

Trophic Links of Leaf-Rolling Weevils (Coleoptera, Rhynchitidae and Attelabidae)

A. A. Legalov

Siberian Zoological Museum, Institute of Animal Systematics and Ecology, Siberian Division, Russian Academy of Sciences,
Novosibirsk, 630091, Russia

Received February 12, 2004

Abstract—The majority of beetle species examined develop on a limited set of plants, comprising species of 1 or 2 genera of the same family or, less frequently, of two closely related families. Some representatives of Rhynchitidae (mainly leaf-rollers) and Attelabidae populate several plant families, which is associated with an increased ability for larval development in dead tissues.

Leaf-rolling weevils (Rhynchitidae and Attelabidae) are obligatory phytophagous species. The World fauna comprises about 1110 species of Rhynchitidae and about 1000 species of Attelabidae (Legalov, 2003). These beetles are widespread, but most species dwell in subtropical and tropical zones. Larval development is associated with vegetative and generative parts of plants. Many species make leaf rolls, where larvae are placed; adult insects also feed on plants during additional feeding. Trophic links of these families are poorly studied. In this relation, the goal of the present study included revealing of these links and also analyzing of beetle population on plants depending on their regional distribution, evolutionary state, and biological peculiarities of Rhynchitidae and Attelabidae. The list of beetle species and their host plants was published earlier (Legalov, 2003); in this publication trophic associations of beetle larvae and adults and various groups of host plants were analyzed. In addition to observations of the author, the data on trophic links were taken from the literature (see References).

TROPHIC LINKS OF RHYNCHITIDAE

Trophic Links of Rhynchitidae of the World Fauna

The family Rhynchitidae is associated with 49 plant families. The largest number of species (Fig. 1) develops on Rosaceae, Fagaceae, and Betulaceae (about 20, 15, and 12%, respectively), comprising about 50% of species of the World fauna. 6% of species were found on Saliaceae and more than 5%, on Fabaceae. Hence, the basis (62.1%) of the World fauna of Rhynchitidae belongs to species associated with 5 plant families; the rest of Rhynchitidae develop on plants of 43 families: 2 species on a single host plant family, on the average.

25 (51%) of the mentioned floral composition in question serve as trophic plants only for Rhynchitidae (Berberidaceae, Bombaceae, Cistaceae, Clusiaceae, Cupressaceae, Dioscoreaceae, Eleagnaceae, Hamamelidaceae, Illiciaceae, Junglandaceae, Menispermaceae, Mimosaceae, Moraceae, Myricaceae, Mersinaceae, Oleaceae, Onagraceae, Pinaceae, Platanaceae, Podocarpaceae, Rhamnaceae, Sonneratiaceae, Symplocaceae, Tamaricaceae, and Vitaceae). More than 18% of Rhynchitidae feed on plants of these families.

Trophic Links of Rhynchitidae of the Temperate Zone

In the temperate zone, Rhynchitidae are associated with 36 plant families. Similarly to the World fauna, the largest number of species is associated with Rosaceae, Fagaceae, and Betulaceae (26, 25, and 11%, respectively), with the number of species developing on plants of the family Betulaceae being somewhat decreased (7.4% against 12.5%). Thus, species developing on plants of these three families form the basis of the fauna of the temperate zone, comprising more than 60% of species. Species, associated with remaining 32 host plant families, are less important in the structure of the fauna. On the average, 2 species of Rhynchitidae develop on plants of each of these families.

Trophic Links of Rhynchitidae of the Tropic Zone

In the tropic fauna, in comparison with the temperate zone, the number of trophic plants somewhat decreases (from 36 to 33). No species, associated with the following 13 families, were found: Dioscoreaceae, Eleagnaceae, Illiciaceae, Junglandaceae, Lamiaceae,

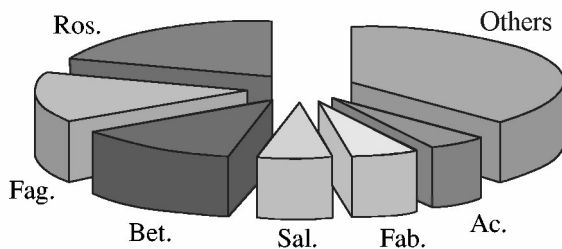


Fig. 1. Links of Rhynchitidae with plant families: Ac., Aceraceae; Sal., Salicaceae; Bet., Betulaceae; Fag., Fagaceae; Ros. Rosaceae.

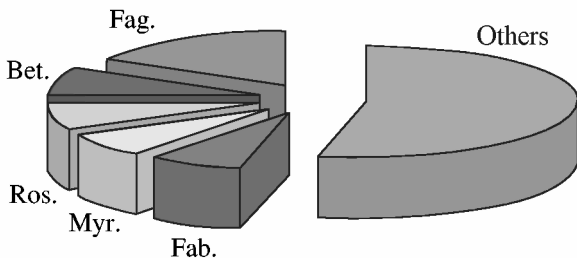


Fig. 2. Links of Attelebidae with plant families. Designations as in Fig. 1.

Magnoliaceae, Malvaceae, Menispermaceae, Onagraceae, Pinaceae, Platanaceae, Ranunculaceae, and Rhamnaceae. At the same time, the list is supplemented with species, associated with 10 other host plant families (Annonaceae, Combretaceae, Euphorbiaceae, Hamamelidaceae, Moraceae, Myrsinaceae, Orchidaceae, Podocarpaceae, Sonneratiaceae, and Sterculiaceae). It should be noted that nearly 7% of the species, dwelling in the temperate zone, are associated with the first group of host plants, whereas about 11% of the species of the tropic fauna are associated with the latter group of host plants. Some other differences are also found in the structure of the fauna. A total fraction of species, developing on Rosaceae and Fagaceae, decreases down to 32% and becomes virtually similar to that typical of the World fauna of Rhynchitidae. A fraction of species, developing on Fabaceae and Betulaceae (7% each), and also on Vitaceae and Myrtaceae (6% each) is also rather large. In the tropics, nearly half of the fauna of Rhynchitidae (43%) is associated with the remaining 27 host plant families.

