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Feeding Behavior of Leaf Beetles (Coleoptera, Chrysomelidae)

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Abstract—The feeding behavior of adult leaf beetles (41 species from 18 genera and 8 subfamilies) was studied for the first time. Beetles of the genera *Chrysolina*, *Chrysomela*, *Cryptocephalus*, *Galeruca*, *Gastrophysa*, *Labidostomis*, *Leptinotarsa*, *Timarcha*, and *Cassida stigmatica* gnaw a leaf from the edge, whereas the representatives of *Donacia*, *Galerucella*, *Lema*, *Lilioceris*, *Oulema*, *Phyllobrotica*, *Plagiodera*, *Zeugophora*, *Hypocassida*, and most species of *Cassida* gnaw the leaf plane. In addition, adults of *Lilioceris merdigera* and *Donacia clavipes* feed on young leaves rolled into a tube. New host plants are reported for the first time: *Hyoscyamus niger* for the larvae of the Colorado potato beetle and *Naumburgia thyrsiflora* for *Galerucella grisescens*.

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The behavior of leaf beetles is now actively studied, with special attention being focused on some aspects related to reproduction, such as mating behavior, aggressive behavior of males, parental care, and defensive behavior of the larvae (Medvedev and Pavlov, 1985, 1987; Jolivet, 1988; Vasconcellos-Neto and Jolivet, 1994; Bieńkowski, 1999; Jolivet, 1999; Konstantinov, 2002, 2004). At the same time, the behavior of beetles feeding on leaves has not been studied yet.

There are extensive data on the food plants of leaf beetles, summarized in a number of reviews (Jolivet and Petitpierre, 1976; Medvedev and Dang Thi Dap, 1982; Jolivet et al., 1986; Medvedev and Roginskaya, 1988; Bourdonné and Doguet, 1991; Buzzi, 1994; Jolivet and Hawkeswood, 1995; Biondi, 1996; Kimoto and Takizawa, 1997). Most species of this group are oligophagous insects adapted to feeding on plants of one particular family (Medvedev and Roginskaya, 1988). The association with a specific food plant affects the distribution, time of flight, oviposition, and other aspects of the leaf-beetle biology.

Beetles of different species gnaw leaves in different manners. This is evident even from the characteristic patterns of damaged leaves that have been described for a number of species (Böving, 1910; Bogdanov-Kat'kov, 1919, 1920; Goecke, 1935; Medvedev and Roginskaya, 1988; Dubeshko and Medvedev, 1989; Savkovskii, 1990).

This communication presents the results of observation of adult leaf beetles of 41 species, 18 genera, and 8 subfamilies, feeding on leaves. The process of feeding on flowers will be described in a separate paper.

MATERIALS AND METHODS

The material was collected in various regions of European Russia (Mordovia, Moscow, Murmansk, Saratov, and Yaroslavl provinces) and in Krasnodar Territory. In the experiments, the beetles were placed in cages and offered the leaves of the plants from which they had been collected. The feeding beetles were observed using the binocular microscope. These experiments were supplemented with observations of feeding in the nature. The samples of damaged leaves were preserved as exsiccatae. The following elements were used to describe the movement of the beetle's head during feeding: tilting the head to the right or to the left in the horizontal plane (Fig. 1*a*), moving the head up or down in the sagittal plane (Fig. 1*b*), and rotating the head to the right (Fig. 1*c*) or to the left (Fig. 1*d*) in the transverse vertical plane.

RESULTS

We have observed several different manners of feeding of leaf beetles. Below they are provisionally subdivided into three groups: (1) feeding on the leaf margin, (2) feeding on the leaf surface, (3) feeding on leaves rolled in tubes.

Feeding on the Leaf Margin

(a) The feeding beetle is positioned on the leaf surface. *Chrysomela vigintipunctata* (Scopoli) (Mordovia, on the grey willow *Salix cinerea*) (Fig. 2, *1*).

