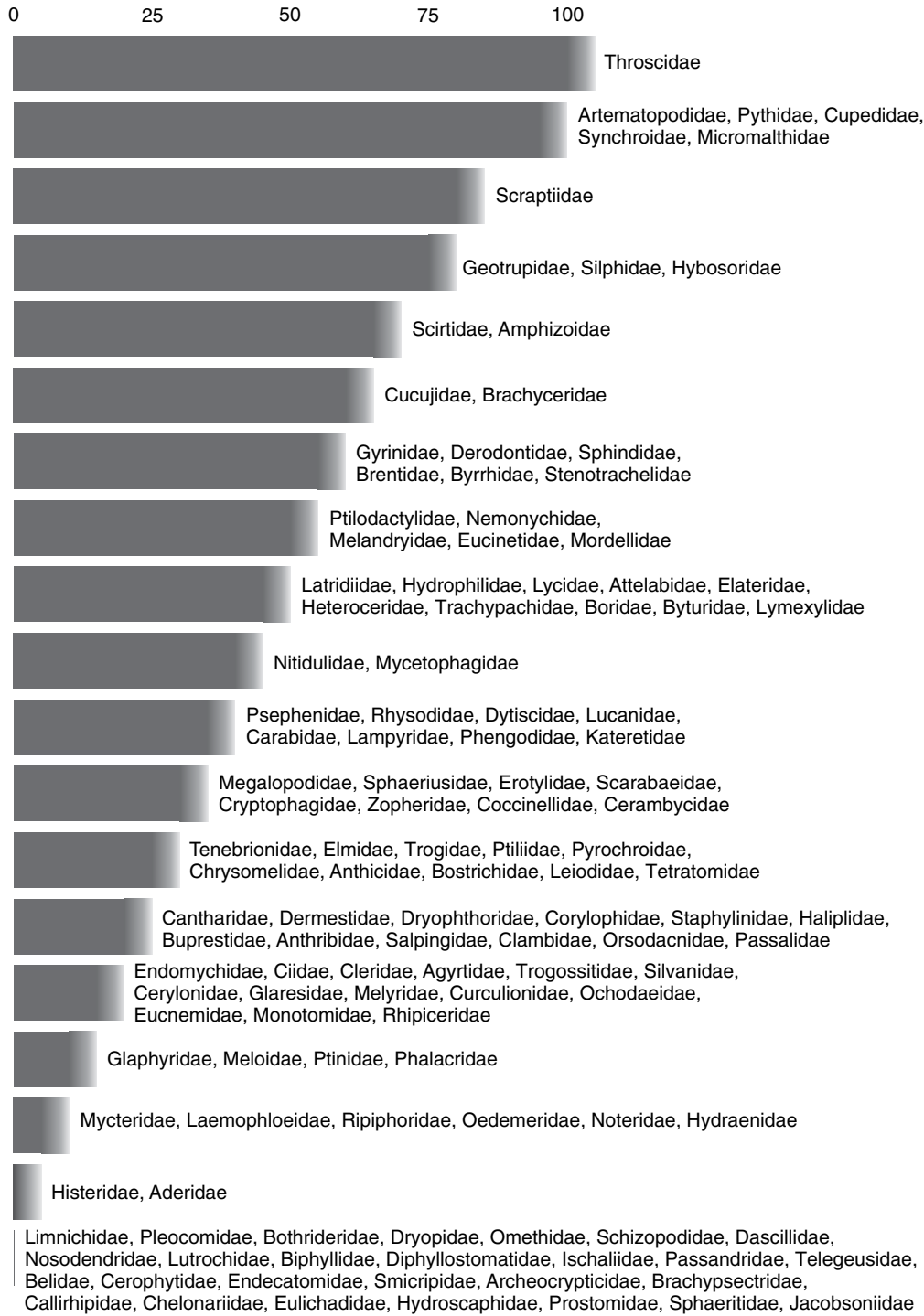


Figure 11.4 Percentage (aggregated in 5% increments) of North American Coleoptera species included in the Barcode of Life Data System (BOLD: <http://www.boldsystems.org>). Percentage coverage is the number of barcoding index numbers (BINs) for a family divided by the number of known species (from Table 11.4). Percentage coverage values of more than 100% indicate poorly known groups in need of further taxonomic and survey research.

many species with cryptic habits; they either burrow in substrates or are myrmecophiles (Histeridae), termitophiles (Histeridae), or parasitoids (Rhipiphoridae). As such, many species in these families have short activity periods as adults and are difficult to collect without taxon-specific techniques. Other examples of taxa with no barcode coverage are the families Pleocomidae and Diphyllostomatidae, both of which are endemic to the West Coast of North America, with small distributions, and are not generally found unless collectors specifically seek them. Of the 129 North American beetle families, 27 (21%) are not yet represented with high-quality barcoding data in BOLD, but most of these families are known only from one to three species with restricted distributions.

For the Canadian fauna, there was an early initiative from 2006 to 2010 to do a barcode inventory of the beetles of Churchill, Manitoba (Woodcock *et al.* 2013). The resulting data set was augmented by the Biodiversity Institute of Ontario through intensive sampling around Guelph, Ontario, Canada, and additional sampling mainly in national parks across Canada. In 2011, a joint effort between the Biodiversity Institute of Ontario and the CNC was initiated to barcode Canadian beetle taxa using pinned specimens in the collection. A first run through all taxa was completed in 2014, with additional sampling still ongoing. The results of these combined efforts yielded 50% barcoding coverage of Canadian beetle species. This level of coverage is higher than for all of North America to the point where most common or widespread species are represented by barcodes. Barcode coverage of 50% of described species or more has been achieved for 57 of the 112 families of Canadian beetles, including diverse families such as the Carabidae, Cerambycidae, and Elateridae. Significant gaps in coverage remain for three of the most diverse families: Chrysomelidae, Curculionidae, and Staphylinidae, which have less than 50% barcode coverage for Canadian species. The gaps in coverage could be efficiently addressed by targeting these groups for future work.

Some families are so poorly known that general barcode efforts have already found many more BINs than the number of described species. This is so for the families Scirtidae, Scaptiidae, and Throscidae, which have 105.0%, 84.8%, and 68.0% barcoding coverage for North America and 212.5%, 180.0%, and 124.0% for Canada. It is obvious from examining the barcoding data that many more species are present in the focal regions than are indicated by the number of described species. These families and others are fertile ground for taxonomists, and highlight the poor state of taxonomy in the backyards of some of the top entomology museum collections in the world.

Two North American genera, *Phyllophaga* and *Serica* (Scarabaeidae: Melolonthinae), were examined for BIN discordance. They were selected because of their high diversity (212 and 100 North American species, respectively; Evans and Smith 2009), with low variation in external morphology. These two factors make these genera likely to have poor COI lineage sorting between species because their similar morphologies suggest that their diversity is a result of a recent speciation explosion. The identification of species in these genera can be accurate using the highly diagnostic genitalic characters. Among BOLD specimens, 16 of the 143 *Phyllophaga* BINs and four of the 36 *Serica* BINs were tagged as discordant, with more than one species based on morphology included (both approximately 11%). This percentage is in line with the findings of Ratnasingham and Hebert (2013) and probably represents the high end of expected BIN discordance error for a group with high recent speciation and poor lineage sorting (whereby descendants of an ancestor species inherit different subsets of variants of the ancestral mitochondrial genome). A good case study for Coleoptera would be to determine whether this percentage changes when more species and more specimens within species are sampled.

DNA Barcoding Detects New Invasive Species Any inventory work can detect new taxa for a focal region, including new species, range extensions, or invasive species. Our analysis of the

barcoding data for North American Coleoptera detected a new invasive species in Canada.

Anthribus nebulosus (Anthribidae) is a predator of scale insects (Hemiptera: Sternorrhyncha), that was intentionally introduced to Virginia, United States, in 1978–79. It is thought to have been introduced elsewhere in North America because of its disjunct distribution (Hoebeke and Wheeler 1991). This Eurasian species also has been recorded from southern New England (Hoebeke and Wheeler 1991) and adjacent regions of Pennsylvania and New Jersey (<http://bugguide.net/node/view/278376/data>). The barcoding records from in and around Guelph, Ontario, Canada, were unexpected because this species had not been observed to spread rapidly and was not first detected in Canada near known localities in the United States. It is unclear whether this disjunct distributional record is a result of a local introduction or an undetected general expansion of the species range. Specimens of *A. nebulosus* were collected in and near Guelph in three separate collecting events and barcoded as part of general survey and inventory efforts. The barcoding data were included in overall Coleoptera and Curculionoidea analyses and were a match within a BIN including identified specimens from Germany. Robert Anderson (Canadian Museum of Nature, Ottawa, Ontario, Canada) confirmed the identification of Guelph specimens. Additional specimens from Ontario in the same BIN were collected in Rouge River National Urban Park and on Beausoleil Island (collectively new country and provincial records).

A false-positive record for an invasive species resulted from a BIN from the root weevil genus *Polydrusus* (Curculionidae: Entiminae), which is widespread globally. Four native and three invasive species are known from North America (Anderson 2002). Specimens from Point Pelee, Guelph, and Rouge River, Ontario, Canada, were collected as part of a general survey to build the barcode library. Our analysis of barcoding data revealed that these specimens shared a BIN with German specimens identified as *Polydrusus corruscus*. This is a Eurasian

willow-feeding species (*Salix*), not previously known from North America. The Ontario specimens deposited in the Biodiversity Institute of Ontario were examined and identified as *Polydrusus impressifrons*, an invasive species previously recorded from North America. The error seems to have originated from misidentified German specimens. This case shows the need to verify identifications of specimens in BOLD before using its results to infer new records of invasive species or other discoveries.

DNA Barcoding Reexamines Species Limits of Holarctic Taxa

Species with a Holarctic distribution are fairly common. Depending on their range and dispersal histories, Nearctic and Palearctic populations of apparent Holarctic species might have been isolated long enough for lineage sorting to occur in fast-evolving gene regions and for the two populations to diverge enough to be considered separate species. Barcoding can be a rapid way to test for such cryptic species. When the Palearctic and Nearctic specimens are sorted to separate BINs, these species should be studied further to determine whether they are different species, using an integrative taxonomic approach. If the barcoding results are supported by morphological, host plant, behavioral, or other characters, then broad-based support has been achieved and the two species should be considered distinct and valid.

The barcoding survey and inventory work in North America and Eurasia has examined numerous Holarctic beetle species. Barcoding has detected two separate BINs (one North American and the other Eurasian) for some species that were formerly considered Holarctic. Species in this category include *Ampedus nigritinus* (Elateridae), *Dictyoptera aurora* (Lycidae), *Grypus equiseti* (Brachyceridae), *Tournotaris bimaculata* (Brachyceridae), and *Dryocoetes autographus* (Curculionidae: Scolytinae). These species should be further investigated to determine whether other data sets support splitting them into separate North American and Eurasian species.

Looking at one specific example, Wood (1982) commented that with *D. autographus*, “The American specimens tend to have the frons more sparsely granulate, the strial punctures slightly larger and not as deep, and the elytral declivity slightly more convex than the European material. The differences are slight, variable, and not suitable for statistical analysis; therefore, I prefer to follow Bright (1963) and recognize only one species.” These recognized morphological differences coupled with the barcoding results suggest a possible basis for considering the Palearctic and Nearctic populations as two separate species.

Also detected were two examples of species with three different BINs for populations in Eurasia, Alaska, and Canada: *Berninelsonius hyperboreus* (Elateridae) and *Eutrichapion viciae* (Brentidae). These examples could indicate multiple cryptic species, or perhaps a slow postglacial range expansion with subsequent population isolation and DNA lineage sorting. More evidence is required to determine the number of species present.

Adventive beetle species in North America also were analyzed, and some had separate BINs for their North American and Eurasian populations. These species include *Brachypterus urticae* (Kateretidae), *Anthocomus equestris* (Melyridae), *Ischnopterapion loti* (Brentidae), and *Tanysphyrus lemnae* (Brachyceridae). More research is needed to explain these genetic distinctions. Possible explanations include misidentifications (as described for *Polydrusus*), and the possibility that the source populations include multiple cryptic species (e.g., *Rhyssemus* and *Aphodius* (Scarabaeidae)). It is also possible that the adventive population originated from a source population with an as-yet-undetected haplotype (i.e., BIN).

DNA Barcoding is Part of the Integrative Taxonomic Approach to Delimiting Species Barcoding and DNA sequence analysis have become a key component of the integrative taxonomic approach to delimiting species. One example is the recent recognition of the scarabs *Rhyssemus*

germanus and *Rhyssemus puncticollis* as separate species, both occurring in Europe and the latter also occurring in North America. *Rhyssemus germanus* was described from Germany, and Brown described *R. puncticollis* much later from Canada. In his description of *R. puncticollis*, Brown (1929) did not mention *R. germanus* or any other Palearctic species, implying that this species was endemic to the Nearctic region. Brown (1950) later synonymized his own species under *R. germanus*, stating that “this species has not been reported previously from America under the name *germanus*, but comparison of the types of *puncticollis* with European specimens shows the names to be synonymous.” The assumption that *R. germanus* was an invasive species to North America, with *R. puncticollis* as a synonym, was supported by Gordon and Cartwright (1980) and others until recently.