Peculiarities of Trophic Links of Rhynchitidae Dwelling in the Temperate and Tropical Zones

Hence, in both geographical zones examined, the majority of Rhynchitidae is associated with the families Rosaceae, Fagaceae, and Betulaceae. In the tem-

perate zone, half of the species is associated with these families, whereas in the tropical zone, only a third of them is. Rhynchitidae of both faunas are associated with host plants of 23 families (Aceraceae, Anacardiaceae, Asteraceae, Berberidaceae, Betulaceae, Cistaceae, Cupressaceae, Ericaceae, Fabaceae, Fagaceae, Lauraceae, Mimosaceae, Myricaceae, Myrtaceae, Oleaceae, Polygonaceae, Rosaceae, Salicaceae, Symlocaceae, Tamaricaceae, Tiliaceae, Ulmaceae, and Vitaceae); however, a smaller number of species develops on these plants in the tropics. Among the species of Rhynchitidae and Attelebidae, representatives of the first family were recorded on 25 host plant families, comprising 37.3% of all the families mentioned in our paper (Berberidaceae, Bombaceae, Cistaceae, Clusiaceae, Cupressaceae, Dioscoreaceae, Eleagnaceae, Hamamelidaceae, Illiceaceae, Junglandaceae, Menispermaceae, Mimosaceae, Moraceae, Myricaceae, Myrsinaceae, Oleaceae, Onagraceae, Pinaceae, Platanaceae, Podocarpaceae, Rhamnaceae, Sonneratiaceae, Symlocaceae, Tamaricaceae, and Vitaceae).

TROPHIC LINKS OF ATTELABIDAE

Trophic Links of Attelebidae of the World Fauna

Representatives of the family Attelebidae were found on plants of 44 families; no Rhynchitidae develop on 20 of these families (more than 45% of floral composition). 16% of leaf-roller species is associated with these families (Arecaceae, Aristolochiaceae, Caprifoliaceae, Celastraceae, Celtidaceae, Clethraceae, Cornaceae, Ebenaceae, Eleocarpaceae, Hydrangeaceae, Lecythidaceae, Melastomataceae, Myrsinaceae, Rubiaceae, Smilacaceae, Staphyleaceae, Styracaceae, Theaceae, Urticaceae, and Verbenaceae).

Species, associated with Fagaceae (16.1%) exceed all the other groups (Fig. 2). More than 7% of leaf-roller species were recorded from the families Betulaceae, Rosaceae, Myrtaceae, and Fabaceae (7–8% of species on average). Species, developing on the latter 5 families, comprise more than 46% of the World fauna. The structure of trophic links of Attelebidae significantly differs from that of Rhynchitidae and Attelebidae combined (see below), being expressed in a decreased significance of Rosaceae (15% in Rhynchitidae and Attelebidae against 8% in Attelebidae) and in the twofold larger significance of Myrtaceae (4% and 7%, correspondingly). Nearly 54% of Attelebidae are associated with other 39 host plant families, with a single species developing on each of 21 families (about 48% of all species).

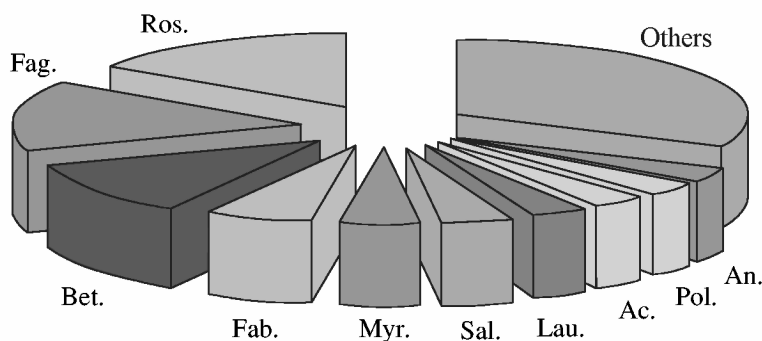


Fig. 3. Links of Rhynchitidae and Attelabidae with plant families. Designations as in Fig. 1.

Trophic Links of Attelabidae of the Temperate Zone

In the temperate zone, Attelabidae were found on host plants of 16 families; only 4 of these families (Lamiaceae, Staphyleaceae, Ulmaceae, and Urticaceae, comprising 25% of families) are not host plants in the tropics and subtropics. More than half of all the species (up to 58%) were recorded on Fagaceae, Betulaceae, and Ulmaceae (24, 21, and 13%, correspondingly). From 2 to 4 species dwell on the families Rosaceae, Fabaceae, Urticaceae, and Polygonaceae. A single species was found on representatives of each of the remaining 9 families.

Trophic Links of Attelabidae of the Tropical Zone

In the tropics and subtropics, the number of host plant families of Attelabidae increases twofold (32 families). The fraction of 20 families (63% of the entire floral composition) strongly increases. These families are Aceraceae, Annonaceae, Arecaceae, Aristolochiaceae, Asteraceae, Combretaceae, Cornaceae, Ebenaceae, Eleocarpaceae, Ericaceae, Euphorbiaceae, Lauraceae, Lecythidaceae, Melastomataceae, Myrtaceae, Orchidaceae, Salicaceae, Sterculiaceae, Theaceae, and Verbenaceae; only tropical leaf-rolling beetles are associated with these families. More than 10 species of Attelabidae (36%) were found on the families Myrtaceae, Fagaceae, and Rosaceae (17, 10, and 8%, correspondingly). Nearly the same number of species develops on plants of the families Fabaceae, Polygonaceae, Betulaceae, Anacardiaceae, Lauraceae, and Combretaceae (4–7% on each family on average). Species, associated with these 9 families, form the basis (more than 70%) of the tropical fauna of Attelabidae. From 2 to 4 species were recorded on 9 families, and plants of 14 families are hosts for a single species of leaf-rolling beetles each.