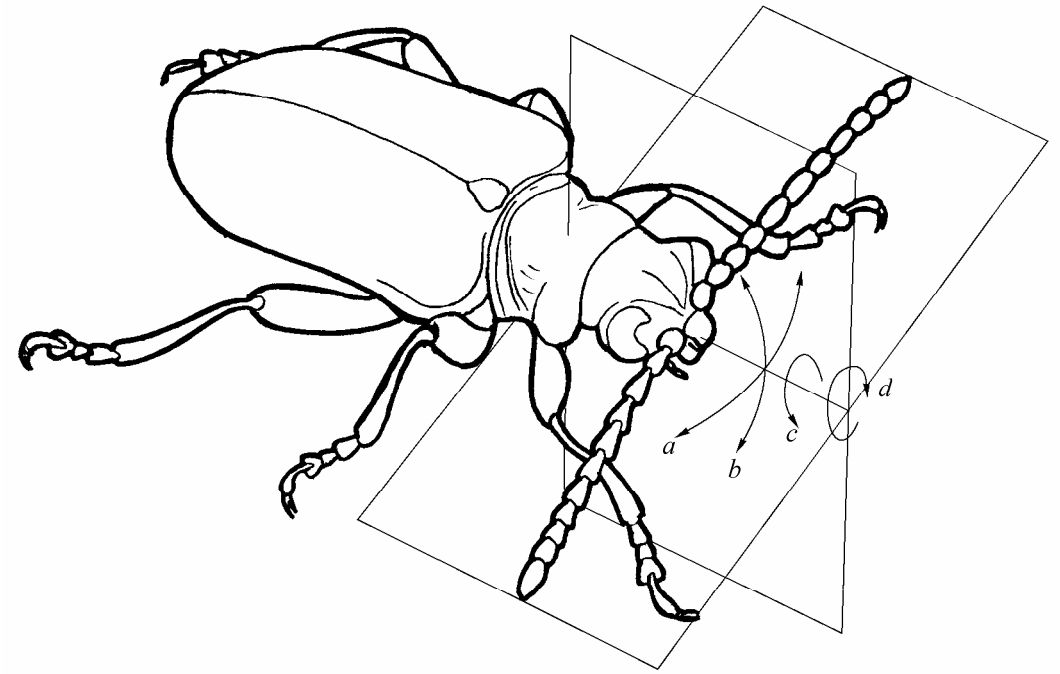

Fig. 1. Movements of the head of a leaf beetle (by the example of *Lilioceris merdigera*) during feeding: tilting to the right or to the left in the horizontal plane (*a*), moving up or down in the sagittal plane (*b*), rotation to the right (*c*) and to the left (*d*) relative to the longitudinal body axis.

The beetle sits on the upper or lower leaf surface near its margin, with the fore and mid tibiae (or only tarsi) grasping the leaf from the opposite side. Having positioned itself with the right side facing the leaf margin, the beetle moves its head down and at the same time rotates it by a small angle to the right, so that the left mandible becomes positioned above the leaf plane, and the right one below it. If the beetle sits with its left side facing the leaf margin, it rotates its head to the left so that the left mandible becomes positioned under the leaf plane, and the right one above it. The beetle gnaws coarse reach-through holes of irregular shape, with only the largest veins left intact.

(b) The feeding beetle is positioned on the leaf margin. *Chrysolina herbacea* (Duftschmid) (Mordovia, on the field mint *Mentha arvensis*). The beetle grasps the leaf with all its tarsi while raising itself above the margin so that the thorax and abdomen do not touch the leaf. It gradually moves its head down, performing a series of bites, then moves its head up and performs another series. In between the series of bites, the beetle advances towards the damaged area.

Chrysolina fastuosa (Scopoli) (Mordovia, on the motherwort *Leonurus quinquelobatus*). The behavior is identical to that of *Ch. herbacea*.

Chrysolina geminata (Paykull) (Yaroslavl Prov., on St. John's wort *Hypericum* sp.). The behavior is identical to that of *Ch. herbacea*. The feeding beetle is positioned with its head towards the leaf apex, since it gets onto the leaf from the stem.

Chrysolina aurichalcea (Gebler in Mannerheim) (Moscow Prov., on the common wormwood *Artemisia vulgaris*). The behavior is identical to that of *Ch. herbacea*. Having completed a series of bites, the beetle moves forward, raises its head, and starts a new series from the intact leaf margin or from the previously made incision, deepening it.

Chrysolina varians (Schaller) (Moscow Prov., on St. John's wort *Hypericum* sp.) (Fig. 3, *1*). The behavior is identical to that of *Ch. herbacea*. Having completed a series of bites, the beetle moves forward, raises its head, and starts a new series from the intact leaf margin or stays in place, deepening the incision to the midrib.

Chrysolina sturmi (Westhoff) (Mordovia, on the ground ivy *Glechoma hederacea*). The behavior is identical to that of *Ch. herbacea*. During a series of bites, the beetle stays in place or moves backwards, and advances after the series has been completed.

Chrysolina polita (Linnaeus) (Moscow Prov., Mordovia, Krasnodar Terr., on the gypsywort *Lycopus europaeus*). The behavior is identical to that of *Ch. herbacea*. The beetle gnaws on the lateral outgrowth of the leaf, starting from its tip or side margin.