Rößner (2012) and Kral and Rakovič (2012) recognized consistent morphological differences between *R. germanus* and *R. puncticollis* and revalidated the latter as a valid species, which they record from Germany and the Czech Republic. Barcoding data corroborate the revalidation of *R. puncticollis*, showing separate BINs for *R. germanus* (German specimens) and *R. puncticollis* (German and Ontario specimens). Independent confirmation robustly supports the hypothesis of two separate and valid species. This new evidence allows researchers to assess whether the true *R. germanus* occurs in North America and whether *R. puncticollis* is actually invasive to North America. Four synonyms based on European specimens need to be reexamined to determine whether they apply to *R. germanus* or *R. puncticollis*.

Another case involves the cryptic dung-feeding scarab species *Aphodius fimetarius* and *Aphodius pedellus*. Until recently, these two species were together named *A. fimetarius*, thought to be native to Europe and invasive to North America. Wilson (2001) found two chromosomal karyotypes in the specimens from Europe and presented subtle morphological characters to support the hypothesis of two

cryptic species. This work was supported and expanded by Miraldo et al. (2014), who included specimens from across the entire range, examined COI mtDNA data, and made an in-depth morphological analysis along with the karyotypic analysis.

Barcoding data from BOLD corroborate the findings of Miraldo et al. (2014), with two clear BINs for *A. fimetarius* from Europe and California and *A. pedellus* from Europe and Canada. *Aphodius fimetarius* and *A. pedellus* are now understood to be cryptic species; both species occur in Europe and North America and both may be invasive to North America. This example highlights how integrative taxonomy and barcoding can reveal cryptic species among common, widespread taxa.

DNA Barcoding Identifies Taxonomic Gaps in Groups with Underestimated Biodiversity The families Scirtidae, Scaptiidae, and Throscidae were identified above as groups where barcoding exposed much hidden species richness. At the generic level, a few spectacular examples are *Ptiliolum* (Ptiliidae), *Cyphon* (Scirtidae), *Trixagus* (Throscidae), and *Anaspis* (Scaptiidae). *Ptiliolum* is known from five species in Canada (Bousquet et al. 2013), but pre-barcoding estimates found “numerous undescribed species occurring in northern and western United States and Canada” (Hall 2000). We found five BINs of *Ptiliolum* from Alberta and Saskatchewan, Canada, although only one species is known from Alberta and none from Saskatchewan (Bousquet et al. 2013). As Hall (2000) indicated, this genus requires taxonomic study because there are many undescribed North American species.

The genus *Cyphon* is also in need of taxonomic revision. Young (2002) commented that the genitalic characters are diagnostic but that the external morphology is homogenous among species so that every specimen requires dissection to confirm identifications. This situation has probably led to the poor taxonomy of this group. The barcoding data yield 21 BINs from North America, and Young (2002) mentions 27 described species. The geographic distribution

of the described species disagrees with that of the BINs, and there are many more BINs than there are described species in Canada, indicating many undescribed North American species.

The genus *Trixagus* was last revised by Yensen (1975) and has six known species in North America, according to Johnson (2002), who cautioned that “this family is in need of general study at all levels.” Using the barcoding data, we found 13 clear North American *Trixagus* BINs. This genus is at least twice as diverse in North America as the taxonomic literature indicates. Because most of the barcoding samples were taken from Canada, we can anticipate more undetected BINs and species in the generally more diverse United States. Yensen (1975) commented that there was much variation in his species definitions, suggesting several cryptic species, as do the barcoding data. The North American Throscidae need a complete taxonomic overhaul. Even with the moderate and general focus of the barcoding to date, the number of North American throscid BINs in BOLD already exceeds the number of known species. This family would be an excellent focal taxon for any taxonomist interested in describing many new North American species.

Anaspis has 13 known North American species but has never undergone a taxonomic revision, and authors have disagreed on whether the genus should be divided into four genera (Pollock 2002). Our barcoding data have recovered 13 BINs from North America, but few specimens from these BINs match any of the described species; they also differ in distribution from the described species. Thus, several North American species in this genus remain undescribed.

Overall, building the barcode library for North American Coleoptera has reached a point where the data are useful in many ways. Most common or widespread species have been barcoded, so clear matches are likely for any new, unidentified specimens compared with BOLD. The barcoding data also help users detect invasive species, re-examine species delimitations, identify cryptic species through

integrative taxonomy, and expose gaps in taxonomic knowledge. The barcode library remains far from complete, so the next steps are to continue to identify and target taxa with poor coverage. This challenge to find DNA-quality specimens will increase, as the bulk of the remaining taxa are cryptic species with small geographical ranges.

11.4 Threatened Beetles

Many beetles are vulnerable to local and global extinction. These beetles often have low powers of dispersal (flightless), occur only in specific

microhabitats, and are distributed over small geographical areas. Beetles of oceanic islands, isolated dunes, caves, mountains, and other ecological islands fit into this category. Currently, 791 species appear on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, of which 12 are listed as extinct, 17 as critically endangered, 47 as endangered, and 45 as vulnerable (Table 11.5). Species on the Red List belong to 22 families. Habitat destruction and the introduction of invasive species continue to threaten most natural ecosystems and their myriad beetle species (Spence and Spence 1988, Kamoun 1996, Martikainen and Kouki 2003, Munks et al. 2004, Abellan et al.

Table 11.5 Number of Coleoptera species on the IUCN (2015) Red List of Threatened Species, by family.

Suborder	Superfamily	Family	EX	CR	EN	VU	NT	LR/NT	LC	DD	Total
Adephaga	—	Carabidae	1	2	2	2	—	1	—	—	8
		Dytiscidae	6	2	8	6	—	—	—	—	22
Polyphaga	Staphylinoidea	Leiodidae	—	—	—	1	1	—	—	—	2
		Silphidae	—	1	—	—	—	—	—	—	1
	Scarabaeoidea	Lucanidae	—	4	6	4	1	1	4	—	20
		Scarabaeidae	—	2	15	15	20	—	302	232	586
	Buprestoidea	Buprestidae	—	—	1	—	—	—	—	—	1
	Byrrhoidea	Elmidae	—	—	—	1	—	—	—	—	1
	Elateroidea	Eucnemidae	—	—	—	1	3	—	7	4	15
		Elateridae	—	—	3	2	7	—	6	38	56
	Bostrichoidea	Bostrichidae	—	—	—	—	1	—	2	—	3
		Ptinidae	—	—	—	—	1	—	—	—	1
	Cleroidea	Trogossitidae	—	—	1	1	—	—	1	3	6
	Cucujoidea	Erotylidae	—	—	—	1	—	—	2	6	9
		Cucujidae	—	—	—	—	1	—	—	1	2
	Tenebrionoidea	Mycetophagidae	—	—	—	—	1	—	—	1	2
		Tenebrionidae	—	—	—	3	—	—	—	—	3
		Anthicidae	—	—	1	—	—	—	—	—	1
Chrysomeloidea	Cerambycidae	—	1	9	8	3	—	8	8	37	
Curculionoidea	Anthribidae	—	4	—	—	1	—	—	—	5	
	Curculionidae	5	1	1	—	—	—	3	—	10	
Total			12	17	47	45	40	2	335	293	791

CR, critically endangered; DD, data deficient; EN, endangered; EX, extinct; LC, least concern; LR/NT, lower risk–near threatened; NT, near threatened; VU, vulnerable. The order of families follows that in Table 11.1.

2005, Davis and Philips 2005, Bouchard et al. 2006, Talley and Holyoak 2006). Because the taxonomy and distribution of most beetles remain unknown, we argue that the number of species currently listed as at-risk represents a gross underestimation of the number that should be targeted for conservation.

11.5 Conclusions

Beetles are a diverse group of arthropods that occur in most non-marine habitats (and a few marine ones). Their influence on science and society is great. Beetles provide essential ecological services and are used as tools in many scientific endeavors, some with large effects on humans. On the other hand, beetles continue to have negative effects on vital industries such as agriculture and forestry. Studies on beetle biodiversity and the conservation of their habitats are necessary to ensure the sustainability of natural ecosystems and critical human activities.

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References

- Abellan, P., D. Sanchez-Fernandez, J. Velasco and A. Millan. 2005. Conservation of freshwater biodiversity: a comparison of different area selection methods. *Biodiversity and Conservation* 14: 3457–3474.
- Acorn, J. 2006. The world's biggest bug is a grub. *American Entomologist* 52: 270–272.
- Ahrens, D., J. Schwarzer and A. P. Vogler. 2014. The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. *Proceedings of the Royal Society B* 281: 20141470.
- Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, S. Buchmann, J. Cane, P. Cox, V. Dalton, P. Feinsinger, M. Ingram, D. Inouye, C. Jones, K. Kennedy, P. Kevan, H. Koopowitz, R. Medellin, S. Medellin-Morales, G. Nabhan, B. Pavlik, V. Tepedino, P. Torchio and S. Walker. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 12: 8–17.
- Alves, L. F. A., V. S. Alves, D. F. Bressan, P. M. O. J. Neves and S. B. Alves. 2004. Natural occurrence of *Metarhizium anisopliae* (Metsch.) Sorok. on adults of the lesser mealworm (*Alphitobius diaperinus*) (Panzer) (Coleoptera: Tenebrionidae) in poultry houses in Cascavel, PR, Brazil. *Neotropical Entomology* 33: 793–795.
- Anderson, R. S. 1995. An evolutionary perspective on diversity in Curculionioidea. *Memoirs of the Entomological Society of Washington* 14: 103–118.
- Anderson, R. S. 2002. Curculionidae Latreille 1802. Pp. 722–815. In R. H. Arnett, Jr., M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. CRC Press, New York, NY.
- Anderson, R. S. and J. S. Ashe. 2000. Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera: Staphylinidae, Curculionidae). *Biodiversity and Conservation* 9: 617–653.
- Andres, A. 1931. Catalogue of the Egyptian Tenebrionidae. *Bulletin de la Société Royale Entomologique d'Égypte* 15: 74–125.
- Archangelsky, M., R. G. Beutel and A. Komarek. 2005. Hydrophiloidea. Introduction, phylogeny. Pp. 157–183. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1. Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Arellano, L. and G. Halffter. 2003. Gamma diversity: derived from and a determinant of

- alpha diversity and beta diversity. An analysis of three tropical landscapes. *Acta Zoologica Mexicana (Nueva Serie)* 90: 27–76.
- Armes, N. J. 1988. The seasonal activity of *Anthrenus sarnicus* and some other beetle pests in the museum environment. *Journal of Stored Products Research* 24: 29–37.
- Arnaldos, M. I., M. D. Garcia, E. Romera, J. J. Presa and A. Luna. 2005. Estimation of postmortem interval in real cases based on experimentally obtained entomological evidence. *Forensic Science International* 149: 57–65.
- Arndt, E., R. G. Beutel and K. Will. 2005. Carabidae Latreille, 1802. Pp. 119–146. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Arnett, R. H., Jr. and M. C. Thomas (eds). 2000. *American Beetles*. Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, New York, NY. 443 pp.
- Arnett, R. H., M. C. Thomas, P. E. Skelley and J. H. Frank. 2002. *American Beetles*. Volume 2. Scarabaeoidea through Curculionioidea. CRC Press, Boca Raton, FL. 861 pp.
- Arrow, G. J. 1931. *The fauna of British India, Including Ceylon and Burma. Coleoptera: Lamellicornia*. Volume 3. Taylor and Francis, London, 428 pp.
- Ashe, J. S. 1986. Subsocial behavior among gyrophaenine staphylinids (Coleoptera: Staphylinidae: Aleocharinae). *Sociobiology* 12: 315–320.
- Bai, M., D. Ahrens, X.-K. Yang and D. Ren. 2012. New fossil evidence of the early diversification of scarabs: *Alloioscarabaeus cheni* (Coleoptera: Scarabaeoidea) from the Middle Jurassic of Inner Mongolia, China. *Insect Science* 19: 159–171.
- Bai, M., R. G. Beutel, C.-K. Shih, D. Ren and X.-K. Yang. 2013. Septiventeridae, a new and ancestral fossil family of Scarabaeoidea (Insecta: Coleoptera) from the Late Jurassic to Early Cretaceous Yixian Formation. *Journal of Systematic Palaeontology* 11: 359–374.
- Balke, M. 2005. Dytiscidae Leach, 1915. Pp. 90–116. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Balke, M., I. Ribera and R. G. Beutel. 2005. The systematic position of Aspidytidae, the diversification of Dytiscoidea (Coleoptera, Adephaga) and the phylogenetic signal of third codon positions. *Journal of Zoological Systematics and Evolutionary Research* 43: 223–242.
- Balke, M., G. Wewalka, Y. Alarie and I. Ribera. 2007. Molecular phylogeny of Pacific island Colymbetinae: radiation of New Caledonian and Fijian species (Coleoptera, Dytiscidae). *Zoological Scripta* 36: 173–200.
- Ball, G. E. and Y. Bousquet. 2000. Carabidae Latreille, 1810. Pp. 32–132. In R. H. Arnett, Jr., and M. C. Thomas (eds). *American Beetles*. Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, New York, NY.
- Ballard, J. W., M. K. Thayer, A. Newton and E. R. Grismer. 1998. Data sets, partitions, and characters: philosophies and procedures for analyzing multiple data sets. *Systematic Biology* 47: 367–396.
- Barraclough, T. G., M. V. L. Barclay and A. P. Vogler. 1998. Species richness: does flower power explain beetle-mania? *Current Biology* 8: 843–845.
- Barth, F. B. 1985. *Insects and Flowers: the Biology of a Partnership*. Princeton University Press, Princeton, NJ. 309 pp.
- Bellamy, C. L. 2003. An illustrated summary of the higher classification of the superfamily Buprestoidea (Coleoptera). *Folia Heyrovskyana, Supplement* 10: 1–197.
- Bellini, R., F. Pederzani, R. Pilani, R. Veronesi and S. Maini. 2000. *Hydroglyphus pusillus*

