

Biology, Ecology, and Evolution of Gall-inducing Arthropods

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Gall-inducing Coleoptera

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ABSTRACT

The gall-inducing habit is not common in Coleoptera. In addition to species of Chrysomeloidea and Curculionoidea, the supposedly most primitive forms of galls or, rather, gall-like swellings on twigs and roots are induced by a considerable number of species of Buprestidae and by a single species each of Nitidulidae and Mordellidae. In Chrysomeloidea, a highly advanced subfamily Lamiinae of Cerambycidae comprises 11 gall inducers, whereas only three species of the other subfamilies induce galls. In the Chrysomelidae, on the contrary, the gallicolous species are confined to the primitive subfamilies Sagrinae, Criocerinae, and Eumolpinae. No gall inducer is known in Bruchinae (the seed beetles), a highly advanced group of Chrysomeloidea. Weevils (Curculionoidea) are the richest in gall inducers among Coleoptera, including species from the higher families Apionidae, Nanophyidae, Eirrhinidae, Curculionidae, and Scolytidae; a few gallers are known in the primitive family Urodontidae. Smaller weevils of several advanced subfamilies of Curculionidae induce a variety of galls on all parts of plants, but more often on the stems and roots. The gall-inducing habit in most weevils seems to be only an extension of several ecological niches like stem- or root-tunneling, pericarp- and perianth-eating. Only in Ceutorhynchinae the gall-inducing habit constitutes a separate niche: several groups of closely related *Ceutorhynchus* species, such as the *C. assimilis* Paykull species-group, induce galls of similar shape on either the stem or the root. One of the most obvious evolutionary advantages of gall induction by small weevils is that it facilitates rapid larval development, enabling the gall-inducing weevils to colonize ephemeral plants in deserts. Gall-inducing Coleoptera elicit less complex plant responses, unlike those of major gall-inducing groups (e.g., gall midges or gall wasps). Compared with the major groups of gall inducers (i.e., Cecidomyiidae, Tenthredinidae, and Cynipidae), the Coleoptera, similarly to Lepidoptera, seem to use plant physiological responses rather infrequently in providing their larvae with mechanical defense and food. The extensive distribution of species of case-bearing Lepidoptera and Chrysomelidae and the variety of habits, involving diverse morphological adaptations, in the moth, leaf-beetle, and weevil larvae suggest that the holometabolous insects with chewing larval mouthparts use their own facilities for purposes of mechanical defense and food.

INTRODUCTION

In spite of a staggering number of phytophagous species and the presence of two large superfamilies (namely, Chrysomeloidea and Curculionoidea) closely associated with plants, the Coleoptera include relatively few gall inducers. The only taxon of the Coleoptera recognized for gall-inducing species is the subfamily Ceutorhynchinae of Curculionidae (Lengerken 1941, Crowson 1981). Lengerken (1941) also lists many Apionidae, Nanophyidae, Mecinini, and Tychiini (Curculionidae: Curculioninae) as gall inducers. Of the at least 400 insect species inducing distinct galls in the European part of the former USSR, only 55 species of Coleoptera induce true galls, 51 belonging to Apionidae and Curculionidae, two to Buprestidae, and one each to Cerambycidae and Scolytidae; many other species of beetles induce less conspicuous swellings on stems and roots (Ermolenko 1991); to these numbers, one species of Buprestidae (*Ovalisia dives* (Guillebeau)) should be added (Bílý 2002). British gall-inducing Coleoptera include 126 species (Bowdrey and Spooner 1996), although some of them are not established as gall inducers. Despite insufficient knowledge of larval development of most weevils, gall inducers appear to be a minor group of Coleoptera.

DEFINITION OF COLEOPTERA AND SYSTEMATICS

Coleoptera are a large, or maybe the largest, order in Insecta. This holometabolous group is subdivided into almost 200 families arranged in four suborders, the largest being Adephaga and Polyphaga. Most Adephaga are either carnivorous or phycophagous species, whereas Polyphaga, with more than 100 families, include several highly advanced families with specialized phytophagous species, including those with xylophagous, xylo-mycetophagous, and mycetophagous habits.

LARVAE AND ADULTS: TYPES AND RANGE OF VARIABILITY

Both the larvae and adults are active feeders with biting mouthparts, playing an important role in most of the terrestrial ecosystems. Feeding behavior is similar in larvae and adults of primitive, mostly predatory and phycophagous taxa. An important, if not predominant, tendency in the evolution of the coleopteran life cycles is the sharing of functions between the adult and larval stages. In primitive carnivorous groups both larvae and adults are agile predators. In the course of evolution, the adult stage specialized for providing better conditions for the offspring development, supplying larvae with both shelter and food. In the most advanced Buprestidae, Cerambycidae, and weevils (Curculionoidea), the larvae have evolved into sedentary organisms, with reduced sensory and locomotory abilities as evidenced by the reduction of the ocelli, antennae, and legs, and depigmentation of the body. Gall induction is, therefore, a phenomenon that is in line with the general tendency in Coleoptera, but it is almost exclusive to its higher phytophagous groups.

PROCESS OF GALL INDUCTION INCLUDING FEEDING OR OVIPOSITIONAL BEHAVIOR OF THE GALL-INDUCING STAGE

In this chapter we are not discussing the peculiarities of coleopteran galls compared with those induced by other arthropods. We use the gall definition by Mani (1964): "Galls are simply pathologically developed cells that have proliferated in a region of the plant, causing an external swelling or modification atypical of the plant as a result of a parasitic organism". Among the abnormalities induced by Coleoptera, there is no absolute way to determine at what stage such an abnormality can be considered a gall.

Information on the process of gall development and on the developmental stages of the gall-inducing Coleoptera is limited. Le Pape and Bronner (1987), Meyer (1987), Vijayaraghavan et al. (1989), and Florentine et al. (2002) describe the physiology of coleopteran galls and the structural alterations in the plant tissues involved. Le Pape and Bronner (1987) have shown that the primary reaction of the plant tissue to the damage caused by the female excavating a hole or a tunnel for an egg is the same as the plant response to the damage caused by feeding. The subsequent changes in the host-plant tissues are activated by chemicals secreted during oviposition; the exochorion probably acts as an intermediate between the gall inducer and the host.

Only the simplest, apparently initial reaction of plant tissues on larval invasion is evident in the most primitive of the coleopteran gall inducers, the Buprestidae. Gall-like swellings on the twigs and roots infested by some buprestid larvae, for example *Metasambus* sp. on *Salix* sp. (Fig. 1), are nonspecific in shape. Plants react similarly to infestation by the larvae of Cerambycidae, Chrysomelidae, Scolytidae, and weevil subfamilies Lixinae and Molytinae (Fig. 2). Single larvae, or sometimes aggregations of larvae, induce spindle-shaped swellings on roots or twigs. Such a reaction benefits



Fig. 1 Root gall possibly induced by *Metasambus* sp. (Buprestidae) on *Salix* sp. (Salicaceae) in Yunnan, China. (Photograph by A.S.K.)

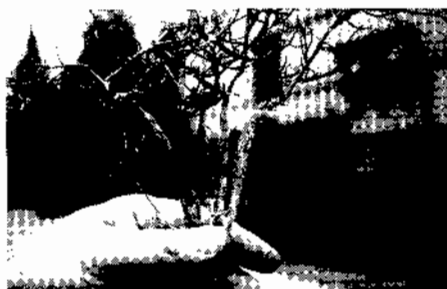


Fig. 2 Root galls induced by *Bothynoderes declivis* Olivier (= *Chromoderus declivis* Olivier, Curculionidae) on *Salsola* sp. (Chenopodiaceae) on the Sea of Azov coast, Russia. (Photograph courtesy M. Cristofaro, Rome)

the larva by increasing the volume of plant tissue available as food. Even in this apparently primitive gall, only meristemic tissues are involved in the growth, a fact repeatedly stressed by Kaplin (1981) with respect to many more-advanced galls.

Species of the more primitive Buprestidae, Cerambycidae, and Chrysomelidae induce galls only on axial organs (i.e., stem and root), whereas the advanced Curculionoidea (the classification by Alonso-Zarazaga and Lyal 1999 is followed here) induce galls on all parts of plants, including leaves and flowers. Noteworthy is the prevalence of trees with soft, rapidly growing stems among hosts of the galling Cerambycidae both in the temperate zone (*Saperda* on Salicaceae) and in the tropics (*Apriona*, *Dihammus*, and *Nupserha* on *Tectona grandis*) (see Table 2). Salicaceae comprise a considerable part of the hosts of galling Buprestidae (see Table 1). On the contrary, conifers are rarely used by gall-inducing Coleoptera as hosts. The tendency to attack axial organs, or organs that are close to axial structures, is retained by higher weevils; for example, *Baris cordiae* Marshall (Curculionidae) induces fusiform galls on the leaf midrib and petioles of *Cordia obliqua* Willd. (Boraginaceae) in India (Krishnamurthy et al. 1977). *Tychius crassirostris* Kirsch, one of a few gallers in the large, predominantly carpophagous *Tychius*, also lays eggs near the leaf midrib of a species of *Melilotus* (Fabaceae) (Ross [1910] cited in Meyer 1987). *Ceutorhynchus*, the most species-rich galling weevil, induces galls on the stem, the leaf midrib, or the root.

Gall-inducing weevils have elaborate and diverse effects on host plants. Even the most primitive gall-inducing weevil, the South African *Urodontus scholtzi* Louw (Urodontidae), affects the architecture of its host shrub (Price and Louw 1996). Infestation of the *Crepis biennis* L. (Asteraceae) stem base by the Western Palearctic *Lixus punctiventris* Boheman (Curculionidae) results in a virescence with polycephaly, that is, proliferation of the host capitulum into numerous new capitula (Meyer 1987). A similar effect is induced by a *Dorytomus* sp. (Curculionidae) larva on *Salix caprea* L. catkin axis (Meyer 1987). *Tychius crassirostris* Kirsch (Curculionidae) induces unusual pod-shaped leaf galls on *Melilotus albus* L. (Fabaceae) (Ross [1910] cited in Meyer 1987). Some antho- and carpophilous higher Curculionidae (e.g., *Anthonomus*, *Curculio*, *Miarus*) induce hypertrophy of the perianth or pericarp, which is not always apparent from the outside (=cryptocecidium). A stem-galling weevil from Argentina, *Conotrachelus albocinereus* Fiedler (Curculionidae: Molytinae), induces a compound effect on its host, *Parthenium hysterophorus* L. (Asteraceae). Larval feeding disrupts the vessel elements in the gall, affecting the movement of metabolites and transpiration in the plant. This, combined with the high level of host specificity of the weevil, makes *C. albocinereus* a promising agent for biological control of the invasive *P. hysterophorus* (Florentine et al. 2002).

HOST PLANTS AND NUTRITIONAL RELATIONSHIPS

Progress in the evolutionary trend leading to gall induction was associated with increase in both the diversity of the infested plant organs and the efficiency in exploiting the host plant's metabolism. High nutrient levels in gall tissues resulted in the rapid development of high biomass coleopteran larvae, when compared with those feeding on decaying woody tissues (Kaplin 1981). Examples of large solitary or aggregated galls on roots are those induced by *Liocleonus clathratus* Olivier (Curculionidae) (Fig. 3). Exploitation of the aerial parts of annuals has probably favored the wide diversification of several groups of small-sized weevils (Apionidae; subfamily Ceutorhynchinae and tribes Tychiini, Smicronychini, and Mecinini of the subfamily Curculioninae in the Curculionidae).



Fig. 3 Large solitary or loosely aggregated galls induced by *Liocleonus clathratus* Olivier (Curculionidae) on *Tamarix* sp. (Tamaricaceae) root in Mongolia. (Photographs by M.G.V.)