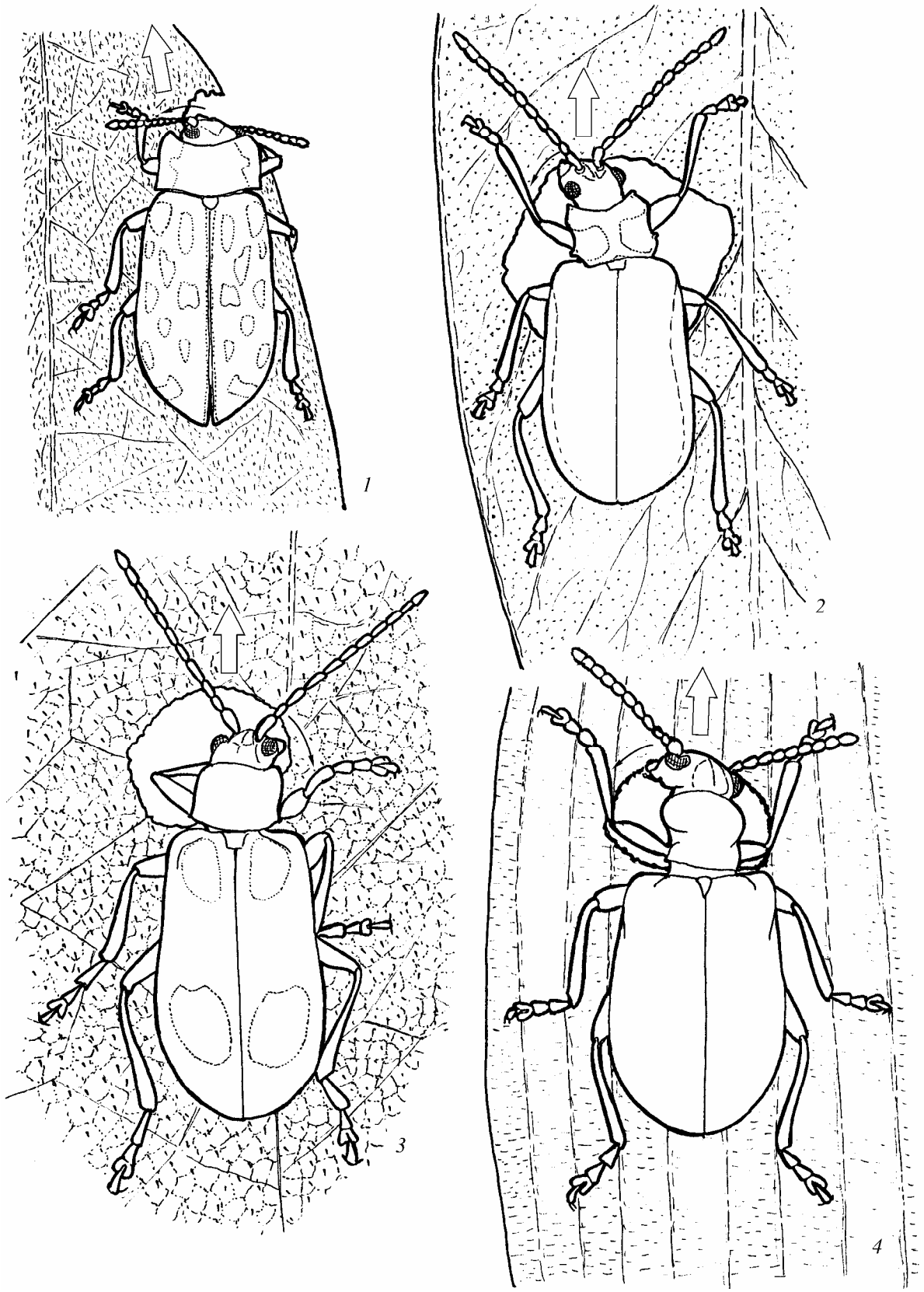

Fig. 2. Feeding of leaf beetles: *Chrysomela vigintipunctata* (*1*), *Galerucella grisescens* (*2*), *Phyllobrotica quadrimaculata* (*3*), and *Lilioceris merdigera* (*4*). The black arrow shows the movements of the head during a single series of bites; the white arrow shows the movements of the beetle between the series of bites.