- (Fabricius) (Coleoptera Dytiscidae): its role as a mosquito larvae predator in rice fields. *Bollettino dell'Istituto di Entomologia "Guido Grandi" della Universita degli Studi di Bologna* 54: 155–163.
- Benecke, M. 1998. Random amplified polymorphic DNA (RAPD) typing of necrophagous insects (Diptera, Coleoptera) in criminal forensic studies: validation and use in practice. *Forensic Science International* 98: 157–168.
- Bernhardt, P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Plant Systematics and Evolution* 222: 293–320.
- Betz, O. 1998. Comparative studies on the predatory behaviour of *Stenus* spp. (Coleoptera: Staphylinidae): the significance of its specialized labial apparatus. *Journal of Zoology* 244: 527–544.
- Betz, O. 2002. Performance and adaptive value of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). *Journal of Experimental Biology* 205: 1097–1113.
- Betz, O. and R. Mumm. 2001. The predatory legs of *Philonthus marginatus* (Coleoptera: Staphylinidae): functional morphology and tarsal ultrastructure. *Arthropod Structure and Development* 30: 77–97.
- Beutel, R. G. 2005. Myxophaga Crowson, 1955. Pp.43–44. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Beutel, R. G. and R. Arce-Pérez. 2005. Sphaeriusidae Erichson, 1845 (Jäch 1999) (= Microsporidae). Pp. 48–49. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Beutel, R. G. and A. Komarek. 2004. Comparative study of thoracic structures of adults of Hydrophiloidea and Histeroidea with phylogenetic implications (Coleoptera, Polyphaga). *Organisms Diversity and Evolution* 4: 1–34.
- Beutel, R. G. and R. A. B. Leschen (eds). 2005a. *Coleoptera, Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. Walter De Gruyter, Berlin, Germany. 567 pp.
- Beutel, R. G. and R. A. B. Leschen. 2005b. Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. *Systematic Entomology* 30: 510–548.
- Beutel, R. G. and I. Ribera. 2005. Adephaga Schellenberg, 1806. Pp. 53–55. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Beutel, R. G. and S. A. Vanin. 2005. Torridincolidae Steffan, 1964. Pp. 46–48. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Beutel, R. G., M. Balke and W. E. Steiner, Jr. 2006. The systematic position of Meruidae (Coleoptera, Adephaga) based on a cladistic analysis of morphological characters. *Cladistics* 22: 102–131.
- Bianchi, F. A. 1937. Notes on a new species of *Pyrophorus* introduced into Hawaii to combat *Anomala orientalis* Waterhouse. *Hawaii Plant Record* 41: 319–333.
- Blodgett, S. L., J. E. Carrel and R. A. Higgins. 1992. Cantharidin contamination of alfalfa hay. *Journal of Medical Entomology* 29: 700–703.
- Blum, M. S. 1981. *Chemical Defenses of Arthropods*. Academic Press, New York, NY. 562 pp.
- Bocák, L., C. Barton, A. Crampton-Platt, D. Chesters, D. Ahrens and A. P. Vogler. 2014. Building the Coleoptera tree-of-life for >8000

- species: composition of public DNA data and fit with Linnean classification. *Systematic Entomology* 39: 97–110.
- Bocáková, M., R. Constantin and L. Bocák. 2012. Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). *Cladistics* 28: 117–129.
- Bologna, M. A. and J. D. Pinto. 2001. Phylogenetic studies of Meloidae (Coleoptera), with emphasis on the evolution of phoresy. *Systematic Entomology* 26: 33–72.
- Booth, D., A. J. A. Stewart and D. Osorio. 2004. Color vision in the glow-worm *Lampyrus noctiluca* (L.) (Coleoptera: Lampyridae): evidence for a green-blue chromatic mechanism. *Journal of Experimental Biology* 207: 2373–2378.
- Bouchard, P. 2002. Phylogenetic revision of the flightless Australian genus *Apterotheca* Gebien (Coleoptera: Tenebrionidae: Coelometopinae). *Invertebrate Systematics* 16: 449–554.
- Bouchard, P., Y. Bousquet, A. E. Davies, M. A. Alonso-Zarazaga, J. F. Lawrence, C. H. C. Lyal, A. F. Newton, C. A. M. Reid, M. Schmitt, S. A. Ślipiński and A. B. T. Smith. 2011. Family-group names in Coleoptera (Insecta). *ZooKeys* 88: 1–972.
- Bouchard, P., T. A. Wheeler and H. Goulet. 2006. Ground beetles (Coleoptera: Carabidae) from alvar habitats in Ontario. *Journal of the Entomological Society of Ontario* 136: 3–23.
- Bourel, B., G. Tournel, V. Hédoïn, M. L. Goff and D. Gosset. 2001. Determination of drug levels in two species of necrophagous Coleoptera reared on substrates containing morphine. *Journal of Forensic Sciences* 46: 600–603.
- Bourel, B., G. Tournel, V. Hédoïn and D. Gosset. 2004. Entomofauna of buried bodies in northern France. *International Journal of Legal Medicine* 118: 215–220.
- Bousquet, Y. 1990. *Beetles Associated with Stored Products in Canada: an Identification Guide*. Canada Department of Agriculture Publication 1837. Ottawa, Ontario.
- Bousquet, Y., P. Bouchard, A. E. Davies and D. S. Sikes. 2013. Checklist of beetles (Coleoptera) of Canada and Alaska. *ZooKeys* 360: 1–44.
- Brackenbury, J. 1999. Water skating in the larvae of *Dixella aestivalis* (Diptera) and *Hydrobius fuscipes* (Coleoptera). *Journal of Experimental Biology* 202: 845–863.
- Brancucci, M. 1979. *Geodessus besucheti* n. gen., n. sp. le premier Dytiscide terrestre (Cole., Dytiscidae, Bidessini). *Entomologica Basiliensia* 4: 213–218.
- Brancucci, M. and G. B. Monteith. 1996. A second *Terradessus* species from Australia (Coleoptera, Dytiscidae). *Entomologica Basiliensia* 19: 585–591.
- Branham, M. A. and J. W. Wenzel. 2003. The origin of photic behaviour and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* 19: 1–22.
- Bright, D. E. 1963. Bark beetles of the genus *Dryocoetes* (Coleoptera: Scolytinae) in North America. *Annals of the Entomological Society of America* 56: 103–115.
- Brockhoff, E. G., J. Bain, M. Kimberley and M. Knížek. 2006. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment on New Zealand and worldwide. *Canadian Journal of Forest Research* 36: 289–298.
- Brown, W. J. 1929. Studies in the Scarabaeidae (II). *Canadian Entomologist* 61: 86–93.
- Brown, E. S. 1954. The biology of the coconut pest *Melittomma insulare* (Col., Lymexylonidae), and its control in the Seychelles. *Bulletin of Entomological Research* 45: 1–66.
- Browne, D. J. and C. H. Scholtz. 1995. Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. *Systematic Entomology* 20: 145–173.
- Browne, D. J. and C. H. Scholtz. 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). *Systematic Entomology* 23: 307–326.
- Browne, D. J. and C. H. Scholtz. 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera). *Systematic Entomology* 24: 51–84.
- Burke, H. R., W. E. Clark, J. R. Cate and P. A. Fryxell. 1986. Origin and dispersal of the boll weevil. *Bulletin of the Entomological Society of America* 32: 228–238.

- CABI [Centre for Agriculture and Bioscience International]. 2015. Distribution maps of plant pests: Coleoptera. <http://www.cabi.org/dmpp/search/?q=&topics=d7e33a7f-34f1-4180-9623-177c5a76597a> [Accessed 31 January 2015].
- Cai, C.-Y., M. K. Thayer, M. S. Engel, A. F. Newton, J. Ortega-Blanco, B. Wang, X.-D. Wang and D.-Y. Huang. 2014. Early origin of parental care in Mesozoic carrion beetles. *Proceedings of the National Academy of Sciences USA* 111: 14170–14174.
- Cambefort, Y. 1994. *Le Scarabée et les Dieux: Essai sur la Signification Symbolique et Mythique des Coleopteres*. Boubée, Paris, France. 224 pp.
- Campbell, J. M., M. J. Sarazin and D. B. Lyons. 1989. *Canadian beetles (Coleoptera) injurious to crops, ornamentals, stored products, and buildings*. Research Branch Agriculture Canada Publication 1826. Ottawa, Ontario.
- Capinera, J. L., D. R. Gardener and F. R. Stermitz. 1985. Cantharidin levels in blister beetles (Coleoptera: Meloidae) associated with alfalfa in Colorado. *Journal of Economic Entomology* 78: 1052–1055.
- Carlton, C. E. and V. M. Bayless. 2007. Documenting beetle (Arthropoda: Insecta: Coleoptera) diversity in Great Smoky Mountains National Park; beyond the halfway point. *Southeastern Naturalist* 6 (Special Issue 1): 183–192.
- Carlton, C. E. and H. W. Robison. 1998. Diversity of litter-dwelling beetles in deciduous forests of the Ouachita highlands of Arkansas (Insecta: Coleoptera). *Biodiversity and Conservation* 7: 1589–1605.
- Carvalho, L. M., P. J. Thyssen, A. X. Linhares and F. A. Palhares. 2000. A checklist of arthropods associated with pig carrion and human corpses in southeastern Brazil. *Memorias do Instituto Oswaldo Cruz* 95: 135–138.
- Caterino, M. S. and N. Dégallier. 2007. A review of the biology and systematics of Chlamydopsinae (Coleoptera: Histeridae). *Invertebrate Systematics* 21: 1–28.
- Caterino, M. S., T. Hunt and A. P. Vogler. 2005. On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). *Molecular Phylogenetics and Evolution* 34: 655–672.
- Catts, E. P. and N. H. Haskell (eds). 1990. *Entomology and Death: a Procedural Guide*. Joyce's Print Shop, Clemson, SC. 182 pp.
- CFIA [Canadian Food Inspection Agency]. 2015. Pests regulated by Canada: insects. <http://www.inspection.gc.ca/plants/plant-pests-invasive-species/insects/eng/1307077188885/1307078272806> [Accessed 31 January 2015].
- Chaddick, P. R. and F. F. Leek. 1972. Further specimens of stored product insects found in ancient Egyptian tombs. *Journal of Stored Products Research* 8: 83–86.
- Chandler, D. S. and S. B. Peck. 1992. Seasonality and diversity of Leiodidae (Coleoptera) in an old-growth and 40 year-old forest in New Hampshire. *Environmental Entomology* 21: 1283–1293.
- Chapman, C. A. and L. J. Chapman. 2003. Fragmentation and alteration of seed dispersal process: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* 35: 382–393.
- Childers, C. C. and R. E. Woodruff. 1980. A bibliography of the coffee bean weevil *Araecerus fasciculatus* (Coleoptera: Anthribidae). *Bulletin of the Entomological Society of America* 26: 384–394.
- Chu, G. S., J. R. Palmieri and J. T. Sullivan. 1977. Beetle-eating: a Malaysia folk medical practice and its public health implications. *Tropical and Geographical Medicine* 29: 422–427.
- Clark, S. M. and E. G. Riley. 2002. Megalopodidae Latreille 1802 – Orsodacnidae Thomson 1859. Pp. 609–616. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Clausen, C. P. 1978. Scarabaeidae. Pp. 277–292. In C. P. Clausen (ed). *Introduced Parasites and Predators of Arthropod Pests and Weeds: a World Review*. United States Department of Agriculture Handbook No. 480. Washington, DC.