Peculiarities of Trophic Links of Attelabidae, Dwelling in the Temperate and Tropical Zones

Comparing the faunas examined, it should be noted that the basis (up to 58%) of the species composition of Attelabidae of the temperate zone consists of forms, developing on Fagaceae, Betulaceae, and Ulmaceae, whereas in the tropics and subtropics, the basic species, forming the fauna, develop on a large number of families (9). The taxa, associated with 2–4 species of Attelabidae, comprise a larger fraction in the temperate zone in comparison with the tropical and subtropical ones (57 and 44%, correspondingly), although the tropics are richer in such taxa (14 families), in comparison with the temperate zone (9 families). The fraction of families, associated with a single species of Attelabidae each, is approximately similar in both zones (25 and 28%). 12 families (Anacardiaceae, Betulaceae, Celcidiaceae, Clethraceae, Fabaceae, Fagaceae, Magnoliaceae, Polygonaceae, Rosaceae, Smilacaceae, Styracaceae, and Tiliaceae) are nearly everywhere populated by leaf-rolling beetles, although species, associated with these plants, comprise 52% and 79% of all the species in tropical and temperate faunas, respectively. The difference in trophic links between these faunas is significantly greater than that in Rhynchitidae, which could be explained by the poverty of the temperate fauna of Attelabidae.

TROPHIC LINKS OF RHYNCHITIDAE AND ATTELABIDAE

Trophic Links of Rhynchitidae and Attelabidae of the World Fauna

At present, associations between Rhynchitidae and Attelabidae and 67 host plant families were established (Legalov, 2003) (table). 1.9% of genera and 1.3% of these beetles develop on 3 families (Pinaceae,

Distribution of the number of genera and species of Rhynchitidae and Attelebidae among higher taxa of host plants

Plants			Number of genera and species			
subclass	order	family	genera	%	species	%
Pinidae	Pinales	Pinaceae	1	0.4	1	0.2
	Cupressales	Cupressaceae	3	1.1	4	0.9
	Podocarpaceae	Podocarpaceae	1	0.4	1	0.2
Magnoliidae		Magnoliaceae	2	0.7	2	0.5
		Annonaceae	3	1.1	3	0.7
		Laurales	Lauraceae	11	4	14
Ranunculidae	Aristolachales	Aristolochiaceae	1	0.4	1	0.2
	Illiciales	Illiciaceae	1	0.4	1	0.2
	Ranunculales	Ranunculaceae	2	0.7	2	0.5
Hamamelididae	Hamamelidales	Berberidaceae	2	0.7	2	0.5
		Hamamelidaceae	1	0.4	1	0.2
	Urticales	Platanaceae	1	0.4	1	0.2
		Celtidaceae	1	0.4	3	0.7
		Ulmaceae	6	2.2	9	2.1
		Moraceae	1	0.4	1	0.2
		Urticaceae	2	0.7	2	0.5
	Fagales	Fagaceae	34	11.3	66	15.3
		Betulaceae	22	7.9	46	10.7
	Caryophyllidae	Myricales	Myricaceae	3	1.1	4
Junglandales		Junglandaceae	1	0.4	1	0.2
Polygonales		Polygonaceae	11	4	13	3
		Theales	Theaceae	1	0.4	1
Dilleniidae		Clusiaceae	1	0.4	1	0.2
		Violales	Cistaceae	3	1.1	3
Tamaricales		Tamaricaceae	1	0.4	3	0.7
Salicales		Salicaceae	9	3.2	18	4.1
Ericales		Clethraceae	1	0.4	1	0.2
		Ericaceae	5	1.8	8	1.9
Ebenales	Styracaceae	3	1.1	3	0.7	
	Symplocaceae	2	0.7	3	0.7	
	Ebenaceae	2	0.7	2	0.5	
Primulales	Myrsinaceae	2	0.7	2	0.5	
Rosidae	Malvales	Eleocarpaceae	1	0.4	1	0.2
		Tiliaceae	5	1.8	6	1.4
	Sterculiaceae	3	1.1	3	0.7	
	Bombaceae	1	0.4	1	0.2	
	Malvaceae	2	0.7	2	0.5	
	Euphorbiales	Euphorbiaceae	5	1.8	6	1.4
	Rosales	Rosaceae	30	10.8	66	15.3
	Grossulariales	Hydrangeaceae	1	0.4	1	0.2

Table (Contd.)

Plants			Number of genera and species			
subclass	order	family	genera	%	species	%
Asteridae	Fabales	Mimosaceae	2	0.7	2	0.5
		Fabaceae	21	7.6	27	6.2
	Myrtales	Lythraceae	2	0.7	2	0.5
		Sonneratiaceae	2	0.7	2	0.5
		Combretaceae	5	1.8	8	1.9
		Lecythidaceae	1	0.4	3	0.7
		Myrtaceae	10	3.6	19	4.4
		Melastomataceae	1	0.4	1	0.2
		Onagraceae	1	0.4	1	0.2
	Rutales	Anacardiaceae	11	4	12	2.8
	Sapindales	Staphyleaceae	1	0.4	1	0.2
		Aceraceae	8	2.9	13	3
	Cornales	Cornaceae	1	0.4	1	0.2
	Celastrales	Celastraceae	1	0.4	1	0.2
	Rhamnales	Rhamnaceae	2	0.7	2	0.5
		Vitaceae	3	1.1	7	1.6
	Eleagnales	Eleagnaceae	1	0.4	1	0.2
	Oleales	Oleaceae	3	1.1	3	0.7
	Gentinales	Rubiaceae	1	0.4	1	0.2
	Dipsacales	Caprifoliaceae	1	0.4	1	0.2
	Lamiales	Verbenaceae	1	0.4	1	0.2
		Lamiaceae	2	0.7	2	0.5
		Asterales	Asteraceae	3	1.1	7
Liliidae	Smilacales	Smilacaceae	1	0.4	2	0.5
		Dioscoreaceae	1	0.4	1	0.2
Arecidae	Orchidales	Orchidaceae	2	0.7	2	0.5
	Arecales	Arecaceae	1	0.4	1	0.2