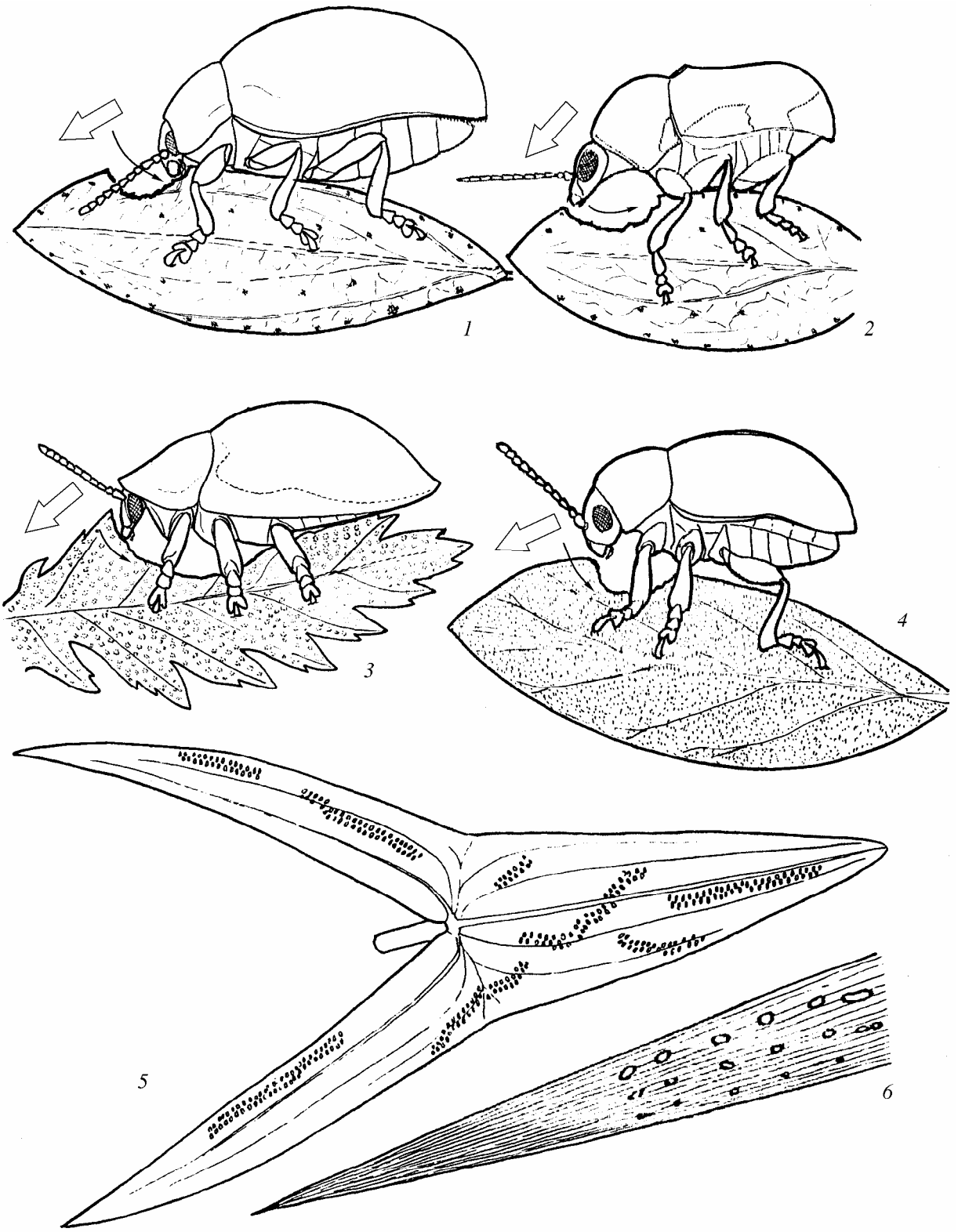

Fig. 3. Feeding of leaf beetles (*1–4*): *Chrysolina varians* (*1*), *Cryptocephalus moraei* (*2*), *Cassida stigmatica* (*3*), and *Gastrophysa polygoni* (*4*); the leaf of *Sagittaria sagittifolia* damaged by *Donacia dentata* (*5*) and the leaf of *Phragmites australis* damaged by *D. clavipes* (*6*). For explanation of the black and white arrows, see Fig. 2.

Leptinotarsa decemlineata (Say) (Saratov Prov., on the black henbane *Hyoscyamus niger*). The behavior is identical to that of *Ch. herbacea*. The beetle sits on the margin of a horizontal leaf, hanging slightly over. All the fore and mid tarsi grasp the leaf, one of the hind tarsi rests on the leaf margin while the other is positioned on the leaf surface. The black henbane is reported here for the first time as a food plant for the larvae of the Colorado potato beetle (*L. decemlineata*). The adults and larvae feeding on henbane were observed in Saratov Prov. (D'yakovka Village, ruderal vegetation near a farm) and in Bashkortostan (Irgizly Village, the Irgizla River valley); the fact of feeding on this plant was confirmed by observations in cages.

Chrysomela populi Linnaeus (Moscow Prov., on the aspen *Populus tremula*). The behavior is identical to that of *Ch. rysolina herbacea*.

Chrysomela tremula Fabricius (Moscow Prov., on the balsam poplar *Populus balsamifera*). The behavior is identical to that of *Ch. herbacea*. The beetle slightly hangs over to one side, with all the tarsi grasping the leaf.

