Fern sawfly larvae *Blasticotoma filiceti* Klug, 1834 (Hymenoptera: Blasticotomidae) are visited by ants: a new kind of trophobiosis

Личинки папоротникового пилильщика Blasticotoma filiceti Klug, 1834 (Hymenoptera: Blasticotomidae) посещаются муравьями: новая разновидность трофобиоза

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KEY WORDS: Blasticotomidae, Formicidae, Hymenoptera, Drosophilidae, trophobiosis, mutualism, life mode, phloem-feeders, miners, zoogeography, range disjunctions, nemoral species.

КЛЮЧЕВЫЕ СЛОВА: Blasticotomidae, Formicidae, Hymenoptera, Drosophilidae, трофобиоз, образ жизни, питание флоэмой, минеры, зоогеография, разрывы ареалов, неморальные виды.

ABSTRACT. Fern sawfly *Blasticotoma filiceti* Klug, 1834 is first recorded in several regions of Central European Russia. Frothy anal excretions of larvae, living in the cells within rachis and feeding mainly on the phloem sap, attract ants and *Drosophila* flies. Interaction of ants with sawfly larvae can be considered as a new kind of trophobiosis: direct (not plant-mediated) hymenopteran-hymenopteran one. Geographical distribution of the species and peculiar life mode of larvae are discussed in detail.

РЕЗЮМЕ. Папоротниковый пилильщик Blasticotoma filiceti Klug, 1834 впервые отмечен в ряде районов центра Европейской России. Пенистые анальные выделения личинок, живущих в ячейках внутри рахиса и питающихся, в основном, соком флоэмы, привлекают муравьёв и дрозофил. Взаимодействие муравьёв с личинками пилильщика может рассматриваться как новая разновидность трофобиоза. Подробно обсуждается распространение вида, а также оригинальный образ жизни личинок.

Introduction

Blasticotomidae is a small family (12 described modern species, and probably at most two genera, *Blasticotoma* Klug, 1834 and *Runaria* Malaise, 1931), now confined to temperate forests of Palaearctic, from England and Scandinavia to southern China, Taiwan and Japan [Shinohara, 1983; Togashi, 1989]. The only fossil blasticotomid was found outside this range, in North America (Early Oligocene of Florissant, Colorado); it was assigned to a separate genus *Paremphytus* Brues, 1908, later either considered possible synonym of *Blasticotoma* or *Runaria*, or synonimized with *Runaria* [Benson, 1942; Smith, 1975; cit. after Shinohara, 1983].

All but one living blasticotomid species are confined to temperate East Asia (Palaearchearctic as defined by Semenov-Tian-Shanskij [1936]), except for *Blasticotoma filiceti* Klug, 1834 (one of its two subspecies is distributed in nemoral and subnemoral zone of Europe and Siberia, see below). At least in Europe *B. filiceti* is a rare, sporadically occurring species, included in regional Red Data Books; it is listed in the Appendix 1 to the Red Data Book of Moscow Region [Zubakin & Tikhomirov, 1998: 536] and included in the Red Data Book of Moscow [Shcherbakov, 2001].

Blasticotomidae represent one of the most archaic living groups within Hymenoptera and are similar to Tenthredinoidea in some characters and to Xyelidae and Pamphiliidae in some other, especially larval characters [Maxwell, 1955]; currently this family is regarded as the basalmost lineage within Tenthredinoidea s.l. [Schulmeister, 2003]. Common ancestors of blasticotomids and remaining tenthredinoids are extinct Xyelotomidae, derivable directly from Xyelidae (the most basal hymenopteran group) [Rasnitsyn, 2002].

The life mode of Blasticotomidae is unique: larva lives in a short, caudally open, tunnel-like cell in the fern rachis and produces copious excretion forming a frothy mass concealing the entrance. Biology of *B. filiceti filiceti* Klug, 1834 is studied in detail [Meijere, 1911]. Host ferns are *Athyrium filix-femina* (L.) Roth. ex Mert. (most usual), *Matteuccia struthiopteris* (L.) Tod., *Dryopteris* spp., *Polystichum* sp., *Pteridium aquilinum* (L.) Kuhn. [Taeger et al., 1998]. The cell is scarcely longer than larva length, with a large posterior opening and one (sometimes two) tiny anterior perforation (on the same or opposite rachis side; no perforation in young larvae). The larva excavates its cell forward only according to its body growth (so it should not be defined as miner) and feeds on the running plant sap (not





Figs 1–2. Blasticotoma filiceti Klug, 1834 1 — two froth masses of larvae on Athyrium filix-femina with characteristic unilateral damage of the frond. Tom' R., Kemerovo Region; 2 — larvae of different instars.