The classification of plants is given according to Takhtadjan (1966), Takhtadjan *et al.* (1978, 1980, 1981, 1982), and also Abramov *et al.* (2001)

Cupressaceae, and Podocarpaceae) of angiosperm plants of the subclass Pinidae (table). All the other genera (98.1%) and species (98.7%) of Rhynchitidae and Attelabidae, taken together, are associated with 2 classes of angiosperm plants. The most abundant beetle fauna was recorded on the families Fagaceae and Rosaceae (15% of beetle species on each family), belonging to the rather remote orders Fagales and Rosales (table). More than one third of the species composition of Rhynchitidae and Attelabidae is associated with these families (Fig. 3). The second place is occupied by species, associated with the family Betulaceae (11%), closely related to Fagaceae. Species,

found on Fabaceae, occupy the fourth place (6.2%). The fraction of Rhynchitidae and Attelabidae, developing on Myrtaceae and Salicaceae (4% on each family), is also rather large. More than half (56%) of all the species concerned are associated with these 6 families (Fig. 3). More, than 10 species (3%) develop on representatives of each of the families Lauraceae, Aceraceae, Polygonaceae, and Anacardiaceae. More than 1% of species (or 5 species) of Rhynchitidae and Attelabidae are associated with each of 6 families (Euphorbiaceae, Tiliaceae, Aceraceae, Vitaceae, Combretaceae, and Ulmaceae). Each of 51 host plant families is populated by 1 to 4 species; 20% of representa-

tives of Rhynchitidae and Attelabidae develop on these plants.

According to their distribution, all host plant families could be subdivided into three groups: temperate, tropical, and cosmopolite one. The beetles studied are associated with 37 mainly tropical families (Anacardiaceae, Annonaceae, Arecaceae, Aristolochiaceae, Bombaceae, Clethraceae, Clusiaceae, Combretaceae, Dioscoreaceae, Ebenaceae, Eleocarpaceae, Ericaceae, Euphorbiaceae, Hamamelidaceae, Iliiaceae, Lauraceae, Lecythidaceae, Lythraceae, Magnoliaceae, Malvaceae, Melastomataceae, Myrtaceae, Orchidaceae, Podocarpaceae, Rhamnaceae, Rubiaceae, Sonneratiaceae, Sterculiaceae, Styracaceae, Symplocaceae, Theaceae, Urticaceae, Verbenaceae, and Vitaceae). The taxa listed comprise more than half (55%) of all weevil host plant species. However, only one third of Rhynchitidae and Attelabidae (35% of genera and 28% of species) develop on these plants. The larger beetle fraction (about 58% of genera and 54% of species) were recorded on representatives of 25 (37% of all families) cosmopolite families (Aceraceae, Asteraceae, Berberidaceae, Caprifoliaceae, Celastraceae, Celcicidae, Cistaceae, Cornaceae, Cupressaceae, Eleagnaceae, Ericaceae, Fabaceae, Fagaceae, Hydrangeaceae, Juglandaceae, Lamiaceae, Myricaceae, Oleaceae, Platanaceae, Ranunculaceae, Rosaceae, Smilacaceae, Staphyleaceae, Tamaricaceae, and Ulmaceae). The poorest fauna (15% of genera and 18% of species) was found on 5 temperate (8%) families (Betulaceae, Onagraceae, Pinaceae, Polygonaceae, and Salicaceae). Interesting data were obtained after calculation of the average number of weevil species (Rhynchitidae and Attelabidae) per plant family. The largest number of species (16 species, or 3.6%) were recorded on plant families, distributed mainly in the temperate zone; 9 (3%) and 3 (1%) species populate cosmopolite and tropical families, respectively. Thus, the largest number of species of the weevils examined develops on cosmopolite and tropical plant families, although the latter comprise half of all the families, associated with Rhynchitidae and Attelabidae.

The widest associations were observed between Rhynchitidae and Attelabidae and dicotyledonous plants (94%), especially those out of rather advanced subclasses Rosidae (40%) and Hamamelididae (31%). The weevils examined are mainly associated with the orders Fagales, Rosales, and Myrtales. Species, developing on families from these orders, comprise nearly half of the entire fauna. Only 5% of all the beetles,

mainly those of the family Attelabidae, develop on monocotyledonous plants. Only representatives of the most primitive Rhynchitidae (1.3%) are associated with gymnospermous plants.

Some peculiarities could be revealed in trophic links of Rhynchitidae and Attelabidae (table). The number of genera, developing on Betulaceae and Fabaceae, is virtually the same. A smaller group is represented by genera, found on Polygonaceae and Anacardiaceae (4% of genera, associated with each family). A total of 52% of genera (a fraction smaller than 62% fraction of species) was recorded from the families Fagaceae, Betulaceae, Fabaceae, Polygonaceae, and Anacardiaceae. 3 beetle genera (more than 1%) develop on 15 host plant families; each of 29 families is associated with a single genus.

Comparing trophic links of Rhynchitidae and Attelabidae, it should be noted that the first weevil family possesses a wider spectrum of host families for their development (49) than the second one (44). At the same time, the fraction of host plant families, where only one of these families can develop, is also larger in Rhynchitidae (51% of families concerned) than in Attelabidae (43%); however, approximately the same fraction of species develop on these host plant groups (18% in Rhynchitidae and 16% in Attelabidae). Representatives of both weevil families were recorded on 24 host plant families (Arecaceae, Anacardiaceae, Annonaceae, Asteraceae, Betulaceae, Combretaceae, Eriaceae, Euphorbiaceae, Fabaceae, Fagaceae, Lamiaceae, Lauraceae, Lythraceae, Magnoliaceae, Malvaceae, Myrtaceae, Orchidaceae, Polygonaceae, Ranunculaceae, Rosaceae, Salicaceae, Sterculiaceae, Tiliaceae, and Ulmaceae); the richest species composition of weevils examined was noted on these families. Species, associated with 6 families (more than 10 beetle species were recorded on plants, belonging to these families) form the basis of the fauna of Rhynchitidae (Fig. 1); the fauna of Attelabidae (Fig. 2) is associated mainly with 5 host plant families. It should be noted that the family Fagaceae is one of the main trophic plant families for both weevil families. Faunas of Rhynchitidae and Attelabidae on Rosaceae and Betulaceae are also rich. Further examination of trophic links would probably result in the enlargement of the species list.