GEOGRAPHICAL DISTRIBUTION OF THE GALL INDUCERS AND THEIR HOSTS

Most of the galls throughout the northern hemisphere are induced by noncoleopteran insects and a wide variety of them develop on willows (*Salix* spp.). Willow vegetation dominates the riparian, floodland, and other wet habitats, hosting the greatest variety of nongalling phytophagous beetles in the boreal and temperate zones of the Asian Far East from Kolyma basin and Kamchatka (about 60–64° N) to South Korea (about 35° N). Over 100 species of Tenthredinidae (Hymenoptera) and some Cynipidae induce the vast majority of galls on willows, some galls being associated with commensal or pseudoparasitic weevils, for example, *Melanapion minimum* Herbst (Apionidae) in galls of Tenthredinidae and Cecidomyiidae (Hoffmann 1958, Dieckmann 1977, Korotyayev and Egorov 1995), *M. naga* Nakane in galls of two species of *Pontania* (Tenthredinidae) (Korotyayev and Egorov 1995), *Curculio salicivorus* Paykull and *C. crux* Fabricius (Curculionidae) in galls of *Pontania* and *Euura* (Tenthredinidae) (Dieckmann 1988). The only coleopteran galls occasionally found on willows are those induced by the cerambycid, *Saperda populnea* (L.) (Figs 4, 5), on thin branches. Larvae of most larger Palearctic species of *Saperda*, including those living on *Populus* spp., show tunneling behavior.



Fig. 4 Stem gall induced by *Saperda populnea* (L.) (Cerambycidae) on *Populus tremula* L. (Salicaceae), longitudinal-sectional view. (After Ermolenko 1991, modified)



Fig. 5 Stem gall induced by *Saperda populnea* (L.) (Cerambycidae) on *Populus gracilis* Grossh. (Salicaceae) in Araks valley, Turkey. (Photograph courtesy V.I. Dorofeyev, St. Petersburg)

Oaks (*Quercus* spp.), dominating broad-leaved forests in the temperate northern hemisphere and widely distributed in northern tropical areas, host the greatest number of specialized phytophagous insects in the Palearctic (Emeljanov 1967), beetles forming a considerable proportion. Yet most galls commonly found on oak leaves and twigs are those induced by Cynipidae (Fig. 6); their vacated dry galls are inhabited by species of Anobiidae (Zerova 2001), and two European species of *Curculio* live as inquiline in leaf and flower galls induced by Cynipidae on oaks.



Fig. 6 Galls induced by Cynipidae (Hymenoptera) on twigs of *Quercus* sp. in Bayburt Province, Turkey. (Vacated dry galls are inhabited in the Ukraine by species of Anobiidae.) (Photograph courtesy V.I. Dorofeyev, St. Petersburg)

Pine trees, playing an even more important role than oaks in the temperate and boreal forests, host only one gall-inducing species of Coleoptera, the specialized weevil *Podapion* (Apionidae). One species of *Podapion*, widely distributed in the North American temperate and boreal forests, induces galls on *Pinus* twigs (Kissinger 1964). Two species of *Podapion* of less frequent distribution are known from Bosnia and Herzegovina (Korotyaev 1993) and Spain (Alonso-Zarazaga 1998). In Eurasia, *Brachonyx pineti* Paykull (Curculionidae: Anthonominae) is common and widespread on *Pinus silvestris* L., sometimes causing considerable damage and supposedly inducing galls on needles (Ermolenko 1991); neither Scherf (1964) nor Dieckmann (1968) provide any information on the galling habit of this weevil. *Macrobrachonyx gounellei* Pic, endemic to the Canary Islands, is probably also associated with *Pinus* sp. (Dieckmann 1968); the biology of *M. gounellei* needs investigation. This species of the monotypic genus is closely related to *B. pineti* but its body size is almost twice that of *B. pineti*. The irregular punctuation of the elytra in *M. gounellei* indicates its more advanced phylogenetic position as compared with *B. pineti* and suggests a gall-inducing larval habit on *Pinus* needles as one of the possible derived traits.

In addition to Tenthredinidae and Cynipidae, the two dipteran families, Tephritidae and Cecidomyiidae (gall midges), induce most of the known galls on temperate herbaceous vegetation (see also the chapters by Yukawa and Rohfritsch, Roskam, Korneyev et al., Roininen et al., and Csóka et al. in this book). The Tephritidae and Cecidomyiidae are abundant in the semi-arid and arid landscapes, whereas Tephritidae are also common in the forest and steppe zones. Tephritids often co-occur with weevils, and sometimes their large, conspicuous galls may be erroneously attributed to weevils, especially when the latter feed on plants in great numbers. For example, *Madarellus undulatus* Say (Curculionidae: Baridinae) proceeding larval development in the *Vitis* (Vitaceae) vine occasionally feeds at adult stage on

flowerheads of the goldenrod *Solidago altissima* L. (Asteraceae), the stems of which often bear large ball galls induced by *Eurosta solidaginis* (Fitch.) (Diptera: Tephritidae) in the temperate North American forests. In the Palearctic Region, tephritids co-occur with weevils of Lixini and Rhyncocillini in flowerheads of many Asteraceae. In contrast to Tephritidae, many species of which induce galls in the flowerheads, no species of the weevil genus *Larinus* induces true galls, although some cause swellings and deformation of the flowerhead.

Little is known about gall-inducing Coleoptera in tropical forests. Symptoms of activity of chewing insects are frequently evident in tropical forests, whereas galls induced by chewing insects are infrequent. In the disturbed vegetation of the urban and agricultural areas of North Vietnam, galls of only one species of Coleoptera, *Hollisiella carbo* Faust (Curculionidae, Baridinae), on twigs of *Fissistigma polyanthum* (Hook. and Thong.) Mes. (Annonaceae) were found during two-month winter collecting; however, many abscised fruits of several species were infested by larvae of Coleoptera, including Curculionoidea (B.A.K., personal observation).

In the Palearctic steppes and deserts, a wide variety of gall-inducing insects occur. Species of *Artemisia* (wormwoods) form a framework of many types of steppe and desert plant communities, and most of the 154 species of Cecidomyiidae (20 genera) monophagous on *Artemisia* induce galls (Fedotova 2000) (Fig. 7). The weevil fauna associated with *Artemisia* in Kazakhstan comprises more than 50 species, dominated probably by the numerous ectophytic at the larval stage species of *Eremochorus* (Hyperinae) and the leaf-mining *Pseudorchesstes* (Rhamphinae), but only three species of the apionid *Taphrotopium* induce galls. The Mongolian weevil fauna is



Fig. 7 *Artemisia* sp. (Asteraceae) in Araks valley, Turkey, usually bears galls induced by several species of Cecidomyiidae (Diptera), but none by weevils, although several species of weevils live on *Artemisia*. (Photograph courtesy V.I. Dorofeyev, St. Petersburg)

overwhelmingly dominated by 74 species of *Stephanocleonus* (Lixinae) with root-feeding larvae (Ter-Minassian 1989, 1990); many of these are associated with *Artemisia*. The next largest numbers of species of weevil taxa living on *Artemisia* belong to *Eremochorus* and *Pseudorchestes* (B.A.K., unpublished data), and *Taphrotopium steveni* Gyllenhal is the only species of *Taphrotopium* known from Mongolia (B.A.K., unpublished data).

A survey of an Eastern European steppe site revealed 168 species of Curculionoidea, mostly of known larval habits, including 14 gall inducers (Korotyayev 2000; B.A.K., unpublished data). Of the gall inducers, three species belong to Apionidae, four to Ceutorhynchinae, four to Mecinini (Curculioninae), two species to *Smicronyx* (Smicronychini, Curculioninae), and one (*Pachycerus cordiger* Germar) to Lixinae, most of which are common at the investigated site.

More than 50 species in 20 genus-group taxa of Oxyonychini (probably the most specialized tribe of the Palearctic Ceutorhynchinae (Curculionidae)) are associated with *Ephedra* (Ephedraceae), a primitive gymnosperm inhabiting the arid Mediterranean and continental Asian regions, yet none induces galls. *Ephedra* does, however, sometimes host large numbers of galls induced by Cecidomyiidae (Fig. 8).



Fig. 8 *Ephedra* sp. (Ephedraceae) in Erzurum Province, Turkey, bears galls induced by Cecidomyiidae (Diptera), but none by weevils, although four species of weevils live on *Ephedra* in this locality. (Photograph courtesy V.I. Dorofeyev, St. Petersburg)

Among the phytophagous insects in the southeastern Kara Kum sand desert in Turkmenistan, Coleoptera was the most species-rich group of endobiont arthropods, dominated by buprestids and weevils (Kaplin 1981). No buprestid (of the 31 species investigated) was found to induce galls, although *Sphenoptera tamarisci beckeri* Dohrn recorded by Kaplin among the 31 species does induce galls (see Table 1). Of the 75 weevil species (Kaplin 1981), the biology and host plants are known only for 30, of which only five induce galls. Only two species of gall-inducing weevils are known on *Haloxylon* (Chenopodiaceae): (1) *Lixus kraatzi* Capiomont infesting shoots (Tokgayev and Nepesova 1964, Soyunov 1991) and (2) an unidentified species of 'small' weevils (Kaplin 1981), while more than 40 species of Cecidomyiidae

are galls on this desert tree. Gall-inducing weevils (all Ceutorhynchinae) seem to dominate in sand deserts on ephemeral and ephemeroïd grasses, whereas gall-inducing cecidomyiids are rare on this ecological plant group.

Numbers and descriptions of gall fauna in the Northern Kara Kum Desert in Turkmenistan (Soyunov 1991) are similar to the findings of Kaplin (1981); in the complex of 76 gall-inducing insects, Coleoptera are represented by five weevils. Four species of *Sphenoptera* (Buprestidae) also induce root galls both in Northern and Southern Kara Kum (see Table 1).

Gall-inducing Coleoptera are also of little importance among insects associated with the plants of the Transaltai Gobi desert communities in Mongolia (Korotyaev et al. 1983). Although Coleoptera were represented more than any other insect order, very few galls occur there. Of the 90 weevil species found, two are galls on roots: *Liocleonus clathratus* Olivier on *Tamarix* (Tamaricaceae) at riverbeds, and *Ulobaris loricata* Boheman on *Atriplex sibirica* L. (Chenopodiaceae) in salt flats. Some of the nine species of the tribe Corimaliini living on *Tamarix* and *Reaumuria* (Tamaricaceae) are probably gall inducers, as also are two species of Ceutorhynchinae. In spite of the harsh arid climate of the Transaltai Gobi, the number of weevil species with ectophytic larvae (10; nine Hyperinae and *Cionus zonovi* Korotyaev) lacking any protective covers (e.g., larval cases), although forming cocoons for pupal stages, is much greater than that of gall inducers.

Chrysomelidae, the second most species-rich family of phytophagous Coleoptera in the Transaltai Gobi fauna, has no galls at all, while species with case-bearing larvae (Clytrinae, Cryptocephalinae) and protective cover-constructing larvae (Cassidinae) comprise a large part of the fauna: 23 of 51 species (B.A.K., unpublished data). Buprestidae, next to Chrysomelidae, in the number of species in the Transaltai Gobi desert communities (B.A.K., unpublished data), include only one gallicolous species, *Sphenoptera tamarisci beckeri* (Alexeev and Volkovitch 1989).

As in the northern hemisphere, only a small number of Coleoptera induce galls in Australia (Blanche 1993) among them six species of endemic genera of Buprestidae (see Table 1).

ASSOCIATED ARTHROPODS IN GALLS

Many of the weevils and some Anobiidae use galls induced by other arthropods for the development of their larvae. Some species of Rhynchitidae live as inquiline and pseudoparasites in the 'leaf packages' made by species of the closely related family Attelabidae, for example, *Paradeporaus depressus* Faust in leaf packages made by *Byctiscus* in the Far East (Egorov 1996). All the species belonging to the South American subfamily Pterocolinae of Rhynchitidae are cleptoparasites of Attelabidae (Hamilton 1998). Inquilineism seems to be characteristic of some genus-group taxa of Apionidae (e.g., *Melanapion* and *Hemiperapion*), but no genus or subgenus of Curculionidae appears specialized for inquilineism. Some inquiline Apionidae, for example, *Hemiperapion mesasiaticum* Ter-Minassian and *Perapion myochroum* Schilsky in Turkmenistan, can develop in shoots when galls of their hosts, psyllids of the genus *Pachypsyllodes*, are rare (Loginova 1978). These two apionids may

infest as much as 30 percent of host galls. Among species of *Anthonomus* (Curculionidae), inquilines occur in many species-groups (Gates and Burke 1972). Moreover, some species may be facultative inquilines, otherwise developing within buds. *Baris* sp. (Curculionidae) lives in galls induced by *Urodontus scholtzi* Louw (Urodontidae) on *Galenia africana* L. (Aizoaceae) in South Africa (Louw 1998).