Gastrophysa polygoni (Linnaeus) (Moscow Prov., Saratov Prov., on the prostrate knotweed *Polygonum aviculare*) (Fig. 3, *4*). The behavior is identical to that of *Ch. rysolina herbacea*. Starting a series of bites, the beetle first gnaws the intact portion of the leaf margin near the place where the preceding series started; then it continues gnawing on the previously damaged margin, moving its head down and deepening the incision.

Timarcha hummeli Faldermann (Krasnodar Terr., on the Persian ivy *Hedera colchica*). The behavior is identical to that of *Ch. herbacea*. The beetle sits on the leaf margin, hanging slightly over to one side.

Galeruca tanaceti (Linnaeus) (Mordovia, on the thistle *Cirsium* sp.). The behavior is identical to that of *Ch. herbacea*. The beetle sits on the margin of an erect leaf with its head directed towards the leaf apex, hanging slightly over to one side; the fore and mid tarsi grasp the leaf, while the tarsi of both hind legs rest on the same side of the leaf surface.

Cryptocephalus moraei (Linnaeus) (Moscow Prov., on St. John's wort *Hypericum* sp.) (Fig. 3, *2*). The behavior is identical to that of *Ch. herbacea*. The abdomen may touch the leaf margin.

Cryptocephalus bipunctatus (Linnaeus) (Krasnodar Terr., on the European dewberry *Rubus caesius* and red raspberry *R. idaeus*). The behavior is identical to that of *Ch. herbacea*.

Labidostomis lepida Lefevre (Mordovia, on the grey willow *Salix cinerea*). Although insects of both sexes were collected, feeding behavior was observed only in the females. The beetle moves its head down in a series of bites, then moves its head up and starts a new series.

Cassida stigmatica Suffrian (Moscow Prov., on the common tansy *Tanacetum vulgare*) (Fig. 3, *3*). The beetle is positioned on the leaf margin grasping it with all the tarsi, with its head protruded maximally from the prothorax and raised. Other details of feeding behavior are identical to those of *Ch. herbacea*.

Feeding on the Leaf Surface

The beetle performs symmetrical, usually alternating series of bites to the right and to the left of the longitudinal body axis. In most species, individual incisions merge into a single hole that usually does not reach the leaf margin. The description below refers to one of the two series of bites (right or left).

Donacia bicolora Zschach (Moscow Prov., on the branched bur-reed *Sparganium erectum*) (Fig. 4, *2*). The beetle sits on the upper or lower surface of the leaf raised above the water. It moves its head down in the sagittal plane until its mandibles become perpendicular to the leaf surface and at the same time tilts it to the left and rotates it slightly to the left relative to the longitudinal axis. The gnawing starts as the head is shifted from the left to the right. Having made an incision 1.5–3 mm long, the beetle rotates its head to the right relative to the longitudinal axis, advances slightly forward, and continues gnawing the leaf, this time from the right to the left. It gnaws a small hole first and then enlarges it lengthwise and sidewise. During feeding the beetle advances slowly onto the damaged area. The incision is only part-through, from several millimeters to 2 cm long and 1–3 mm wide, with rough margins. It runs along the leaf, not crossing any veins.

Donacia aquatica (Linnaeus) (Moscow Prov., on the narrowleaf bur-reed *Sparganium angustifolium*). The behavior is identical to that of *D. bicolora*. The incisions are made on floating leaves, always on the upper surface.

Donacia cinerea Herbst (Moscow Prov., on the broadleaf cattail *Typha latifolia*). The behavior is identical to that of *D. bicolora*. The incisions are made on both sides of the leaves raised above the water.