Trophic Links of Rhynchitidae and Attelabidae of the Temperate Zone

Representatives of the temperate fauna develop on representatives of 42 host plant families. At the same

time, trophic links with 14 families were revealed only in the temperate zone. In the tropical fauna, species, developing mainly on cosmopolite and temperate families, are absent, but species (17%) associated with the families Annonaceae, Arecaceae, Aristolochiaceae, Combretaceae, Cornaceae, Ebenaceae, Eleocarpaceae, Euphorbiaceae, Hamamelidaceae, Lecythidaceae, Melastomataceae, Moraceae, Myrsinaceae, Orchidaceae, Podocarpaceae, Sonneratiaceae, Sterculiaceae, Theaceae, and Verbenaceae, being most diverse in the tropics and subtropics, are added. Some other changes are also observed in the structure of the species composition of tropical plants, in comparison with the temperate fauna. The fraction of species, developing on Rosaceae and Fagaceae, decreases down to 39%, becoming virtually similar to that in the entire fauna; at the same time, the number of species, associated with Fagaceae, increases, occupying the first place. The number of species, associated with Rosaceae, decreases nearly twofold (13%). Such an abundance of species of Rhynchitidae and Attelabidae in these plant families could be explained by the cosmopolite distribution of Fagaceae and Rosaceae. Probably, situation with Rhynchitidae and Attelabidae, developing on Rosaceae, changes in the tropics, owing to decrease in the number of representatives of Rosaceae towards the equator; however, close relations between subtropical and tropical faunas of Rhynchitidae and Attelabidae hamper this analysis, at least at present. The fraction of species, developing on the cosmopolite families Fabaceae (8%) and Betulaceae (7%), and also on the mainly tropical and subtropical families Myrtaceae (8%) and Lauraceae (5%), is rather high in the tropical fauna. Nearly half of the fauna of Rhynchitidae and Attelabidae is associated with the other 41 plant families. More than 5 species were found on 6 plant families. From 1 to 4 species were recorded on representatives of the rest 35 families. It should be noted that nearly 40% of host plant families are associated with 1 species each, and 23%, with 2 species.

*Peculiarities of Trophic Links of Rhynchitidae
and Attelabidae, Dwelling in the Temperate
and Tropical zones*

Comparison of the data obtained demonstrates that the richest fauna of Rhynchitidae and Attelabidae is associated with the widespread families Rosaceae and Fagaceae, and also with the cosmopolite Betulaceae, in both temperate and tropical and subtropical zones. In the temperate zone, significance of Salicaceae and Aceraceae as host plants increases, whereas the role of

Fabaceae, Myrtaceae, and Lauraceae is rather high only in the tropics. In both zones, Rhynchitidae and Attelabidae develop on host plants of 28 families (Aceraceae, Anacardiaceae, Asteraceae, Berberidaceae, Betulaceae, Celcidaceae, Cistaceae, Clethraceae, Cupressaceae, Ericaceae, Fabaceae, Fagaceae, Lauraceae, Magnoliaceae, Mimosaceae, Myricaceae, Myrtaceae, Oleaceae, Polygonaceae, Rosaceae, Salicaceae, Smilacaceae, Styracaceae, Symplocaceae, Tamaricaceae, Tiliaceae, Ulmaceae, and Vitaceae); however, the fraction of species, associated with these families, is somewhat higher in the temperate zone (93%), in comparison with the tropical one (83%). Peculiarities of the temperate fauna also include the fact that its basis is formed of species, feeding on 3 host plant families (58%), whereas in the tropical and World faunas, this group comprises 6 families (56 and 60% of species, respectively).

DIAPASON OF TROPIC LINKS

Diapason of trophic links differs in different species of Rhynchitidae and Attelabidae. The majority of species of Rhynchitidae (77%) develop on species of a single host plant family. 19% of species were noted in plants of 2 or 3 families. Only 5% of Rhynchitidae are associated with 4–9 host plant families. They mainly include representatives of the genus *Bystiscus*. Each of the genera *Eugnamptus*, *Deporaus*, *Temnocerus*, and *Neocoenorhinus* contains a species with similar wide trophic links. The situation is analogous in Attelabidae. The largest number of species (84%) is associated with a single host plant family. A significantly smaller number of species (9%) was found on representatives of 2 families. 3 families are populated by only 4% of leaf-rollers (Attelabidae). Only representatives of the subfamily Apoderinae can dwell on 4 or more plant families. According to this analysis, the overwhelming majority of species of Rhynchitidae and Attelabidae (80%) develop on representatives of a single family of plants and, most frequently, only on several closely related genera. 16% of weevils were found on representatives of 2 or 3 families. Only 4% of the fauna are able to develop on representatives of many families (from 4 to 9). This group includes mainly leaf-rolling species.

Nearly two thirds (58%) of the fauna of Rhynchitidae are associated with a single plant genus. The number of species, associated with 2–5 genera, is also rather significant, whereas the number of species, developing on more than 6 genera, constitutes only 6%

of species. Attelabidae are even more specialized than Rhynchitidae. For example, 75% of their species are associated with a single plant genus; 18% of species were found on 2 or 3 genera. Only 6% of species are associated with 4–8 plant genera. In Rhynchitidae and Attelabidae on the whole, the fraction of monophagous species constitutes 65%. 20% of species successfully develop on 2 or 3 genera. Only 12% of the species adapted to host plants of 4–12 genera.