Species of *Dorytomus*, *Curculio*, and *Anthonomus* (Curculionidae), and probably all five species of the Palearctic *Melanapion* (Apionidae), are inquilines in the galls of Tenthredinidae on *Salix* spp. (Salicaceae). *Dorytomus leucophyllus* Motschulsky also often uses roll galls induced by Tenthredinidae (A.G. Zinovjev, personal communication) on leaves of *Salix* sp. as shelters in Kamchatka. Inquilinous weevils live in galls induced by advanced gallers, namely the Tenthredinidae, Cynipidae, and Cecidomyiidae, belonging to the youngest and most progressive insect orders Hymenoptera and Diptera, whereas Curculionoidea are an old superfamily of the old order Coleoptera. This probably means that gall induction has arisen as a very progressive habit in different phyletic branches of weevils.

GALL INDUCTION IN DIFFERENT GROUPS OF COLEOPTERA

Gall induction in Coleoptera occurs almost exclusively in the most advanced superfamilies, Chrysomeloidea and Curculionoidea. Among the more primitive Coleoptera, gall induction is occasional but not rare in the predominantly xylobiontic Buprestidae. Other examples are *Brachyleptus algiricus* Grouvelle (Nitidulidae), which causes deformations of the seed capsule in two papaveraceous hosts in Algeria, and *Mordellistena brevicauda* Boheman (Mordellidae), which causes twig swellings on *Euphorbia nicaeensis* All. (Euphorbiaceae) in southern Europe (Lengerken 1941).

Galls or gall-like swellings on stems, twigs, or roots induced by buprestid larvae are probably the simplest, maybe mechanical, reaction of plant tissues to larval feeding. The gall occurrence pattern in Cerambycidae, with wood-boring or subcortical larvae, is similar to that in buprestids. Transition from woody plants to herbs is not known to give rise to gall induction in the Buprestidae or Cerambycidae, even in the species-rich herbivorous *Agapanthia*, *Phytoecia*, and the largest Palearctic genus *Dorcadion* with rhizophagous larvae. Such a transition in several groups of Curculionoidea, including the predominantly xylophilous Scolytidae, indicates the possible origin of the galling habit. *Hylobius transversovittatus* Goeze (Curculionidae), a herbivorous species of the mostly dendrophilous nongalling genus *Hylobius*, induces galls on the root crown of *Lythrum salicaria* L. (Lythraceae). *Thamnurgus*, the only Palearctic truly gall-inducing scolytid, is one of a few genera associated with herbs. Chrysomelidae is a vast group of moderately to strictly specialized plant feeders including many species of small to medium size, with a larval diversity probably greater than in any other insect family (Imms 1957); it includes a few species which induce galls, mostly simple stem swellings caused by larvae. The most advanced group of the Chrysomeloidea, the Bruchinae (seed-beetles), is entirely specialized for feeding on seeds during larval stages. The hypothesized phylogenetic

lineage from the stem-galling Sagrinae to the seed-feeding *Rhaebus* (Bruchinae) has no examples within Coleoptera, whereas the stem gall-inducing habit has apparently arisen from seed feeding in Urodontidae (Louw 1993) and many genera of Curculionidae (see below). The gall-inducing habit is more or less widely distributed in Curculionoidea.

Buprestidae

Among buprestids (jewel beetles, flat-headed borers), the larvae of only a few species are known to induce gall-like swellings of stems and roots of their host plants (Table 1). These species belong to only two distantly related subfamilies, Chalcophorinae (Poecilonotini and Sphenopterini) and Agrilinae (Agrilini and Coraebini) (classification after Volkovitsh 2001). Gall-inducing behavior usually occurs only in some species of large genera, while other species of those genera (e.g., *Sphenoptera*, *Agrilus*, *Cisseis*) induce no galls. It seems that gall-like swellings develop as a protective reaction of host plants only if the larvae develop inside slender stems, branches, and roots.

Table 1 Gall-inducing Buprestidae

Taxa	Distribution	Host plant	References
Subfamily			
Chalcophorinae			
Tribe Poecilonotini			
<i>Poecilonota</i>			
<i>P. bridwelli</i> Van Dyke	USA: California	<i>Populus fremontii</i> Wats. (Salicaceae). Gall-like swellings on limbs	Nelson 1965, Bellamy and Scholtz 1986
<i>Ovalisia</i>			
<i>O. dives</i> (Guillebeau)	Central, Southern, and Eastern Europe, Western Siberia	<i>Salix</i> spp. (Salicaceae), <i>Sorbus aria</i> Crantz (Rosaceae). Gall-like swellings on branches	Bilý 2002
Tribe Sphenopterini			
<i>Sphenoptera</i>			
<i>S. (Chilostetha) jugoslavica</i> Obenberger	South of Eastern Europe, North America (introduced)	<i>Centaurea diffusa</i> Lam. (Asteraceae). Root galls	R.L. Westcott (personal communication) in Bellamy and Scholtz 1986
<i>S. (Chrysoblemma) bifulgida</i> Reitter	Middle Asia*	<i>Salsola</i> spp. (Chenopodiaceae). Root galls	Krivosheina 1975b, Bellamy and Scholtz 1986

(Contd.)

*Russian literature distinguishes Middle Asia and Central Asia. Middle Asia is the climatic and natural region that includes the Asian republics of the former USSR and neighboring parts of Afghanistan; the region is characterized by warm winters and maximum rainfalls in spring and autumn. Central Asia is the climatic region that includes Mongolia and a large area of western China; it is characterized by an extreme continental climate with harsh winters and maximum rainfall in late summer. In the English-language literature Middle Asia is incorporated in Central Asia.

Table I (Contd.)

Taxa	Distribution	Host plant	References
<i>S. (Chrysoblemma) tamarisci</i> (Klug)	Middle Asia	<i>Climacoptera turcomanica</i> (Litv.) Botsch., <i>Salsola leptoclada</i> Gand., <i>Suaeda arcuata</i> Bge., <i>S. acuminata</i> (C.A. Mey.) (Chenopodiaceae). Root galls	Krivosheina 1975a, b (as <i>S. pseudoignita</i> Alexeev)
<i>S. (Chrysoblemma) scovitzii</i> Faldermann	Transcaucasia, Middle Asia, Turkey, Iran, Afghanistan, Israel	<i>Climacoptera turcomanica</i> (Litv.) Botsch., <i>Salsola leptoclada</i> Gand. (Chenopodiaceae). Root galls	Krivosheina 1975a, b
<i>S. (Chrysoblemma) tamarisci beckeri</i> Dohrn (as <i>S. beckeri</i> Dohrn)	Transcaucasia, Middle Asia, Turkey, Iran, Afghanistan, Mongolia	<i>Climacoptera turcomanica</i> (Litv.) Botsch., <i>Horaninovia ulicina</i> Fisch. et Mey., <i>Salsola leptoclada</i> Gand., <i>Atriplex sibirica</i> L. (Chenopodiaceae). Root swellings	Krivosheina 1975a, b; Kaplin 1981; Alexeev and Volkovitch 1989
<i>S. (Tropeopeltis) gnidiaphaga</i> Bellamy	South Africa	<i>Gnidia burchelli</i> (Meisn.) Gilg. (Thymelaeaceae). Stem galls	Bellamy and Scholtz 1986
<i>S. (Tropeopeltis) loranthiphaga</i> Bellamy	South Africa	<i>Loranthus zeyheri</i> Harv. (Loranthaceae). Basal stem galls	Bellamy and Scholtz 1986
Subfamily Agrilinae Tribe Agrilini <i>Agrilus</i>			
<i>A. anxius</i> Gory	North America	<i>Crataegus</i> sp. (Rosaceae). Irregular twig and branch annulations	Felt 1940, Bellamy and Scholtz 1986
<i>A. champlaini</i> Frost	USA: Connecticut	<i>Ostrya virginica</i> Willd. (Betulaceae). "Reared from galls"	Frost 1912, Bellamy and Scholtz 1986
<i>A. crataegi</i> Frost	North America	<i>Crataegus</i> sp. (Rosaceae). Globose twig swellings	Felt 1940 (as <i>A. politus</i>), Bellamy and Scholtz 1986
<i>A. cuprescens</i> (Ménétriés) (as <i>A. aurichalceus</i> Redtenbacher, <i>A. viridis</i> auct., <i>A. chrysoderes</i> Abeille de Perrin, <i>A. rubicola</i> Abeille de Perrin)	Palaearctic, North America (introduced)	<i>Rosa</i> spp. (Rosaceae). Twig galls (swellings)	Fisher 1928, Felt 1940, Alexeev 1957, Bellamy and Scholtz 1986, Bílý 2002
<i>A. politus</i> (Say)	North America	<i>Salix</i> sp. (Salicaceae). Globose constricted twig swellings	Felt 1940, Bellamy and Scholtz 1986
<i>A. politus pseudocoryli</i> Fisher	North America	<i>Corylus</i> sp., <i>C. americana</i> Marsh (Betulaceae). Galls	Fisher 1928, Felt 1940, Bellamy and Scholtz 1986

(Contd.)

Table 1 (Contd.)

Taxa	Distribution	Host plant	References
<i>A. ruficollis</i> (Fabricius)	North America	<i>Rubus</i> spp. (Rosaceae). Elongate swellings or galls on the canes	Fisher 1928, Bellamy and Scholtz 1986
Tribe Coraebini			
<i>Cisseis</i>			
<i>C. acuducta</i> (Kirby)	Australia	<i>Dillwynia retorta</i> (Wendl.) Druce (Fabaceae). Root galls	Froggatt 1892 (as <i>Ethon marmoratum</i> Laporte et Gory), Hawkeswood and Peterson 1982, Turner and Hawkeswood 1995a
<i>Cisseis</i> sp. near <i>C.</i> <i>nitiventris</i> Carter	Australia	<i>Dillwynia retorta</i> (Wendl.) Druce (Fabaceae). Root galls	Turner and Hawkeswood 1995a
<i>Dinocephalia</i> <i>D. cyaneipennis</i> (Blackburn)	Australia	<i>Casuarina distila</i> Vent. (Casuarinaceae). Galls on branches	Froggatt 1894, Hawkeswood and Peterson 1982 (as <i>Paracephala</i> <i>cyaneipennis</i>)
<i>Ethonion</i>			
<i>E. affine</i> (Laporte et Gory)	Australia	<i>Pultenaea stipularis</i> Sm., <i>P.</i> <i>flexilis</i> Sm. (Fabaceae). Stem galls	Froggatt 1892, Hawkeswood and Peterson 1982, Bellamy and Scholtz 1986, Hawkeswood 1988, Volkovitsh and Hawkeswood 1990 (as <i>Ethon affine</i>)
<i>E. corpulentum</i> (Boheman)	Australia	<i>Dillwynia retorta</i> (Wendl.) Druce (Fabaceae). Root galls	Froggatt 1892 (as <i>D.</i> <i>ericifolia</i> Sm.), Hawkeswood and Peterson 1982, Bellamy and Scholtz 1986, Hawkeswood and Turner 1992 (as <i>Ethon corpulentum</i>)
<i>E. fissiceps</i> (Kirby)	Australia	<i>Dillwynia retorta</i> (Wendl.) Druce, <i>D. floribunda</i> Sm. (Fabaceae). Stem galls	Hawkeswood and Turner 1992, Turner and Hawkeswood 1995b (as <i>Ethon</i> <i>fissiceps</i>)
<i>Eupristocerus</i>			
<i>E. cogitans</i> Weber	North America	<i>Alnus rugosa</i> Spreng, <i>A. incana</i> (L.) Moench (Betulaceae). "Forming galls"	Knull 1920, Bellamy and Scholtz 1986
<i>Metasambus</i>			
<i>Metasambus</i> sp. n. pr. <i>hoschecki</i> Obenberger (V. Kubán det.)	China (Yunnan)	<i>Salix</i> sp. Root galls (Fig. 1)	M.G.V., unpublished data

Cerambycidae

Cerambycidae (longhorned wood-boring beetles) include over 25,000 species whose larvae develop inside axial plant parts. Although most longhorned wood-boring beetles develop in dead or dying wood, many live in healthy portions of plants. A small number of them induce galls as a result of feeding activity within the plant. Indeed, some cerambycids cause barely visible swellings on plants. However, we shall consider only those species that usually induce an obvious swelling on the host plant.

