

The Agromyzid Fauna of Iceland and the Faroes, with Appendices on the *Phytomyza milii* and *robustella* Groups (Diptera, Agromyzidae).

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Introduction.

Six species of Agromyzidae identified by Professor E. M. Hering were recorded for Iceland in Professor Carl H. Lindroth's "Insektenfauna Islands" (1931). Subsequently Rydén (1953) published a brief paper which altered one of the earlier identifications, and gave his own identifications of some twenty specimens in the Zoological Museum, Copenhagen. Nielsen, Ringdahl and Tuxen's (1954) volume on the Diptera in the Zoology of Iceland series contains summaries of Hering's and Rydén's records, but no new information apart from a record of mines found on *Ranunculus*. In the course of this work I have found that a number of Rydén's records require correction.

Last year (1962) the Lund University Expedition to Iceland, led by Professor Lindroth, brought back about 160 further specimens, mostly from the Skaftafell area in South-East Iceland. Mr. Hugo Andersson of Lund University Museum kindly made this material available to me for study.

The only previous published records of Agromyzidae from the Faroes refer to three species. *Phytomyza ranunculi* Schrank was recorded by Hansen (1881)* (as *flavoscutellata* Fallén), and having seen his specimens in the material sent me from Copenhagen I can confirm that his records are correct. Becker (1915) recorded further specimens of this species and added "*Phytomyza pullula* Zetterstedt" and "*P. obscurella* Fallén". Neither of the last two records is however acceptable as it stands. According to Hendel (1931-6) the name *pullula* Zett. was used for *P. tenella* Meigen and *P. ranunculi* Schrank form *praecox* Meigen. The several records of "*P. obscurella* Fall." can hardly refer to the monophagous species on *Aegopodium* for which the name is now used, as that plant is a rare introduced weed on the Faroes. In view of these doubts about the identifications I cannot accept the records of these species. Becker's specimens (also at Copenhagen) are in very poor condition and the only identification I was able to confirm was that of an example of *P. ranunculi* Schrank (which he called *flavoscutellata* Fall.).

However there is a large additional material of Faroese Agromyzidae (over 160 specimens) in the Zoological Museum, Copenhagen, which Mr. Leif Lyneborg was kind enough to allow me to study. Although this material mostly dates from 1926 it has not previously been determined.

The study of the Agromyzidae has been perplexed in the past by the inadequacy of the external morphology to characterise the species of many groups. Many species were recognised as distinct from their life-history, but the external differences given in the keys to the adults were not sufficiently clear-cut to enable caught material to be identified with accuracy. Consequently there are numerous inaccurate identifications of caught specimens in the literature and it is very difficult to have any

*) Hansen also gives "*Agromyza vagans* Fallén", but according to Hendel (1931-6) this name refers to a *Meoneura* sp. (*Milichiidae*). The specimen in question is no longer identifiable.

confidence in records not based upon bred material. Fortunately this situation can be remedied, as the male genitalia give excellent specific and generic characters. Their paramount importance has been clearly demonstrated by Nowakowski (1962) in his "Introduction to a systematic Revision of the Family Agromyzidae". I agree fully with that author that "an immediate task for specialists is to describe carefully and methodically and give figures of the male genitalia of all known species of the Agromyzidae". In order to leave no doubt about the identity of the species recorded in this paper, it has been necessary to figure at least the aedeagus of all species of which males were available. In many cases I have dissected the holotype (if male) or paratypes of the species concerned. Only by this means was it possible to track down some species in difficult groups, such as *Phytomyza evanescens* Hendel, *P. archangelicae* Hering, *P. opacella* Hendel and *P. taraxacoecis* Hering.

Although nearly all the material recorded in this paper was caught, the life-history of most of the species is known, and the species which have not been bred are all closely related to species of known life-history. Having regard to the limited flora of Iceland and the Faroes I have been able to suggest the probable life-history of all these unbred species, and I will be surprised if any of these conjectures prove mistaken. I would emphasise that the assessment of relationship which these conjectures involve has been made possible entirely by examination of the male genitalia, which give excellent group as well as specific characters. The key to *Phytomyza* based on external characters given in Hendel's (1931-6) monograph and subsequently expanded on many occasions does not always reflect natural relationship, as the external characters are remarkably uniform in many groups of *Phytomyza*, and it was not possible to break the genus down into natural groups using these characters. But study of the genitalia allows the genus to be divided along much more natural lines, and the life-history of many of the unbred species can be reasonably conjectured from the group relationship which can be established by this means.

This paper includes an essay on the significance and probable origins of the Icelandic and Faroese Agromyzid fauna. The Diptera have generally not featured prominently in zoogeographical work for two reasons: (i) the published records for many

groups are few and often unreliable, and (ii) their powers of active dispersal and the possibility of involuntary dispersal by wind or convection currents make them less satisfying subjects for zoogeographical study than earth-bound forms (such as many of the Carabidae (Coleoptera) which figure so prominently in Professor Lindroth's work). On the first point there is absolutely no reason for inaccuracy in identifying Agromyzidae provided that the male genitalia are examined, and I hope that the figures with this paper will leave future workers in no doubt about the identity of the species before me. The question of dispersal is however more difficult, and I have set out my views later in this paper. In the case of the Agromyzidae the close host-association acts as a further check against conclusions drawn from the distribution of the flies, particularly when, as in the case of Iceland, the origins of the flora of an area have been studied in detail (see Steindorsson, 1962).

In the course of this work I have had cause to investigate several difficult groups, and have therefore figured the aedeagus of a number of other species besides those represented in the Icelandic and Faroese material. For instance I dissected five other species of the *robustella* group of *Phytomyza* before finally discovering that the Faroese male belonged to *P. taraxacocecis* Hering. The results of this latter investigation have been included as Appendix II of this paper.

Location of Material.

The Faroese material all belongs to the Zoological Museum, Copenhagen, apart from a few duplicates retained by the author. Most of it was collected by J. P. Kryger in 1926.

The majority of the Icelandic material was collected by the Lund University Expedition in 1962 and belongs to the Zoological Institute at Lund University, Sweden (apart from a few duplicates retained by the author). The earlier Icelandic material of six species included in Lindroth's "Insektenfauna Islands" (1931), which includes all the three specimens of *Liriomyza richteri* Hering, belongs to the Göteborg Natural History Museum. Other material collected by Tuxen, Jørgensen, Gigja, Heding, Spärck, Cloudsley-Thompson and Böcher belongs to the Zoological Museum, Copenhagen.

In quoting the records of each species I have omitted the col-

lector's name in the case of Kryger's 1926 Faroese material and the 1962 material brought back by the Lund University Expedition to Iceland (these two sources representing the bulk of the material), but have indicated material from other sources by the collector's name or otherwise.

Summary of Records and taxonomic Comment.

Agromyza ?nigrociliata Hendel, 1931.

Faroes — 2 ♀♀, Sandur, 13. vii. 26.

These two specimens are the only Agromyzinae in the material before me. I cannot be completely certain of the identity of the species as the group to which they belong, the *ambigua* group, is in need of comprehensive revision.

Specimens attributed to *A. nigrociliata* Hd. are very common in northern Europe, and I expect that the Faroese species, when more material including males can be obtained, will prove identical with a European species. In view of the uncertain identification I have generally omitted reference to this species in the discussion on the origin of the Agromyzid fauna later in this paper.

Petersen (1956) records a single example of *Dacnusa eros* Nixon (Hym. Braconidae) from Norðfjörður in East Iceland. This species is known to me as a parasite of the larvae of *A. nigrociliata* Hd. in England, so that its occurrence in Iceland can only suggest that this or a related *Agromyza* species will be found there.

Ecology. The larvae of all members of the *ambigua* group are leaf-miners on Gramineae.

Cerodontha (Dizygomyza) lindrothi sp. nov.

Greenland — Holotype ♂, Eqaaluit-landet (Julianehaab), 16. vii. 48 (leg. Vibe);
2 ♂♂ paratypes, Julianehaab, Frederiksdal, 30. vi. 48 (Vibe);
♀ paratype, Hekla Havn, 24. vii. 1892 (leg. Deichmann).
N. Iceland — Paratype ♂, Mælifell, Skagafjarðarsýsla, 13. vi. 33 (leg. Tuxen).
S.E. Iceland — Paratype ♂, Skaftafell, 22. vii. 62.