- Cline, A. R., T. R. Smith, K. Miller, M. Moulton, M. Whiting and P. Audisio. 2014. Molecular phylogeny of Nitidulidae: assessment of subfamilial and tribal classification and formalization of the family Cybocephalidae (Coleoptera: Cucujoidea). *Systematic Entomology* 39: 758–772.
- Cloudsley-Thompson, J. L. 1964. On the function of the sub-elytral cavity in desert Tenebrionidae (Col.) *Entomologist's Monthly Magazine* 100: 148–151.
- Cognato, A. I., J.-H. Sun, M. A. Anducho-Reyes and D. R. Owen. 2005. Genetic variation and origin of red turpentine beetle (*Dendroctonus valens* LeConte) introduced to the People's Republic of China. *Agricultural and Forest Entomology* 7: 87–94.
- Contag, C. H., S. D. Spilman, P. R. Contag, M. Oshiro, B. Eames, P. Dennerly, D. K. Stevenson, and D. A. Benaron. 1997. Visualizing gene expression in living mammals using a bioluminescent reporter. *Photochemistry and Photobiology* 66: 523–531.
- Costa, C., S. Casari-Chen and A. Vanin. 1992. On the larvae of Tetralobini (Coleoptera, Elateridae). *Revista Brasileira de Entomologia* 36: 879–888.
- Craighead, F. C. 1950. Insect enemies of eastern forests. *United States Department of Agriculture Miscellaneous Publications* 657: 1–679.
- Crawford, C. S., W. P. Mackay and J. G. Cepeda-Pizarro. 1993. Detritivores of the Chilean arid zone (27–32°S) and the Namib Desert: a preliminary comparison. *Revista Chilena de Historia Natural* 66: 283–289.
- Dacke, M., P. Nordström and C. H. Scholtz. 2003. Twilight orientation to polarised light in the crepuscular dung beetle *Scarabaeus zambeziensis*. *Journal of Experimental Biology* 206: 1535–1545.
- Dai, Z., S. N. Gorb and U. Schwarz. 2002. Roughness-dependent friction force of the tarsal claw system in the beetle *Pachnoda marginata* (Coleoptera, Scarabaeidae). *Journal of Experimental Biology* 205: 2479–2488.
- Darlington, P. J., Jr. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs* 13: 37–61.
- Davies, R. H. and C. Wray. 1995. Contribution of the lesser mealworm beetle (*Alphitobius diaperinus*) to carriage of *Salmonella enteritidis* in poultry. *Veterinary Record* 137: 407–408.
- Davis, A. L. V. 1994. Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents from Australia. *Journal of Natural History* 28: 383–399.
- Davis, A. L. V. and T. K. Philips. 2005. Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. *Environmental Entomology* 34: 1081–1088.
- Davis, A. L. V., C. H. Scholtz, P. W. Dooley, N. Bham and U. Kryger. 2004. Scarabaeinae dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *South African Journal of Science* 100: 415–424.
- De Clerck-Floate, R. A., B. M. Wikeem and R. S. Bouchier. 2005. Early establishment and dispersal of the weevil, *Mogulones cruciger* (Coleoptera: Curculionidae) for biological control of houndstongue (*Cynoglossum officinale*) in British Columbia, Canada. *Biocontrol Science and Technology* 15: 173–190.
- Deleurance-Glaçon, S. 1963. Recherches sur les Coléoptères troglobies de la sous-famille des Bathysciinae. *Annales des Sciences Naturelles (Zoologie)* 5: 1–172.
- de Souza, A. M. and A. X. Linhares. 1997. Diptera and Coleoptera of potential forensic importance in southeastern Brazil: relative abundance and seasonality. *Medical and Veterinary Entomology* 11: 8–12.
- Dickens, J. C., J. E. Oliver, B. Hollister, J. C. Davis and J. A. Klun. 2002. Breaking a paradigm: male-produced aggregation pheromone for the Colorado potato beetle. *Journal of Experimental Biology* 205: 1925–1933.
- Dickerson, W. A., A. L. Brashear, J. T. Brumley, F. L. Carter, W. J. Grefenstette and F. A. Harris (eds). 2001. *Boll Weevil Eradication through*

1999. The Cotton Foundation. Memphis, TN. 627 pp.
- DiZinno, J. A., W. D. Lord, M. B. Collins-Morton, M. R. Wilson and M. L. Goff. 2002. Mitochondrial DNA sequencing of beetle larvae (Nitidulidae: Osmatida) recovered from human bone. *Journal of Forensic Sciences* 47: 1337–1339.
- Donlan, E. M., J. H. Townsend and E. A. Golden. 2004. Predation of *Caretta caretta* (Testudines: Cheloniidae) eggs by larvae of *Lanelater sallei* (Coleoptera: Elateridae) on Key Biscayne, Florida. *Caribbean Journal of Science* 40: 415–420.
- Douglas, H. 2011. Phylogenetic relationships of Elateridae inferred from adult morphology, with special reference to the position of Cardiophorinae. *Zootaxa* 2900: 1–45.
- Doyen, J. T. 1976. Marine beetles (Coleoptera excluding Staphylinidae). Pp. 497–519. In L. Cheng (ed). *Marine Insects*. North-Holland Publishing, Amsterdam.
- Duan, J. J., M. S. Paradise, J. G. Lundgren, J. T. Bookout, C. J. Jiang and R. N. Wiedenmann. 2006. Assessing nontarget impacts of Bt corn resistant to rootworms: tier-1 testing with larvae of *Poecilus chalcites* (Coleoptera: Carabidae). *Environmental Entomology* 35: 135–142.
- Dubitskii, A. M., R. T. Akhmetbekova and V. V. Nazarov. 1975. Aquatic beetles (Coleoptera: Dytiscidae) in mosquito control. *Izvestiya Akademii Nauk Kazakhskoi SSR Seriya Biologicheskaya* 13: 47–51.
- Edwards, P. B. and H. H. Aschenborn. 1987. Patterns of nesting and dung burial in *Onitis* dung beetles: implications for pasture productivity and fly control. *Journal of Applied Ecology* 24: 837–851.
- Eidmann, H. H. 1992. Impact of bark beetle on forests and forestry in Sweden. *Zeitschrift für Angewandte Entomologie* 114: 193–200.
- Ellers-Kirk, C. and S. J. Fleischer. 2006. Development and life table of *Acalymma vittatum* (Coleoptera: Chrysomelidae), a vector of *Erwinia tracheiphila* in Cucurbits. *Environmental Entomology* 35: 875–880.
- Eppo [European and Mediterranean Plant Protection Organization]. 2015. A1 and A2 lists of pests recommended for regulation as quarantine pests. <http://www.eppo.int/QUARANTINE/quarantine.htm> [Accessed 31 January 2015].
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36: 74–75.
- Erwin, T. L. 1991. Natural history of the carabid beetles at the BIOLAT Biological Station, Rio Manu, Pakitza, Peru. *Revista Peruana de Entomologia* 33: 1–85.
- Escalona, H. E., J. F. Lawrence, M. Wanat and A. Ślipiński. 2015. Phylogeny and placement of Boganiidae (Coleoptera, Cucujoidea) with a review of Australian and New Caledonian taxa. *Systematic Entomology* 40: 628–651.
- Estrada, A. and R. Coates-Estrada. 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 11: 1903–1918.
- Evans, A. M., D. D. McKenna, C. L. Bellamy and B. D. Farrell. 2014. Large-scale molecular phylogeny of metallic wood-boring beetles (Coleoptera: Buprestoidea) provides new insights into relationships and reveals multiple evolutionary origins of the larval leaf-mining habit. *Systematic Entomology* 40: 385–400.
- Evans, A. V. and A. B. T. Smith. 2009. An electronic checklist of the New World chafers (Coleoptera: Scarabaeidae: Melolonthinae). Version 3 [online]. <http://museum.unl.edu/research/entomology/SSSA/NW-Melo-v3.pdf> [Accessed 30 December 2014].
- Farrell, B. D. 1998. “Inordinate fondness” explained: why are there so many beetles? *Science* 281: 553–557.
- Farrell, B. D., A. S. Sequeira, B. O’Meara, B. B. Normark, J. H. Chung and B. H. Jordal. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). *Evolution* 55: 2011–2027.
- Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash and J. D. Thomson. 2004. Pollination syndromes and floral specialization. *Annual*

- Review of Ecology, Evolution and Systematics* 35: 375–403.
- Fincher, G. T. 1981. The potential value of dung beetles in pasture ecosystems. *Journal of the Georgia Entomological Society* 16: 301–316.
- Fish, F. E. and A. J. Nicastro. 2003. Aquatic turning performance by the whirligig beetle: constraints on maneuverability by a rigid biological system. *Journal of Experimental Biology* 206: 1649–1656.
- Forrest, T. G., M. P. Read, H. E. Farris and R. R. Hoy. 1997. A tympanal hearing organ in scarab beetles. *Journal of Experimental Biology* 200: 601–606.
- Franc, V., P. Hrasko and M. Snopko. 1989. Use of entomologic findings in forensic medicine and criminology. *Soudni Lekarstvi* 34: 37–45.
- Frank, J. H. and K. Kanamitsu. 1987. *Paederus*, sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. *Journal of Medical Entomology* 24: 155–191.
- Frantsevich, L., Z. Dai, W. Y. Wang and Y. Zhang. 2005. Geometry of elytra opening and closing in some beetles (Coleoptera, Polyphaga). *Journal of Experimental Biology* 208: 3145–3158.
- Freitag, R. 1979. Carabid beetles and pollution. Pp. 485–506. In T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (eds). *Carabid Beetles: Their Evolution, Natural History, and Classification*. Junk, The Hague.
- Freuler, J., G. Blandenier, H. Meyer and P. Pignon. 2001. Epigeal fauna in a vegetable agroecosystem. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 74: 17–42.
- Gagliano-Candela, R. and L. Aventaggiato. 2001. The detection of toxic substances in entomological specimens. *International Journal of Legal Medicine* 114: 197–203.
- Garcia-Salazar, C. G., F. E. Gildow, S. J. Fleischer, D. Cox-Foster and F. L. Lukezic. 2000. ELISA versus immunolocalization to determine the association of *Erwinia tracheiphila* in *Acalymma vittatum* (F.) (Coleoptera: Chrysomelidae). *Environmental Entomology* 29: 542–550.
- Gaston, K. J. 1991. The magnitude of global insect species richness. *Conservation Biology* 5: 283–296.
- Geisthardt, M. 2003. Tenebrionidae (Insecta, Coleoptera) as an indicator for climatic changes on the Cape Verde Islands. *Special Bulletin of the Japanese Society of Coleopterology* 6: 331–337.
- Gilbert, M., N. Fielding, H. F. Evans and J.-C. Grégoire. 2003. Spatial pattern of invading *Dendroctonus micans* (Coleoptera: Scolytidae) populations in the United Kingdom. *Canadian Journal of Forest Research* 33: 712–725.
- Goddard, J. 2000. *Physician's Guide to Arthropods of Medical Importance*. 3rd edition. CRC Press, Boca Raton, FL.
- Goldberg, L. 1996. A history of pest control measures in the anthropology collections, National Museum of Natural History, Smithsonian Institution. *Journal of the American Institute for Conservation* 35: 23–43.
- Gordon, R. D. and O. L. Cartwright. 1980. The Western Hemisphere species of *Rhyssemus* and *Trichiorhyssemus* (Coleoptera: Scarabaeidae). *Smithsonian Contributions to Zoology* 317: 1–29.
- Gorb, S. 2001. *Attachment Devices of the Insect Cuticle*. Kluwer Academic Press. Dordrecht, Sweden. 305 pp.
- Graczyk, T. K., R. Knight and L. Tamang. 2005. Mechanical transmission of human protozoan parasites by insects. *Clinical Microbiology Reviews* 18: 128–132.
- Grebennikov, V. V. 2009. Discheramocephalini, a new pantropical tribe of featherwing beetles (Coleoptera: Ptiliidae): description of new taxa and phylogenetic analysis. *Systematic Entomology* 34: 113–136.
- Grebennikov, V. and A. F. Newton. 2009. Good-bye Scydmaenidae, or why the ant-like stone beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera). *European Journal of Entomology* 106: 275–301.
- Grebennikov, V. V. and C. H. Scholtz. 2004. The basal phylogeny of Scarabaeoidea (Insecta: Coleoptera) inferred from larval morphology. *Invertebrate Systematics* 18: 321–348.

- Greer, L. and A. A. Szalay. 2002. Imaging of light emission from the expression of luciferases in living cells and organisms: a review. *Luminescence* 17: 43–74.
- Grimaldi, D. and M. S. Engel. 2005. *Evolution of the Insects*. Cambridge University Press, New York, NY. 772 pp.
- Grove, S. J. and N. E. Stork. 2000. An inordinate fondness for beetles. *Invertebrate Taxonomy* 14: 733–739.
- Gunter, N. L., Z. Levkaničová, T. H. Weir, A. Ślipiński, S. L. Cameron and L. Bocák. 2014. Towards a phylogeny of the Tenebrionoidea (Coleoptera). *Molecular Phylogenetics and Evolution* 79: 305–312.
- Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269–288.
- Hald, B., A. Olsen and M. Madsen. 1998. *Typhaea stercorea* (Coleoptera: Mycetophagidae), a carrier of *Salmonella enterica* serovar infantis in a Danish broiler house. *Journal of Economic Entomology* 91: 660–664.
- Halfpfter, G. and L. Arellano. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica* 34: 144–154.
- Halfpfter, G. and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana* 12–14: 3–312.
- Hall, W. E. 2000. Ptiliidae Erichson, 1845. Pp. 233–246. In R. H. Arnett and M. C. Thomas (eds). *American Beetles*. Volume 1. Archostemata, Myxophaga, Adepaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, FL.
- Hall, W. E. 2005. Ptiliidae Erichson, 1845. Pp. 251–261. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1. Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Hammond, P. M. 1979. Wing-folding mechanisms of beetles, with special reference to special investigations of adepagan phylogeny (Coleoptera). Pp. 113–180. In T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (eds). *Carabid Beetles: Their Evolution, Natural History, and Classification*. Junk, The Hague, Netherlands.
- Hammond, P. H. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. Pp. 197–254. In W. J. Knight and J. D. Holloway (eds). *Insects and the Rain Forests of South East Asia (Wallacea)*. Royal Entomological Society of London, London, UK.
- Hammond, P. M. 1995. Described and estimated species numbers: an objective assessment of current knowledge. Pp. 29–71. In D. Allsopp D. L. Hawkesworth and R. R. Colwell (eds). *Microbial Diversity and Ecosystem Function*. CAB International, Wallingford, UK.
- Hanley, R. S. and M. A. Goodrich. 1995. Review of mycophagy, host relationships and behavior in the New World Oxyporinae (Coleoptera: Staphylinidae). *Coleopterists Bulletin* 49: 267–280.
- Hansen, M. 1991. The hydrophiloid beetles: phylogeny, classification and a revision of the genera (Coleoptera, Hydrophiloidea). *Biologiske Skrifter, Kongelige Danske Videnskabernes Selkab* 40: 1–367.
- Hansen, M. 1997. Phylogeny and classification of the staphyliniform beetle families. *Biologiske Skrifter, Kongelige Danske Videnskabernes Selkab* 48: 1–339.
- Harris, F. 1966. Observations on the lesser mealworm, *Alphitobius diaperinus* (Panz.). *Journal of the Georgia Entomological Society* 1: 17–18.
- Harris, K. F. 1981. Arthropod and nematode vectors of plant viruses. *Annual Review of Phytopathology* 19: 391–426.
- Hemachandra, K. S., N. J. Holliday, P. G. Mason, J. J. Soroka and U. Kuhlmann. 2007. Comparative assessment of the parasitoid community of *Delia radicum* in the Canadian prairies and Europe: a search for classical biological control agents. *Biological Control* 43: 85–94.