Bowdrey and Spooner (1996) list two species of gall-inducing cerambycids in England (*Saperda populnea* (L.) and *S. carcharias* (L.)); Duffy (1953) lists six species worldwide (*Apriona swainsoni* Hope, *Nupserha variabilis* Gahan, *Xylotrechus aceris* Fisher, *Desmocerus aureipennis piperi* Webb, *Dihammus cervinus* Hope, and *Archodontes melanopus* (L.)); Felt and Joutel (1904) treat only *Saperda*, but list and illustrate five gall-inducing species (*S. concolor* LeConte, now in *S. inornata* Say; *S. obliqua* Say; *S. fayi* Bland; *S. puncticollis* Say, herein not considered a true gall inducer; and *S. moesta*, now in *S. populnea* (L.)); Solomon (1995) lists six species in the United States (*Saperda inornata* Say, *S. populnea* (L.), *S. cretata* Newman, *S. fayi* Bland, *Oberea delongi* Knull, and *Xylotrechus aceris* Fisher); Byers (2002) lists four (*Oberea perspicillata* Haldeman [included erroneously in the Buprestidae under the name *Oberea bimaculata*], *Xylotrechus aceris* Fisher, *Saperda inornata* Say, and *S. populnea* (L.)). *Saperda fayi* Bland has been recorded by Nielsen (2002) and *Saperda calcarata* Say by North Dakota State University (2002).

Table 2 lists 15 species of Cerambycidae that induce galls on their host plants. Although the Lamiinae (and, in particular, the genus *Saperda*) are well documented, Prioninae, Lepturinae, and Cerambycinae also include gall-inducing species.

Table 2 Gall-inducing Cerambycidae

Species	Common name	Subfamily	Primary host(s)
<i>Archodontes melanopus</i> (L.)	(none found in literature)	Prioninae	<i>Quercus</i> , <i>Celtis</i>
<i>Desmocerus aureipennis piperi</i> Webb	golden-winged elder borer	Lepturinae	<i>Sambucus</i>
<i>Xylotrechus aceris</i> Fisher	gall-making maple borer	Cerambycinae	<i>Acer</i>
<i>Apriona swainsoni</i> Hope	(none found in literature)	Lamiinae	<i>Butea</i> , <i>Tectona</i>
<i>Dihammus cervinus</i> Hope	teak canker borer	Lamiinae	<i>Tectona</i> , <i>Gmelina</i>
<i>Nupserha variabilis</i> Gahan	(none found in literature)	Lamiinae	<i>Thunbergia</i> , <i>Tectona</i> , <i>Gmelina</i>
<i>Oberea delongi</i> Knull	poplar twig borer	Lamiinae	<i>Populus</i>
<i>Oberea perspicillata</i> Haldeman	raspberry cane borer	Lamiinae	<i>Rubus</i>
<i>Saperda calcarata</i> Say	large poplar borer	Lamiinae	<i>Populus</i> , <i>Salix</i>
<i>Saperda carcharias</i> (L.)	—	Lamiinae	<i>Populus</i> , <i>Salix</i>
<i>Saperda cretata</i> Newman	spotted apple-tree borer	Lamiinae	<i>Malus</i> , <i>Crataegus</i>
<i>Saperda fayi</i> Bland	thorn limb borer	Lamiinae	<i>Crataegus</i>
<i>Saperda inornata</i> Say	poplar gall borer	Lamiinae	<i>Salix</i> , <i>Populus</i>
<i>Saperda obliqua</i> Say	alder borer	Lamiinae	<i>Alnus</i>
<i>Saperda populnea</i> (L.)	small poplar borer	Lamiinae	<i>Salix</i> , <i>Populus</i>

Archodontes melanopus (L.) (occurring in the southeastern United States from Florida to Texas) is the only species of prionine in which the gall-inducing habit has been recorded. This species (then known as *Mallodon melanopus*) induces large galls on the roots of oaks, retarding their growth and sometimes leading to the death of the tree (H.G. Hubbard, cited in Riley 1884). *Desmocerus aureipennis piperi* Webb (occurring in the western United States to the northern Rocky Mountains) is the only lepturine for which the gall-inducing habit is recorded. This cerambycid (then known as *Desmocerus piperi*) induces a 25 cm diameter gall at the bases of elderberry (*Sambucus* spp.) stems (Craighead 1923). One species of Cerambycinae, *Xylotrechus aceris* Fisher, induces small galls on trunks of young red maples (*Acer rubrum* L.) in the northeastern United States and southeastern Canada; a pupal chamber is made either above or below the gall, and the adult emerges through the gall wall (Craighead 1923).

Most gall-inducing Cerambycidae are Lamiinae. *Apriona swainsoni* Hope, in northern India, Myanmar, and east to Vietnam, is one of the few beetles that develops in two host plants. It begins feeding in the stem of *Butea* sp. (Fabaceae), inducing a gall, and prior to the molting of the final instar moves from the *Butea* to the teak tree (*Tectona grandis* L.) to complete its metamorphosis (Beeson and Bhatia 1939). *Dihammus cervinus* Hope, the teak canker borer, shows a pattern in host preference similar to that of *Apriona swainsoni*. Its large gall-like swelling at the base of the teak tree (0.3–1 m above ground level) sometimes causes such a weakening that the tree will break at the gall site (Beeson and Bhatia 1939). *Nupserha variabilis* Gahan is another species that may undergo development in two hosts. It begins larval feeding inside *Thunbergia* liane, inducing a large gall; when fully grown, the larva passes into the adjacent teak tree where it pupates (Beeson and Bhatia 1939). This species also occurs throughout northern India and Myanmar. *Oberea delongi* Knull, the poplar twig borer, occurs in the northeastern United States and causes small elongate swellings on poplar branches (Solomon 1995). *Oberea perspicillata* Haldeman, the raspberry cane borer on *Rubus* sp., is listed in Solomon (1995) and Byers (2002), but Solomon's description of the larval development and damage shows no indication of gall induction. If galls are indeed induced by the raspberry cane borer, they are not nearly as conspicuous as the wilting of stems, consequent to the infestation.

Saperda includes the most known examples of gall-inducing Cerambycidae. Five species, mostly occurring in the United States, induce galls (Felt and Joutel 1904, Solomon 1995). *Saperda inornata* Say, the poplar gall borer (referred previously as *S. concolor*), induces conspicuous stem galls on willow and poplar trees. These galls may occur serially on one stem and each may be twice the diameter of the unaffected portion of the stem. *Saperda populnea* (L.) attacks the same hosts as *S. inornata* and occurs in both Eurasia and the United States. Its galls (Figs 4, 5) are smaller, ovoid and less conspicuous than those of other *Saperda* species (Fig. 9a–e) on willows and poplars. *Saperda fayi* Bland, the thorn limb borer, induces galls (0.5–3.7 cm) on hawthorn branches (Fig. 9a). Populations can build to such high levels that they cause

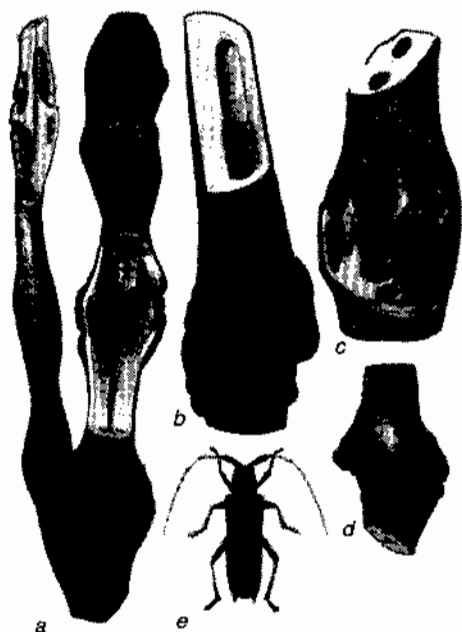


Fig. 9 Galls induced by *Saperda* spp. (Cerambycidae) and an adult insect (e). (a) Hawthorn (*Crataegus* sp., Rosaceae) branch with galls of *Saperda fayi* Bland; (b) alder (*Ainus* sp., Betulaceae) stem with external view of gall of *S. obliqua* Say; (c) alder stem with gall of *S. obliqua* exposed internally; (d) alder stem with gall of *S. obliqua*; (e) adult of *S. obliqua*. (All figures drawn by J.H. Joutel and adapted from Felt and Joutel 1904)

damage to hawthorns (Nielsen 2002). *Saperda cretata* Newman, the spotted apple-tree borer, causes similar gall-like swellings on bark, primarily of apple trees (*Malus domestica* Borkh., Rosaceae), but also of serviceberry (*Amelanchier arborea* L., Rosaceae), hawthorn (*Crataegus* sp.), and crabapple trees (*Malus* sp., Rosaceae). *Saperda calcarata* Say, the large poplar borer, can be destructive to poplar trees because of its large body size and often high populations in individual trees. Although Solomon (1995) does not indicate galling, North Dakota State University (2002) mentions that larval feeding induces spindle-shaped twig galls. *Saperda obliqua* Say (Fig. 9 e), the alder borer occurring in the northeastern United States, produces prominent, deformed swellings on stems of alder (Fig. 9 b–d).

Statistically, there must be many more cerambycids that induce galls since host plants and immature stages are known for only 10–20 percent of them. Only through intensive fieldwork and rearing can the list of gall-inducing cerambycids be expanded.

Chrysomelidae

Gall inducers are rare among leaf beetles. The larvae of some live inside roots or underground stems (*Longitarsus*, *Aphthona*, *Psylliodes*). Many Sagrinae,

and some Criocerinae and Eumolpinae induce galls. Early records (Lengerken 1941) indicate a flea beetle, *Psylliodes napi* Fabricius, as a potential gall inducer on *Cardamine* spp. (Brassicaceae). However, this record needs confirmation since galls on *Cardamine* are more likely to be induced by a weevil, *Ceutorhynchus pectoralis* Weise (Curculionidae). The following gall-inducing taxa are known: eumolpine *Odontionopa sericea* Gyllenhal (Cox and Windsor 1999), criocerine *Ortholema abnormis* Heinze, and other species of *Ortholema* (Jolivet and Hawkeswood 1995). Cox and Windsor (1999) and Jolivet and Hawkeswood (1995) have considered *Ortholema* to be transitional between criocerines and sagraeines although no information is available on the structure of galls.

The best-known leaf beetles that are gallicolous in the larval stage are sagraeines (Jolivet and Hawkeswood 1995). Sagraeine larvae tunnel the above-ground stems of host plants. From one to 20 larvae of *Sagra* species occur in one stem. The stem galls are simple swellings around the larval feeding sites (Fig. 10). Larvae of *Sagra* construct cocoons inside the gall where pupation occurs. The adults cut holes before exiting. Larvae of *Atalasis* also induce galls on stems, each gall containing one larva in an elongate chamber. Larval excreta accumulate at both ends of the chamber. Pupation possibly occurs in the soil (Jolivet and Hawkeswood 1995).

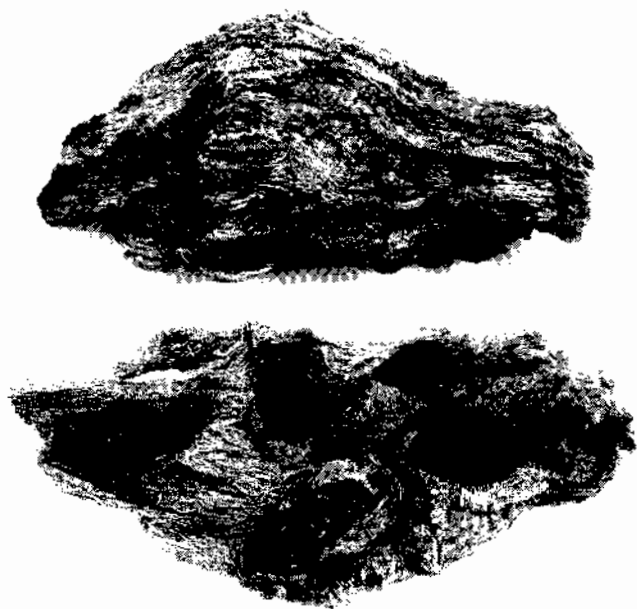


Fig. 10 Stem gall with multiple pupal chambers, induced by *Sagra* sp. (Chrysomelidae) on an unknown plant from India (USNM, specimen label includes the text "given to Bridwell by C. Schaefer, 1920"). (Photographs by A.S.K.)

