The Agromyzidae (Diptera) Feeding Particularities on Some Genera of Ranunculaceae

SAULIUS PAKALNIŠKIS

Institute of Ecology, Vilnius University, Akademijos 2, LT–08412, Vilnius, Lithuania; e–mail: saupak@ekoi.lt

PAKALNIŠKIS S. 2004. THE AGROMYZIDAE (DIPTERA) FEEDING PARTICULARITIES ON SOME GENERA OF RANUNCULACEAE. – *Latv. entomol.*, 41: 93-99.

Abstract: There were the life stories of 47 Agromyzidae (Diptera) species on 11 genera of ranunculaceous plants studied, including their host specialization, feeding character and localization of mine as well as pupation particularities. The agromyzid larvae colonizing the assimilative, generative as well as support organs of certain host–plant show a high level of specialization. On the other hand, almost all the mining types may be characteristic to one species (e.g. *Phytomyza clematidis* on *Ranunculus lingua*). Further bionomic data on several poorly known species are provided in this report for the first time. Also some possible micro-evolutionary ways of the feeding behaviour are discussed in present paper.

Key words: Agromyzidae, Ranunculaceae, bionomics, feeding behaviour, Lithuania.

Introduction

The ranunculaceous plants form an old, rich in species as well as unique family of Magnoliophyta, widespread in temperate to arctic areas over the Holarctic and partially in temperate areas of southern hemisphere. Because of the particular chemical stuffs there are almost no polyphagous Agromyzidae on Ranunculaceae.

There are predominantly (more than 100) representatives of *Phytomyza* genus feeding on Ranunculaceae. Some of them demonstrate certainly distinctive morphological characters and were placed in the *Napomyza* up to 1994. Many species groups of *Phytomyza* are represented on Ranunculaceae and species group limits are here almost invisible. These groups are descended on this plant family more probably than reverberate a result of several colonisations. Thus K.A. Spencer (1990) considered that Agromyzidae are on Ranunculaceae primary, not secondary, and that means they are 'inherited'. This proposition, being correct generally, cannot be aimed at all Agromyzidae though.

The agromyzid larvae (and *Phytomyza* particularly) attack all the plant–organs of Ranunculaceae and form there rather all types of mines, represent in even narrow geographical areas. This species complex is a good model for studies on evolution of the host specialization and larval feeding behaviour. This paper provides new biological data on some poorly known species and discusses on particularities of feeding specialization.

Methods

Author in Lithuania and contiguous districts of neighbouring countries collected early stages of Agromyzidae between 1980 and 2003, with the consequent imago rearing in laboratory. Material is deposited in the Institute of Ecology, Vilnius.

The species are laid out in the list below, taking into account their morphological resemblance. The six species with note of interrogation marked need a formal confirmation by rearing of imagines or even imago males (in case of *P. platonoffi*).

Results

There were 47 species of Agromyzidae found feeding on 11 genera of Ranunculaceae during the investigation. These phytophagoes host specialization range varies here between the monophagy and oligophagy and does not overstep a plant genus limits mostly. Only 3 species colonise plants of 2–3 relate genera, three species feed on 2 most relate genera of different plant tribes (Isopyreae and Thalictreae). But *Phytomyza clematidis* colonize only selective plant species, which represent 2 genera of different tribes (Anemoneae and Ranunculeae), choosing even different organs of each host. And *Phytomyza actaeae* can feed on selective plant species of 2 genera from different subfamilies (Helleboroideae and Ranunculoideae).

Two last phenomena are most interesting since analysing the evolution of feeding behaviour and host specialization in Agromyzidae and may be considered to be a kind of 'selective oligophagy' rather confirmable with the xenophagy (cf. Spencer 1999).

List of species

Phytomyzinae

Phytomyza ? albimargo Hering, 1925
Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Anemone nemorosa.* Larva leaves the mine through an upper leaf surface, pupating in the ground.
Lithuania: Spalviškiai environs, 56º16'N, 24º58'E, mines and puparia collected only.