- Hinton, H. E. 1945. *A Monograph of the Beetles Associated with Stored Products*. British Museum, London, UK. 443 pp.
- Hoebeke, E. R. and A. G. Wheeler. 1991. *Anthribus nebulosus*, a Eurasian scale predator in the eastern United States (Coleoptera: Anthribidae): notes on biology, recognition, and establishment. *Proceedings of the Entomological Society of Washington* 93: 45–50.
- Hoffman, W. A. 1933. *Rhizopertha dominica* F. is a library pest. *Journal of Economic Entomology* 26: 293–294.
- Holst, N. and W. G. Meikle. 2003. *Teretrius nigrescens* against larger grain borer *Prostephanus truncatus* in African maize stores: biological control at work? *Journal of Applied Ecology* 40: 307–319.
- Hood, W. M. 2004. The small hive beetle, *Aethina tumida*: a review. *Bee World* 85: 51–59.
- Hörschemeyer, T. 2005. Archostemata Kolbe, 1908. Pp. 29–42. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 1. Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Howard, R. W., R. A. Jurenka and G. J. Blomquist. 1986. Prostaglandin synthetase inhibitors in the defensive secretion of the red flour beetle *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). *Insect Biochemistry* 16: 757–760.
- Howden, H. F. 1982. Larval and adult characters of *Frickius* Germain, its relationship to the Geotrupini, and a phylogeny of some major taxa in the Scarabaeoidea (Insecta: Coleoptera). *Canadian Journal of Zoology* 60: 2713–2724.
- Howden, H. and A. Howden. 2001. Change through time: a third survey of the Scarabaeinae (Coleoptera: Scarabaeidae) at Welder Wildlife Refuge. *Coleopterists Bulletin* 55: 356–362.
- Howe, R. W. 1959. Studies on beetles of the family Ptinidae. XVII. Conclusions and additional remarks. *Bulletin of Entomological Research* 50: 287–326.
- Hu, G. Y. and Frank, J. H. 1995. Biology of *Neohyphnus pusillus* (Sachse) (Coleoptera: Staphylinidae) and its predation on immature horn flies in the laboratory. *Coleopterists Bulletin* 49: 43–52.
- Hughes, J., S. J. Longhorn, A. Papadopoulou, K. Theodorides, A. de Riva, M. Mejia-Chang, P. G. Foster and A. P. Vogler. 2006. Dense taxonomic EST sampling and its applications for molecular systematics of the Coleoptera (beetles). *Molecular Biology and Evolution* 23: 268–278.
- Hughes, R. D., P. Ferrar, A. Macqueen, P. Durie, G. T. McKinney and F. H. W. Morley. 1975. Introduced dung beetles and Australian pasture ecosystems: papers presented at a symposium during the meeting of the Australian and New Zealand Association for the Advancement of Science at Canberra in January 1975. *Journal of Applied Ecology* 12: 819–837.
- Hurst, J. J., J. Meinwald and T. Eisner. 1964. Defense mechanisms of arthropods – XII. Glucose and hydrocarbons in the quinone-containing secretion of *Eleodes longicollis*. *Annals of the Entomological Society of America* 57: 44–46.
- IUCN [International Union for Conservation of Nature]. 2015. IUCN Red List of threatened species. www.iucnredlist.org [Accessed 13 November 2015].
- Ivie, M. A. 2002. Bostrichidae Latreille 1802. Pp. 223–244. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Jäch, M. A. 1998. Annotated check list of aquatic and riparian/littoral beetle families of the world (Coleoptera). Pp. 25–42. In M. A. Jäch and L. Ji (eds). *Water Beetles of China*. Volume II. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien, Austria.
- Jäch, M. A., R. G. Beutel, J. A. Delgado and J. A. Diaz. 2005. Hydraenidae Mulsant, 1844. Pp. 224–251. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera,

- beetles. Volume 1: Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Jackson, T. A. and M. G. Klein. 2006. Scarabs as pests: a continuing problem. *Coleopterists Society Monographs* 5: 102–119.
- Jameson, M. L. and B. C. Ratcliffe. 2002. Series Scarabaeiformia Crowson 1960 (= Lamellicornia): Superfamily Scarabaeoidea Latreille 1802: introduction. Pp. 1–5. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Jankielsohn, A., C. H. Scholtz and S. V. Louw. 2001. Effect of habitat transformation on dung beetle assemblages: a comparison between a South African nature reserve and neighboring farms. *Environmental Entomology* 30: 474–483.
- Japan-MAFF [Japanese Ministry of Agriculture, Forestry and Fisheries]. 2014. Quarantine Pest List. <https://www.ippc.int/en/countries/japan/reportingobligation/2014/03/quarantine-pest-list-revised-on-24-february-2014/> [Accessed 18 January 2016].
- Jelínek, J., C. Carlton, A. Cline and R. Leschen. 2010. Nitidulidae Latreille, 1802. Pp. 390–407. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Johns, C. V., C. Stone and L. Hughes. 2004. Feeding preferences of the Christmas beetle *Anoplognathus chloropyrus* (Coleoptera: Scarabaeidae) and four paropsine species (Coleoptera: Chrysomelidae) on selected *Eucalyptus grandis* clonal foliage. *Australian Forestry Journal* 67: 184–190.
- Johnson, P. J. 2002. Throscidae Laporte, 1840. Pp. 158–159. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Jordal, B. H., R. A. Beaver, B. B. Normark and B. D. Farrell. 2002. Extraordinary sex ratios and the evolution of male neoteny in sib-mating *Ozopemon* beetles. *Biological Journal of the Linnean Society* 75: 353–360.
- Josephson, R. K., J. G. Malamud and D. R. Stokes. 2001. The efficiency of an asynchronous flight muscle from a beetle. *Journal of Experimental Biology* 204: 4125–4139.
- Kamoun, S. 1996. Occurrence of the threatened *Cicindela senilis frosti* Varas-Arangua in an inland salt marsh in Riverside County, California (Coleoptera, Cicindelidae). *Coleopterists Bulletin* 50: 369–371.
- Kaplan, J. K. 2003. We don't cotton to boll weevil 'round here anymore. *Agricultural Research* February 2003: 4–8.
- Karras, D. J., S. E. Farrell, R. A. Harrigan, F. M. Henretig and L. Gealt. 1996. Poisoning from "Spanish fly" (cantharidin). *American Journal of Emergency Medicine* 14: 478–483.
- Kaufman, P. E., S. J. Long, D. A. Rutz and C. S. Glenister. 2000. Prey- and density-mediated dispersal in *Carcinops pumilio* (Coleoptera: Histerida), a predator of house fly (Diptera: Muscidae) eggs and larvae. *Journal of Medical Entomology* 37: 929–932.
- Kellner, R. L. L. 2001. Suppression of pederin biosynthesis through antibiotic elimination of endosymbionts in *Paederus sabaesus*. *Journal of Insect Physiology* 47: 475–483.
- Kellner, R. L. L. 2003. Stadium-specific transmission of endosymbionts needed for pederin biosynthesis in three species of *Paederus* rove beetles. *Entomologia Experimentalis et Applicata* 107: 115–124.
- Kergoat, G. J., P. Bouchard, A.-L. Clamens, J. L. Abbate, H. Jourdan, R. Jabbour-Zahab, G. Genson, L. Soldati and F. L. Condamine. 2014a. Cretaceous environmental changes led to high extinction rates in a hyperdiverse beetle family. *BMC Evolutionary Biology* 14 (220): 1–13.
- Kergoat, G. J., L. Soldati, A.-L. Clamens, H. Jourdan, R. Jabbour-Zahab, G. Genson, P. Bouchard and F. L. Condamine. 2014b. Higher-level molecular phylogeny of darkling beetles (Coleoptera, Tenebrionidae). *Systematic Entomology* 39: 486–499.

- Kevan, P. and H. G. Baker. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28: 407–453.
- Kim, J.-J., E. A. Allen, L. M. Humble and C. Breuil. 2005. Ophistomatoid and basidiomycetous fungi associated with green, red, and grey lodgepole pines after mountain pine beetle (*Dendroctonus ponderosae*) infestation. *Canadian Journal of Forest Research* 35: 274–284.
- Kirejtshuk, A. G. and D. Azar. 2013. Current knowledge of Coleoptera (Insecta) from the Lower Cretaceous Lebanese amber and taxonomical notes for some Mesozoic groups. *Terrestrial Arthropod Reviews* 6: 103–134.
- Kirejtshuk, A. G. and A. Nel. 2013. Current knowledge of Coleoptera (Insecta) from the Lowermost Eocene Oise amber. *Insect Systematics & Evolution* 44: 175–201.
- Kirejtshuk, A. G., P. E. Chetverikov, D. Azar and P. A. Kirejtshuk. 2016. Ptismidae fam. nov. (Coleoptera, Staphyliniformia) from the Lower Cretaceous Lebanese amber. *Cretaceous Research* 59: 201–213.
- Kishimoto, H. and I. Adachi. 2008. Predation and oviposition by predatory *Stethorus japonicus*, *Oligota kashmirica benefica*, and *Scolothrips takahashii* in egg patches of various spider mite species. *Entomologia Experimentalis et Applicata* 128: 294–302.
- Klimaszewski, J., R. Pace, T. D. Center and J. Couture. 2010. A remarkable new species of *Himalusa* Pace from Thailand (Coleoptera, Staphylinidae, Aleocharinae): phytophagous aleocharine beetle with potential for bio-control of skunkvine-related weeds in the United States. *ZooKeys* 35: 1–12.
- Koch, C. 1958. Preliminary notes on the coleopterological aspect of the arrow poison of the Bushmen. *Pamphlet of the South African Biological Society* 20: 49–54.
- Kolibáč, J. 1992. Revision of Thanerocleridae n. stat. (Coleoptera, Cleroidea). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 65: 303–340.
- Kolibáč, J. 2004. Metaxinidae fam. nov., a new family of Cleroidea (Coleoptera). *Entomologica Basiliensia* 26: 239–268.
- Kolibáč, J. 2005. A review of the Trogossitidae. Part 1: morphology of the genera (Coleoptera, Cleroidea). *Entomologica Basiliensia et Collectionis Frey* 27: 39–159.
- Kolibáč, J. 2010. Cleridae Latreille, 1802. Pp. 257–261. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. Walter De Gruyter, Berlin, Germany.
- Korte, A., I. Ribera, R. G. Beutel and D. Bernhard. 2004. Interrelationships of Staphyliniform groups inferred from 18S and 28S rDNA sequences, with special emphasis on Hydrophiloidea (Coleoptera, Staphyliniformia). *Journal of Zoological Systematics and Evolutionary Research* 42: 281–288.
- Kovarik P. W. and M. S. Caterino. 2005. Histeridae Gyllenhal, 1808. Pp. 190–222. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, beetles. Volume 1. Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. Walter de Gruyter, Berlin, Germany.
- Kral, D. and M. Rakovič. 2012. Faunistic records from the Czech Republic – 338. Coleoptera: Scarabaeidae: Aphodiinae. *Klapalekiana* 48: 291–292.
- Kritsky, G. 1991. Beetle gods of ancient Egypt. *American Entomologist* 37: 85–89.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture Ecosystems & Environment* 74: 187–228.
- Kulshrestha, P. and D. K. Satpathy. 2001. Use of beetles in forensic entomology. *Forensic Science International* 120: 15–17.
- Kukalová-Peck, J. and R. G. Beutel. 2012. Is the Carboniferous †*Adiphlebia lacoana* really the “oldest beetle”? Critical reassessment and