External Morphology. Frons parallel-sided, twice as wide as an eye. In profile (fig. 23d) the orbits are very broadly visible above the eye; cheeks only narrowly visible around the eye; jowls about $\frac{1}{4}$ of the eye-height in their middle. All four orbital bristles are of about the same length. Orbital setulae very few, near the bases of the lower orbital bristles. Male antennae (fig. 23d)

with the 3rd segment very much enlarged and clothed in dense white hairs. The arista is conspicuously flattened in its basal $\frac{1}{3}$ to $\frac{1}{2}$. The female antennae are similar in appearance to those of the male, but are somewhat smaller: as in the male the arista is obviously swollen basally.

Dorsocentrals (3+1) decreasing in length forwards. Acrostichals in 4 regular rows reaching the hind dorsocentral. About 9-10 postsutural intra-alar hairs in roughly three rows.

Wing not significantly different from that figured by Hendel (1931-6) for *luctuosa* Meigen, the 3rd and 4th costal segments being of about equal length, in a ratio of 3.0—3.5 with the 2nd segment. Last segment of m_{3+4} about the same length as the penultimate. The r-m cross-vein lies a little beyond the middle of the discal cell.

Wing-length 2.2—2.3 mm.

Colour. Predominantly black. Mesonotum grey dusted over a strong black subshine. Legs dark except for the yellow tips of the front femora. Squamal fringe dull white or ochreous.

♂ genitalia (figs. 23 a-c). The aedeagus is very close to those of the European *C. (D.) luctuosa* (Meigen) and *C. (D.) effusi* (Karl) (figured by Nowakowski, 1959, figs. 66—67), but differs obviously in that the distiphallus in lateral view is less sinuate. In ventral view the degree of divergence of the tubules of the distiphallus is intermediate between that figured for *luctuosa* and *effusi*. The ejaculatory bulb (fig. 23 c) is larger and more strongly sclerotised than in those species.

Dr. J. T. Nowakowski, who is working on a monograph of the European species of *Cerodontha*, has confirmed that this species is not known to him from Europe. He states (personal communication) that "nach Genitalien steht sie neben *luctuosa*, äusserlich dagegen ähnelt den europäischen Vertretern der *crassiseta*-Gruppe". If the only female before me is typical, the sexual dimorphism of the antennae is much less than in *luctuosa*, because of the acquisition by the female of enlarged antennae approaching those of the male, bearing a conspicuous fringe of hairs around the 3rd segment.

The genitalia of all five males were examined.

I am pleased to dedicate this species to Professor Carl H. Lindroth in recognition of his work on the fauna of the North

Atlantic Islands. All the material belongs to the Zoological Museum, Copenhagen, except for the Skaftafell specimen, which is among the material brought back by the Lund University Expedition. The paratype from Mælifell, Iceland, was previously recorded by Rydén (1953) as "*Dizygomyza luctuosa* Meig."

Ecology. The Skaftafell specimen was taken according to Mr. Andersson's notes "on the heath with *Carex capitata* L., *C. nigra* (L.) Reichard, *C. saxatilis* L., *Juncus balticus* Willd. and *Salix phylicifolia* L.". The first four are all possible hosts. I do not know the details of the other captures.

***Cerodontha (Dizygomyza) ? caricicola* Hering, 1926.**

Faroes — ♀ Mýrarnar, near Vestmanna, Streymoy, 23. vi. 26 (350—375 metres):
♀ Tórshavn, Streymoy, 27. vi. 26.

Dr. J. T. Nowakowski has kindly examined these two females and states (personal communication) that they belong to the "Überart *morosa* Meigen"; although it is not possible to give a certain identification on the basis of the females only, he considers that the species is very probably the common European *C. (D.) caricicola* Hering.

***Liriomyza richteri* Hering, 1927, Dtsch. ent. Z., 47: 157—8.**

S. Iceland — ♀, Gröf (Skaftártunga), 27. vi.; ♀, Þórsmörk, Húsadalur, 13. vi.
S.E. Iceland — ♂, Skaftafell, 30. vi.

Designation of lectotype. Hering (1927) in his original description designated a pair of specimens as the "types" of this species. These were taken on 17. vii. 26 at Renntierinsel, near Alexandrowsk, on the Murman Coast of Arctic Russia. In accordance with Article 74(a) of the 1961 International Code of Zoological Nomenclature, I formally designate the male as lectotype, and have labelled it accordingly. Its genitalia are figured at figs. 1 a-c. This action is in accordance with Professor Hering's wish (personal communication).

The three Icelandic examples of this species were recorded in Lindroth (1931) and no further material has been taken. I am satisfied that the genitalia of the Icelandic male are identical with those of the lectotype. Both the lectotype and the Icelandic specimens have a yellow third antennal segment, in conformity with the original description, which reads: "Fühler ganz gelb, das dritte Glied rund, am Oberrande normal rein gelb, ohne

Schwärzung." Hendel's (1931-6) key is misleading as this species is included with those with a darkened third antennal segment — he states that the description was based on the ♀ syntype, which, he says, has a darkened third antennal segment. Rydén's records from Sweden also refer to a species with conspicuously darkened antennae, which he took widely in Sweden from Skåne province to Torne Lappmark. I have examined this material and dissected two males. Their distiphallus is somewhat differently shaped and I consider that they belong to another species.

This species belongs to the *flaveola* group, characterised as well as on genital characters by the colour of the femora. The group needs revision, and it is clear that the name *Liriomyza flaveola* Fallén has been widely used for more than one species. It is possible that other material of *L. richteri* Hg. exists which has been confused with related species, so that it would be unwise to place much emphasis on the restricted known distribution. But pending a revision of the *flaveola* complex I am only prepared to accept the holotype and the Icelandic specimens as certainly *richteri*.

Ecology. Lindroth (1931) gives details of the localities where the Icelandic specimens were captured. Two were taken on pasture and meadowland; the capture of the third on birch (*Betula* sp.) was no doubt fortuitous. The life-history is unknown, but the larvae may be expected to be leaf-miners on Gramineae, like other members of the *flaveola* group.

***Phytomyza angelicae* Kaltenbach, 1874.**

S.E. Iceland — 4 ex. from larvae in mines on *Angelica sylvestris* L., Skaftafell, 30. vii. 62, adults emerged 18. ii. 63, 26. ii. and 9. iii. (2 ex.).

The genitalia (figs. 2 a-c) of an Icelandic male agree with those of Southern English material. Mr. Andersson has also sent me the pressed mines, which are typical of this species.

***Phytomyza archangelicae* Hering, 1937, Blattminen M.-und N.-Europas: 566.**

Phytomyza nilssoni Rydén, 1956, Opusc. Ent., 21: 199—200. **Syn. nov.**
Faroese — 3 ♂♂ 4 ♀♀, Kirkjubøur and Kirkjubøholtur, Streymoy, 3. vi. 26.

The genitalia (figs. 3 a-c) of two Faroese males were examined and compared with those of a male bred by Dr. H. Buhr from *Angelica archangelica* L. at Neuhaus, Mecklenburg, Germany,

emerged 6. vii. 36 (one of the series which includes the holotype); they appear completely identical. Rydén's *Phytomyza nilssoni* is also identical according to the genitalia (I have dissected the holotype ♂, labelled "Abisko*, Torne Lappmark", emerged 11. viii. 54 from larva in *Angelica archangelica* L.). Rydén's specimens were considered to be distinct as they all possess four dorsocentral bristles, as in most Phytomyzinae. The typical series of *P. archangelicae* Hg. lack the second (counting from front to back — the third if one counts in the opposite direction in Hendel's fashion) dorsocentral. I consider that the identical form of the aedeagus almost certainly indicates that the two series are conspecific, as there is considerable variation in the aedeagus of different species in the Umbelliferae-feeding species of *Phytomyza*; furthermore Professor Hering informs me that one female of his original series has four dorsocentrals on one side only. The Faroese examples all have four dorsocentrals but there is some variation in their position.

It is however possible that the loss of the second dorsocentral in most of the typical series may be a character found in only part of the species' range, in which case the name *nilssoni* might be retained as a subspecific name for the northern (and Faroese) population which lack this feature. But I cannot consider the existing material from only four localities sufficient to establish a subspecific distinction of this kind.

Hering (1956) described the larva of *P. nilssoni* Ryd. from the typical locality — Abisko — and concluded that in larva and in mine this species was "extraordinarily similar" to his *P. archangelicae*. The only difference found — 24-28 bulbs on the hind spiracles for *nilssoni* as against 20-22 for *archangelicae* — may be no more than individual variation, and requires checking on a more numerous material.