Phytomyza pulsatillae Hering, 1924
Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Pulsatilla patens* and *P. pratensis*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza hendeli Hering, 1923
Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Anemone nemorosa.* Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza ranunculivora Hering, 1934
Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus acris, R. lanuginosus* and *R. polyanthemos*. Larva leaves the mine through a lover leaf surface, pupation takes place in the opening, and the yellowish puparium remains hung in the opening or falls down.

Phytomyza linguae Lundquist, 1947
Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus lingua*. Larva leaves the mine through an upper leaf surface, pupation takes place on the leaf blade, puparium is black and stuck to the leaf in some centimetres from the opening away.
Not a synonym of *P. ranunculivora* (cf. Pakalniškis, 1996b).

Phytomyza pulsatillicola Hering, 1962
Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Pulsatilla patens* and *P. pratensis*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza anemonantheae Spencer, 1969
Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Anemone sylvestris.* Pupation takes place inside.

Phytomyza ? aconiti Hendel, 1920
Helleboroideae: Delphineae. Upper–surface leaf mines in *Aconitum napellus*. Several larvae feed together, leaving the mine through an upper leaf surface and pupating in the ground. The species can feed on *Delphinium* spp. as well (Spencer, 1996, 1999).
Lithuania: Šilainiai, 54º56'N, 23º52'E, mines and puparia collected only. An introduced species, doubtless.

Phytomyza aconitophila Hendel, 1927
Helleboroideae: Delphineae. Upper–surface leaf mines in *Aconitum septentrionale*. Larva leaves the mine through an upper leaf surface, pupating in the ground. Introduced species.

Phytomyza actaeae Hendel, 1922
Helleboroideae: Cimicifugeae. Upper–surface leaf mines in *Actaea spicata*. Pupation takes place internally. M. Beiger recorded (1980) in Poland *Clematis alpina* (Ranunculoideae: Anemoneae) to be next host plant.

Phytomyza rydeni Hering, 1934
Ranunculoideae: Ranunculeae. Upper–surface

leaf mines in *Ranunculus acris*. Some larvae are feeding together usually, and pupation takes place in the mine.

Phytomyza trollii Hering, 1930Helleboroideae: Trollieae. Upper–surface leaf mines in *Trollius europaeus*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza ignota Pakalniškis, 1994

Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Pulsatilla pratensis*. Pupation takes place inside (under the upper epidermis) or rarely larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza ? kaltenbachi Hendel, 1922

Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Clematis vitalba* and relate spp. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Lithuania: Kryžiokai, 54º48'N, 25º21'E; Merkinė, 54º10'N, 24º11'E; Šilainiai, 54º56'N, 23º52'E; Tamošava, 54º36'N, 24º34'E. Mines and puparia collected only. An introduced species, doubtless.

Phytomyza palionisi Pakalniškis, 1998

Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus cassubicus*. Pupation takes place inside, under the lower epidermis.

Phytomyza anemones Hering, 1925

Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Anemone nemorosa*. Pupation takes place inside, under the upper epidermis.

Phytomyza fallaciosa Brischke, 1881

Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus acris, R. lanuginosus* and *R. lingua,* with some larvae feeding together. Pupation takes place inside, under the lower epidermis.

Phytomyza trolliivora Hering, 1935

Helleboroideae: Trollieae. Upper–surface leaf mines in *Trollius europaeus*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza calthophila Hering, 1931

Helleboroideae: Trollieae. Upper–surface leaf mines in *Caltha palustris*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza ? calthivora Hendel, 1934

Helleboroideae: Trollieae. Upper–surface leaf mines in *Caltha palustris*. Larva leaves the mine through a lower leaf surface, puparium remains hung in the opening.

Lithuania: Marcinkonys environs, 54º05'N, 24º27'E, mines and puparia collected only.

Phytomyza ~~?~~soenderupi Hering, 1941

Helleboroideae: Trollieae, Internal petiole mines in *Caltha palustris*, sometimes (if some larvae are feeding together) appearing in the surface irregularly and even in basal part of leaf blade (just as *P. stolonigena*), pupation takes place inside.