- description of a new Permian beetle family. *European Journal of Entomology* 109: 633–645.
- Kumar, P. 1988. Flesh eating behaviour of *Alphitobius diaperinus* Panz. (Tenebrionidae; Coleoptera). *Indian Journal of Entomology* 48: 113–115.
- Kundrata, R. and L. Bocák. 2011. The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta* 40: 364–378.
- Kundrata, R., M. Bocáková and L. Bocák. 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* 76: 162–171.
- Kundrata, R, N. L. Gunter, H. Douglas and L. Bocak. 2016. Next step toward a molecular phylogeny of click-beetles (Coleoptera: Elateridae): redefinition of Pityobiinae, with a description of a new subfamily Parablacinae from the Australasian Region. *Austral Entomology* 55: 291–302.
- Kutalek, R. and A. Kassa. 2005. The use of gyrinids and dytiscids for stimulating breast growth in East Africa. *Journal of Ethnobiology* 25: 115–128.
- Lacey, E. S., M. D. Ginzel, J. G. Mallar and L. M. Hanks. 2004. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. *Journal of Chemical Ecology* 30: 1493–1507.
- Lamb, A. B., S. M. Salom, L. T. Kok and D. L. Mause. 2006. Confined field release of *Laricobius nigrinus* (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in Virginia. *Canadian Journal of Forest Research* 36: 369–375.
- Larsen, K. J. and T. W. Work. 2003. Differences in ground beetles (Coleoptera: Carabidae) or original and reconstructed tallgrass prairies in northeastern Iowa, USA, and impact of 3-year spring burn cycles. *Journal of Insect Conservation* 7: 153–166.
- Lawrence, J. F. 1987. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of Elateriformia. *Invertebrate Taxonomy* 2: 1–53.
- Lawrence, J. F. 2010a. Endecatommidae LeConte, 1861. Pp. 206–209. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Lawrence, J. F. 2010b. Lymexylidae Fleming, 1821. Pp. 229–235. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Lawrence, J. F., R. G. Beutel and R. A. B. Leschen. 2010. Derodontiformia. Introduction, phylogeny. Pp. 179–180. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Lawrence, J. F. and E. B. Britton. 1994. *Australian Beetles*. Melbourne University Press, Melbourne, Victoria. 192 pp.
- Lawrence, J. F., A. M. Hastings, M. J. Dallwitz, T. A. Paine and E. J. Zurcher. 1999. *Beetles of the World. CD-ROM, Version 1.0*. CSIRO Division of Entomology, Canberra, Australia.
- Lawrence, J. F. and R. A. B. Leschen. 2010. Acanthocnemidae Crowson, 1964. Pp. 262–265. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Lawrence, J. F. and A. F. Newton, Jr. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1006. In J. Pakaluk and S. A. Ślipiński (eds). *Biology*,

- Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Warszawa, Muzeum i Instytut Zoologii Polska Akademia Nauk, Poland.
- Lawrence, J. F. and S. A. Ślipiński. 2010. Dermestidae Latreille, 1804. Pp. 198–206. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Lawrence, J. F. and S. A. Ślipiński. 2013. *Australian Beetles*. Volume 1. Morphology, classification and keys. CSIRO Publishing. Collingwood, Victoria, Australia. 576 pp.
- Lawrence, J. F. and S. A. Ślipiński. 2014. Orsodacnidae C. G. Thomson, 1859. Pp. 184–189. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 3. Morphology and systematics (Phytophaga). Walter de Gruyter, Berlin, Germany.
- Lawrence, J. F., A. Ślipiński, R. G. Beutel and A. F. Newton. 2013. A possible larva of *Lepicerus inaequalis* Motschulsky (Coleoptera: Myxophaga: Lepiceridae) from Panama. *Zootaxa* 3701: 393–400.
- Lawrence, J. F., A. Ślipiński, A. E. Seago, M. K. Thayer, A. F. Newton and A. E. Marvaldi. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* 61: 1–217.
- Lepesme, P. 1947. *Les Insects des Palmiers*. P. Lecavalier, Paris, France. 903 pp.
- Leschen, R. A. B. 2011. World review of *Laricobius* (Coleoptera: Derodontidae). *Zootaxa* 2908: 1–44.
- Leschen, R. A. B. and R. Beutel. 2010. Phycosecidae Crowson, 1952. Pp. 265–268. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Leschen, R. A. B. and R. G. Beutel (eds). 2014. *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 3. Morphology and systematics (Phytophaga). Walter De Gruyter, Berlin, Germany.
- Leschen, R. A. B., R. G. Beutel and J. F. Lawrence (eds). 2010. *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany. 786 pp.
- Lethbridge, R. C. 1971. The hatching of *Hymenolepis diminuta* eggs and penetration of the hexacanth in *Tenebrio molitor*. *Parasitology* 62: 445–456.
- Lindgren, C. J., J. Corrigan and R. A. De Clerck-Floate. 2002. *Lythrum salicaria* L., purple loosestrife (Lynthaceae). Pp. 383–390. In P. G. Mason and J. T. Huber (eds). *Biological Control Programmes in Canada, 1981–2000*. CABI Publishing, Wallingford, UK.
- Lindroth, C. H. 1961–1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementa* 20, 24, 29, 33, 34, 35: 1–1192 + i–xlvi.
- Lindroth, C. H. 1974. *Coleoptera: Family Carabidae*. Royal Entomological Society of London, UK. 148 pp.
- Lindroth, C. H. 1985–1986. *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Scandinavian Science Press Ltd., Copenhagen, Denmark. 225 pp.
- Lingafelter, S. W. and E. R. Hoebeke. 2002. *Revision of the genus Anoplophora (Coleoptera: Cerambycidae)*. Entomological Society of Washington, Washington, DC. 235 pp.
- Lloyd, J. E. 1983. Bioluminescence and communication in insects. *Annual Review of Entomology* 28: 131–160.
- Löbl, I. and A. Smetana (eds). 2011. *Catalogue of Palaearctic Coleoptera*. Volume 7. Curculionoidea I. Apollo Books, Stenstrup, Denmark. 373 pp.
- Löbl, I. and A. Smetana (eds). 2013. *Catalogue of Palaearctic Coleoptera*. Volume 8. Curculionoidea II. Brill, Netherlands. 700 pp.

- Lobo, J. M. and A. L. V. Davis. 1999. An intercontinental comparison of dung beetle diversity between two mediterranean-climatic regions: local versus regional and historical influences. *Diversity and Distributions* 5: 91–103.
- Lobo, J. M., J. Hortal and F. J. Cabrero-Sañudo. 2006. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions* 12: 111–123.
- Lopez, P. D., E. Lugo, S. Valle, P. Espinoza, M. M. Lopez, M. Delgado, P. Rivera, I. Garcia Avila. 1997. Aquatic insects as biological control agents of mosquito larvae in Nicaragua. *Revista Nicaraguense de Entomologia* 39: 27–30.
- Lord, N. P., C. S. Hartley, J. F. Lawrence, J. V. McHugh, M. F. Whiting and K. B. Miller. 2010. Phylogenetic analysis of the minute brown scavenger beetles (Coleoptera: Latridiidae), and recognition of a new beetle family, Akalyptoischiidae fam. n. (Coleoptera: Cucujoidea). *Systematic Entomology* 35: 753–763.
- Losey, J. E. and M. Vaughan. 2006. The economic value of ecological services provided by insects. *BioScience* 56: 311–323.
- Lövei, G. L. and K. D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* 41: 231–256.
- Lundheim, R. and K. E. Zachariassen. 1993. Water balance of over-wintering beetles in relation to strategies for cold tolerance. *Journal of Comparative Physiology. B. Biochemical, Systemic, and Environmental Physiology* 163: 1–4.
- Lundkvist, E., J. Landin, M. Jackson and C. Svensson. 2003. Diving beetles (Dytiscidae) as predators of mosquito larvae (Culicidae) in field experiments and in laboratory tests of prey preference. *Bulletin of Entomological Research* 93: 219–226.
- Luterek, D. 1966. Observations on the larvae of some species of click beetles (Col., Elateridae) feeding on mushrooms. *Polskie Pismo Entomologiczne (B)* 3–4: 341–345.
- Mackie, T. T., G. W. I. Hunter and C. B. Worth. 1945. *A manual of tropical medicine*. W. B. Saunders, Philadelphia, PA. 727 pp.
- Maddison, D. R., M. D. Baker and K. A. Ober. 1999. Phylogeny of carabid beetles as inferred from 18S ribosomal DNA (Coleoptera: Carabidae). *Systematic Entomology* 24: 103–138.
- Maddison, D. R., W. Moore, M. D. Baker, T. M. Ellis, K. A. Ober, J. J. Cannone and R. R. Gutell. 2009. Monophyly of terrestrial adephagan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). *Zoologica Scripta* 38: 43–62.
- Magagula, C. N. 2003. Changes in carabid beetle diversity within a fragmented agricultural landscape. *African Journal of Ecology* 41: 23–30.
- Magura, T., B. Tothmeresz and Z. Elek. 2003. Diversity and composition of carabids during a forestry cycle. *Biodiversity and Conservation* 12: 73–85.
- Maier, C. A., M. A. Ivie, J. B. Johnson and D. R. Maddison. 2010. A new northern-most record for the family Hydroscaphidae (Coleoptera: Myxophaga), with description of a new Nearctic species. *Coleopterists Bulletin* 64: 289–302.
- Majer, K. 1994. A review of the classification of the Melyridae and related families (Coleoptera, Cleroidea). *Entomologica Basiliensia* 17: 319–390.
- Majer, K. 2002. Subfamilial classification of the family Malachiidae (Coleoptera, Cleroidea). *Entomologica Basiliensia* 24: 179–244.
- Marshall, C. J. and J. K. Liebherr. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography* 27: 203–216.
- Marske, K. A. and M. A. Ivie. 2003. Beetle fauna of the United States and Canada. *Coleopterists Bulletin* 57: 495–503.
- Martikainen, P. and J. Kouki. 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation* 12: 1815–1831.
- Mason, P. G., J. T. Huber and S. M. Boyetchko. 2002. Introduction. Pp. xi–xiv. In P. G. Mason

- and J. T. Huber (eds). *Biological Control Programmes in Canada, 1981–2000*. CABI Publishing, Wallingford, UK.
- Matthews, E. G. and J. F. Lawrence. 2015. Trachelostenini sensu novo: redescription of *Trachelostenus* Solier, *Myrmecodema* Gebien and *Leaus* Matthews & Lawrence, based on adults and larvae, and descriptions of three new species of *Leaus* (Coleoptera: Tenebrionidae). *Zootaxa* 4020: 289–312.
- McClain, E., M. K. Seely, N. F. Hadley and V. Gray. 1985. Wax blooms in tenebrionid beetles on the Namib Desert: correlations with environment. *Ecology* 66: 112–118.
- McCutcheon, G. S. 2002. Consumption of tobacco budworm (Lepidoptera: Noctuidae) by hooded beetle (Coleoptera: Anthicidae) and bigeyed bug (Hemiptera: Lygaeidae). *Journal of Agricultural and Urban Entomology* 19: 55–61.
- McElrath, T. C., J. A. Robertson, M. C. Thomas, J. Osborne, K. B. Miller, J. V. McHugh and M. F. Whiting. 2015. A molecular phylogenetic study of Cucujidae s.l. (Coleoptera: Cucujoidea). *Systematic Entomology* 40: 705–718.
- McElroy, W. D. and M. A. Deluca. 1983. Firefly and bacterial luminescence: basic science and applications. *Journal of Applied Biochemistry* 5: 197–209.
- McKenna, D. D., B. D. Farrell, M. S. Caterino, C. W. Farnum, D. C. Hawks, D. R. Maddison, A. E. Seago, A. E. Z. Short, A. F. Newton and M. K. Thayer. 2015b. Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. *Systematic Entomology* 40: 35–60.
- McKenna, D. D., A. S. Sequeira, A. E. Marvaldi and B. D. Farrell. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proceedings of the National Academy of Sciences USA* 106: 7083–7088.
- McKenna, D. D., A. L. Wild, K. Kanda, C. L. Bellamy, R. G. Beutel, M. S. Caterino, C. W. Farnum, D. C. Hawks, M. A. Ivie, M. L. Jameson, R. A. B. Leschen, A. E. Marvaldi, J. V. McHugh, A. F. Newton, J. A. Robertson, M. K. Thayer, M. F. Whiting, J. F. Lawrence, S. A. Ślipiński, D. R. Maddison and B. D. Farrell. 2015a. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* 40: 835–880.
- Medeiros, L. and G. R. P. Moreira. 2002. Moving on hairy surfaces: modifications of *Gratiana spadicea* larval legs to attach on its host plant *Solanum sisymbriifolium*. *Entomologia Experimentalis et Applicata* 102: 295–305.
- Miller, L. K. 1978. Physical and chemical changes associated with seasonal alterations in freezing tolerance in the adult northern tenebrionid, *Upis ceramboides*. *Journal of Insect Physiology* 24: 791–796.
- Miller, K. B. and J. Bergsten. 2014. The phylogeny and classification of predaceous diving beetles (Coleoptera: Dytiscidae). Pp. 49–172. In D. A. Yee (ed). *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae)*. Springer, New York, NY.
- Miraldo, A., F.-T. Krell, M. Smalén, R. B. Angus and T. Roslin. 2014. Making the cryptic visible – resolving the species complex of *Aphodius fimetarius* (Linnaeus) and *Aphodius pedellus* (De Geer) (Coleoptera: Scarabaeidae) by three complementary methods. *Systematic Entomology* 39: 531–547.
- Mittal, I. C. 1993. Natural manuring and soil conditioning by dung beetles. *Tropical Ecology* 34: 150–159.
- Moore, I. and E. F. Legner. 1976. Intertidal rove beetles (Coleoptera: Staphylinidae). Pp. 521–551. In L. Cheng (ed). *Marine Insects*. North-Holland Publishing, Amsterdam, Netherlands.
- Morgan, R. E., P. de Groot and S. M. Smith. 2004. Susceptibility of pine plantations to attack by the pine shoot beetle (*Tomicus piniperda*) in southern Ontario. *Canadian Journal of Forest Research* 34: 2528–2540.
- Moura, M. O., C. J. de Carvalho and E. L. Monteiro-Filho. 1997. A preliminary analysis of insects of medico-legal importance in Curitiba,