*) The type locality given in Rydén's (1956) original description is Kopparåsen, not Abisko (both localities are in Torne Lappmark). I cannot be certain whether the published description or the labelling is in error. Three paratypes of *nilssoni* which I have also seen are in fact labelled "Kopparåsen". But, as the Abisko specimen is clearly labelled as the type and the emergence date accords with the description, I prefer to take Abisko as the type locality and consider that Kopparåsen was named in the published description through oversight.

Phytomyza atricornis Meigen, 1838.

- Faroës — ♂♀, Tórshavn, Streymoy, 19. vii., 22. viii. 26; ♂, Kirkjubøur, Streymoy, 27. vii. 26; ♂♀, Nólsoy, 26. vii. 26; ♂, Svinoy, 16. viii. 26.
- S.E. Iceland — 4 ex., Skaftafell, 30. vi. (see Lindroth, 1931); 2 ♂♂, Skaftafell, 19. and 22. vii. 62; ♂, Hornafjörður, 12. viii. 62; 36 ex., Bæjarstaðaskógur, 3. viii. 62.
- S. Iceland — 1 ex., Hnauсар (Meðalland), 18. vii. (see Lindroth, 1931).
- N. Iceland — ♂, Skiðastaðalaug, Skagafjarðarsýsla, 27. vii. 33 (Tuxen).
- Note: The other records for N. Iceland given by Rydén (1953) refer to *P. tenella* Meigen.

The genitalia of this species are figured as figs. 4 a and 4 b. Ecology. I agree with Hering's view (in Lindroth, 1931) that the main host of this species in localities such as Skaftafell is probably *Taraxacum*. However there are other plants which this species might be expected to attack, such as *Leontodon autumnalis* L., which was growing at Bæjarstaðaskógur, or various Cruciferae. Bæjarstaðaskógur, where this species was taken in numbers, is a locality with hot springs, and so is Skiðastaðalaug.

Phytomyza evanescens Hendel, 1920.

- Faroës — 5 ♂♂ 15 ♀♀, Tórshavn, Streymoy, meadow with *Caltha*, 14. vi. 26; ♂, Bø near Tórshavn, Streymoy, 25. vi. 26; 2 ♀♀, Stykkið, Streymoy, 19. ix. 25; 3 ♂♂ 4 ♀♀, Lorvik, Eysturoy, 29. vi. 26.

The genitalia of a Faroese male are figured at figs. 5 a-f. In investigating the identity of this species I also examined males from the following localities:

- Holotype ♂, Ragusa, Dalmatia, 19. v. (Naturhistorisches Museum, Wien)
- Berisal, Valais, Switzerland, 1. viii. 56 (K. A. Spencer)
- Stupsk (formerly Stolp), Pomerania, Poland, 28. vi. 24 (Warsaw Zoological Institute)
- München, Bayern, Germany, v. 1870 (Naturhistorisches Museum, Wien)
- Ulricehamn, Västergötland, Sweden, 8. vi. 46 (Rydén's collection, Lund)
- Mullhyttan, Närke, Sweden, 25. vii. 52 (" " ")
- Björkliden, Torne Lappmark, Sweden, 26. vi. 54 (" " ")

The genitalia of this species show several interesting features. In many Agromyzidae the last tergite before the epandrium (or 9th tergite) is a fused tergite, which is considered (see Hennig, 1958) to consist of tergites 6—8. In *P. evanescens* however a narrow additional tergite is present immediately before the epandrium (fig. 5 e). I consider that this should provisionally be called tergite 8, and the preceding tergite 6+7. It is clear that this

small tergite 8 belongs to the groundplan of the Agromyzidae as it occurs in a number of disjunct groups including *Melanagromyza* (Agromyzinae) and *Cerodontha* subgenus *Dizygomyza*. However the lateral extensions of this tergite in *Phytomyza evanescens* are probably secondary, associated with the development of other appendages around the genitalia. In most *Phytomyza* species the 8th tergite is fused with the preceding tergite 6+7 (for instance in *P. milii* Kaltenbach and the *obscura* group s.l.), but a separately developed tergite 8 is retained by *P. cineracea* Hendel and *P. opaca* Hendel.

A very striking character of the Faroese males are the enormously elongate surstyli which project beneath the abdomen. The surstyli are of some taxonomic interest, particularly in *Liromyza* Mik and related genera, and I was tempted at first to suppose that this character was very significant. But in fact the presence of the surstyli is not constant within this species. The Ulricehamn (Sweden) and Munich males completely lack this feature and the holotype ♂ is an intermediate form having only small surstyli (fig. 5g). The presence of the swelling with long hairs on the epandrium near the base of the surstyli is linked with the development of the surstyli, as the examples which lack the latter lack this feature too.

Another variable feature is the hypandrial apodeme, which is developed into an elongate appendage (as in fig. 5d) in some specimens but absent in others.

In contrast with these variable characters of the surrounding appendages the aedeagus itself is perfectly constant in form, and shows that this species is very closely related to *P. cineracea* Hendel, a species whose larvae feed in *Ranunculus* stems.

It is possible that the striking variation in the peripheral characters of the male genitalia can be used, when more material is available, to demonstrate geographical races of this species. At least in the Faroese material — the only series available from the same locality — the development of the surstyli is constant. Ecology. The life-history of *P. evanescens* Hendel is not known, but the fact that the species was swept in numbers in a "meadow with *Caltha*" on the Faroes, and is very closely related to *P. cineracea*, convinces me that the larvae should be sought in the stems or roots of *Caltha*.*

*) See next page.

Phytomyza fallaciosa Brischke, 1880, Blattmin. Danzigs: 6.*Phytomyza mimica* Hering, 1928, Zool. Jahrb., Abt. Syst., 55: 573.*Phytomyza pseudohellebori* Hendel, 1936, Flieg. pal. Reg., 59: 459. **Syn. nov.**

Faroes — 6 ♂♂ 7 ♀♀, Tórshavn area, Streymoy, 14. vi. 26 (1 ♀), 14—24. vii. 26 (11 ex.), 26. viii. 26 (1 ♀); ♂, Kirkju, Fugloy, 13. vi. 26; ♀, Lorvik, Eysturoy, 29. vi. 26.

S.E. Iceland — 4 ex., Skaftafell, 18—19. vii. 62; 1 ♂, Bæjarstaðaskógur, 3. viii. 62.

The synonymy of *P. mimica* Hering was made by Hering (1957). Having examined the genitalia of the type ♂ (bred from *Ranunculus repens* L., Gartz (Oder), emerged 19. vi. 24 (Hering 3430)), I agree with this synonymy. *Phytomyza pseudohellebori* Hd. is also synonymised following my examination of the genitalia of the type ♂ (Curland, Libau). Mr. K. A. Spencer tells me that he had previously formed this same opinion from study of the external characters. I have also examined males of this species from Poland, Finland (Hoplax) and southern England (bred from *Ranunculus repens* L. and *R. acris* L.). The genitalia of a Faroese specimen are shown at figs. 6 a-d.

Ecology. The four Skaftafell specimens were taken in places where *Ranunculus acris* L., a known larval host-plant, was growing — the description of the localities which Mr. Andersson has supplied me reads "cliffs with small stream" (1 example taken), "under rock with dripping water and very small pool" (1 example taken), and "meadow slope with rich vegetation" (2 examples taken). This is a very hardy species which in southern England shows marked aestivation — after the first generation larvae in May or June, no further larvae are found until October and November.

Phytomyza hedingi Rydén, 1953, Ent. Medd., 26: 467-8.

N.W. Iceland — Type ♀, Arngerðareyri, Isafjarðardjúp, 12. viii. 33 (Heding).

The difference given by Rydén (in a correction note issued in 1954 to his 1953 paper) that *P. penicilla* Hendel has "r₅ im ganzen allmählich zurückgebogen, an der Mündung gerade", but

*) (page 403) *Phytomyza soenderupi* Hering, which was bred from the leaf-stalks of *Caltha*, does not belong to the *cineracea* group, but appears related according to the genitalia to *P. opaca* Hendel, an alpine species of unknown ecology. An interesting difference between the two species is that *P. opaca* Hd. retains the separate 8th tergite, but in *P. soenderupi* Hg. this is fused with tergite 6+7.

P. hedingi "r₅ gerade", is completely imaginary. However I have provisionally listed *hedingi* as a good species particularly as the known host plant of *penicilla* — *Lactuca serriola* L. — does not occur on Iceland. Only when the male is obtained will it be possible to check if Rydén's species is a good one.

Phytomyza milii Kaltenbach, 1864. *Phytoph.* 21: 248,
and 1874, *Pfl.-Feinde*: 761.