Рис. 1–2. Blasticotoma filiceti Klug, 1834 1 — две личиночные пенистые массы на женском кочедыжнике с характерным односторонним повреждением вайи. Кемеровская обл., р. Томь; 2 — личинки разных возрастов.

on the modified plant tissue as gallers). Cells occur both in the upper, foliate and lower, naked rachis parts; sometimes several more or less close-set larval cells are found in one rachis, adjacent ones being directed tailto-tail and often concealed by a common frothy mass. The froth is less watery than that of cercopoid nymphs, stable, non-adhesive, resembles the beaten egg white, and turns brownish with time; it is absent within the cell and originates from the caudal end of larva during pushing movements of the anal segment. Grown larvae occurring in July–August are easy to notice by their froth and characteristic unilateral browning of rachis and pinnules (Fig.1); in some years they are locally abundant, in others impossible to find. Mature larvae leave cells and pupate in soil without cocoon; rearing attempts were unsuccessful; fern fronds broke easily at the abandoned larval cells. Adults, especially males, are extremely rare (516 larvae and only 4 females were collected by Verzhutsky [1973]) and occur in late Mayearly July. Oviposition scars on rachises are blackish and conspicuous; some larvae fail to develop. Parasitoids of B. filiceti are Shawiana foveolator (Thomson, 1892) (Braconidae: Exothecinae) [Belokobylskij & Tobias, 1986] and Tetrastichus rasnitsyni Kostjukov, 2001 (Eulophidae) [Kostjukov, 2001].

Observations

On July 21, 1987 a froth mass produced by the *B. filiceti* larva was encountered on *A. filix-femina* in the country house ('dacha') garden near Snigiri, 40 km WNW Moscow. The find was totally unexpected, because the nearest records of this species were from Karelia and Ukraine. Since then, several dozen larvae were collected in natural biotopes from the following localities in Central European Russia:

Moscow Region: Istra R. valley 5 km SSW Snigiri (55°51′N 37°01′E); 5 km NW Ramenskoe (55°35′N 38°11′E); Malakhovka (55°40′N 38°05′E); 5 km N Faustovo (55°28′N 38°30′E); Losinyi Ostrov at NE edge of Moscow (55°50′N 37°50′E);

Tver' Region: Volga R. valley 15 km WNW Dubna (56°47′N 36°54′E);

Kostroma Region: Unzha R. valley 5 km ENE Ugory (58°09'N 44°25'E).

The host fern is usually *A. filix-femina*, occasionally *M. struthiopteris* or *Dryopteris filix-mas* (L.) Schott. Larvae, found from July to August, are locally abundant in some years and very rare in the others; no adults were collected or reared. Larval cell is excavated nearer to one side of the rachis, almost cutting one of two symmetrical vascular bundles. The rear end of larval body is shaped like elytral declivity in Scolytidae. Mature larva, if alarmed, sometimes leaves the cell, coils ring-like and starts twist and turn like a caterpillar. Braconid parasitoids are quite common, they pupate in the host cells. Empty sawfly cells are sometimes used as shelters by occasional visitors (small beetles and beetle larvae, true bugs, mites).

Froth masses, especially brownish ones, often attract ants *Myrmica rubra* (Linnaeus, 1758), *M. rugino*-

dis Nylander, 1846 and Lasius sp., various small flies, and occasionally vespine wasps. The ants spend much time near the froth and feed on its substance. A kind of combat between conspecific ants (M. ruginodis), presumably belonging to the different colonies, was once observed around the froth masses. Young larvae seem to produce no much froth, older ones show perfect froth masses, and only mucous brownish remnants of froth are sometimes found at the cells of fully grown larvae (this may be owing to activities of ants and other insect visitors). Drosophila species (D. histrio Meigen, 1830, D. testacea von Roser, 1840, D. transversa Fallén, 1823) are often attracted to and oviposit at the froth turning brownish; their larvae were found near or in abandoned sawfly cells and sometimes pupate within.

In August 2001 numerous *B. filiceti* larvae were observed in West Siberia, Kemerovo Region, Tom' R. valley 10 km NE Ust'-Naryk (54°23′N 87°32′E), very close to the locality reported by Rasnitsyn [1969]. The larvae were common both on *M. struthiopteris* and *A. filix-femina*, and actively visited by ants *M. rubra* and *Formica lemani* Bondroit, 1917.