Curculionoidea, excluding Scolytidae

Galling is apparently a derived mode of life in weevils, judging from the scarcity or absence of gall inducers in the most primitive families of Curculionoidea, species of which are associated with reproductive plant organs and are usually characterized by tunneling larvae. The Urodontidae is one of the most ancient weevil families, which includes predominantly carpophagous larvae, and some of them are gall inducers. Two of the 21 South African *Urodontus* species induce stem galls on woody species of Aizoaceae, whereas the congeners develop in seedpods of Aizoaceae and other families (Louw 1993).

Gall-inducing species are common in Apionidae, Nanophyidae, and Curculionidae, the most advanced families of Curculionoidea. Gall inducers are apparently absent in the primitive families associated with pteridophytes. Only one gall inducer, *Hypselus ater* Boheman (= *Anchonoides bonariensis* Brèthes), is known on a South American monocotyledon, *Sagittaria montevidensis* Cham. and Schlect. (Alismataceae) (Houard [1933] cited in Meyer 1987). *H. ater* is the only gall inducer known in Erihrinidae, the family that is closest to, but more primitive than Curculionidae and is associated mostly with monocotyledons. No gallicolous species is known in the three large advanced families, Dryophthoridae, living mostly on monocotyledons, and Rhynchitidae and Attelabidae, developing on a wide range of dicotyledons. Many species of Rhynchitidae live as inquiline in the leaf rolls made by Attelabidae, but they do not match apionids in gall-inducing behavior.

Among higher weevils, gall induction is typical of the advanced groups. In the Apionidae, species of many apparently young herbivorous Palearctic genera induce galls. In the Nanophyidae, *Titanomalía komaroffi* Faust (Corimaliini) induces galls on woody branches of *Tamarix* sp. (Tamaricaceae), whereas most other Corimaliini develop in flowers and fruits, including an unidentified species which induces floral galls on *Tamarix troupii* Hole in India (Vijayaraghavan et al. 1989). Species of several Palearctic genera of Nanophyini induce galls on the stem or lower parts of the midrib of *Lythrum* (Lythraceae) and *Ctenomeropsis nigra* Walzl induces galls on the young shoots of *Erica* (Ericaceae). The host range and variety of galls induced by Curculionidae are much wider than those in Apionidae and Nanophyidae.

Of the approximately 400 European species of Curculionidae with described larval habits (Scherf 1964), about 10 percent induce galls on all organs of a variety of dicotyledons. Relatively few species of the more primitive subfamilies Molytinae, Lixinae, and Cryptorhynchinae induce simple galls on roots or twigs (Figs 2, 3, 11a, b). Gall inducers are most numerous in the highly advanced Ceutorhynchinae, Baridinae, and Curculioninae sensu lato (especially in the tribes Mecinini and Tychiini).

A common European molytine, *Hylobius transversovittatus* Goeze, induces swellings at the stem-root transition zone of *Lythrum salicaria* L. (Lythraceae). The predominantly Holarctic genus *Hylobius* includes over 20 species

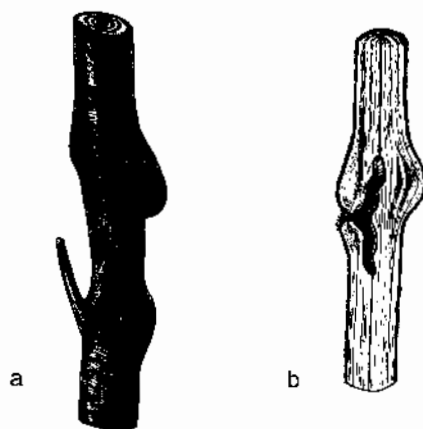


Fig. 11 Galls induced by *Cryptorhynchus lapathi* L. (Curculionidae) on twig of *Alnus* sp. (Betulaceae). (a) external view; (b) longitudinal-sectional view. (After Ermolenko 1991)

developing on trees, and three Palearctic species on herbs. Of these three, only *H. transversovittatus* induces swellings. A similar mode of larval development occurs in other comparatively large-bodied beetles (Buprestidae and weevils of the subfamily Lixinae) that develop in twigs, shoots, or roots of small herbaceous plants or semi-shrubs. Gall induction is also common in small-bodied weevils whose larvae develop in great numbers within one root, for example, *Ulobaris loricata* Boheman (Baridinae) on Chenopodiaceae in Middle Asia and Central Asia.

Lixinae induce more diverse galls: well-developed ones on twigs in desert bushes, spindle-shaped swellings on roots (e.g., two species of *Bothynoderes* (= *Chromoderes*), namely *B. declivis* Olivier (Fig. 2) and *B. affinis* Schrank (= *fasciatus* Müller)), and single or multiple galls on roots (e.g., *Lioctonus clathratus* Olivier on *Tamarix*, *Hypolixus tigrinus* Reitter on *Suaeda arcuata* Bge. and *S. paradoxa* Bge. (Chenopodiaceae) in Tajikistan (Nikulina 1989)). The gall-inducing habit occurs in some genera of the two tribes, Lixini and Cleonini.

Several advanced groups of Curculionidae induce different types of galls. Species of the nominotypical subgenus of *Smicronyx* (Smicronychini: Curculioninae) induce spherical galls on host stems, mostly *Cuscuta* spp. (Convolvulaceae), whereas the larvae of other species of *Smicronyx* (sensu stricto) developing on *Cuscuta* are either seed feeders or stem borers; the bulk of the subgenera *Pachyphanes*, *Pseudosmicronyx*, and *Desmoris* develop in seeds of Asteraceae (Anderson 1962). Palearctic *Tychius crassirostris* Kirsch (Tychiini: Curculioninae) induces leaf galls on *Melilotus* spp. (Fabaceae), whereas larvae of most of its congeners develop in pods feeding on seeds (Fig. 12). Of the more than 20 European species of *Sibinia*, also Tychiini, most develop in seed capsules of the Caryophyllaceae; only one species (*Sibinia* sp. near *femoralis* Gyllenhal) induces stem galls on *Silene otites* L. (Caryophyllaceae), whereas *S. femoralis* develops in the capsules of *Tunica saxifraga* L. (Caryophyllaceae) in Slovakia (Dieckmann 1988). A Middle Asian

relative of *Sibinia* sp. near *femoralis*, *S. taschkentica* Faust (considered conspecific with it by Caldara (1985)), develops in the capsules of *Silene nana* Kar. and Kir. in Turkmenistan (Kaplin 1981). *Mecinus janthinus* Germar (Mecinini: Curculioninae) develops inside the peduncles of *Linaria* spp. (Scrophulariaceae) without inducing galls, whereas closely related *M. heydeni* Wencker and *M. collaris* Germar induce spindle-shaped swellings of the stem of *Linaria* spp. and *Plantago* spp. (Plantaginaceae), respectively (Scherf 1964). Species of *Rhinusa* and *Gymnetron* (Mecinini) may either develop in the capsules or induce root galls (Fig. 13) or stem galls, the latter sometimes several centimeters in diameter (*Gymnetron hispidum* Brullé on *Linaria* spp.). Some Holarctic and tropical Baridinae induce gall-like swellings on leaf midribs and petioles (e.g., *Baris cordiae* Marshall on *Cordia obliqua* Willd., Boraginaceae; Krishnamurthy et al. 1977, Mani 2000), on tree branches, shoots, or roots, but no genus-group taxon of this subfamily comprises exclusive gallers. Ceutorhynchinae is the only weevil taxon that includes a great number of gall-inducing species-groups.

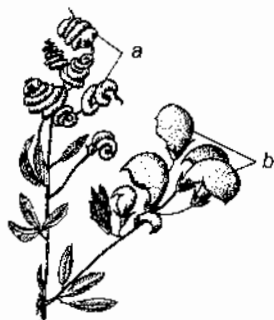


Fig. 12 Fruit galls induced by *Tychius medicaginis* Bris. (Curculionidae) on *Medicago sativa* L. (Fabaceae). a—normal fruits; b—galls. (After Ermolenko 1991)



Fig. 13 Root galls induced by *Rhinusa* sp. (Curculionidae) on *Linaria* sp. (Scrophulariaceae). (After Ermolenko 1991)

The subfamily Ceutorhynchinae is distributed worldwide with over 1,200 described species of small (1.3–7 mm, usually about 2 mm long) robust weevils whose moderately long rostrum is placed between coxae in repose. Ceutorhynchinae is a highly advanced group of the true weevils. Most Ceutorhynchinae are specialized to a narrow host range, and many are monophagous, at least within much of the species range. They feed on all plant organs and induce galls on many species of plants. The biology of most Ceutorhynchinae and their host-plant relationships are little known, but the gall-inducing habit is common in the largest genus, *Ceutorhynchus*, which comprises about 300 species in the Holarctic and Afrotropical (including southern Africa) Regions. With a few exceptions, not discussed herein, species of *Ceutorhynchus* develop on Brassicaceae. Larval habits are known for much less than half of the European *Ceutorhynchus* species, and available information on galling in this group is preliminary, except for the investigations by Le Pape and Bronner (1987).

The distribution of the gall-inducing habit is evidently nonstochastic among Palearctic *Ceutorhynchus*, most of the known gall inducers belonging to the *C. chalybeus* Germar and *C. assimilis* Paykull species-groups. The target organ is usually consistent and types of galls are also mostly similar among closely related *Ceutorhynchus* species. Species of the *C. chalybeus* group induce stem galls of irregular shape (Fig. 14), and those of the *C. assimilis* group induce subspherical or irregular-shaped, single or multiple galls on roots (Figs 15, 16). Host ranges of the species of these groups may be broad. Both *C. chalybeus* and *C. assimilis* attack and damage many economically important Brassicaceae. Monophagous species are also present in both groups: the *C. chalybeus* group includes the eastern European *C. wellschmiedi* Dieckmann on *Crambe tataria* Sebeok, and almost sympatric with it is *C. cardariae* Korotyaev on *Cardaria draba* (L.) Desv.; the *C. assimilis* group includes



Fig. 14 Stem galls induced by *Ceutorhynchus chalybeus* Germar (Curculionidae) on *Erucastrum armoracioides* (Czern. ex Turcz.) Cruchet (Brassicaceae) in Erzurum Province, Turkey. (Photograph courtesy V.I. Dorofeyev, St. Petersburg)



Fig. 15 Galls induced by *Ceutorhynchus assimilis* Payk. (Curculionidae) on a root crown of *Cardaria draba* (L.) Desv. (Brassicaceae) (coin diameter = 20.5 mm). (Photograph courtesy M. Cristofaro, Rome)

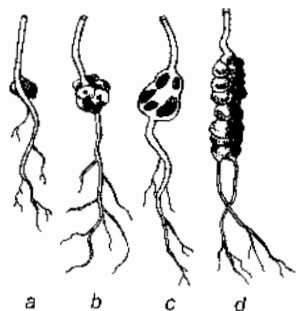


Fig. 16 Root galls induced by *Ceutorhynchus plumbeus* Bris. (Curculionidae) on *Erysimum cheiranthoides* L. (Brassicaceae). (a) Single-chambered; (b) aggregated, external view; (c) longitudinal-sectional view of aggregated gall; (d) linearly arranged galls. (After Lengerken 1941)

monophagous species and those probably associated with a few species of a single genus [*C. dubius* Brisout on *Berteroa incana* (L.) DC., *C. wagneri* Smreczynski on *Alyssum calycinum* L. (Smreczynski 1974), *C. subpilosus* Brisout on *A. calycinum* in Europe (Smreczynski 1974) and Georgia (Caucasus) (Korotyaev and Cholokava 1989), *C. plumbeus* Brisout on *Erysimum cheiranthoides* L. in Europe (Dieckmann 1972), and *C. khnzoriani* Korotyaev on the same host in West Sayan mountains in Eastern Siberia (B.A.K., unpublished data)].