Thus, the main part of weevils examined become adapted to development on a small number of plants, as a rule, belonging to 1 or 2 genera of the same family or, less frequently, of two closely related families. Some representatives of advanced groups (mainly leaf-rollers) could populate several, sometimes even remote plant families. For such species, not the host plant species, but its part, where a larva develops, is important. It could be explained by the development of larvae in dead plant tissues, because a female gnaws conductive tubules and part of the plant with the laid eggs dies. However, even these polyphagous species possess preferable plants.

The largest number of species of weevils examined develops on cosmopolite and tropical plant families. In all the zones, the richest fauna of Rhynchitidae and Attelabidae was noted on representatives of widespread families Rosaceae and Fagaceae, and also on cosmopolite Betulaceae. In the temperate zone, the role of Salicaceae and Aceraceae as host plants increases; Fagaceae, Myrtaceae, and Lauraceae are very important in feeding of tropical species. The spectrum of trophic plant families is wider in Rhynchitidae (49) in comparison with Attelabidae (44).

Thus, angiosperm plants, which appeared in the early Cretaceous (Abramov *et al.*, 2001) and, probably, caused the Cretaceous biocenotic crisis, strongly affected insects (Zherikhin, 1980). The development of diversity of angiosperm plants (about 250 thousand modern species) that served as a basis for the formation of various ecological groups of Rhynchitidae and Attelabidae and allowed them to populate different parts of plants. The appearance of the leaf plate was most important, because beetles started to roll it, providing the successful development of larvae. In the Paleogene, all this resulted in the appearance of many new tribes of Rhynchitidae and in the formation of a new family Attelabidae that completely passed to leaf rolling. Thus the ability to develop on angiosperm plants has strongly influenced the evolution of Rhynchitidae and Attelabidae, providing their diversity.

ACKNOWLEDGMENTS

This work was supported by the grant of the Lavrentiev Competition of youth projects of the Siberian Branch of the Russian Academy of Sciences no. 70, the prize of the European Academy for young scientists of Russia for 2003, the grant of the Russian Science Support Foundation for 2004, and Russian Foundation for Basic Research, project no. 04-04-48727a.

REFERENCES

1. Abramov, I.V., Abramov, I.I., Agaponov, N.P., *et al.*, *Biology: the Major Biological Glossary* (Bolshaya Rossiiskaya Entsiklopediya, 2001) [in Russian].
2. Azarova, N.A., "Leaf-Rolling Weevils (Coleoptera, Attelabidae) of the Kuril Islands," *Entomol. Obozr.* **53** (4), 783–790 (1974).
3. Azarova, N.A., "Contributions to the Fauna and Ecology of Some Species of Leaf-Rolling Weevils (Coleoptera, Attelabidae)," in *New Data on Insects of the Russian Far East* (Vladivostok, 1980), pp. 36–42 [in Russian].
4. Azarova, N.A. and Kupyanskaya, A.N. "Leaf-Rolling Weevils (Coleoptera, Attelabidae) in Urban and Suburban Plantings of Primorskii Territory," in *The Role of Insects in Forest Biogeocenoses of the Russian Far East* (Vladivostok, 1972), pp. 39–149 [in Russian].
5. Dieckmann, L. "Beitrage zur Insectenfauna der DDR: Coleoptera: Curculionidae (Rhynomacerinae, Rhynchitinae, Attelabinae, Apoderinae)," *Beitr. Entomol.* **24** (1–4), 5–54 (1974).
6. Dubeshko, L.N. and Malikova, G.E., "Coleopterans of the Malomorskii Islands," in *Insects and Arachnids of Siberia* (Irkutsk, 1989), pp. 6–33 [in Russian].
7. Egorov, A.B., "Family Attelabidae, or Leaf-rolling Weevils," in *A Key to Insects of the Russian Far East* (Vladivostok, 1996), Vol. 3, No. 3, pp. 199–215 [in Russian].
8. Erol, T., "Turkiye Attelabidae (Coleoptera) familyasi turleri uzerinde faunistic ve sistematik calismalar," *Turk. Entomol. Derg.* **18** (1–3), 41–50, 89–102, 175–192 (1994).
9. Garcia, M., Andreazze, R., Ronchi-Teles, B., and Pamplona, "Ocorrencia e danos de *Hybolabus amazonicus* Voss e H. Columbus Voss (Coleoptera, Attelabidae) em castanha-do-brasil (*Bertholletia excelsa* Humb. Et Bonpl., Lecythydaceae)," *Anais Soc. Entomol. Brasil.* **26** (1), 313–315 (1997).
10. Gardner, J.S.M., "Immature Stages of Indian Coleoptera (Curculionidae)," *Indian Forest Rec.* **20** (2), 1–49 (1934).
11. Hamilton, R.W., "The Genus *Pselaphorhynchites* (Coleoptera, Rhynchitidae) in America North of Mexico," *Ann. Entomol. Soc. Amer.* **64**, 982–996 (1971).