Range of B. filiceti

The species comprises two subspecies:

Euro-Siberian *B. filiceti filiceti:* northern and central Europe: England, Netherlands, Germany, Norway, Sweden, Finland, Poland, Hungary [Benson, 1951; Móczár & Zombori, 1973; Taeger et al., 1998; Nasjonal rødliste..., 1999; Watson & Dallwitz, 2003, etc.]; Ukraine (Uzhgorod, Lvov, Kiev and Chernigov regions) [Ermolenko, 1972]; European Russia (Karelia, Moscow, Tver' and Kostroma regions) [Zhelokhovtsev, 1988; Shcherbakov, 2001 and this paper]; South Siberia: Kemerovo Region (Tom' River N of Altai Mts.), Krasnoyarsk Province, mountains around SW end of Baikal Lake (Primorsky and Khamar-Daban ranges, Tunka Valley; Irkutsk Region and Buryatia) [Rasnitsyn, 1969; Verzhutsky, 1973, 1974, 1981].

B. filiceti subsp. indet.: Russian Far East (Khabarovsk Province [Verzhutsky, 1973], Sakhalin and Kuril Islands [Ermolenko, 1994]).

East-Asiatic *B. filiceti pacifica* Malaise, 1931: Russian Far East (southern Maritime Province) [Gussakovskij, 1935]; Japan (Hokkaido, Honshu) [Togashi, 1989]. (*B. smithi* Shinohara, 1983, very similar to *B. filiceti pacifica*, is found in the mountains of Taiwan, at the southernmost extremity of the family range, ca. 24°N [Shinohara, 1983])

The range of *B. filiceti* as currently known is essentially tripartite, with one major disjunction from near Moscow to near Novokuznetsk, and another from Baikal to Amur. Such ranges are termed Europe–West-Siberia–Far-East disjunctive [Dubatolov & Kosterin, 2000] and reported for a number of animal and plant species, e.g. *Arge metallica* Klug, 1834 [Ermolenko, 1972: fig.59], *Yponomeuta evonymellus* (Linnaeus, 1758) [Gershenson, 1981], *Parus palustris* Linnaeus, 1758 [Stegmann,

1938: fig.36], and Asperula odorata L. [Tolmachev, 1974: fig.31]. However, taking into account a "cryptic habit" of B. filiceti, we may expect that its western, Ural-Siberian disjunction will be at least partly filled with future finds, and the range may eventually appear as having only one major disjunction in Transbaikalia, similar to those of e.g. Macrophya duodecimpunctata (Linnaeus, 1758) with its two subspecies, Euro-Siberian and East-Asiatic [Benson, 1950: fig.6], Cicadetta montana (Scopoli, 1772) [Kudryasheva, 1979: fig.13], and Nebria livida (Linnaeus, 1758) [Kryzhanovsky, 1982]. The range of N. livida is similar to that of B. filiceti in being restricted to rather narrow latitudinal zone, and demonstrates that the eastern disjunction may also be filled with possible finds in northern China. Such range disjunctions were traditionally dated to Tertiary, preglacial times, e.g. to Miocene for B. filiceti [Verzhutsky,

The B. filiceti range is much narrower than those of its commoner host ferns A. filix-femina and M. struthiopteris, and fits (except for Baikalian finds) in the zone of broad-leaved (nemoral) forests, outlined in European Russia and West Siberia with the range of small-leaved lime *Tilia cordata* Miller and its allies [Sokolov et.al., 1986] (*Tilia* series *Cordatae* Maleev, 1949: *T. cordata* = sibirica Bayer and T. amurensis Rupr. = taquetii Schneid.). Siberian finds of B. filiceti are restricted to refuges of the nemoral flora: lime forests of the Kemerovo Region, black ('chernevaya') taiga (fir-aspen taiga enriched with nemoral herbaceous species and considered to be subnemoral forest) of Altai and northern slopes of Sayan and Khamar-Daban Mts. [Ermakov, 1998]. The zone of nemoral forests (i.e. containing at least lime or elm), now broadly interrupted in Siberia, was last restored as continuous belt during the Holocene climatic optimum (9,000 to 5,000 years B.P.); after its breakup some nemoral species of Lepidoptera diverged into the western and eastern subspecies, and East-Asiatic origin can be traced for those nemoral species that occur both in Europe and Siberia [Dubatolov & Kosterin, 2000]. By analogy, one may assume that B. filiceti and M. duodecimpunctata are of eastern origin, and their subspecies separated in the Holocene.