Phytomyza intermedia Spencer, 1957, *Ent. Gaz.*, 8: 21—22. **Syn. nov.**

Faroes — ♂ 2 ♀♀, Tórshavn, Streymoy, 6—7. ix. 25; 20 ♂♂ 23 ♀♀, Tórshavn area, Streymoy, 2. vii. 26 (1 ♀), 25. vii.—26. viii. 26 (42 ex.); 2 ♂♂ 3 ♀♀, Kirkjubøholmur, Streymoy, 3. vi. 26; ♂ Vestmanna, Streymoy, 22. vi. 26; ♂♀, Klaksvík, Borðoy, 12. viii. 26.
S.E. Iceland — ♂, Skaftafell, 23. vii. 62.

(Note: the female recorded in Lindroth (1931) was not the true *P. milii* Kalt., as Rydén (1953) says — see below under *P. opacella* Hendel.)

Phytomyza intermedia Spencer is synonymised following my examination of the genitalia of a paratype ♂, caught on 9. vi. 54 at Hampstead, London (the holotype ♀ was taken in this same locality on 24. vi. 54). The main reason for Spencer's failure to recognise his species as *milii* is to be found in couplet 153 of the key in Hendel's (1931-6) monograph, where a split is made between species whose second costal segment is $3\frac{1}{2}$ —4 times as long as the fourth, and those in which the ratio is $1\frac{1}{2}$ —3. In fact it is impossible to divide the species in this way because the range of intra-specific variation of this character is too great. In his description of *P. intermedia* Spencer gives the average value of this ratio as 3.3 (♂) and 3.4 (♀). My own measurements agree with these figures. The extreme range is however at least 2.9—4.0. In Griffiths (1957) it was shown that the extreme range of *P. adjuncta* Hering was 2.8—4.2. This character can be a very useful one if series of a species are available, and the result can be conveniently expressed in graph form. But it cannot be used as a fundamental division in a key which is intended to identify individual specimens.

Other males whose genitalia were examined in the course of this work were:

2 ♂♂ from larvae 2. vii. 54 on *Milium effusum* L., Chesham, Buckinghamshire, England, emerged 4. and 8. vii. 54 (K. A. Spencer).

3 ♂♂, Darenth (Kent), Chippenham Fen (Cambs.) and Woodwalton Fen (Hunts.), Southern England, v.—vi.

To illustrate the range of variation in the aedeagus two examples have been figured (figs. 12 and 13), one Faroese and one British. This variation does not appear to be of geographical significance as one of the British males is very similar to the Faroese example figured, and the latter are not constant among themselves. The variation lies in the size and sclerotisation of the paraphalli. The homology of the different sections of the aedeagus in the *milii* group is not completely clear, but I have given my interpretation on fig. 12a, trying to homologise my use of the terms with those proposed by Nowakowski (1959) for the *Phytomyza obscura* group. The important group character, if my interpretation is correct, is the displacement of the distiphallus so that it arises from the apex of the basiphallus, above the paraphalli.

I believe that I am using the term *milii* group for the first time in this paper. The species which I include here are *P. milii* Kalt., *P. luzulae* Hering, *P. opacella* Hendel and the new subspecies described in Appendix I. More information on the differentiation of these species is to be found in that Appendix.

Ecology. According to the data which Mr. Andersson has supplied me, the single Icelandic specimen was taken in a "canyon with water dripping down". Grasses which he noted growing there were *Festuca*, *Agrostis* and *Poa glauca* M. Vahl. If the presence of the specimen was not fortuitous, the larvae should be found on one or more of these genera. I have no ecological data for the Faroese material, but it may be noteworthy that this species was the commonest Agromyzid taken by Kryger in the cultivated area around Tórshavn in 1926. I doubt if there is any significance in the fact that the species was so numerous on the Faroes in that year, but only one specimen has been taken yet in Iceland — like many other insects the abundance of Agromyzid species may vary markedly from one year to another.

***Phytomyza nigra* Meigen, 1830.**

- Faroës — 2 ♂♂ 2 ♀♀, Tórshavn area, Streymoy, 29. iv. 25 (♂), 21. viii. 26 (♂♀), 7. ix. 26 (♀); ♂, Stórvatn (135 metres), Eiði, Eysturoy, 10. viii. 26; ♀, Tvøroyri, Suðuroy, 29. v. 26.
- S.E. Iceland — 1 ex., Skaftafell, from pasture (Lindroth, 1931); 24 ex., Skaftafell, 18. vii.—2. viii. 62; 5 ex., Hornafjörður, 11—12. viii. 62.
- S. Iceland — 1 ex., Gröf (Skaftártunga), from meadowland, 27. vi. (Lindroth, 1931).

E. Iceland — ♂, Egilsstaðir, 13. viii. 31 (Jørgensen).

N. Iceland* — ♀, Stafn, Svartárdalur, Húnavatnsýsla, 30. vii. 33 (Tuxen).

The characteristic genitalia of this species are figured at figs. 7 a and 7 b. The Icelandic and Faroese males agree with my other preparations of Southern English material.

Ecology. Examples of this species were taken at Skaftafell from several different biotopes, including cultivated land, meadow slopes, birch wood, heath and beside a spring. The birch wood and "meadow slope with rich vegetation" yielded five and four examples respectively, but otherwise the species was taken in ones or twos only. As far as it is possible to deduce any common denominator for these different biotopes, I can only observe that the genera *Festuca*, *Agrostis* and *Anthoxanthum* occur in most of them, according to Mr. Andersson's notes. The larvae of this species attack a wide range of Gramineae, and there may of course be more than one main host in Iceland.

Phytomyza opacella opacella Hendel, 1936, Flieg. pal. Reg., 59: 447.

Phytomyza lindrothi Rydén, 1953, Ent. Medd., 26: 465—6. **Syn. nov.**

Faroese — 2 ♂♂, Ljósa Vatn, Streymoy, 12. vi. 26.

S.E. Iceland — ♀, Skaftafell, 18. vii. 62 (meadow slope with rich vegetation); ♂, Skaftafell, 17. viii. 62 (birch wood); 3 ♀♀, Hornafjörður, 11—12. viii. 62 (grazed grassland).

S. Iceland — ♀, Þorsmörk, Langadalur, 15. vi., from luxuriant herbage beside a stream (recorded by Lindroth (1931) as *P. milii* Kaltenschach, and made the holotype of *P. lindrothi* by Rydén (1953)).

E. Iceland — ♀, Egilsstaðir, 9. viii. 31 (Jørgensen).

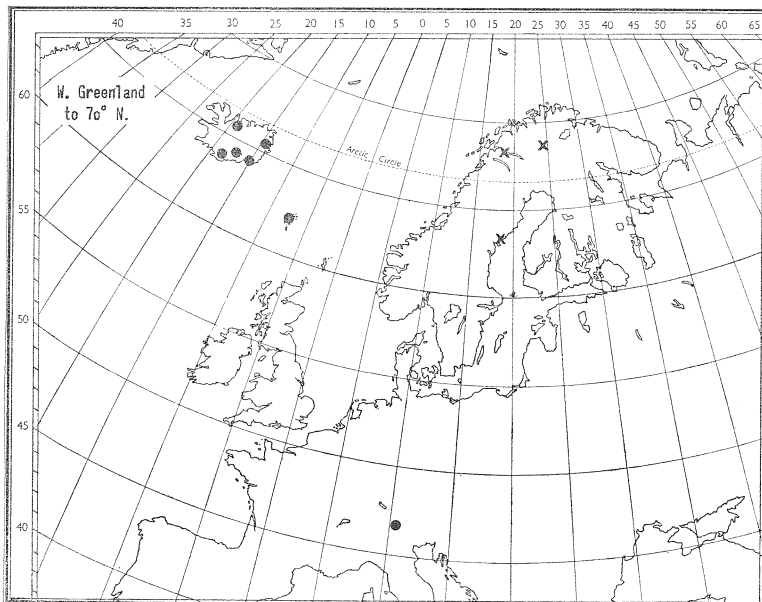
N. Iceland — ♀, Mælifell, Skagafjarðarsýsla, 13. ix. 32 (Tuxen).

Rydén's *P. lindrothi* is clearly a female of *P. opacella* Hd. The Icelandic and Faroese males of this species agree completely in their genitalia (figs. 14 a-d) with Hendel's holotype from Trafoi in the Italian Alps. This appears to be the only central European specimen.

Rydén recorded this species from northern Sweden. Study of this material has revealed some differences between it and the typical form, and it has therefore been described as a new subspecies in Appendix I.