The gall-inducing habit may be considered a well-defined niche in *Ceutorhynchus* corresponding to other niches like seed feeding, leaf mining, and stem and root tunneling. This habit is apparently progressive, as it has no derivatives within *Ceutorhynchus*, which probably includes the most gall-inducing species among Coleoptera. Even species not closely related to *C. assimilis*, such as *C. plumbeus* and *C. subpilosus*, have larval stages that induce root galls. A similar habit possibly occurs in the larvae of *C. alliaricola* Colonnelli, living on *Alliaria petiolata* (Bieb.) Cavara and Grande (Brassicaceae) in Italy, in *C. invisus* Fall in North America, and in *C. grenieri* Brisout and *C. melitensis* Schultze in the western Mediterranean. Investigation of larval habits of the last two species is necessary, as to date they are the most advanced and apparently most xerophilous – or at least thermophilous – representatives of the *C. assimilis* group (sensu lato).

The evolutionary importance of the gall-inducing habit for *Ceutorhynchus* may primarily be in increasing the number of species which can exploit a host plant. This is shown by the weevil complex associated with *Cardaria draba*, where 25 percent of the *Ceutorhynchus* species are gall inducers. One of them, *C. cardariae* Korotyaev, inducing galls at leaf bases, is monophagous, whereas the root galler *Ceutorhynchus assimilis* is not host-specific. *C. dubius* Brisout, one of the three or four monophagous *Ceutorhynchus* on *Berteroa incana*, induces root galls. Yet many crucifers hosting a multi-species weevil assemblage seem to lack host-specific gall inducers. For example, *Sisymbrium loeselii* L., *Descurainia sophia* L., and *Alliaria petiolata* have several specialized seed feeders, and many nonhost-specific *Ceutorhynchus* attack their root crown and roots, but no specialized gall inducer is known. *A. petiolata* is often infested by a nonhost-specific gall inducer, *Ceutorhynchus chalybeus*; probably *C. alliaricola* Colonnelli is a galler specific to this plant.

The gall-inducing habit enables weevils to use short-lived plants with slender stems as hosts. This is impressively exemplified by the spherical galls (about 3 mm diameter) induced by *Ceutorhynchus hirtulus* Germar on the filiform stem of *Erophila verna* (L.) Bess., or by spindle-shaped stem galls induced by *Ceutorhynchus atomus* Boheman on *Arabidopsis thaliana* (L.) Heynh. (Fig. 17). This ability of *Ceutorhynchus* to use short-lived plants with slender stems as hosts has favored its colonization of deserts; in the



Fig. 17 Stem gall induced by *Ceutorhynchus atomus* Boheman (Curculionidae) on *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae). (After Ermolenko 1991)

Kara Kum sand desert, weevils of this genus are predominant on ephemeral plants (Kaplin 1981). One of the few groups of *Ceutorhynchus* living in the desert communities, the *C. viator* Faust species-group, includes the two most common gall-inducing species, *C. intermixtus* Voss and *C. confusus* Schultze (Kaplin 1981). Possibly other species of this group, *C. viator*, *C. klementzorum* Korotyaev, *C. languidus* Schultze, *C. kandaharicus* Voss, *C. dieckmanni* Kryzhanovskaya, and *C. madinae* Korotyaev, also induce galls on aerial parts of their host plants.

Galling is an advantageous mode of life judging from the wide variety of species in the groups with gall-inducing larvae, as, for example, in the *C. assimilis* group. This group comprises about 20 species distributed throughout most of the Holarctic Region, many of them common in natural areas; *C. assimilis* also often damages economically important plants. Species of this group induce galls of similar appearance, mostly on roots. Although variation in gall shape and distribution on the host plant are limited, this group shows high species richness.

Scolytidae

Thamnurgus, a bark-beetle, induces galls on herbaceous plants (Lengerken 1941). Adults of *Thamnurgus kaltenbachii* Bach sever the stem of *Lamium album* L. (Lamiaceae) just above the site of oviposition. A spindle-shaped gall (up to 10 mm long) develops at the top of the stem, and the apical portion of the stem dries out, whereas the basal part of the stem remains normal. The larvae grow in galls (Balachowsky 1949). This species infests also *Origanum vulgare* L., *Stachys* sp., *Teucrium scorodonia* L., *Betonica officinalis* L. (all Lamiaceae), and a few other species of Lamiaceae.

Thamnurgus delphinii Rosenhauer, living on several species of *Consolida* (Ranunculaceae) in the Mediterranean, induces galls on the stems (Lengerken 1941). Small (5–10 mm), red or brown, spindle-shaped galls with large larval chambers are induced on the stem portion close to the petioles. *T. euphorbiae* (Küster) induces club-shaped galls on the terminal regions of shoots of *Euphorbia* (Lengerken 1941).

Another herbivorous scolytid is *Hylastinus obscurus* (Marsham) living on herbaceous legumes (Fabaceae). It infests preferentially *Trifolium pratense* L., but can breed in *Medicago* spp., *Melilotus* spp., *Lathyrus* spp., *Vicia* spp., and some nonherbaceous Fabaceae including *Laburnum* spp. and *Ulex europaeus* L. *H. obscurus* originated in western and southern Europe, but was introduced into Canada, the United States, and Chile. In the United States it causes extensive damage to clover and alfalfa. Galleries of this species develop in the lower part of the stem or in the roots. The species overwinters as young adults or larvae in clover roots. New adults tunnel less-vigorous plants in spring. The galleries have basically two branches, and the eggs are deposited in the gaps along the margins. The larvae mine at random through the root tissues. Pupation occurs in late summer, with one generation each year (Wood 1982). The galls induced by *H. obscurus* have not been described in

detail (Lengerken 1941); infestation by adult scolytids and larvae reduces plant vigor, and results in poor development of flowers.

The bark-beetles breeding in twigs and thin branches of trees sometimes also induce gall-like structures. In high infestations in twigs of Scots-pine (*Pinus sylvestris* L.), the bark beetle *Pityogenes quadridens* Hartig induces nodelike teratological bulges, especially where branching occurs.

EVOLUTIONARY TRENDS OF GALL INDUCTION IN COLEOPTERA

The gall-inducing habit seems to increase in the course of evolution of the Coleoptera. Gall induction has originated apparently from larvae exploiting a nonspecific reaction of the plant tissue to injury by the ovipositing female or, maybe, by the feeding larva. This habit arose probably several times in the evolution of Coleoptera and has become established in three phyletic lineages: the superfamilies Buprestoidea (Buprestidae), Chrysomeloidea (Cerambycidae and Chrysomelidae), and Curculionoidea (Urodontidae, Apionidae, Nanophyidae, Eirrhinidae, Curculionidae, and Scolytidae). Initially galls were induced only on stems, shoots and roots. Of the two species-rich families of wood-boring beetles, the Buprestidae and Cerambycidae, the Buprestidae have evolved with more gall-inducing species, but the Cerambycidae have developed more elaborate gall-inducing habits. The initial stage of forming a gall-like swelling by buprestid larvae may probably be associated with a characteristic type of larval movement. *Agilus cuprescens* and *Ovalisia dives* make circular or dense spiral tunnels over short distances within a twig, and galling larvae of *Sphenoptera* develop in short distances within a root. Larvae of species of the mentioned genera that gnaw long tunnels (e.g., *Agilus viridis*) induce no galls. The gall-inducing habit probably arose independently in Buprestidae and Cerambycidae with their similar bionomics to achieve maximal nourishment in minimal substratum, and this constitutes one of the endobiotic strategies.

Within Cerambycidae, the most advanced subfamily Lamiinae includes most of the known gallers. Two species of Lamiinae, *Apriona swainsoni* Hope and *Nupserha variabilis* Gahan, progress larval development in the stems of two hosts which grow rapidly: first in a liane (*Butea* sp. and *Thunbergia* sp., respectively), then in the trunk of their host, the teak tree *Tectona grandis* L. (Verbenaceae). This unusual mode of life is paralleled by the weevil, *Smicronyx quadrifur* Casey (Curculionidae), inducing galls in several species of *Cuscuta* and tunneling for pupation into the stems of *Veronica noveboracensis* (L.) Michx. (Asteraceae) which supports the weak-stemmed *Cuscuta* (Anderson 1970). Host shift by the *Smicronyx* larvae appears to be driven by the insufficient size of the *Cuscuta* stem to house the mature weevil larvae. Gall induction by many other *Smicronyx* species is a possible alternative to solve such a spatial problem. Therefore we would expect a similar life style in some cerambycids living in woody climbers: showing a shift from the first to the second host, although a gall may not be induced on the first host.

The most advanced superfamily of the Coleoptera, the Curculionoidea, has widened its range of target organs to include the entire plant. The tendency in the evolution of the gall-inducing habit within particular groups of weevils is rather the diversification of galls on the same organ of different plants than successive exploitation of different parts of the plant. Of the three closely related species of the *Sibinia femoralis* Gyllenhal species-group (Curculionidae: Curculioninae), one is a stem galler, and the other two are carpophagous, but no instance of closely related species inducing galls on different organs is known. The structure of galls on vegetative organs is usually simple and does not vary distinctly. In many species galls on stem or roots coalesce into irregular masses (Fig. 16 b), or a large part of a stem may be strongly swollen and contain many separated weevil larvae (Fig. 18). In the weevil subfamily Ceutorhynchinae, the richest in galling Coleoptera, gall induction seems to be derived mostly from stem tunneling. In the tribes Mecinini and Tychiini (Curculionidae: Curculioninae), some galling species are related to carpophagous ones, and at least in the predominantly carpophagous *Tychius* the descent of the gall-inducing habit from feeding on seeds is most likely. The same is probably true for '*Ceutorhynchus*' *bituberculatus* Faust, a xeromorphous Middle Asian weevil inducing galls on a root crown of *Koelipinia macrantha* C. Winkl. (Asteraceae). The systematic position of this species is uncertain but its closest relative is probably *Glocianus*, all species of which develop in flowerheads of Asteraceae, in particular *Scorzonera*, closely allied to *Koelipinia*. Gall induction also occurs, in a few examples, in the anthophagous *Anthonomus* and carpophagous *Curculio* (Curculionidae), but no transition from leaf mining to galling is known in Coleoptera. In most cases, the galling habit more or less broadens the larval habits of Coleoptera to involve additional host-plant organs or tissues (e.g., leaf gall induced by *Tychius crassirostris* Kirsch on *Melilotus*),



Fig. 18 Stem gall induced by *Euprotopion kueenburgerorum* Schilsky (Apionidae) on a species of Apiaceae, in Kop Pass, Bayburt Province, Turkey. (Photograph courtesy V.I. Dorofeyev, St. Petersburg)

but does not form an additional niche. Exceptions are several fairly large species-groups of *Ceutorhynchus*, uniting species which induce galls of similar shape either on stem (viz., *C. viator* and *C. chalybaeus* species-groups) or root (viz., *C. assimilis* group), and a few highly xeromorphous oligotypical desert genera of the weevil subfamilies Ceutorhynchinae and Lixinae (e.g., *Eugeniodecus*). It thus seems to be a secondarily derived trait in Coleoptera.

CONCLUSION

The major groups of gallers all over the world are small and minute holo- and hemimetabolous insects with sedentary or slow-moving larvae characterized by either external digestion or sucking mouthparts.

Holometabolous plant-feeding insects with chewing mouthparts, the two largest taxa being Lepidoptera and Coleoptera, protect their larvae by their own behavioral patterns and metabolic processes rather than by exploiting host-plant metabolism to provide food and shelter. The predominance of the number of species of gall midges with their external mode of larval digestion, and the small hemimetabolous insects (e.g., Thysanoptera and Hemiptera [Psylloidea, Aphidoidea, and Coccoidea]) with sucking mouthparts over the number of chewing holometabolous insects appears overwhelming. Three holometabolous taxa with chewing mouthparts in the larval stages (the Cynipidae and Chalcidoidea with small or minute sedentary larvae, and the Tenthredinidae with large, freely mobile larvae) are the distinct exceptions that constitute the major groups of gall inducers in the boreal (Tenthredinidae) and temperate (Cynipidae) forests of the northern hemisphere, and in the forests of the southern hemisphere (Chalcidoidea).