Larval lifestyle of Blasticotomidae

Blasticotomid larvae (Fig. 2) were classified as stemborers [Benson, 1951], petiole-miners [Hering, 1957], or sometimes even as petiole-gallers [Labandeira & Phillips, 1996]. Some insect gallers were only recently recognized as such, because their galls are externally inconspicuous ('cryptic', 'rudimentary'), and presence of nutritive tissue is sometimes evident only in the cell structure modification (stem galls of some Eurytomidae and Cynipidae [Zerova et al., 1988], leaf galls of some Cecidomyiidae [Rohfritsch, 1999]). The term 'galler' seems not applicable for blasticotomid lifestyle: there is no evidence of nutritive tissue, and copious sweetish excreta indicate that the food composition is far from

optimal. Probably those miners that feed on the parenchymatic cell sap in spot mines [Gerasimov, 1952] approximate the blasticotomid life mode most closely, but the difference is still large.

A supposition that blasticotomid larvae feed chiefly on the phloem sap agrees with: (i) it is the only constant food source in the cell; (ii) vascular bundles in the fern rachis contain central xylem elements surrounded by the phloem [Meyer, 1948] that is easily accessible to the larva; and (iii) frothy excretions of larvae attract ants and other insects preferring sugary food. Larvae of Blasticotomidae represent a peculiar case of phloemfeeder with chewing mouthparts (phloem feeding is otherwise restricted to piercing-and-sucking Hemiptera [Douglas, 2006]). A special term, 'phloeminer', may be proposed for endophytic insect grazer feeding chiefly on the phloem sap and producing liquid (frothy) excretion. This lifestyle, now restricted to Blasticotomidae, is probable for their ancestors (Xyelotomidae) and some other extinct symphytans, and was possibly more widespread in the past, when fern-like plants were more diverse. Similarity of phloeminer to typical miners is confirmed by the fact that its parasitoid, S. foveolator is recorded also on *Phyllonorycter rajella* (Linnaeus, 1758) (Lepidoptera Gracillariidae) mining leaves of *Alnus* spp.

Trophobiosis of *B. filiceti* with ants

The term 'trophobionts' was coined by Wasmann [1894, cit. after Wilson, 1971] for arthropods that provide social insects with honeydew or nutritive secretions in exchange for protection from parasites and predators. In broader sense, trophobiosis is a mutualistic relation between different species, one receiving the food, another protection; by such definition even protective ant-plant interactions [Heil & McKey, 2003] are trophobiotic. The best known are the trophobiosis of Hymenoptera, Isoptera, some other insects, and even tetrapods with phloem-feeding Homoptera and Heteroptera [Wilson, 1971; Delabie, 2001; Fölling et al., 2001], and that of ants with larvae of lycaenid and riodinid butterflies [Pierce et al., 2002]. The only type of hymenopteran-hymenopteran trophobiosis recorded so far is plant-mediated: honeydew-secreting galls of some Cynipidae, known already to ancient Greeks [Theophrastus, 287 BC, cit. after Washburn, 1984], and of few Cecidomyiidae, are tended by ants [Bequaert, 1924; Kovalev, 1965; Abe, 1988]. Unlike ant-cynipid relationship, interaction of Blasticotoma with ants is direct, not mediated by plant. In yet another type of trophobiosis, ants mechanically stimulate the larvae of Tortricidae living in silken shelters, and feed on their anal liquid containing sugar and amino acids [Maschwitz et al., 1986]. Among known types of trophobiosis, ant-tortricid relationship is the most similar to the case of *Blasti*cotoma, but stimulation by ants was not observed in the latter. The ant-blasticotomid association is facultative, nevertheless, sawfly larvae apparently receive some protection from parasitoids due to ant attendance, and we can consider these interactions as a new kind of trophobiosis, referable to the same type as the anttortricid case.

Cercopoid nymphs feeding principally on xylem sap produce spittle mass from sugar-free anal liquid to protect themselves. Their spittle is sometimes used by female eumenid wasps or ants in nest or aphid-tent construction [Beiko, 1986; Henderson et al., 1990]. On the contrary, the 'honeyspittle' of *Blasticotoma* represents both an attractive food resource for ants that compete for this 'candyfloss', and a protection against parasitoids in the absence of ants.

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