*) The specimen recorded by Rydén (1953) from Akureyri is definitely not *nigra* but I am not able to give any alternative identification on the basis of a female.

Rydén (1949) also described "*Phytomyza opacella* Hd. form *borealis* nov. form." on the basis of a single swept female from Marsfjäll in northern Sweden. The alleged difference between it and the typical form is the shining abdomen; but I am very doubtful of its identification as *opacella*. The practice of erecting new taxa on the basis of a single caught female is to be condemned. As the external characters of the black-frons species of



Distribution of *Phytomyza opacella opacella* Hendel and *P. opacella glacialis* ssp. nov.

● *opacella opacella* × *opacella glacialis*

Phytomyza are so confusing, I am not at present able to suggest the species to which Rydén's "*borealis*" may belong. The known distribution of *opacella* is given on the map.

Ecology. The life-history of *P. opacella* Hd. is unknown, but, as it clearly belongs to the *milii* group according to the genitalia, the larvae may be expected to be leaf-miners on some monocotyledon — probably of the family Gramineae. Most of the Icelandic captures have been from meadow and grassland, but the male was taken in birch wood.

Phytomyza ranunculi Schrank, 1803.

- Faroes — 4 ♀♀, Tórshavn, Streymoy, 14. vi. 26, 24. vii. 26, 26. viii. 26, 8. ix. 25; ♀, Kirkjubøur, Streymoy, 27. viii. 26; ♀, Saksunardalur, Streymoy, 10. ix. (see Becker, 1915); ♂♀, Nólsoy, 26. vii. 26; ♂♀, Lørvík, Eysturoy, 29. vi. 26; ♂, Stóra Vatn (135 metres), Eiði, Eysturoy, 10. viii. 26; ♂, Svinoy, 16. viii. 26; ♂, Churchyard at Miðvágur, Vágar, 2. ix. 12; ♀, Vágar, 20. viii. 26; 3 ♂♂ 3 ♀♀, Bøsdalafossur, Sörvágsvatn, Vágar, 30. viii.—2. ix. (Becker, 1915).
Hansen's (1881) two specimens in the Zoological Museum, Copenhagen, have been seen and belong to this species, but the precise locality is not given.
- S.E. Iceland — ♀ bred from mine on *Ranunculus acris* L., Skaftafell, emerged 20. viii. 62.
- S.W. Iceland — Nielsen, Ringdahl and Tuxen (1954) record the finding of mines on *Ranunculus acronitifolius* L. and *R. repens* L. at Reykjavík, 3. and 17. vii. 50, which they think may have been caused by this species.
- N. Iceland — ♀, Steinbogi in Mælifellsá, Skagafjarðarsýsla, 25. vii. 33 (Tuxen), the holotype of "var. *islandica*" Rydén.

The genitalia of one of Hansen's (1881) Faroese specimens are figured at figs. 8 a and 8 b. The distiphallus is somewhat differently shaped from that of the specimen illustrated by Nowakowski (1962). Unfortunately it was not possible to check the range of variation in the other Faroese males, as they had previously been preserved in some medium which had hardened the soft tissue around the aedeagus, so that the delicate distiphallus could not be freed without damage.

I have also dissected nine specimens from various localities in Skåne province, Sweden, collected by Rydén, and a number of my own bred material from southern England. The distiphallus is subject to considerable variation both in the number of coils and their position. The Faroese specimen figured is extreme in having only one complete coil, and agrees in this respect (but not in position) with one Swedish male. In other specimens there are up to seven complete coils. There is also variation in the position of the distiphallus. In most specimens it is coiled upwards in the vertical plane (as fig. 8 a), but in some downwards in the same plane (as in Nowakowski's (1962) figure). In one specimen the coils lie in the horizontal plane. One Swedish specimen is remarkable in that the coils are not fully formed, and the distiphallus is represented by a curious S-shaped band.

It is of course possible that more than one species is involved, but, since there appears to be a continuous range of variation, I prefer to consider, at least for the present, that there is only one. The variation in the form of the distiphallus shows no obvious link with colour variation between the individuals concerned.

No seasonal dimorphism is observable in the Icelandic and Faroese material before me (although in Southern England for instance this is a constant and characteristic feature of this species) and all the specimens correspond more or less to the colour form *flavoscutellata* Fallén. The apparent absence of seasonal dimorphism in part of this species' range merits further investigation. I note that Rydén (1954) records only form *flavoscutellata* from Lappland.

The separation by Rydén (1953) of his "var. *islandica*" seems to me pointless. The character given — more extensive dark side spots of the scutellum than in form *flavoscutellata* — is no more than a trivial feature of a single specimen and does not characterise any separately recognisable race or seasonal form. I have therefore discarded the name. The classification of "var. *islandica*" as a melanic form by Nielsen, Ringdahl and Tuxen (1954) is erroneous. The spring form which can be taken commonly in England and elsewhere in Europe (form *praecox* Meigen) is much darker in many respects.

Ecology. I have no definite biotypical data for this species in Iceland or the Faroes apart from the breeding record, but it may be of significance that it was caught in more localities on the Faroes than any other species. It has long been known as a very hardy species and Hering (1951) refers to the larvae feeding under snow. In Southern England the larvae can be found commonly in November and December.

***Phytomyza taraxacoecis* Hering, 1949.**

Faroes — 2 ♂♂, Stóra Vatn, Eidi, Eysturoy, 8. viii. 26; ♀, Kirkjubøur, Streymoy, 27. vii. 26.

For the distinction of this species from other members of the *robustella* group reference should be made to Appendix II.

Ecology. The larvae have been found in "gall-mines" in the leaf-bases of *Taraxacum officinale* agg., but the host in the Faroes must be *Taraxacum spectabile* agg., as no species of the *T. officinale* agg. occur there.

Phytomyza tenella Meigen, 1830, Syst. Besch. VI: 195.

- Faroes — 10 ♂♂ 10 ♀♀, Tórshavn area, Streymoy, 26. vi.—26. viii. 26; ♀, Klaksvík, Borðoy, 12. viii. 26; 2 ♂♂, Sandur, 26. viii. 12, mountain slope; 4 ♂♂ 8 ♀♀, Sandur, 12—13. vii. 26.
- S.E. Iceland — 2 ex., Skaftafell, 1. vii., from birch wood (Lindroth, 1931); 5 ex., Skaftafell, 21—27. vii. 61 (Böcher); 34 ex., Skaftafell, 18—29. vii. 62; 19 ex., Hornafjörður, 11—13. viii. 62.
- S. Iceland — 1 ex., Hliðarendakot (Fljótshlíð), 3. vi. (Lindroth, 1931).
- E. Iceland — ♂♀, Egilsstaðir, 12. viii. 31 (Jørgensen).
- N. Iceland — 1 ex., Slúttnes (in Mývatn), 20. viii. (Lindroth, 1931); 5 ex., Mælifell, Skagafjarðarsýsla, 24. vii. 33 (Tuxen); ♀, same locality, 10. vii. 33 (Tuxen); ♂, Skiðastaðalaug, Skagafjarðarsýsla, 27. vii. 33 (Tuxen); 2 ♀♀, Orravatn, Skagafjarðarsýsla, 18. vii. 33 (Tuxen); ♂, Svartá bei Starrastaðir, Skagafjarðarsýsla, 12. viii. 32 (Tuxen).
- N.W. Iceland — 3 ex., 50 km. N.E. of Borgarnes, 30. vii. 47 (Cloudsley-Thompson).

Identity of holotype. Meigen in his original description states that this species was taken by Winthem. According to Becker (1902) there is no example of this species in the Meigen collection in Paris, so the single male in the Winthem collection in the Naturhistorisches Museum, Vienna, must be considered the holotype. I have labelled it accordingly.

The genitalia of the holotype are figured at figs. 9 a-c. Their paraphalli differ from those of the Faroese male figured at figs. 10 a-c in being less elongate in lateral view and more widely separated in ventral view. I consider this variation to be intra-specific, but have figured the observed differences in case further material should ever suggest that more than one species may be involved. In the course of this work I also examined the genitalia of males from the following localities:

- St. Gilgen, Austria (Naturhistorisches Museum, Wien)
 Prater, Wien, Austria (" " ")
 Bèrisal, Switzerland (K. A. Spencer)

These specimens all agree closely with the Faroese and Icelandic material (preparations were made of three Faroese and three Icelandic males).