Latvia: Rucava environs, 56º10'N, 21º08'E, puparia collected 28.08.2003, 2 females and 3 males emerged.

Phytomyza socia Brischke, 1881

Ranunculoideae: Anemoneae. Upper–surface leaf mines in *Hepatica nobilis* and *Pulsatilla pratensis*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza abdominalis Zetterstedt, 1848

Ranunculoideae: Anemoneae. Upper–surface mines in over-wintered leaves of *Hepatica nobilis*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza ranunculicola Hering, 1949

Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus acris* and *R. bulbosus*. Pupation takes place inside, under the upper epidermis.

Phytomyza albifrons Groschke, 1957

Isopyroideae: Thalictreae. Upper–surface leaf mines in *Thalictrum aquilegifolium*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza thalictricola Hendel, 1925

Isopyroideae: Thalictreae. Upper–surface leaf mines in *Thalictrum flavum*. Larva leaves the mine through an upper leaf surface, pupating in the ground. New to Belarus: Ritshany environs, 55º41'N, 26º41'E, 25.06.1985, larvae in *T. flavum*, 2 females emerged.

Phytomyza aquilegiae Hardy, 1849

Isopyroideae: Isopyreae and Thalictreae. Upper–surface leaf mines in *Aquilegia vulgaris, Thalictrum aquilegifolium, T. flavum, T. lucidum*

and *T. minus*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Phytomyza subrostrata Frey, 1946

Helleboroideae: Trollieae. Larvae feed in flower heads and peduncles of *Trollius europaeus* as well as mine a stem or petiole internally (cf. Pakalniškis, 1998b), pupating in stem (petiole) hole.

Phytomyza ? platonoffi Spencer, 1976

Helleboroideae: Trollieae. Upper–surface mines in lower parts of stem and petiole of *Trollius europaeus*. Pupation takes place in the ground. Lithuania: Agailės, 56º06'N, 22º54'E. A male is lacking for confirmation.

Phytomyza soenderupiella Spencer, 1976

Ranunculoideae: Anemoneae. Larva feeds in a stem of *Pulsatilla pratensis*, no more particularities are known. Only imagines have been found in Lithuania (Pakalniškis 1998c).

Phytomyza clematidis Kaltenbach, 1859

Ranunculoideae: Anemoneae and Ranunculeae. The species was described from flower heads and peduncles of *Clematis vitalba*, and further found (Pakalniškis 1995) feeding on *Ranunculus acris, R. auricomus, R. lanuginosus* and in all over-ground organs of *R. lingua*. Pupation takes place in mine, in stem hole (most usually) or in the ground (rarely).

Phytomyza murina Hendel, 1935

Isopyroideae: Thalictreae. Larva feeds in a seed capsule of *Thalictrum minus*, pupating internally, and *P. fennoscandiae* Spencer, 1976 is a junior synonym of this species very likely (Pakalniškis 2000).

Phytomyza enigmoides Hering, 1937

Ranunculoideae: Ranunculeae. Larva forms primary surface stems mine in *Ranunculus cassubicus*, than mines it internally, pupating in stem hole (Pakalniškis, 1998b).

Phytomyza albipennis Fallén, 1823

Ranunculoideae: Ranunculeae. The first host plant established. Larva forms primary surface stem mine in *Ranunculus acris*, than mines it internally, pupating in stem hole.

Phytomyza evanescens Hendel, 1920

Ranunculoideae: Ranunculeae. Larva forms primary surface stem mine in *Ranunculus acris* and *R. lanuginosus*, than mines it internally, pupating in stem hole.

Phytomyza nigritula Zetterstedt, 1838

Ranunculoideae: Ranunculeae. Larva forms primary surface stem mine in *Ranunculus acris, R. cassubicus* and *R. lanuginosus*, than mines it internally, pupating in stem hole.