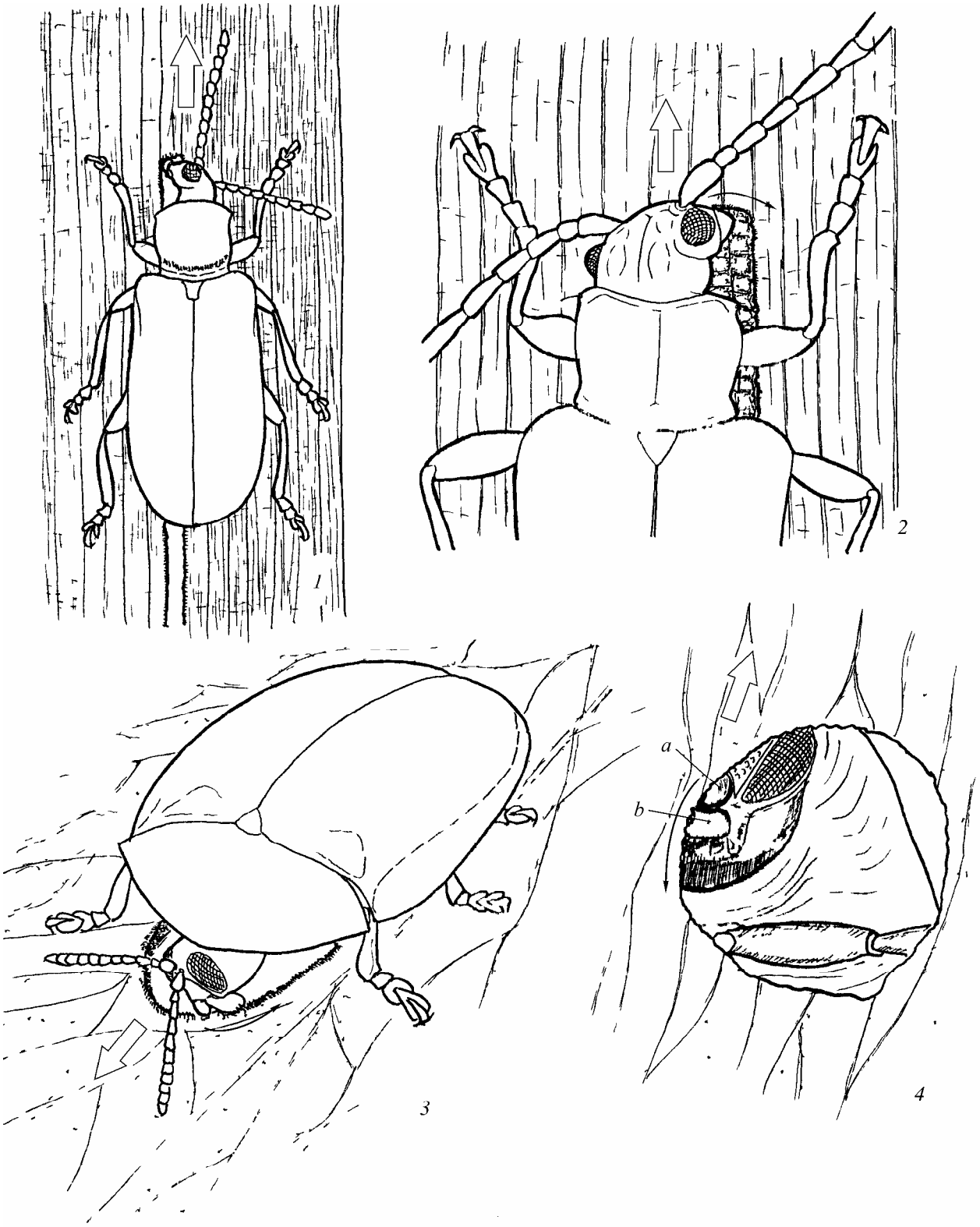

Fig. 4. Feeding of leaf beetles: *Oulema erichsonii* (*1*), *Donacia bicolora* (*2*), and *Cassida rubiginosa* (*3–4*), observed from the upper leaf side (*3*) and from the lower leaf side, through the incision (*4*). Left (*a*) and right (*b*) mandibles. For explanation of the black and white arrows, see Fig. 2.

Donacia clavipes Fabricius (Moscow Prov., on the common reed *Phragmites australis*). The behavior is identical to that of *D. bicolora*. The incisions are made on both sides of the leaves raised above the water.

Donacia crassipes Fabricius (Moscow Prov., on the white water-lily *Nymphaea candida* and yellow pond-lily *Nuphar lutea*). The beetle sits on the upper surface of the floating leaf. It moves its head down and gnaws separate holes 0.5–0.75 mm long and 1.5 mm wide in the pulp. In experiments with captive beetles, the leaf was after some time covered with such small holes arranged without any specific pattern.

Donacia dentata Hoppe (Moscow Prov., on the arrowhead *Sagittaria sagittifolia* and European water plantain *Alisma plantago-aquatica*). The beetle sits on the upper surface of leaves raised above the water. The behavior is identical to that of *D. crassipes*, except that individual small holes form characteristic undulate tracks (Fig. 3, *5*). The presence of *D. dentata* in a water body can be easily detected by such traces.

Donacia marginata Hoppe (Moscow Prov., on the branched bur-reed *Sparganium erectum*). The behavior is identical to that of *D. bicolora*. The incision is positioned along the leaf but may deviate from the longitudinal direction and cross some veins.

Donacia semicuprea Panzer (Moscow Prov., on the reed mannagrass *Glyceria maxima*). The behavior is identical to that of *D. bicolora*. The incisions are made on both sides of leaves raised above the water.

Donacia sparganii Ahrens (Moscow Prov., on the narrowleaf bur-reed *Sparganium angustifolium*). The behavior is identical to that of *D. bicolora*. The incisions are made on floating leaves, always on the upper surface.