Colour Variation. Most of the Icelandic and Faroese specimens have dark abdomens and do not show any extensive yellow coloration as often occurs in specimens from central Europe. But a few, including the three examples from N.W. Iceland, do have extensively yellow abdomens. The colour of the head too is

variable. While many specimens (especially from Skaftafell and Egilsstaðir) have typical pale yellow frons and face, there are many with grey-dusted orbits and the centre of the frons deep orange yellow. Rydén (1953) was confused by this variation and attributed the darker specimens to *P. atricornis* Meigen and *P. sibirica* Hendel. Genitalia studies show clearly that this variation is intraspecific.

One female, taken in the birch wood at Skaftafell on 18. vii. 62, is remarkable because its frons, face and jowls are entirely reddish black. The other eleven specimens taken on that occasion were however the typical pale form. Melanism is well-known in several Icelandic Coleoptera, Lepidoptera and other dipterous families, but this is the only striking example of its occurrence in the Agromyzid material which I have examined (the classification of *P. ranunculi* "var. *islandica*" Rydén as a melanic form by Nielsen, Ringdahl and Tuxen (1954) was erroneous). A discussion of this phenomenon is found in Lindroth (1931).

Ecology. Hendel (1931-6) suggested that the larvae fed in the seeds of *Euphrasia*, as he had swept the flies in numbers off *Euphrasia rostkowiana* Hayne (the specimens in question are, I think, those from St. Gilgen in his collection). The genitalia confirm that there is a close relationship between this species and *P. varipes* Macquart, whose larvae feed on *Rhinanthus* seeds. As far as I know Hendel's suggestion has not previously been confirmed by breeding, but I succeeded in obtaining one puparium from seeds of *Euphrasia nemorosa* (Pers.) H. Mart. emend. Löhr, collected at Beachy Head, Sussex, England on 22. viii. 62, which yielded a female *tenella* on 13. vi. 63.

P. tenella Mg. is the most numerous Agromyzid in the Icelandic material and was taken from many different localities. Habitats where it was taken in numbers were on dry heavily-grazed grassland at Hornafjörður (13 examples, 11. viii. 62) and on heath at Skaftafell (nineteen of the 1962 Skaftafell specimens were from this habitat). Thirteen examples including the single melanic female were taken in birch wood, but only a single specimen was taken on swampy ground. It seems established from these records that this species is primarily associated with drier habitats.

Note. *Phytomyza nigrifemur* Hering, 1934 is according to the genitalia a very different species from *P. tenella* Mg.; however

the difference in the colour of the palpi given in Hering's (1949a) emendation to Hendel's (1931-6) key is not clear-cut. The only significant external difference which I have noticed lies in the shape of the third antennal segment, which is very short in *nigrifemur*. Rydén's (1951) suggested synonymy of *P. nigrifemur* Hg. with *P. zonata* Zetterstedt is in my opinion doubtful. The holotype of *zonata* is unfortunately a female (from Gottland, Sweden); although very close to *tenella* I think it is probably not identical because its second costal segment is 2.6 times as long as the fourth — in the *tenella* series before me this ratio exhibits a range of 1.8—2.3. The identity of *zonata* can only be settled in the context of a revision of this group, particularly the large material which Rydén obtained in Scandinavia.

***Phytomyza varipes* Macquart, 1835.**

- Faroes — 2 ♀♀, Tórshavn area, Streymoy, 15. and 28. vii. 26; 5 ♀♀, Lørvík, Eysturoy, 29. vi. 26.
 S.E. Iceland — 2 ex., Skaftafell, 30. vi. (pasture) and 1. vii. (birch wood) (Lindroth, 1931); 32 ex., Skaftafell, 17—30. vii. 62; 2 ex., Bæjarstaðaskógur, 5. viii. 62.
 S. Iceland — 1 ex., Breiðabólstaður (Síða), 15—16. vii. (Lindroth, 1931).
 E. Iceland — ♀, Egilsstaðir, 8. viii. 31 (Jørgensen).
 N. Iceland — ♀, Mælifell, Skagafjarðarsýsla, 15. vii. 33 (Tuxen); ♂, Skiðastaðalaug, Skagafjarðarsýsla, 27. vii. 33 (Tuxen).
 N.W. Iceland — ♀, Brjánslækur, vii. 33 (Gígja).*

Lindroth (1931) also states that in some notes by F. W. Edwards on the Icelandic Diptera was the following entry: "*Phytomyza varipes* Macq.(?). Bred from fruit of *Rhinanthus minor*", but no precise locality was given.

The male genitalia are figured at figs. 11 a-c. They show a definite affinity with those of *P. tenella* Meigen. This species is easily recognised on external characters, and published records can generally be accepted.

The Icelandic and Faroese material shows some colour variation. The third antennal segment is in most specimens yellow, but in a few brown. The femora in most specimens are more or less dark, only obscurely yellow. As in many examples of *tenella* the yellow coloration on the abdomen is less extensive in the Icelandic and Faroese material than in that from central Europe. Ecology. The larvae of this species are well-known as seed-feeders in *Rhinanthus* spp. In Iceland *Rhinanthus minor* Ehrh. is

*) according to Rydén (1953) — this specimen has not been re-examined.

a common plant and, apart from the breeding record, was noted as growing at Breiðabólstaður and Skaftafell when this species was caught. At Skaftafell four specimens were taken on 18. vii. 62 on "cliffs with small stream" where *Rhinanthus minor* was growing, and five more on 19. vii. 62 "under a rock with dripping water and a small pool", also where the same plant grew (the quotations are from Mr. Andersson's notes).

Phytomyza sp.

Phytomyza continua Hendel, Rydén, 1953, Ent. Medd., 26: 468.

S. Iceland — ♀, Rauðumýrarmúli, north of Laugarvatn, 10. vii. 32 (Spärck).

This specimen was called *Phytomyza continua* Hendel by Rydén, but I do not consider it possible to give an accurate identification on the basis of a single female. It does appear to represent a different species from any of the others before me, so I have listed it as *Phytomyza* sp.

Keys for Identification.

The following keys based on external characters may prove useful to local Dipterists for identification. They are not intended to be phylogenetic. It cannot be overemphasised however that the identity of many species should be checked from the male genitalia before publishing records.

References are made to the figures in Hendel's (1931-6) monograph in "Die Fliegen der paläarktischen Region". The numbers after the species names have the following significance:

- ¹The external characters of this species are sufficiently distinct to allow firm identification.
- ²This species should not be confused on external characters with any other species known from Iceland and the Faroes, but other similar species occur elsewhere.
- ³Confirmation of identity from the male genitalia should always be sought; records based on females alone can only be accepted with reserve.
- ⁴Species requiring further investigation (inadequate material available).

A. AGROMYZINAE.

Subcostal vein not reaching the costa separately, fused with r_1 distally (Hendel fig. 25).

Entirely black species; six dorsocentrals decreasing in length markedly forwards; squamal fringe black. Costa only to r_{4+5} . Lower cross-vein present (compare Hendel figs. 126—127).....

..... *Agromyza ?nigrociliata* Hendel⁴

B. PHYTOMYZINAE.

Subcostal vein reaching the costa separately, although it may be weakened to little more than a fold distally (Hendel fig. 26).

1. Lower cross-vein present. Costa to m_{1+2} 2.
- Lower cross-vein absent. Costa to r_{4+5} (*Phytomyza* Fallén) 3.
2. Extensive yellow coloration, including the scutellum; antennae entirely yellow. Femora black with yellow tips (compare Hendel's description of *L. flaveola* Fallén)..... **Liriomyza richteri** Hering²
- Largely black species. Third antennal segment at least of male conspicuously enlarged (see fig. 23 d)..... **Cerodontha (Dizygomyza)** spp.
3. Rear upper orbital bristle very weak or absent: only one lower orbital. Scutellum yellow in centre. Second antennal segment yellow. Only two or three pairs of acrostichals present (Hendel fig. 467)..... **P. ranunculi** Schrank¹
- Scutellum dark, except sometimes in *P. fallaciosa* Brischke. Two upper orbital bristles always clearly developed..... 4.
4. Rear upper orbital bristle obviously shorter than the front. Acrostichals 3—4 rowed 5.
- Rear upper orbital more or less equal in length to the front..... 6.
5. Frons dark **P. archangelicae** Hering³
- Frons bright yellow (Hendel fig. 353)..... **P. angelicae** Kaltenbach²
6. 3rd antennal segment yellow or brown. Acrostichals 2—3 rowed. Femora streaked with yellow. ♀ ovipositor very elongate, as long as the rest of the abdomen (Hendel fig. 493)..... **P. varipes** Macquart¹
- 3rd antennal segment black. Femora dark except at their tips. Ovipositor not elongate 7.
7. Acrostichals in at least 3—4 rows 8.
- Acrostichals at most 2—3 rowed 11.
8. Labellum projecting downwards (Hendel fig. 404). Orbits raised above the eye in profile; orbital setulae partly in two rows. Mesonotum and pleura very matt. Frons brown or ochreous. Squamal fringe brown or ochreous. Enlarged surstyli projecting below abdomen in male **P. evanescens** Hendel³
- Labellum not so. Orbital setulae 1-rowed 9.
9. Frons ochreous yellow. Mesonotum and pleura very matt **P. sp.**⁴ (p. 414)
- Frons wholly or mainly dark. At least pleura more or less shining. 10.
10. 3rd antennal segment a little longer than high with a short fringe of hairs apically. Orbits not raised in profile (Hendel fig. 438). Mesonotum more or less shining..... **P. milii** Kaltenbach³
- 3rd antennal segment rounded, without fringe. Orbits raised above the eye in profile. Wing membrane tinged with brown. Frons often partly ochreous. Mesonotum somewhat matt **P. opacella opacella** Hendel³
11. Eyes densely haired (Hendel fig. 443). Mesonotum matt grey. Frons yellow-ochreous..... **P. nigra** Meigen¹
- Eyes with at most a few inconspicuous hairs. Frons normally yellow low 12.