Phytomyza notata Meigen, 1830

Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ranunculus repens*. Pupation takes place in the ground. Also 3 further *Ranunculus* species are known (Spencer, 1976) being hosts of this species.

Phytomyza stolonigena Hering, 1949

Ranunculoideae: Ranunculeae. Upper–surface mines in leaves and petioles of *Ranunculus lanuginosus* and *R. repens*. No specimens were reared after description. Only mines have been found in Lithuania (Ostrauskas et all., 2003) as well.

Phytomyza ranunculi (Schrank, 1803)

Ranunculoideae: Ranunculeae. Upper–surface leaf mines in *Ficaria verna* (new host plant established), common on *Ranunculus acris, R. auricomus, R. bulbosus, R. flammula, R. lanuginosus, R. lingua, R. repens* and *R. sceleratus*. Larva leaves the mine through an upper leaf surface, pupating in the ground. The species feeds also on *Myosurus* occasionally (Spencer, 1999).

Phytomyza caulinaris Hering, 1949

Ranunculoideae: Ranunculeae. Upper–surface stem mines in *Ranunculus acris*. Pupation takes place in the ground.

Phytomyza jonaitisi Pakalniškis, 1996

Isopyroideae: Thalictreae. Internal mines in petiole of *Thalictrum aquilegifolium*. Pupation takes place in the stem hole (Pakalniškis, 1998b).

Phytomyza minuscula Goureau, 1851

Isopyroideae: Isopyreae and Thalictreae. Upper–surface leaf mines in *Aquilegia vulgaris*, *Thalictrum aquilegifolium, T. flavum, T. lucidum* and *T. minus*. Larva leaves the mine through an upper leaf surface, pupating in the ground.

Calycomyza subapproximata (Sasakawa, 1955)

Isopyroideae: Thalictreae. Internal stem mines in *Thalictrum flavum, T. lucidum* and *T. minus*.

Pupation takes place in stem hole (Pakalniškis, 1998b).

Agromyzinae

Ophiomyia ranunculicaulis Hering, 1949

Ranunculoideae: Ranunculeae. Upper–surface stem mines in *Ranunculus acris* and *R. lanuginosus.* Pupation takes place in mine, under epidermis.

Ophiomyia aquilegiana Lundquist, 1947

Isopyroideae: Isopyreae and Thalictreae. Upper–surface stem mines in *Aquilegia vulgaris, Thalictrum aquilegifolium, T. flavum* and *T. minus*. Several petiole mines were detected, too. Pupation takes place in mine, under epidermis.

Ophiomyia definita Spencer, 1971

Isopyroideae: Thalictreae. The first host plant established. Larvae form inconspicuous surface stem mines in the finest upper branches of *Thalictrum minus,* pupating in mine, under epidermis. Puparium is pale brown to shiny–black, with 4 (rarely 3 to 7) bulbs on each posterior spiracle. *O. sueciae* Spencer, 1976 is a junior synonym of this species (Scheirs et all., 2000).New to Lithuania: Gerdašiai, 53°58'N, 23°53'E, puparia collected 05.08.1997, and 1 male emerged; puparia 18.05.1998, 1 female emerged; puparia 20–28.08.1998, 3 females and 3 males emerged. Kalviai, 55°05'N, 23°21'E, 1 male swept 28.05.1992; puparia 20.06.1999, 1 female emerged. Merkinė, 54°10'N, 24°11'E, puparia 04.04.1999, 1 male emerged. Ražiškiai, 54°48'N, 23°54'E, puparia 28.06.1999, 1 female and 1 male emerged.

Ophiomyia ivinskisi Pakalniškis, 1996

Isopyroideae: Thalictreae. Upper–surface stem mines in *Thalictrum flavum, T. lucidum T. minus*, usually hidden under a leaf stalk base. Pupation takes place in mine, under epidermis.

Discussion

Calycomyza subapproximata represents a poorly investigated species group characteristic by darker coloration and was confirmed (Pakalniškis, 1998b) to mine stems internally, whereas the rest species of genus with known biology are leaf miners on Asteraceae predominantly. The phylogeny of genus stays indefinite.