- State of Parana. *Memorias do Instituto Oswaldo Cruz* 92: 269–274.
- Munks, S., K. Richards, J. Meggs, M. Wapstra and R. Corkrey. 2004. Distribution, habitat and conservation of two threatened stag beetles, *Hoplogonus bornemisszai* and *H. vanderschoori* (Coleoptera: Lucanidae) in north-east Tasmania. *Australian Zoologist* 32: 586–596.
- Nahrung, H. F. 2004. Biology of *Chrysophtharta agricola* (Chapuis), a pest of eucalypt plantations in Victoria and Tasmania. *Australian Forestry Journal* 67: 59–66.
- NAPIS [National Agricultural Pest Information System, USA]. 2015. Pest Tracker. <http://pest.ceris.purdue.edu/index.php> [Accessed 31 January 2015].
- Naylor, L. H. 1999. Reporter gene technology: the future looks bright. *Biochemical Pharmacology* 58: 749–757.
- Neboiss, A. 1968. Larva and pupa of *Cupes varians* Lea, and some observations on its biology (Coleoptera: Cupedidae). *Memoirs of the National Museum of Victoria* 28: 17–19.
- Neboiss, A. 1984. Reclassification of *Cupes* Fabricius (s. lat.) with descriptions of new genera and species (Cupedidae: Coleoptera). *Systematic Entomology* 9: 443–477.
- Newton, A. F. 1997. Review of Agyrtidae (Coleoptera), with a new genus and species from New Zealand. *Annales Zoologici* 47: 111–156.
- Newton, A. F. 1998. Phylogenetic problems, current classification and generic catalog of world Leiodidae (including Cholevidae). Pp. 41–178. In P. M. Giachino and S. B. Peck (eds). *Phylogeny and Evolution of Subterranean and Endogean Cholevidae (= Leiodidae)*. Proceedings of XX International Congress of Entomology, Florence, 1996. Museo Regionale di Scienze Naturali, Torino, Italy.
- Newton, A. F. 2005. Leiodidae Fleming, 1821. Pp. 269–280. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1. Morphology and systematics. Walter de Gruyter, Berlin, Germany.
- Nichols, D. S., T. I. Christmas and D. E. Greig. 1990. Oedemerid blister beetle dermatosis: a review. *Journal of the American Academy of Dermatology* 22: 815–819.
- Nielsen, E. S. and L. A. Mound. 1999. Global diversity of insects: the problems of estimating numbers. Pp. 213–222. In P. H. Raven and T. Williams (eds). *Nature and Human Society: the Quest for a Sustainable World*. National Academy Press, Washington, DC.
- Niemela, J., J. R. Spence, D. Langor, Y. Haila and H. Tukia. 1993. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. Pp. 29–50. In K. J. Gaston, T. R. New and M. J. Samways (eds). *Perspectives on Insect Conservation*. Intercept Limited, Andover, UK.
- Nummelin, M. and I. Hanski. 1989. Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. *Journal of Tropical Ecology* 5: 549–552.
- O'Brien, C. W. 1995. Curculionidae, premiere biocontrol agents (Coleoptera: Curculionidae). *Memoir of the Entomological Society of Washington* 14: 119–128.
- Onore, G. 1997. A brief note on edible insects in Ecuador. *Ecology of Food and Nutrition* 36: 277–285.
- Paine, T. D., K. F. Raffa and T. C. Harrington. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 42: 179–206.
- Pakaluk, J., S. A. Ślipiński and J. F. Lawrence. 1994. Current classification and family-group names in Cucujoidea (Coleoptera). *Genus* 5: 223–268.
- Parker, J. 2016. Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News* 22: 65–108.
- Paulus, H. F. 2004. *Urtea graeca* nov. gen. et nov. spec., der erste Vertreter der tropischen Atractocerinae in Europa sowie eine Beschreibung von *Hymaloxylon aspoECKi* nov. spec. aus Yunnan (China) (Coleoptera, Cucujiformia, Lymexyliidae, Atractocerinae nov. status). *Denisia* 13: 277–290.

- Payne, J. A., E. W. King and G. Beinhart. 1968. Arthropod succession and decomposition of buried pigs. *Nature* 219: 1180–1181.
- Peck, S. B. 2005. A checklist of the beetles of Cuba with data on distributions and bionomics (Insecta: Coleoptera). *Arthropods of Florida and Neighboring Areas* 18: 1–241.
- Peck, S. B. 2006. Distribution and biology of the ectoparasitic beaver beetle *Platypsyllus castoris* Ritsema in North America (Coleoptera: Leiodidae: Platypsyllinae). *Insecta Mundi* 20: 85–94.
- Peck, S. B. and M. C. Thomas. 1998. A distributional checklist of the beetles (Coleoptera) of Florida. *Arthropods of Florida and Neighboring Areas* 16: 1–180.
- Pervez, A. and Omkar. 2006. Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*: a review. *Biocontrol Science and Technology* 16: 111–128.
- Peter, C. I. and S. D. Johnson. 2005. Anther cap retention prevents self-pollination by elaterid beetles in the South African orchid *Eulophia foliosa*. *Annals of Botany* 97: 345–355.
- Peters, B. C. and C. J. Fitzgerald. 1996. Anobiid pests of timber in Queensland: a literature review. *Australian Forestry* 59: 130–135.
- Philips, T. K. 2001. A record of *Micromalthus debilis* (Coleoptera: Micromalthidae) from Central America and a discussion of its distribution. *Florida Entomologist* 84: 159–160.
- Philips, T. K. 2002. Anobiidae Fleming 1821. Pp. 245–260. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Piel, J., I. Höfer and D. Hui. 2004a. Evidence for a symbiosis island involved in horizontal acquisition of pederin biosynthetic capabilities by the bacterial symbiont of *Paederus rufipes* beetles. *Journal of Bacteriology* 186: 1280–1286.
- Piel, J., G. Wen, M. Platzer and D. Hui. 2004b. Unprecedented diversity of catalytic domains in the first four modules of the putative pederin polyketide synthase. *ChemBioChem* 8: 93–98.
- Piel, J., D. Butzke, N. Fusetani, D. Hui, M. Platzer, G. Wen and S. Matsunaga. 2005. Exploring the chemistry of uncultivated bacterial symbionts: antitumor polyketides of the pederin family. *Journal of Natural Products* 68: 472–479.
- Pinto, J. D. and M. A. Bologna. 2002. Meloidae Gyllkenthal 1810. Pp. 522–529. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Pitman, A. J., A. M. Jones and E. B. Gareth Jones. 1993. The wharf-borer *Nacerdes melanura* L., a threat to stored archaeological timbers. *Studies in Conservation* 38: 274–284.
- Pitman, A. J., E. B. Gareth Jones and P. Oevering. 2003. An overview of the biology of the wharf borer beetle (*Nacerdes melanura* L., Oedemeridae) a pest of wood in marine structures. *Biofouling* 19: 239–248.
- Plavilstshikov, N. N. 1958. Coleoptera. Cerambycidae. Part 3. Lamiinae. Part 1. *Fauna of USSR* 23: 1–592. [In Russian].
- Poland, T. M. and D. G. McCullough. 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104: 118–124.
- Polilov, A. A. 2008. Anatomy of the smallest Coleoptera, featherwing beetles of the tribe Nanosellini (Coleoptera, Ptiliidae), and limits of insect miniaturization. *Entomological Review* 88: 26–33.
- Polilov, A. A. 2015. How small is the smallest? New record and remeasuring of *Scydosella musawasensis* Hall, 1999 (Coleoptera, Ptiliidae), the smallest known free-living insect. *ZooKeys* 526: 61–64.
- Pollock, D. A. 2002. Scaptiidae Mulsant, 1856. Pp. 564–567. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank. *American Beetles*. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Pollock, D. A. and B. B. Normark. 2002. The life cycle of *Micromalthus debilis* LeConte (1878) (Coleoptera: Archostemata: Micromalthidae): historical review and evolutionary perspective. *Journal of Zoological Systematics and Evolutionary Research* 40: 105–112.

- Porch, N. and S. Elias. 2000. Quaternary beetles: a review and issue for Australian studies. *Australian Journal of Entomology* 39: 1–9.
- Potter, D. A. and D. W. Held. 2002. Biology and management of the Japanese beetle. *Annual Review of Entomology* 47: 175–205.
- Quintero, I. and T. Roslin. 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. *Ecology* 86: 3303–3311.
- Raffa, K. F. and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53: 27–49.
- Rajapakse, S. 1981. Beetle marasmus. *British Medical Journal* 283: 1316–1317.
- Ramos-Elorduy, J., J. M. Pino and V. H. C. Martínez. 2009. Edible aquatic Coleoptera of the world with an emphasis on Mexico. *Journal of Ethnobiology and Ethnomedicine* 5: 1–10.
- Ratcliffe, B. C., M. L. Jameson and A. B. T. Smith. 2002. Scarabaeidae Latreille 1802. Pp. 39–81. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*. Volume 2. Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, FL.
- Ratnasingham, S. and P. D. N. Hebert. 2013. A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PLoS ONE* 8 (8): e66213.
- Rea, N. 1997. Biological control: premises, ecological input and *Mimosa pigra* in the wetlands of Australia's top end. *Wetlands Ecology and Management* 5: 227–242.
- Rees, D. J., B. C. Emerson, P. Oromí and G. M. Hewitt. 2001. Reconciling gene trees with organism history: the mtDNA phylogeography of three *Nesotes* species (Coleoptera: Tenebrionidae) on the western Canary Islands. *Journal of Evolutionary Biology* 14: 139–147.
- Reid, C. A. M. 2000. Spilopyrinae Chapuis: a new subfamily in the Chrysomelidae and its systematic placement. *Invertebrate Taxonomy* 14: 837–862.
- Reid, C. A. M. 2014. Chrysomelidae Latreille 1802. Pp. 11–15. In R. A. B. Leschen and R. G. Beutel (eds). 2014. *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 3. Morphology and systematics (Phytophaga). Walter De Gruyter, Berlin, Germany.
- Ribera, I., J. Mateu and X. Belles. 2005. Phylogenetic relationships of *Dalyat mirabilis* Mateu, 2002, with a revised molecular phylogeny of ground beetles (Coleoptera, Carabidae). *Journal of Zoological Systematics and Evolutionary Research* 43: 284–296.
- Ribera, I., R. G. Beutel, M. Balke and A. Vogler. 2002. Discovery of Aspidytidae, a new family of aquatic Coleoptera. *Proceedings of the Royal Society of London B* 269: 2351–2356.
- Ribera, I. and A. P. Vogler. 2004. Speciation of Iberian diving beetles in Pleistocene refugia (Coleoptera, Dytiscidae). *Molecular Ecology* 13: 179–193.
- Ribera, I., A. P. Vogler and M. Balke. 2008. Phylogeny and diversification of diving beetles (Coleoptera: Dytiscidae). *Cladistics* 24: 563–590.
- Robertson, J. A., A. Ślipiński, M. Moulton, F. W. Shockley, A. Giorgi, N. P. Lord, D. D. McKenna, W. Tomaszewska, J. Forrester, K. B. Miller, M. F. Whiting and J. V. McHugh. 2015. Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology* 40: 745–778.
- Rößner, E. 2012. *Die Hirschkäfer und Blatthornkäfer Ostdeutschlands (Coleoptera: Scarabaeoidea)*. Verein der Freunde & Förderer des Naturkundemuseums Erfurt e.V., Erfurt, Germany. 508 pp.
- Rosa, S. P. 2010. Second record of bioluminescence in larvae of *Xantholinus* Dejean (Staphylinidae, Xantholinini) from Brazil. *Revista Brasileira de Entomologia* 54: 147–148.
- Sagegami-Oba, R., Y. Oba and H. Ôhira. 2007. Phylogenetic relationships of click beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: insights into the evolution of bioluminescence in Elateridae. *Molecular Phylogenetics and Evolution* 42: 410–421.