Donacia versicolorea (Brahm) (Moscow Prov., on the floating pondweed *Potamogeton natans*). The behavior is identical to that of *D. bicolora*. The incisions (often through) occur on the upper surface of floating leaves.

Donacia vulgaris Zschach (Moscow Prov., on the narrowleaf bur-reed *S. angustifolium* and the broadleaf cattail *Typha latifolia*). The behavior is identical to that of *D. bicolora*. The incision is positioned along the leaf but may deviate from the longitudinal direction and cross some veins; on floating leaves of *S. angustifolium* it is always located on the upper surface, and on the raised leaves of *T. latifolia*, on both surfaces.

Galerucella grisescens (Joannis) (Mordovia, on the tufted loosestrife *Naumburgia thyrsiflora*) (Fig. 2, *2*). The beetle rotates its head by a small angle to the right and performs a series of bites gradually turning the head and pronotum to the left in the horizontal plane; then the head and pronotum are turned to the right and the head is rotated by a small angle to the left relative to its initial position, after which another series of bites is performed. The mandibles grasp the leaf from both sides. The beetle raises itself slightly on its legs over the leaf surface and gradually advances to the through incision, its legs widely spread and its tarsi resting on the sides of the incision. The tufted loosestrife is reported here for the first time as a food plant for the adults of *G. grisescens*. The pupae of this species were collected from this plant in the nature, and the beetles emerging from them were observed to feed on the leaves.

Phyllobrotica quadrimaculata (Linnaeus) (Mordovia, on the marsh skullcap *Scutellaria galericulata*) (Fig. 2, *3*). The beetle sits on the upper surface of the leaf and does not raise itself on its legs during feeding; other behavioral traits are identical to those of *Galerucella grisescens*, described above.

Lema cyanella (Linnaeus) (Krasnodar Terr., on the thistle *Cirsium* sp.). The behavior is identical to that of *Galerucella grisescens*. The incision is rounded or oval, 1–3 mm wide, only part-through, with the epidermis of the opposite leaf surface remaining intact. During feeding, one mandible is positioned on the leaf surface while the other sinks into the pulp.

Lilioceris merdigera (Linnaeus) (Moscow Prov., on the lily of the valley *Convallaria majalis* (Fig. 2, *4*). The beetle sits on the upper leaf surface parallel to its longitudinal axis. Its head rotates by 45° to the right, and its pronotum, also to the right but by a smaller angle. A series of several bites is performed as the head is tilted to the left in the horizontal plane. The mandibles grasp the leaf from both sides (the left one from above and the right one from below). After the series is complete, the head and pronotum are rotated to a different direction and the feeding is resumed. The fore and mid legs sometimes provide a somewhat springy support for the body: it is pressed to the leaf as the mandibles converge, and raised from it as they are brought apart. In between the series of bites the beetle advances onto the incision. The incision is large, through, sometimes damaging all the veins except the main arcuate ones.

Oulema erichsonii (Suffrian) (Moscow Prov., on grasses (Poaceae)) (Fig. 4, *1*). The beetle moves its head down in the sagittal plane and tilts it by 90° in the horizontal plane relative to the longitudinal body axis. After a series of several rapid bites, it tilts its head by 90° in the opposing direction and continues feeding. The beetle advances onto the incision simultaneously with gnawing. The incision is shaped as a long and narrow, mostly complete groove between the parallel veins.

Zeugophora flavicollis (Marsham) (Moscow Prov., on the balsam poplar *P. balsamifera*). Sitting on the upper leaf surface, the beetle moves its head down in the sagittal plane and gnaws the leaf pulp, leaving even the finest veins intact. It gradually advances in the process of feeding. The incision is only part-through.

Plagiodera versicolora (Laicharting) (Mordovia, on the grey willow *Salix cinerea*). The incision is through, not extending to the leaf margin. Its shape is different on the young and old leaves. The incisions on young leaves are large and irregular, with only the midrib and large lateral veins remaining intact. On older leaves the beetle gnaws only the pulp, leaving even the finest veins intact.

Cassida viridis Linnaeus (Mordovia, on the gypsywort *Lycopus europaeus*). The beetle moves its head up in the sagittal plane so that the mandibles become perpendicular to the leaf surface, after which the head is rotated to the right and at the same time tilted to the right in the horizontal plane. A series of bites is performed as the head is tilted to the left in the horizontal plane. When a series is complete, the beetle rotates its head to the left, tilting it to the left in the horizontal plane, and starts a new series of bites during which the head is tilted to the right. The mandibles grasp the leaf from both sides (as in Fig. 4, *4*). The legs and body remain static during gnawing. The beetle advances slowly between the series of bites as the incision is enlarged. The incisions are through, rounded, 3–5 mm wide.