Majority of species groups of *Ophiomyia* have representatives on Fabaceae, also species most resembling other genera are known there. That shows a later origin of this 'supergenus', thus *Ophiomyia* miners are secondary on Ranunculaceae, and no pair of species is truly monophyletic here.

Inside the rather archaic Magnoliopsida class only Ranunculidae (and Ranunculaceae namely) are colonised by numerous *Phytomyza* species. There are known by one *Phytomyza* species feeding on relate subclasses Magnoliidae and Hamamellididae, and no species on most relate Caryophyllidae (cf. Spencer, 1999).

Thus the only probable candidates to be primary Ranunculaceae miners are *Phytomyza* species (no *Napomyza* feed on this family plants). Trying to reconstruct a phylogeny of feeding behaviour of these species, such tendencies or stages manifest them self:

1) larva mines the leaf blade pupating in the ground (as a rule) or internally (*P. anemonantheae, P. actaeae, P. anemones, P. clematidis* (in a leaf of *Ranunculus lingua*), *P. fallaciosa, P. ignota* (occasionally), *P. palionisi, P. ranunculicola, P. rydeni*);

2) puparium has posterior spiracles widely protuberant and stays to hang in the exit hole (*P. ranunculivora*), that is characteristic for some non related species of aquatic environment (Spencer, 1990); another way is to adhere puparium to the leaf blade as it does *P. linguae*;

3) larva mines the leaf blade and petiole (leaf–stalk) like *P. stolonigena*;

4) larva mines the petiole internally, pupating therewith (*P. subrostrata*) or in the stem hole (*P. jonaitisi*);

5) larva mines the stem surface, pupating in the ground (*P. caulinaris*);

6) larva forms up to 10 cm long linear, down stretching surface mine in the upper part of stem, which usually has a spiral shape, later mines the stem internally and pupates therewith (*P. albipennis, P. enigmoides, P. evanescens, P.*

nigritula);
7) larva eats the seed–buds (*P. murina, P. subrostrata*) and later mines peduncle (flower-stalk) and a part of stem internally (*P. clematidis, P. subrostrata*).
The stem mining in *Phytomyza* on Ranunculaceae is secondary most probably, because the oldest forms of this family, very scantly represent in tropics, are shrubs and lianas, and the leaf–blade, leaf–midrib or petiole mining could be modified to the stem–rind mining and to the internal stem–pith mining consequently in further herbaceous forms only.
The feeding behaviour of many *Phytomyza* species is definite, but *P. subrostrata* can mine generative organs as well as petiole and stem internally (Pakalniškis, 2000). *P. clematidis* feeds in flower–buds, blossoms and mines internally the stem of *Clematis vitalba* (cf. Kaltenbach, 1859), *Ranunculus acris, R. lanuginosus* and *R. lingua* (cf. Pakalniškis, 1995). On the next host it mines leaf blades as well. If larva finds the leaf axle in its way, it moves along the petiole internally to reach a bud.
Some competition exists among the blossom miners, and species colonize different plants. So *Phytomyza murina* is closely relate to further European species confirmed to feed (Rougemont, 1912; Hering, 1949) within the blossoms and seed capsules of *Anemone* (*P. franzi* Hering, 1944), *Aquilegia* (*P. krygeri* Hering, 1949) and *Thalictrum aquilegifolium* (*P. thalictri* Escher–Kündig in Rougemont, 1912).
Hosts of four further relate species are as follows: *Ranunculus acris* (*Phytomyza albipennis, P. evanescens*), *R. cassubicus* (*P. enigmoides*), *R. lanuginosus* (*P. evanescens*). But *P. nigritula* was found in stems of all three *Ranunculus* species.
The *Ophiomyia* species mine different parts of stem of *Thalictrum minus*. Blossom mines of *O. ivinskisi* are findable in the lower parts, *O. aquilegiana* mines the upper part (and leaf stalks occasionally), and larvae of *O. definita* mine the thinnest branches.
The species of the same *Phytomyza ranunculi* species group mine leaves of *Ranunculus* spp. (*P. notata, P. ranunculi*), leaves and petioles consequently (*P. stolonigena*) or stems only (*P. caulinaris*).
Closely related species feed on comparatively remote hosts or different plant organs often. Any competition for food resources is practically unlikely possible among the leaf miners; it comes out through the highest trophic chain – the Hymenoptera parasitoids (Jonaitis, Pakalniškis, 2000). A change of host plant usually means an accidental change of biotope and some possibility to escape the specific parasitoids. Some effect also cold result a cardinal change of the feeding behaviour on the same host plant.