The specialized and widely diversified holometabolous plant feeders, Lepidoptera and Coleoptera, include a comparatively small number of gall inducers (Meyer 1987, Zerova and Dyakonchuk 1991). There is no climatic zone, natural region, or plant taxon where Coleoptera would be a leading group of gall inducers. Instead of provoking plant responses, the advanced taxa of Coleoptera, like those of Lepidoptera (Fig. 19), have developed complex adult and/or larval behavioral patterns to provide the progeny with food and shelter, such as (1) forming of leaf-packages by adult leaf-beetles (Chrysomelidae) of the subfamily Hispinae (Dang Thi Dap 1981) and by weevils of the family Attelabidae and (2) construction of larval cases (Clytrinae, Cryptocephalinae) or protective skins (Cassidinae) (all Chrysomelidae) or cocoonlike chambers around the larvae of Cleonini (Curculionidae), feeding on roots. The 'sand tubes' constructed by *Cleonidius poricollis* Mannerheim (Cleonini: Lixinae) larvae on roots of *Descurainia pinnata* (Walt.) Britton (Brassicaceae) in Texas (O'Brien and Marshall 1987) are of a particular interest because they are similar to the galls induced by *Hypolixus tigrinus* Reitter (Lixini: Lixinae) on roots of *Suaeda paradoxa* Bge. (Chenopodiaceae) in Tajikistan (Nikulina 1989) and are of principally the same kind as galls of *Liocleonus clathratus* (Figs 3a-c) on *Tamarix* roots. Chambers of various kinds are made by larvae apparently of many Cleonini

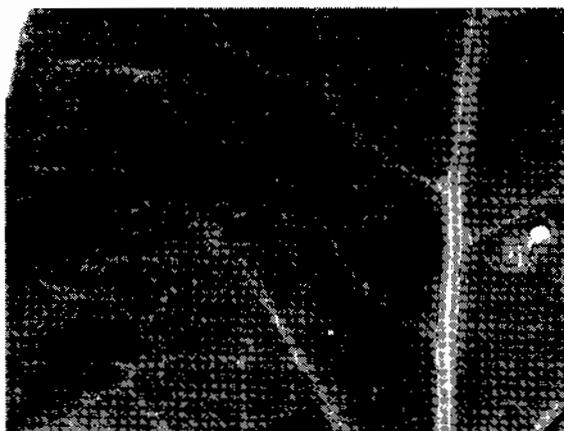


Fig. 19 Leaf of *Beta macrorhiza* Stev. (Chenopodiaceae) with a larva of Gelechioidea(?) (Lepidoptera) under a silk cover encrusted with excrements, and a larva of *Cassida (Deloyala) seraphina* Ménériés (Chrysomelidae) (new host record), in Erzincan Province, Turkey. (Photograph courtesy L. Gültekin, Erzurum)

feeding on roots; some construct rather loose ones from plant detritus and excrements, e.g., *Coniocleonus astragali* Ter-Minassian and Korotyaev on *Oxytropis* sp. (Fabaceae) in the Arctic (Korotyaev and Ter-Minassian 1977); others (*Mongolocleonus gobiensis* Voss on *Zygophyllum* sp. (Zygophyllaceae)) make hard chambers from gypsum-rich soil particles in Gobi deserts (B.A.K., unpublished data). This larval habit is probably not less common than the gall-inducing habit in rhizophagous Lixinae, showing the ability of these weevils to use both ways of protecting larvae.

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REFERENCES

- Alexeev, A.V. 1957. Jewel-beetles of Stalingrad Province (Coleoptera, Buprestidae). [in Russian] Uchenye Zapiski Orekhovo-Zuevskogo Pedagogicheskogo Instituta, 10: 115–158.
- Alexeev, A.V., and M.G. Volkovitch. 1989. A review of jewel-beetles (Coleoptera, Buprestidae) of Mongolian People's Republic. [in Russian] Nasekomye Mongolii, 10: 301–368.
- Alonso-Zarazaga, M.A. 1998. The genus *Podapion* Riley, 1883 in the Old World: a new species and biogeographical implications (Coleoptera: Apionidae: Apioninae), pp. 133–143. In E. Colonnelli, S. Louw, and G. Osella. [eds.]. Taxonomy, ecology and distribution of Curculionoidea (Coleoptera: Polyphaga), Proceedings of a Symposium, 28 August 1996, Florence, Italy, XX International Congress of Entomology. Museo regionale di Scienze naturali, Torino, Italy.
- Alonso-Zarazaga, M.A., and C.H.C. Lyal. 1999. A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae). Entomopraxis, Barcelona, Spain.
- Anderson, D.M. 1962. The weevil genus *Smicronyx* in America north of Mexico. Proceedings of the United States National Museum, 3456: 185–372.
- Anderson, D.M. 1970. Dodder weevils in simultaneous association with parasitic plants and their hosts. Science, 168: 132–133.
- Balachowsky, A. 1949. Faune de France, 50. Coléoptères Scolytides. Le Chevalier, Paris, France.
- Beeson, C.F.C., and B.M. Bhatia. 1939. On the biology of the Cerambycidae (Coleopt.). Indian Forcst Records, New Series, Entomology 5 (1). Government of India Press, New Delhi, India.
- Bellamy, C.L., and C.H. Scholtz. 1986. Two new species of gall-forming *Sphenoptera* Solier (Coleoptera, Buprestidae). Coleopterists Bulletin, 40: 117–126.
- Blanche, K.R. 1993. Insect-induced galls on Australian vegetation, pp. 49–55. In P.W. Price, W.J. Mattson, and Y.N. Baranchikov. [eds.] 1993. The ecology and evolution of gall-forming insects. General Technical report NC-174. USDA, North-Central Experiment Station, Forest Service, St. Paul, Minnesota, USA.
- Bowdrey, J.P., and B.M. Spooner. 1996. Checklist of British galls and gall-causing organisms. 2. Coleoptera: preliminary list. Cecidology, 11: 36–71.
- Bílý, S. 2002. Summary of the bionomy of the Buprestid beetles of Central Europe (Coleoptera: Buprestidae). Acta Entomologica Musei Nationalis Pragae, Suppl. 10.
- Byers, J. 2002. Gall-making insects. <http://www.wcrl.ars.usda.gov/cec/insects/gallmake.htm>. USDA, USA.
- Caldara, R. 1985. Revisione delle *Sibirina* paleartiche (Coleoptera Curculionidae). Memorie della Società Entomologica Italiana, 62/63 (1983–1984): 24–105.
- Carver, M., G.F. Gross, and T.E. Woodward. 1991. Hemiptera, pp. 429–509, In The insects of Australia. CSIRO, Melbourne University Press, Carlton, Victoria, Australia.
- Cox, M.L., and D.M. Windsor. 1999. The first instar larva of *Aulacoscelis* sp. and *Megascelis puella* Lacordaire (Coleoptera: Chrysomelidae: Aulacoscelinae, Megascelinae) and their value in the placement of the Aulacoscelinae and Megascelinae, pp. 51–70. In M.L. Cox. [ed.] 1999. Advances in Chrysomelidae biology, I. Backhuys Publishers, Leiden, The Netherlands.
- Craighead, F.C. 1923. North American cerambycid larvae, a classification and the biology of North American cerambycid larvae. Bulletin 27, new series. Canada Department of Agriculture, Ottawa, Canada.
- Crowson, R.A. 1981. The biology of the Coleoptera. Academic Press, New York, USA.
- Dang, Thi Dap. 1981. Zhuki-listoedy (Coleoptera, Chrysomelidae) Vietnam [Leaf-beetles (Coleoptera, Chrysomelidae) of Vietnam]. Ph.D. thesis, Institute of Evolutionary Morphology and Ecology of Animals, Academy of Sciences of the USSR, Moscow, USSR.
- Dieckmann, L. 1968. Revision der westpaläarktischen Anthonomini (Coleoptera: Curculionidae). Beiträge zur Entomologie, 17: 377–564.
- Dieckmann, L. 1972. Beiträge zur Insektenfauna der DDR: Coleoptera — Curculionidae: Ceutorhynchinae. Beiträge zur Entomologie, 22: 3–128.
- Dieckmann, L. 1977. Beiträge zur Insektenfauna der DDR: Coleoptera — Curculionidae (Apioninae). Beiträge zur Entomologie, 27: 7–143.

- Dieckmann, L. 1988. Beiträge zur Insektenfauna der DDR: Curculionidae (Curculioninae: Ellescini, Acalyptini, Tychiini, Anthonomini, Curculionini). Beiträge zur Entomologie, 38: 365–468.
- Duffy, E.A.J. 1953. A monograph of the immature stages of British and imported timber beetles (Cerambycidae). British Museum (Natural History), London, UK.
- Egorov, A.B. 1996. Sem. Rhynchitidae – rinkhitidy [Family Rhynchitidae], pp. 199–215. In G.S. Lafer, A.B. Egorov, G.O. Krivolutsкая, A.N. Kupyanskaya, A.S. Lelej, and P.G. Nemkov. [eds.] Opredelitel' nasekomykh Dal'nego Vostoka Rossii [A key to insects of the Russian Far East]. Volume 3. Coleoptera, pt. 3. Dal'nauka, Vladivostok, Russia.
- Emeljanov, A.F. 1967. Some characteristics of the distribution of oligophagous insects over host plants, pp. 28–65. In Doklady na XIX ezhegodnykh chteniyakh pamyati N.A. Kholodkovskogo 1 aprelya 1966 [Reports on the XIX annual readings in memory of N.A. Kholodkovskii, April 1, 1966]. [in Russian] Nauka, Leningrad, USSR.
- Ermolenko, V.M. 1991. Zhestkokrylye-galloobrazovateli [Coleopterous gall-makers], pp. 154–211. In E.N. Savchenko. [ed.] 1991. Nasekomye-galloobrazovateli kul'turnykh i dikorastuschikh rastenii yevropeiskoi chasti SSSR. Ravnokrylye, cheshuyekrylye, zhestkokrylye, poluzhestkokrylye [Gall-forming insects on cultivated and wild plants of the European part of the USSR. Homoptera, Lepidoptera, Coleoptera, Heteroptera]. Naukova Dumka, Kiev, Ukraine, USSR.
- Falkovitsh, M.I. 1979. Lepidoptera of the Middle Asian deserts. D.Sc. thesis, [in Russian] Zoological Institute, Leningrad, USSR.
- Fedotova, Z.A. 2000. Gallitsy-fitofagi (Diptera, Cecidomyiidae) pustyn' i gor Kazakhstana: morfologiya, biologiya, rasprostranenie, filogeniya i sistematika [Phytophagous gall-midges (Diptera, Cecidomyiidae) of the deserts and mountains of Kazakhstan: morphology, biology, distribution, phylogeny and systematics]. State Academy of Agriculture, Samara, Russia.
- Felt, E.P. 1940. Plant galls and gall makers. Comstock, Ithaca, New York, USA.
- Felt, E.P., and L.H. Joutel. 1904. Monograph of the genus *Saperda*. New York State Museum, Bulletin 74, Entomology.
- Fisher, W.S. 1928. A revision of the North American species of the buprestid beetles belonging to the genus *Agrilus*. Bulletin of the United States National Museum, 145: 1–347.
- Florentine, S.K., A. Raman, and K. Dhileepan. 2002. Responses of the weed *Parthenium hysterophorus* (Asteraceae) to the stem gall-inducing weevil *Conotrachelus albocinereus* (Coleoptera: Curculionidae). Entomologia Generalis, 26: 195–206.
- Froggatt, W.W. 1892. Gall-making buprestids. Proceedings of the Linnean Society of New South Wales, 7: 323–326.
- Froggatt, W.W. 1894. On the life-histories of Australian Coleoptera (Part II). Proceedings of the Linnean Society of New South Wales, 19: 113–125.
- Frost, C.A. 1912. New species of Coleoptera of the genus *Agrilus*. Canadian Entomologist, 44: 245–252.
- Gates, D.B., and H.R. Burke. 1972. Review of the gall-inhabiting weevils of the genus *Anthonomus*, with description and biology of a new species (Coleoptera: Curculionidae). Annals of the Entomological Society of America, 65: 1215–1224.
- Hamilton, R.W. 1998. Taxonomic revision of the New World Pterocolinae (Coleoptera: Rhynchitidae). Transactions of the American Entomological Society, 124: 203–269.
- Hawkeswood, T.J. 1988. A review of larval host records for twelve Australian Buprestidae (Coleoptera). Giornale Italiano di Entomologia, 4: 81–88.
- Hawkeswood, T.J., and M. Peterson. 1982. A review of larval host records for Australian jewel beetles (Coleoptera: Buprestidae). Victorian Naturalist, 99: 240–251.
- Hawkeswood, T.J., and J.R. Turner. 1992. Review of the biology and host plants of *Ethon fissiceps* (Kirby) and other *Ethon* species (Coleoptera: Buprestidae). Giornale Italiano di Entomologia, 6: 169–174.
- Hoffmann, A. 1958. Coléoptères curculionides (troisième partie). Faune de France (Paris), 62: 1209–1839.
- Imms, A.D. 1957. A general textbook of entomology. Ninth edition. Methuen, London, UK.