Cassida denticollis Suffrian (Moscow Prov., on the common tansy *Tanacetum vulgare*). The behavior is identical to that of *C. viridis*. The pronotum of a feeding beetle is slightly raised in the sagittal plane, allowing the head to be positioned perpendicular to the leaf. The incisions are through, oval (3 × 5 mm) or irregular-shaped, and may extend to the leaf margin.

Cassida rubiginosa Müller (Moscow Prov., on the thistle *Cirsium* sp.) (Fig. 4, *3*, *4*). The behavior is identical to that of *C. viridis*. The incisions are either through or part-through, with the epidermis of the opposing leaf surface remaining intact even in case of extensive damage. Both variants of incision could be observed in the same individual feeding on the same leaf. The pronotum tilts slightly up and down during each bite. The thorax, abdomen, and all legs remain static during the series of bites.

Cassida vibex Linnaeus (Moscow Prov., on the thistle *Cirsium* sp.). The behavior is identical to that of *C. viridis*.

Hypocassida subferruginea (Schrank) (Krasnodar Terr., on the bindweed *Convolvulus* sp.). The behavior is identical to that of *C. viridis*. The incisions are rounded or oval, 2–4 mm wide, or larger and irregularly shaped, usually not reaching the leaf margin.

Feeding on the Leaf Rolled into a Tube

The adults of *Lilioceris merdigera* (Moscow Prov., on the lily of the valley *Convallaria majalis*; Murmansk Prov., on the May lily *Maianthemum bifolium*) and *Donacia clavipes* (Moscow Prov., on the common reed *Phragmites australis*) (Fig. 3, *6*) feed on young, still unexpanded leaves at the beginning of the warm season. The beetle gnaws a deep hole through several layers of the rolled leaf; later, with the leaf expanded, the trace of a single feeding act appears as a row of holes arranged perpendicular to the longitudinal leaf axis.

DISCUSSION

The leaf beetles can be subdivided into three types according to the position of their mouthparts: prognathous, hypognathous, and opistognathous (Medvedev and Roginskaya, 1988), with the mandibles directed forwards, downwards, and down-backwards, respectively. The above characteristics refer to the resting position of the mandibles. During feeding, however, the mouthparts are brought to the most convenient position for gnawing, namely perpendicular to the leaf surface. To assume this position, the representatives of the subfamilies Donaciinae and Criocerinae (the prognathous type) move the head down (Figs. 2, *4*; 4, *1, 2*), whereas the species of the subfamily Cassidinae (the opistognathous type), on the contrary, raise the head up (Figs. 3, *3*; 4, *3*). In other words, the head of these leaf beetles becomes functionally hypognathous.

The manner of feeding is related to the shape of the leaf, the venation pattern, and the size and proportions of the beetle body. Feeding on the leaf surface is possible for the beetles whose head is sufficiently movable in the horizontal plane. This mode of feeding is typical of all the studied representatives of Donaciinae, Criocerinae, and Zeugophorinae. Beetles of the subfamily Cassidinae also have quite movable heads, allowing them to gnaw through the leaf while resting on its surface.

Some of the species considered above feed by marginal gnawing even though the beetles are positioned on the surface during feeding: the head is partly sunk into the perforation and assumes the position with the mandibles grasping the leaf from both sides, so that the leaf plane almost coincides with the sagittal plane of the head. This mode of feeding is observed in large species (*Chrysomela*, *Galerucella*, *Phyllobrotica*, *Lilioceris*, *Oulema*, and *Cassida*), whereas such a small beetle as *Zeugophora flavicollis* can only gnaw through the epidermis on one side of the leaf and consume the pulp. On the other hand, some reed beetles of the genus *Donacia*, including large forms with motile heads, are also characterized by part-through incisions (Fig. 4, *2*).

In many representatives of the subfamily Chrysomelinae the head is sunk into the prothorax and can only move up and down in the sagittal plane. The only mode of feeding open to such forms is gnawing on the leaf margin (Fig. 3, *1*, *4*). The adults of most of the species studied position themselves directly on the leaf margin during feeding (Fig. 3, *1*, *4*). The beetles *Chrysomela vigintipunctata*, on the contrary, sit on the leaf surface at the margin (Fig. 2. *1*), which may be related to their body shape: they have a wide body and short legs preventing them from keeping on the margin. Some of the observed individuals of *Ch. fastuosa* and *Ch. polita* tried gnawing the leaf from the surface. However, since these beetles could not tilt their heads to the right or left in the horizontal plane or rotate them along the longitudinal axis, they could not feed in this way and soon moved onto the leaf margin.

In conclusion, it should be noted that the modes of feeding of leaf beetles and the corresponding damage patterns are quite diverse and in many cases species-specific. Further studies of these aspects, together with obtaining new data on their food plants, will be essential both for taxonomy and phylogeny of leaf beetles and for identification of agricultural and forest pests.

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