12. Hamilton, R.W., "The Genus *Haplorhynchites* (Coleoptera, Rhynchitidae) in America North of Mexico," *Ann. Entomol. Soc. Amer.* **67**, 787–794 (1974).
13. Hamilton, R.W., "A New Subgenus of *Auletobius* Desbrochers," *Southwest. Entomol.* **8** (1), 67–72 (1984).
14. Hamilton, R.W., "Biological Data on the Two North American Rhynchids (Coleoptera: Curculionoidea) Associated with the Sweet Fern, *Comptonia peregrine* L., with Description, Illustrations, and Comparisons of Their Immature Stages," *J. Kans. Entomol. Soc.* **56** (4) 511–522 (1983a).
15. Hamilton, R.W., "The Genus *Merynychites* in America North of Mexico," *Southwest. Entomol.* **10** (10), 49–64 (1985).
16. Hamilton, R.W., "A Revision of the Weevil Genus *Eugnamptus* Schoenherr (Coleoptera, Rhynchitidae) in America North of Mexico," *Trans. Amer. Entomol. Soc.* **115** (4), 475–502 (1990).
17. Hamilton, R.W., "Revision of the New World Genus *Pilolabus* Jekel (Coleoptera, Attelabidae)," *Trans. Amer. Entomol. Soc.* **120** (4), 369–411 (1994).
18. Hamilton, R.W., "A New Species of *Euscelus* Schoenherr from Mexico (Coleoptera, Attelabidae)," *Coleopt. Bull.* **51** (4), 364–370 (1997).
19. Hamilton, R.W., "Taxonomic Revision of the New World Pterocolinae (Coleoptera, Rhynchitidae) in America North of Mexico," *Trans. Amer. Entomol. Soc.* **124** (3–4), 203–269 (1998).
20. Hamilton, R.W., "New Species of *Euscelus* Schoenherr from Central America (Coleoptera, Attelabidae)," *Coleopt. Bull.* **55** (4), 453–470 (2001).
21. Hong, K.-J., Park, S.-W., and Woo, K.-S., "Coleoptera: Anthribidae, Rhynchitidae, Attelabidae, Brentidae, Apionidae, Dryophthoridae," *Insecta Koreana* **20** (Suppl.), 1–180 (2001).
22. Isaev, A.Yu. and Savitskii, M.Yu., "Contributions to the Knowledge of Seed Beetles (Coleoptera: Chrysomeloidea, Bruchidae) and Weevil-Like Beetles (Curculinoidea: Urodonidae (Bruchellidae), Nemonychidae, Anthribidae, Attelabidae) of Ulyanovsk Province," in *Natural Historic Investigations in Simbirsk-Ulyanovsk Region in the End of the Century* (Ulyanovsk, 1999), pp. 95–100 [in Russian].
23. Kâno, H., "Die biologischen Gruppen der Rhynchitiden, Attelabinen und Apoderinen," *J. Fac. Agric. Hokkaido Imper. Univ.* **20** (1), 1–36 (1930).
24. Korotyayev, B.A., "New Data on the Synonymy and Distribution of Weevils in Russia (Coleoptera: Curculionoidea)," *Zoosyst. Ross.* **8** (1), 137–138 (1999).
25. Lee, Ch.-Yu. and Morimoto, K., "Larvae of the Weevil Family Attelabidae of Japan. Part 1. Subfamily Attelabinae (Insecta: Coleoptera)," *J. Fac. Agric. Kyushu Univ.* **32** (3–4), 215–237 (1988).
26. Lee, Ch.-Yu. and Morimoto, K., "Larvae of the Weevil Family Attelabidae of Japan: Part 2. Subfamily Rhynchitidae (Insecta: Coleoptera)," *J. Fac. Agric. Kyushu Univ.* **32** (3–4), 239–254 (1988a).
27. Legalov, A.A., "Revision der holarktischen Auletini (Coleoptera, Attelabidae)," *Rus. Entomol. J.* **10** (1), 33–66 (2001).
28. Legalov, A.A., "The Taxonomy, Classification, and Phylogeny of Leaf-rolling Weevils (Coleoptera: Rhynchitidae, Attelabidae) of the World Fauna," CD-ROM (Novosibirsk, 2003).
29. Liang, X., Seven New Species of the *Euscelophilus* (Coleoptera, Attelabidae) from Yunnan, Southwest China," *Japan J. Entomol.* **62** (3), 483–496 (1994).
30. Marshall, G.A.K., "Two New Species of Curculionidae (Col.) from Haiti," *Bull. Entomol. Res.* **17** (53–54) (1926).
31. Osella, G. and Zuppa, A.M., "New and Remarkable Curculinoidea (Coleoptera) from Macronesia," *Bocagiana*, No. 191, 1–12 (1998).
32. Rafiquizzaman, M. and Maiti, B., "Dormancy of Mango Cutting leaf Weevil, *Eugnamptus marginellus* Fst. (Coleoptera, Curculinoidea)," *Crop. Res.* **8** (2), 283–286 (1999).
33. Riedel, A., "Taxonomy, Phylogeny, and Zoogeography of the Weevil Genus *Euops* (Insecta: Coleoptera: Curculionoidea) in the Papuan Region," PhD Thesis (Munich, 2002).
34. Sawada, Y., "How to Identify the Cradles Made by Attelabid Weevils," *Nature Study* **32** (4), 41–44 (1986).
35. Sawada, Y., "A Revision of the Tribe Deporaini of Japan (Coleoptera, Attelabidae): I. Description of Taxa. 1. Genera *Apoderites*, *Eusproda*, *Chokkirius*, and *Paradeporaus*," *Kontyû* **55** (4), 654–665 (1987).
36. Sawada, Y., "A Systematic Study of the Family Rhynchitidae of Japan (Coleoptera, Curculinoidea)," *Humans and Nature*, No. 2, 1–93 (1993).
37. Singh, R.N. and Thangavelu, K., "Report of *Apoderus tranquebaricus* Fabricius (Attelabidae: Coleoptera) Feeding on *Terminalia arjuna* Bedd.," *Indian Forester* **120** (4), 376–377 (1994).
38. Takhtadjan, A.L., *The Classification and Phylogeny of Angiosperm Plants* (Nauka, Moscow, 1966) [in Russian].
39. Takhtadjan, A.L., Lazarenko, A.S., Grushvitskii, I.V., et al., *The Life of Plants, Vol. 4. Mosses. Club Mosses. Horsetails. Ferns. Gymnosperm Plants*, (Prosveshchenie, Moscow, 1978), Vol. 4 [in Russian].
40. Takhtadjan, A.L., Grubov, V.I., Grushvitskii, I.V., et al., *The Life of Angiosperm Plants* (Prosveshchenie, Moscow, 1980), Vol. 5 [in Russian].
41. Takhtadjan, A.L., Artyushenko, Z.T., Grudzinskaya, I.A., et al., *The Life of Angiosperm Plants* (Prosveshchenie, Moscow, 1981), Vol. 6 [in Russian].
42. Takhtadjan, A.L., Fedorov, A.A., Budantsev, L.Yu., et al., *The Life of Plants, Vol. 4, Part 2. Mosses. Club Mosses. Horsetails. Ferns. Gymnosperm Plants*, (Prosveshchenie, Moscow, 1981), Vol. 4, Part 2 [in Russian].