References

Beiger M. 1980. Studies on mining insects of the Tatry National Park. 11. Materials concerning the morphology, taxonomy and systematics of some *Phytomyza* Fallén species (Diptera, Agromyzidae). – Bull. Soc. Amis Sci. et lettres Poznań. Ser. D, 20: 135–143.

Hering E.M. 1949. Neue palaearktische Agromyziden. – Notul. ent., 29: 18–32.

Jonaitis V., Pakalniškis S. 2000. Long–term dynamics of biocenotic relations of insects. In: Jonaitis V. (ed.) The Inter–Ecosystematic Relationships of Insects and Their Dynamics. Institute of Ecology. Vilnius: 227–238.

Kaltenbach J.H. 1859. Die deutschen Phytophagen aus der Klasse der Insecten (C). – Verh. natur. Ver. preuss. Rheinl., 16: 216–299.

Ostrauskas H., Pakalniškis S., Taluntytė L. 2003. The species composition of plant mining dipterans (Insecta: Diptera) of greenhouse surroundings in Lithuania. Ekologija, 3: 3-11.

Pakalniškis S. 1994. The Lithuanian Agromyzidae (Diptera). Descriptions of 6 new species and other notes. – Acta entomologica Lituanica, 12: 5–34.

Pakalniškis S. 1995. Addition to the fauna list of Lithuanian Agromyzidae (Diptera). - In:

New and Rare for Lithuania Insect Species. Records and Descriptions of 1994–1995. Vilnius: 177–182.

Pakalniškis S. 1996a. On the bionomics and knowledge of Agromyzidae (Diptera) feeding on plant stems. – Ekologija, 3: 19–24.

Pakalniškis S. 1996b. The Lithuanian Agromyzidae (Diptera). Descriptions of 4 new species and other notes. - In: Lietuvos entomologų darbai (Lietuvos entomologų draugijos 30–mečiui). Vilnius: 17–34.

Pakalniškis S. 1998a. Interesting Agromyzidae finds in Lithuania. – Ekologija, 1: 18–23.

Pakalniškis S. 1998b. On the bionomics and knowledge of Agromyzidae (Diptera) feeding on plant stems. Report 2. – Ekologija, 2: 36–42.

Pakalniškis S. 1998c. Agromyzidae (Diptera) species new to Lithuania and neighbouring countries. – Acta Zoologica Lituanica, 8, 3: 73–80.

Pakalniškis S. 2000. New data on the bionomics and distribution of Agromyzidae (Diptera) with the description of a new species. – Acta Zoologica Lituanica, 10, 1: 59–62.

Rougemont F. de, 1912. Détails biologiques sur la Phytomyza de Thalictrum. – Mitt. schweiz. ent. Ges., 12: 82–87.

Scheirs J., De Bruyn L., Tschirnhaus M. von 2000. Redescription of Cerodontha mellita Spencer and Ophiomyia definita Spencer (Diptera Agromyzidae). – Faune de Belgique, 136: 79–84.

Spencer K.A. 1976. The Agromyzidae (Diptera) of Fennoscandia and Denmark. – Fauna ent. scand., 5, 1–2: 1–606.

Spencer K.A. 1990. Host Specialization in the World Agromyzidae. – Ser. ent., 45: 1–444.

Received: October 31, 2003.