- Jolivet, P., and T.J. Hawkeswood. 1995. Host-plants of Chrysomelidae of the World. An essay about the relationships between the leaf-beetles and their food-plants. Backhuys Publishers, Leiden, The Netherlands.
- Kaplin, V.G. 1981. Kompleksy chlenistonogikh zhivotnykh, obitayuschiye v tkanyakh rastenii peschanykh pustyn' [Arthropod complexes in tissues of plants in sand deserts]. Ylym, Ashkhabad, Turkmenia, USSR.
- Kissinger, D.G. 1964. Curculionidae of America north of Mexico. A key to the genera. Taxonomic Publications, South Lancaster, Massachusetts, USA.
- Knull, J.N. 1920. Notes on Buprestidae with descriptions of new species (Coleop.). Entomological News, 31: 4-12.
- Korotyaev, B.A. 1993. *Magdalis mariae* Formánek from Bosnia belongs actually to the Nearctic apionid genus *Podapion* (Coleoptera: Curculionidae, Apionidae). Zoosystematica Rossica, 1: 75-77.
- Korotyaev, B.A. 2000. On unusually high diversity of rhynchophorous beetles (Coleoptera, Curculionoidea) in steppe communities of the North Caucasus. [in Russian] Zoologicheskii Zhurnal, 79: 242-246. [English translation: Entomological Review, 80 (8): 1020-1026.]
- Korotyaev, B.A., and A.O. Cholokava. 1989. A review of the weevil subfamily Ceutorhynchinae (Coleoptera, Curculionidae) of the fauna of Georgia. [in Russian] Entomologicheskoye Obozrenie, 68: 154-177. [English translation: Entomological Review, 68 (4): 117-140.]
- Korotyaev, B.A., and A.B. Egorov. 1995. Review of the weevil genus *Melanapion* Wagn. (Coleoptera, Apionidae) and contribution to the knowledge of the related genera of the fauna of the Far East. [in Russian] Entomologicheskoye Obozrenie, 74: 855-883.
- Korotyaev, B.A., A.L. Lvovsky, and A.G. Kirejtshuk. 1983. Insect fauna of the Transaltai Gobi, pp. 65-71. In Kompleksnaya kharakteristika pustynnykh ekosistem Zaaltaiskoi Gobi [Complex characteristics of the desert ecosystems of the Transaltai Gobi]. [in Russian] Puschino, USSR.
- Korotyaev, B.A., and M.E. Ter-Minassian. 1977. Review of the weevil genus *Coniocleonus* Motsch. (Coleoptera, Curculionidae) in Eastern Siberia and the Far East. [in Russian] Entomologicheskoye Obozrenie, 56: 823-832.
- Krishnamurthy, K.V., A. Raman, and T.N. Ananthkrishnan. 1977. Studies on plant galls from India. 2. Leaf galls of *Cordia obliqua* Willd. (= *Cordia myxa* Linn.) (Boraginaceae). Ceylon Journal of Science, 12: 73-84.
- Krivosheina, N.P. 1975a. Regularities of the formation of rhizobiont insect complexes on desert plants, pp. 95-117. In B.M. Mamaev and F.N. Pravdin. [eds.] 1975. Nasekomye kak komponenty biogeotsenoza saksaulovogo lesa [Insects in the *Haloxylon* forest biogeocoenosis]. [in Russian] Nauka, Moscow, USSR.
- Krivosheina, N.P. 1975b. The biology of the rhizobiont insects on desert plants, pp. 127-158. Biologiya nasekomykh-rizobiontov pustynnykh rastenii. In B.M. Mamaev and F.N. Pravdin. [eds.] 1975. Nasekomye kak komponenty biogeotsenoza saksaulovogo lesa [Insects in the *Haloxylon* forest biogeocoenosis]. [in Russian] Nauka, Moscow, USSR.
- Lengerken, H. v. 1941. Von Käfern erzeugte Pflanzengallen. Entomologische Blätter, 37: 121-159.
- Leonova, T.G. 1982. 33. *Artemisia* L. - Sharilzh [Mongolian common name of *Artemisia*], pp. 245-253. In V.I. Grubov. Opredelitel' sosudistykh rastenii Mongolii (s atlasom) [A key to vascular plants of Mongolia (with atlas)]. [in Russian] Nauka, Leningrad, USSR.
- Le Pape, H. and R. Bronner. 1987. The effects of *Ceuthorrhynchus napi* (Curculionidae, Coleoptera) on stem tissues of *Brassica napus* var. *oleifera*, pp. 207-212. In V. Labeyrie, G. Farbes, and D. Lachaise. [eds.] Insects - plants. W. Junk Publishers, Dordrecht, The Netherlands.
- Loginova, M.M. 1978. Psyllids, or jumping plant lice (Homoptera, Psylloidea) of Repetek, pp. 113-129. In N.T. Nechayev, and V.G. Kaplin. [eds.] Biotsenologicheskoye issledovaniya v Vostochnykh Karakumakh [Biocenological investigations in Eastern Kara Kum]. Ylym, Ashkhabad, USSR.
- Louw, S. 1993. Seed-feeding Urodontidae weevils and the evolution of the galling habit, pp. 186-193. In P.W. Price, W.J. Mattson, and Y.N. Baranchikov. [eds.] The ecology and evolution of gall-forming insects. General Technical report NC-174. USDA, North-Central Experiment Station, Forest Service, St. Paul, Minnesota, USA.

- Louw, S. 1998. The gall-inhabiting weevil (Coleoptera) community on *Galenia africana* (Aizoaceae): co-existence or competition?, pp. 122–126. In G. Cs6ka, W.J. Mattson, G.N. Stone, and P.W. Price. [eds.] The biology of gall-inducing arthropods. General Technical report NC-199. USDA, North-Central Experiment Station, Forest Service, St. Paul, Minnesota, USA.
- Mani, M.S. 1964. Ecology of plant galls. W. Junk Publishers, The Hague, The Netherlands.
- Mani, M.S. 2000. Plant galls of India. Second edition. Science Publishers Inc., New Hampshire, USA.
- Meyer, J. 1987. 3.324 Cecidogenous Coleoptera, pp. 189–198. In Plant galls and gall inducers. Gebrüder Borntraeger, Berlin, Stuttgart, Germany.
- Naumann, I.D. 1991. Hymenoptera, pp. 916–1000. In The insects of Australia. CSIRO, Melbourne University Press, Carlton Victoria, Australia.
- Nelson, G.H. 1965. Notes on the Buprestidae: part IV, with a new synonym in *Chrysobothris*. Bulletin of the Brooklyn Entomological Society, 59/60: 37–41.
- Nielsen, G.R. 2002. The thorn-limb borer, *Saperda fayi*. <http://www.uvm.edu/extension/publications/el/el235.htm>. University of Vermont Extension, USA.
- Nikulina, O.N. 1989. On the biology of weevils of the genus *Ilixus* F. (Coleoptera, Curculionidae) developing in semishrubs and herbaceous plants in Tajikistan. (in Russian). Entomologicheskoye Obozrenie, 68: 511–521.
- North Dakota State University. 2002. Insect and disease management guide for woody plants in North Dakota (poplar borer, *Saperda calcarata*). <http://www.ext.nodak.edu/extpubs/plantsci/trees/f1192-3.htm>. North Dakota State University, USA.
- O'Brien, C.W., and G.B. Marshall. 1987. Unusual larval "sand tube" construction in the weevil genus *Cleonidius* (Coleoptera: Curculionidae: Cleoninae) in West Texas. The Southwestern Entomologist, 12: 357–360.
- Price, P.W. and S. Louw. 1996. Resource manipulation through architectural modification of the host plant by a gall-forming weevil *Urodonotus scholtzi* Louw (Coleoptera: Anthribidae). African Entomology, 4: 103–110.
- Riley, C.V. 1884. Annual Report of US Commissioner of Agriculture: 285–418.
- Scherf, H. 1964. Die Entwicklungsstadien der mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 506. Verlag Waldemar Kramer, Frankfurt am Main, Germany.
- Smreczynski, S. 1974. Klucze do oznaczania owadów Polski. Czesc 19. Chrzaszczce – Coleoptera, zeszyt 98 c, Rykowiec – Curculionidae, Podrodzina Curculioninae, Plemliona: Barini, Coryssomerini, Ceutorhynchini. Polskie Towarzystwo Entomologiczne, Warsaw, Poland.
- Solomon, J.D. 1995. Guide to insect borers of North American broadleaf trees and shrubs. Agricultural Handbook No. 706. United States Department of Agriculture, Forest Service, Washington, D.C., USA.
- Soyunov, O.S. 1991. Kompleksy nasekomykh Severnykh Karakumov [Insect complexes in northern Kara Kum]. Ylym, Ashkhabad, Turkmenia, USSR.
- Ter-Minassian, M.E. 1989. Weevils of the subfamily Cleoninae (Coleoptera, Curculionidae) in the fauna of Mongolia. [in Russian] Nasekomye Mongolii [Insects of Mongolia], 10: 393–412.
- Ter-Minassian, M.E. 1990. Some results of further study of the genus *Stephanocleonus* (Coleoptera, Curculionidae). [in Russian] Nasekomye Mongolii [Insects of Mongolia], 11: 242–244.
- Tokgayev, T.B., and M.G. Nepesova 1964. Contribution to the knowledge of the fauna and ecology of weevils (Coleoptera, Curculionidae) of Southeastern Turkmenia. [in Russian] Izvestiya Akademii Nauk TSSR. Seriya biologicheskikh nauk, 1: 53–59.
- Turner, J.R., and T.J. Hawkeswood. 1995a. A note on the biology and host plant of *Cisseis* sp. near *C. nitidiventris* Carter (Coleoptera: Buprestidae) from Australia. Mauritania (Altenburg), 15: 313–316.
- Turner, J.R., and T.J. Hawkeswood. 1995b. A new larval host plant for the Australian jewel beetle *Ethon fissiceps* (Kirby) (Coleoptera: Buprestidae). Mauritania (Altenburg), 15: 317–319.
- Vijayaraghavan, M.R., Shah, Rajesh, and S.S. Sehgal. 1989. Induction of floral galls by *Nanophyes* sp. (Curculionidae: Coleoptera: Insecta) on *Tamarix troupitii* Hole (Tamaricaceae). Proceedings of the Indian National Science Academy, 55: 397–406.

- Volkovitsh, M.G. 2001. The comparative morphology of antennal structures in Buprestidae (Coleoptera): evolutionary trends, taxonomic and phylogenetic implications. Part 1. Acta Musei Moraviae, Scientiae Biologicae (Brno), 86: 43-169.
- Volkovitsh, M.G., and T.J. Hawkeswood. 1990. The larvae of *Agrilus australasiae* Laporte & Gory and *Ethon affine* Laporte & Gory (Insecta: Coleoptera: Buprestidae). Spixiana, 13: 43-59.
- Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, 6. Brigham Young University, Provo, Utah, USA.
- Zerova, M.D. 2001. A new species of the genus *Eurytoma* Illiger (Hymenoptera, Eurytomidae) from the Crimea. [in Russian] Entomologicheskoye Obozrenie, 80: 740-743.
- Zerova, M.D., and L.A. Dyakonchuk. 1991. Comparative characteristics of gall-inducing insect groups, pp. 7-10. In E.N. Savchenko. [ed.] 1991. Nasekomye-galloobrazovateli kul'turnykh i dikorastuschikh rastenii yevropeiskoi chasti SSSR. Ravnokrylye, cheshuyekrylye, zhestkokrylye, poluzhestkokrylye [Gall-inducing insects on cultivated and wild plants of the European part of the USSR. Homoptera, Lepidoptera, Coleoptera, Heteroptera]. [in Russian] Naukova Dumka, Kiev, Ukraine, USSR.