43. Ter-Minasyan, M.E., "Family Attelabidae, Leaf-Rolling Weevils," in *Forest Pests* (Nauka, Moscow, 1955), Vol. 2, pp. 581–592 [in Russian].
44. Voss, E., "Die Unterfamilien Attelabinae und Apoderinae (Col. Curc.), 18. Beitrag zur Kenntnis der Curculioniden," *Stettiner Entomol. Zeit.* **85** (1–2), 1–78, 191–304 (1925).
45. Voss, E., "Die Unterfamilien Attelabinae und Apoderinae (Col. Curc.), 18. Beitrag zur Kenntnis der Curculioniden. II. Apoderinae," *Stettiner Entomol. Zeit.* **87** (1), 1–89, (1926a).
46. Voss, E., "Die Unterfamilien Attelabinae und Apoderinae (Col. Curc.), 18. Beitrag zur Kenntnis der Curculioniden. II. Apoderinae," *Stettiner Entomol. Zeit.* **87** (2), 141–197 (1926b).
47. Voss, E., "Eine Rhynchites-Art als Schädling an *Cinnamomum camphora* (Col. Curc.) (30. Beitrag zur Kenntnis der Curculioniden)," *Zeit. Wiss. Insektenbiol.* **24**, 256 (1926c).
48. Voss, E., "Monographie der Rhynchitinen-Tribus Bystiscini, VI. Teil der Monographie der Rhynchitinae-Pterocolinae (31. Beitrag zur Kenntnis der Curculioniden)," *Koleopterol. Rundschau* **16** (5), 191–208 (1930).
49. Voss, E., "Monographie der Rhynchitinen-Tribus Rhynchitini, 2. Gattungsgruppe: Rhynchitina, VI. Teil der Monographie der Rhynchitinae-Pterocolinae (41. Beitrag zur Kenntnis der Curculioniden)," *Koleopterol. Rundschau* **18** (3–4), 153–189 (1932).
50. Voss, E., "Monographie der Rhynchitinen-Tribus Auletini, III. Teil der Monographie der Rhynchitinae-Pterocolinae (37. Beitrag zur Kenntnis der Curculioniden)," *Stettiner Entomol. Zeit.* **94** (1), 108–136, 273–286 (1933).
51. Voss, E., "Monographie der Rhynchitinen-Tribus Auletini, III. Teil der Monographie der Rhynchitinae-Pterocolinae (37. Beitrag zur Kenntnis der Curculioniden)," *Stettiner Entomol. Zeit.* **95** (1), 109–344 (1934).
52. Voss, E., "Ein Beitrag zur Kenntnis der Attelabiden Javas (57. Beitrag zur Kenntnis der Curculioniden)," *Tijdschrift voor Entomol.* **78** (1–2), 95–125 (1935a).
53. Voss, E., "Ein Beitrag zur Kenntnis der Attelabiden Javas. Tribus Auletini, III. Teil der Monographie der Rhynchitinae-Pterocolinae (37. Beitrag zur Kenntnis der Curculioniden)," *Stettiner Entomol. Zeit.* **96** (2), 108–136, 229–241 (1935b).
54. Voss, E., "Ein Beitrag zur Kenntnis der Attelabiden Javas. Tribus Deporaini sowie der Unterfamilien Pterocolinae-Oxycorininae (Allocorynini), VII. Teil der Monographie der Rhynchitinae-Pterocolinae (37. Beitrag zur Kenntnis der Curculioniden)," *Stettiner Entomol. Zeit.* **99**, 59–116, 302–363 (1938).
55. Voss, E., "Rhynchitinen, Attelabinen und Cossoninen aus dem Congo Gebiet (Col., Curc.). (76. Beitrag zur Kenntnis der Curculioniden)," *Rev. Zool. Bot. Afr.* **32** (1), 42–64 (1939).
56. Voss, E., "Monographie der Rhynchitinen-Tribus Rhynchitini. 2. Gattungsgruppe: Rhynchitina. VII. Teil der Monographie der Rhynchitinae-Pterocolinae," *Mitt. Münch. Entomol. Ges.* **31**, 628–680 (1941).
57. Voss, E., "Curculionidae: Oxycorininae, Belinae, Archolabinae, Attelabinae, Apoderinae," *Coleopterorum Catalogus*, Suppl. 110, 1–34; 144, 1–19 (1953).
58. Voss, E. "Neue und bekannte, vorwiegend Indonesische Curculioniden (Coleoptera)," *Treubia Reinward. Ann. Bogorensis* **24** (1), 7–17 (1957).
59. Voss, E., "Monographie der Rhynchitinen-Tribus Rhynchitini, 2. Gattungsgruppe: Rhynchitina Coleoptera- Curculionidae), VII. Teil der Monographie der Rhynchitinae-Pterocolinae," (195. Beitrag zur Kenntnis der Curculioniden)," *Entomol. Arb. Mus. G. Grey* **20**, 117–375 (1969).
60. Zhang, X., Yang, C., and Gao, Zh., "Two New Species of *Attelabus* (Coleoptera: Attelabidae) from China," *Sinozoologia*, No. 12, 207–209 (1995) [in Chinese].
61. Zherikhin, V.V., "Insects in Terrestrial Ecosystems," in *Historic Development of the Class of Insects* (Nauka, Moscow, 1980) [in Russian].
62. Zimmerman, E.C., *Australian Weevils (Coleoptera, Curculionoidea), Vol. 1. Anthribidae to Attelabidae* (CSIRO Publications, 1994), Vol. 1.