12. Sides of mesonotum partly yellow. Frons clear yellow. Sometimes scutellum marked with yellow in its centre... **P. fallaciosa** Brischke²
 -. No yellow on sides of mesonotum or scutellum..... 13.
13. Front coxae marked with yellow. 3rd antennal segment more or less quadrate (Hendel fig. 486)..... **P. tenella** Meigen²
 -. Front coxae dark..... 14.
14. 3rd antennal segment with conspicuous fringe of long hairs. Large species (wing-length 3 mm.)..... **P. hedingi** Rydén⁴
 -. 3rd antennal segment without fringe..... 15.
15. Large species (wing-length 2.5—3 mm.). Acrostichals strongly developed..... **P. taraxacocecis** Hering²
 -. Smaller species (about 2 mm.). Not more than two pairs of acrostichals present, sometimes none (Hendel fig. 362). **P. atricornis** Meigen²

Significance and Origin of the Agromyzid Fauna.

Lindroth in his "Insektenfauna Islands" (1931) after a detailed analysis of the composition of the Icelandic insect fauna concluded that*:

(i) The Icelandic fauna is high boreal and typically European. It clearly lacks any originally Greenlandic/American or Arctic elements. The fauna of the tertiary land-bridge between Europe and North America is absent and must have been lost early in the ice-age.

(ii) A postglacial entry of the entire fauna from Europe is unthinkable as, although there has been no postglacial land connection with Europe, the Icelandic fauna contains many European species for which overseas dispersal is highly improbable (e. g. flightless beetles).

(iii) An interglacial entry of an European fauna over a land-bridge via the Faroes must be postulated at a time when the climate was boreal (hence the absence of a definite arctic element in the fauna).

(iv) Part of this fauna survived the last glaciation in an ice-free coastal zone (which may now lie beneath the sea), probably in two separate main areas — near Hornafjörður in the South-East and beneath Mýrdalsjökull in the extreme South.

Tuxen (1944) thought that, if there was an ice-free coastal zone, particularly favourable conditions for survival would have been found in the vicinity of hot springs, but hot springs by themselves could not have stopped the advance of land ice.

*) Abridged from Lindroth (1931), page 567.

In "The Faunal Connections between Europe and North America" (1957) Lindroth retains his earlier views with the modification that he considers on geological grounds that the postulated land-bridge might have to be removed back to the last-but-one interglacial period (the Mindel-Riss).

Investigations of the flora have led to the same conclusion that the majority of Icelandic species have survived at least one period of glaciation. Steindorsson (1962), on the basis of the distribution of local plants on the island, lists six probable refuge areas; these are: (i) the Vestfirðir, (ii) the coastal region of Breiðafjörður (both in N.W. Iceland), (iii) the land surrounding Eyjafjörður (N. Iceland), (iv) the Austfirðir (E. Iceland) extending to Hornafjörður (S.E. Iceland), (v) the central region of South Iceland particularly near Mýrdalsjökull and (vi) the vicinity of Hvalfjörður (S.W. Iceland). Refuges (i), (iii) and (iv) in particular contain many very localised plants, but only three plants are given by Steindorsson as having their centres of distribution in refuge (v), which is one of Lindroth's postulated survival areas. The southern part of Steindorsson's refuge (iii) corresponds with Lindroth's south-eastern survival area, but extends for some distance beyond it to the North.

It is outside the scope of this paper to discuss the reasons for this partial discrepancy between the conclusions on survival areas based on faunal and floral evidence. The essential point is that both botanists and zoologists are agreed that many species survived on the island during at least part of the ice-age.

Spärck (1929) concluded that part of the Faroese fauna too arrived by a land connection during an interglacial period. The relationship between the Faroese and Icelandic faunas is so close that conclusions on the age of one must inevitably hold good for the other.

One of the most important facts in favour of the postulated land-bridge to Iceland via the Faroes is the large number of species common to both areas. For the Coleoptera Lindroth (1957) calculated that 38 out of 56 (68%) species native to Iceland were common to the Faroes. A similar calculation for Collembola (in Lindroth, 1931) gave 44 out of 75 species (58.6%).

While the available material of Agromyzidae from Iceland and the Faroes is still limited, it is sufficient to enable a general assessment to be made of the significance and origins of the

fauna. My purpose in the succeeding parts of this section is to draw what conclusions can be drawn from the available evidence and to see how far they are compatible with Lindroth's views. The principal factors to be considered have been grouped under the following headings: (a) Outside Distribution, (b) Distribution within Iceland and the Faroes, (c) Host-plant Association, and (d) Dispersal.

(a) Outside Distribution.

The known distribution outside Iceland and the Faroes of the species recorded in this paper (excluding the four species of doubtful identity) may be summarised as follows.

(Note: The records for Greenland in this table are based on material I am now studying, and have not previously been published.)

Species common to Iceland and the Faroes.

<i>Phytomyza atricornis</i> Meigen	— Cosmopolitan, except South America and Greenland (probably of holarctic origin).
” <i>fallaciosa</i> Brischke	— Central and Northern Europe (including Great Britain and Scandinavia).
” <i>militi</i> Kaltenbach	— Central and Northern Europe (including Great Britain and Scandinavia).
” <i>nigra</i> Meigen	— Holarctic: Europe, Japan, North America.
” <i>opacella</i> Hendel	— Italian Alps (Trafoi), Scandinavia, Greenland.
” <i>ranunculi</i> Schrank	— Holarctic: Europe, Japan, North America, Greenland.
” <i>tenella</i> Meigen	— Central and Northern Europe (including Great Britain and Scandinavia).
” <i>varipes</i> Macquart	— Central and Northern Europe (including Great Britain and Scandinavia), Greenland.

Species found in Iceland only.

<i>Cerodontha (Dizygomyza) lindrothi</i> sp. nov.	— Greenland.
<i>Liriomyza richteri</i> Hering	— Murman Coast (U. S. S. R.).
<i>Phytomyza angelicae</i> Kaltenbach	— Europe (including Great Britain and Scandinavia) — subsp. <i>kibunensis</i> Sasakawa in Japan.

Species found in the Faroes only.

- Phytomyza archangelicae* Hering — Mecklenburg (Germany), Swedish Lapland.
 „ *evanescens* Hendel — Scandinavia, Central Europe, Dalmatia.
 „ *taraxacocecis* Hering — Germany, England.

Summarised according to the areas from which the species probably migrated to Iceland and the Faroes, these results read as follows:

- Iceland: 9 species of European origin (8 of which are confirmed also for the Faroes, but only 3 of which reach Greenland).
 1 species doubtfully of Arctic distribution.
 1 species in common with Greenland only (probably of Nearctic origin).
 Faroes: 11 species, all of European origin, of which 8 reach Iceland and 3 also Greenland.

The Agromyzid fauna of Iceland can thus be seen to be predominantly an extension of the European fauna, and the Faroese fauna is entirely so. There are no confirmed endemic species or subspecies. Two species — *Phytomyza nigra* Meigen and *P. ranunculi* Schrank — have a continuous holarctic distribution, being found both in Japan and North America, but at least the former must be considered part of the European element in the Icelandic fauna, as it does not occur in Greenland. For the purpose of the above summary I have assumed that the same is the case with *P. ranunculi* Schrank. The cosmopolitan *P. atricornis* Meigen is also absent from Greenland and has therefore been considered a European element in the Icelandic fauna.