- Sandorini, P. 2001. Aphrodisiacs past and present: a historical review. *Clinical Autonomic Research* 11: 303–307.
- Scheffler, P. Y. 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology* 21: 9–19.
- Scholtz, C. H. and V. V. Grebennikov. 2005. Scarabaeiformia Crowson, 1960. Pp. 345–366. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 1. Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin, Germany.
- Schweigkofler, W., W. J. Otrosina, S. L. Smith, D. R. Cluck, K. Maeda, K. G. Peay and M. Garbelotto. 2005. Detection and quantification of *Leptographium wageneri*, the cause of black-stain root disease, from bark beetles (Coleoptera: Scolytidae) in Northern California using regular and real-time PCR. *Canadian Journal of Forest Research* 35: 1798–1808.
- Scott, M. P. 1998. The ecology and behavior of burying beetles. *Annual Review of Entomology* 43: 595–618.
- Seres, A. and N. Ramírez. 1995. Biología floral y polinización de algunas monocotiledoneas de un bosque nublado venezolano. *Annals of the Missouri Botanical Garden* 82: 61–81.
- Short, A. E. Z. and M. Fikáček. 2013. Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). *Systematic Entomology* 38: 723–752.
- Short, A. E. Z., L. J. Joly, M. García, A. L. Wild, D. D. Bloom and D. R. Maddison. 2015. Molecular phylogeny of the Hydroscaphidae (Coleoptera: Myxophaga) with description of a remarkable new lineage from the Guiana Shield. *Systematic Entomology* 40: 214–229.
- Sikes, D. S. 2004. The beetle fauna of Rhode Island. An annotated checklist. *The Biota of Rhode Island*. Volume 3. Rhode Island Natural History Survey, Kingston, Rhode Island. vi + 295 pp.
- Sikes, D. S. 2005. Silphidae Latreille, 1807. Pp. 288–296. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, beetles. Volume 1. Morphology and systematics. Walter De Gruyter, Berlin, Germany.
- Ślipiński, S. A. and J. F. Lawrence. 2010. Cerylonidae Billberg, 1820. Pp. 422–432. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Ślipiński, S. A., R. A. B. Leschen and J. F. Lawrence. 2011. Order Coleoptera Linnaeus, 1758. In Z.-Q. Zhang (ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 203–208.
- Ślipiński, S. A., N. Lord and J. F. Lawrence. 2010. Bothrideridae Erichson, 1845. Pp. 411–422. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Ślipiński, S. A. and W. Tomaszewska. 2010. Coccinellidae Latreille, 1802. Pp. 454–472. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Smith, A. B. T. 2006. A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. *Coleopterists Society Monographs* 5: 144–204.
- Smith, A. B. T. and A. Paucar. 2000. Taxonomic review of *Platycoelia lutescens* (Scarabaeidae: Rutelinae: Anoplognathini) and a description of its use as food by the people of the Ecuadorian Highlands. *Annals of the Entomological Society of America* 93: 408–414.

- Smith, A. B. T., D. C. Hawks and J. M. Heraty. 2006. An overview of the classification and evolution of the major scarab beetle clades (Coleoptera: Scarabaeoidea) based on preliminary molecular analyses. *Coleopterists Society Monographs* 5: 35–46.
- Smith, D. M. and J. D. Marcot. 2015 The fossil record and macroevolutionary history of the beetles. *Proceedings of the Royal Society B* 282: 20150060.
- Smith, K. G. V. 1986. *A Manual of Forensic Entomology*. Cornell University Press, Ithaca, NY. 205 pp.
- Sole, C. L., C. H. Scholtz and A. D. S. Bastos. 2005. Phylogeography of the Namib Desert dung beetles *Scarabaeus (Pachysoma)* MacLeay (Coleoptera: Scarabaeidae). *Journal of Biogeography* 32: 75–84.
- Sörensson, M. 1997. Morphological and taxonomical novelties in the world's smallest beetles, and the first Old World record of Nanosellini (Coleoptera: Ptiliidae). *Systematic Entomology* 22: 257–283.
- Spangler, P. J. and W. E. Steiner, Jr. 2005. A new aquatic beetle family, Meruidae, from Venezuela (Coleoptera: Adephaga). *Systematic Entomology* 30: 339–357.
- Spector, S. 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopterists Society Monographs* 5: 71–83.
- Spence, J. R. and D. H. Spence. 1988. Of ground-beetle and men: introduced species and the synanthropic fauna of western Canada. *Memoirs of the Entomological Society of Canada* 144: 151–168.
- Stolz, U., S. Velez, K. V. Wood, M. Wood and J. L. Feder. 2003. Darwinian natural selection for orange bioluminescent color in a Jamaican click beetle. *Proceedings of the National Academy of Sciences USA* 100: 14955–14959.
- Stork, N. E. 1999a. The magnitude of biodiversity and its decline. Pp. 3–32. In J. Cracraft and M. Novacek (eds). *The Living Planet in Crisis: Biodiversity, Science and Policy*. American Museum of Natural History, NY.
- Stork, N. E. 1999b. Estimating the number of species on Earth. Pp. 1–7. In W. Ponder and D. Lunney (eds). *The Other 99%: the Conservation and Biodiversity of Invertebrates*. Royal Zoological Society of New South Wales, Sydney, Australia.
- Strom, B. L., S. R. Clarke and P. J. Shea. 2004. Efficacy of 4-allylanisole-based products for protecting individual loblolly pines from *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Canadian Journal of Forest Research* 34: 659–665.
- Strother, K. O., C. D. Steelman and E. E. Gbur. 2005. Reservoir competence of lesser mealworm (Coleoptera: Tenebrionidae) for *Campylobacter jejuni* (Campylobacterales: Campylobacteraceae). *Journal of Medical Entomology* 42: 42–47.
- Švácha, P. and J. F. Lawrence. 2014a. Vesperidae Mulsant, 1839. Pp. 16–49. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, beetles. Volume 3. Morphology and systematics (Phytophaga)*. Walter de Gruyter, Berlin, Germany.
- Švácha, P. and J. F. Lawrence. 2014b. Disteniidae J. Thomson, 1861. Pp. 60–76. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, beetles. Volume 3. Morphology and systematics (Phytophaga)*. Walter de Gruyter, Berlin, Germany.
- Švácha, P., J.-J. Wang and S.-C. Chen. 1997. Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). *Annales de la Société Entomologique de France* 33: 323–369.
- Tabor, K. L., C. C. Brewster and R. D. Fell. 2004. Analysis of the successional patterns of insects on carrion in southwestern Virginia. *Journal of Medical Entomology* 41: 785–795.
- Talley, T. S. and M. Holyoak. 2006. The effects of dust on the federally threatened valley elderberry longhorn beetle. *Environmental Management* 37: 647–658.
- Tarasov, S. and F. Génier. 2015. Innovative bayesian and parsimony phylogeny of dung

- beetles (Coleoptera, Scarabaeidae, Scarabaeinae) enhanced by ontology-based partitioning of morphological characters. *PLoS ONE* 10 (3): e0116671.
- Thayer, M. K. 2005. Staphylinidae Latreille, 1802. Pp. 296–344. In R. G. Beutel and R. A. B. Leschen (eds). *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom*. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 1. Morphology and Systematics. Walter de Gruyter, Berlin, Germany.
- The Coleopterists Society. 2007. Home page. <http://www.coleopsoc.org/> [Accessed 21 March 2016].
- Tomaszewska, W. 2010. Endomychidae Leach, 1815. Pp. 442–454. In R. A. B. Leschen, R. G. Beutel and J. F. Lawrence (eds). *Handbook of Zoology*. Arthropoda: Insecta. Coleoptera, beetles. Volume 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter De Gruyter, Berlin, Germany.
- Tostowaryk, W. 1971. Coleopterous predators of the Swaine jack-pine sawfly, *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae). *Canadian Journal of Zoology* 50: 1139–1146.
- Tschinkel, W. R. 1975. A comparative study of the chemical defensive system of tenebrionid beetles: chemistry of the secretions. *Journal of Insect Physiology* 21: 753–783.
- Turchetto, M. and S. Vanin. 2004. Forensic entomology and globalization. *Parassitologia* 46: 187–190.
- Tyndale-Biscoe, M. 1994. Dung burial by native and introduced dung beetles (Scarabaeidae). *Australian Journal of Agricultural Research* 45: 1799–1808.
- Underwood, T. J., D. W. Tallamy and J. D. Pesek. 1997. Bioluminescence in firefly larvae: a test of the aposematic display hypothesis (Coleoptera: Lampyridae). *Journal of Insect Behavior* 10: 365–370.
- USDA-APHIS [United States Department of Agriculture – Animal and Plant Health Inspection Service]. Regulated pest list. https://www.aphis.usda.gov/wps/portal/aphis/ourfocus/planthealth?1dmy&uril=wcm%3Apath%3A/aphis_content_library/sa_our_focus/sa_plant_health/sa_import/sa_permits/sa_plant_plant_products/sa_prohibited/sa_quarantine/ct_regulated_pest_list [Accessed 31 January 2015].
- Utsunomiya, Y. and K. Masumoto. 1999. Edible beetles (Coleoptera) from northern Thailand. *Elytra* 27: 191–198.
- VanLaerhoven, S. L. and G. S. Anderson. 1999. Insect succession on buried carrion in two biogeoclimatic zones of British Columbia. *Journal of Forensic Sciences* 44: 32–43.
- Varchola, J. M. and J. P. Dunn. 1999. Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. *Agriculture Systems and Environment* 73: 41–49.
- Viviani, V. R. 2002. The origin, diversity, and structure function relationships of insect luciferases. *Cellular and Molecular Life Sciences* 59: 1833–1850.
- Vulinec, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. *Biotropica* 34: 297–309.
- Wallace, M. G. 2005. Observations of urban dung beetles utilizing dog feces (Coleoptera: Scarabaeidae). *Coleopterists Bulletin* 59: 400–401.
- Watson, D. W., P. E. Kaufman, D. A. Rutz and C. S. Glenister. 2001. Impact of the darkling beetle *Alphitobius diaperinus* (Panzer) on establishment of the predaceous beetle *Carcinops pumilio* (Erichson) for *Musca domestica* control in caged-layer poultry houses. *Biological Control* 20: 8–15.
- Watts, C. H. S. and W. F. Humphreys. 1999. Three new genera and five new species of Dytiscidae (Coleoptera) from under-ground waters in Australia. *Records of the South Australian Museum* 32: 121–142.
- Weber, D. C., D. L. Rowley, M. H. Greenstone and M. M. Athanas. 2006. Prey preference and host suitability of the predatory and parasitoid carabid beetle, *Lebia grandis*, for several species of *Leptinotarsa* beetles. *Journal of Insect Science* 6: 1–14.

- Wheeler, Q. D. 1986. Revision of the genera of Lymexylidae (Coleoptera: Cucujiformia). *Bulletin of the American Museum of Natural History* 183: 113–210.
- Wilson, C. J. 2001. *Aphodius pedellus* (DeGeer), a species distinct from *A. fimetarius* (Linnaeus) (Coleoptera: Aphodiidae). *Tijdschrift voor Entomologie* 144: 137–143.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6: 1–1359.
- Wood, S. L. and D. E. Bright. 1992. A catalog of Scolytidae and Platypodidae (Coleoptera), part 2 (volumes A and B): taxonomic index. *Great Basin Naturalist Memoirs* 13: 1–1553.
- Woodcock, T. S., E. E. Boyle, R. E. Roughley, P. G. Kevan, R. N. Labbee, A. B. T. Smith, H. Goulet, D. Steinke and S. J. Adamowicz. 2013. The diversity and biogeography of the Coleoptera of Churchill: insights from DNA barcoding. *BMC Ecology* 13: 40.
- Work, T., J. Klimaszewski, E. Thiffault, C. Bourdon, D. Pare, Y. Bousquet, L. Venier and B. Titus. 2013. Initial responses of rove and ground beetles (Coleoptera, Staphylinidae, Carabidae) to removal of logging residues following clearcut harvesting in the boreal forest of Quebec, Canada. *ZooKeys* 258: 31–52.
- Wyatt, T. D. 1986. How a subsocial intertidal beetle, *Bledius spectabilis*, prevents flooding and anoxia in its burrow. *Behavioral Ecology and Sociobiology* 19: 323–331.
- Yeates, D. K., M. S. Harvey and A. D. Austin. 2003. New estimates for terrestrial arthropod species-richness in Australia. *Records of the South Australian Museum, Monograph Series* 7: 231–241.
- Yensen, E. 1975. A revision of the North American species of *Trixagus* Kugelann (Coleoptera: Throscidae). *Transactions of the American Entomological Society* 101: 125–166.
- Young, D. K. 2002. Scirtidae Fleming, 1821. Pp. 87–89. In R. H. Arnett, M. C. Thomas, P. E. Skelley and J. H. Frank. *American Beetles*. Volume 2. Polyphaga: Scarabaeoidea through Curculionioidea. CRC Press, Boca Raton, FL.
- Zachariassen, K. E. 1991. Routes of transpiratory water loss in a dry-habitat tenebrionid beetle. *Journal of Experimental Biology* 157: 425–437.
- Zelazny, B. and E. Pacumbaba. 1982. Phytophagous insects associated with cadang-cadang infected and healthy coconut palms in southeastern Luzon, Philippines. *Ecological Entomology* 7: 113–120.