The distribution of *Liriomyza richteri* Hering is interesting as the species is otherwise known only from the Murman Coast. It is possible that its distribution is of the Arctic type, but unfortunately the likelihood that it may have been confused with related species if taken elsewhere is too great to allow the description "Arctic" to be anything more than doubtful at present.

The existence of a single non-European species in Iceland is particularly interesting. The presence of a Greenlandic/American element in the Icelandic fauna and flora is clearly established, although it is proportionately very small. Steindorsson (1962) gives only 6 American plants not occurring in Europe out of a total Icelandic flora of 429 indigenous higher plants. Insects of American origin include *Simulium vittatum* Zetterstedt (Dipt. Simuliidae) and several Lepidoptera. It is most probable that *Cero-*

dontha (*Dizygomyza*) *lindrothi* sp. nov. belongs to this element, although I have not yet been able to confirm its occurrence in North America (unfortunately the subgenus has been little studied there).

Of the twelve species considered to have reached Iceland and the Faroes from Europe, ten are widely distributed species which should probably be classed as "commonboreal". Two species are of more restricted distribution. *Phytomyza archangelicae* Hering, although its distribution is very inadequately known, will probably prove to be high- and middle-boreal, as its principal host, *Angelica archangelica* L., is native in Scandinavia, Denmark and Eastern Europe (Clapham, Tutin and Warburg, 1952); the parasite has not however been found in Iceland and Greenland where its host is also widespread. *Phytomyza opacella* Hendel undoubtedly has a restricted boreo-alpine or arctic-alpine distribution. From central Europe the only known specimen of this latter species is the holotype taken in the Italian Tyrol. Scandinavian specimens differ in several respects and have been described as a new subspecies in Appendix I.

The predominantly European origin of the Icelandic fauna and the high proportion of species common to both Iceland and Faroes agrees completely with results obtained in other groups. In a fauna which was mainly the result of postglacial overseas dispersal, whether by air currents or human agency, the high proportion of species common to the two areas and the overwhelming predominance of European species in Iceland would not be expected. The observed facts thus completely accord with Lindroth's thesis of a land-bridge.

(b) Distribution within Iceland and the Faroes.

Lindroth (1931) divided Iceland for faunistic purposes into eight areas corresponding to the eight points of the compass — North, North-West, West, South-West, South, South-East, East and North-East. Species which are found in all or most of these (though usually omitting the largely barren central plateau) he called panislandic. Species with more restricted distribution were generally found in the South and South-East, and an analysis of these distributions in conjunction with other factors, such as the means of dispersal of the insects concerned, led him to the conclusion that there had been an ice-free coastal zone in the South and South-East. The species whose distribution has re-

mained centred in this area include a disproportionately high proportion of those with poor means of dispersal, including many flightless forms.

The available Agromyzid material is not a suitable basis for a detailed analysis. There is a very large material from the South-East, a little from the South and North, but no more than a few specimens from the other regions. Consequently I have classed species which occur in the North as well as the South or South-East as probably panislandic. In addition there are four species which have only been taken in the South or South-East. The breakdown is as follows:

- Probably panislandic — *Cerodontha (Dizygomyza) lindrothi* sp. nov.
Phytomyza atricornis Meigen.
 „ *nigra* Meigen.
 „ *opacella* Hendel.
 „ *ranunculi* Schrank.
 „ *tenella* Meigen.
 „ *varipes* Macquart.
- South and South-East
 Iceland only — *Liriomyza richteri* Hering.
Phytomyza angelicae Kaltenbach.
 „ *fallaciosa* Brischke.
 „ *milii* Kaltenbach.

In addition there are two species of doubtful identity represented by single specimens only — *Phytomyza hedingi* Rydén from Isafjarðaröjúp in N. W. Iceland and the *Phytomyza* sp. ("continua" sensu Rydén) from near Laugarvatn in S. Iceland.

These distributions must, as already said, be regarded as very provisional on account of the lack of material from many areas. But even when a clearer picture can be obtained it is *a priori* doubtful whether the horizontal distribution within Iceland of active winged insects such as the Agromyzidae will provide useful evidence for the origin of the fauna. Existing distributions will more likely be dependent on factors now in operation, and are unlikely to retain an earlier pattern. Exceptions may however occur in the case of species whose food-plant or biotope is of very localised occurrence, as they may have been unable to bridge the gap from their original to other areas, which would now be suitable for their development.

A striking confirmation of the possibility of survival through a period of glaciation is provided by the fauna of Skaftafell in the South-East. The significance of this locality lies in the fact

that here a rich fauna and flora extends right to the edge of permanent ice, and, if there was an ice-free coastal zone during the last glaciation, there is unlikely to have been any climatic obstacle to the survival there of most of the species which can today be found at Skaftafell. Now it is a striking fact that, apart from the two doubtful species, all eleven Icelandic Agromyzids have been taken in the Skaftafell district, and some of them are very common there. I therefore feel confident in asserting that the species of Agromyzidae now found in Iceland are sufficiently hardy to have survived the last glaciation, if there was an ice-free coastal zone.

There are some insects in Iceland which are always or usually associated with hot springs. As an exceptionally rich vegetation is found in the neighbourhood of many of these springs they should be of particular interest to the student of Agromyzidae. Tuxen (1944) studied the animal communities in and around these springs, and reference should be made to his work for further details. Only one Agromyzid is mentioned in his work — *Phytomyza atricornis* Meigen; however he did obtain a number of other specimens and, in the list of material under each species in this paper, those collected by Tuxen are all from localities where hot springs are found. However I do not know any details of the circumstances of capture, and, as only one or two flies were caught on each occasion, probably not much significance can be attached to the records as they stand. All the species concerned have also been taken in localities where there are no hot springs. In 1962 the Lund University Expedition took a series of thirty-nine Agromyzids at Bæjarstaðaskógur, a hot spring area near Skaftafell. Thirty six of these specimens are *Phytomyza atricornis* Meigen. It seems established therefore that this species finds conditions especially favourable near hot springs, but it is not confined to such localities.

There are no records of Agromyzidae from the largely barren central area of Iceland, but this may of course be due to less intensive collecting.

The Faroese Agromyzid material was mainly taken on the largest island, Streymoy, and is clearly not sufficient evidence on which to base an analysis of the distribution within the islands of the species taken. However I have summarised the

existing records, as far as they go, according to islands in the following table:

Streymoy	— All Faroese species except <i>Agromyza ?nigrociliata</i> Hendel.
Eysturoy	— <i>Phytomyza evanescens</i> Hendel, <i>P. fallaciosa</i> Brischke, <i>P. nigra</i> Meigen, <i>P. ranunculi</i> Schrank, <i>P. taraxacoecis</i> Hering, <i>P. varipes</i> Macquart.
Nólsoy	— <i>Phytomyza atricornis</i> Meigen, <i>P. ranunculi</i> Schrank.
Svínoy	— „ <i>atricornis</i> Meigen, <i>P. ranunculi</i> Schrank.
Fugloy	— „ <i>fallaciosa</i> Brischke.
Borðoy	— „ <i>milii</i> Kaltenbach, <i>P. tenella</i> Meigen.
Vágar	— „ <i>ranunculi</i> Schrank.
Sandoy	— <i>Agromyza ?nigrociliata</i> Hendel, <i>Phytomyza tenella</i> Meigen.
Suðuroy	— <i>Phytomyza nigra</i> Meigen.

(c) Host-plant Association.

Three species of Agromyzidae have been bred in Iceland — *Phytomyza ranunculi* Schrank from mines in *Ranunculus acris* L., *P. varipes* Macquart from seeds of *Rhinanthus minor* Ehrh. and *P. angelicae* Kaltenbach from mines on *Angelica sylvestris* L. However the life-history of several other species is known in Europe, and all the unbred species (except for the unidentified *Phytomyza* sp. which is omitted from the table below) are closely related to species of known life-history, so that their probable life-history can be conjectured (the justification of these conjectures has been given under the species concerned). The known and probable host-plants are given in the following table (the larvae are leaf-miners unless otherwise stated):

Species common to Iceland and the Faroes.

<i>Phytomyza atricornis</i> Meigen	— Polyphagous on many dicotyledons (especially Compositae and Cruciferae).
„ <i>fallaciosa</i> Brischke	— <i>Ranunculus</i> .
„ <i>milii</i> Kaltenbach	— Various Gramineae.
„ <i>nigra</i> Meigen	— Various Gramineae.
„ <i>opacella</i> Hendel	— Unknown, but probably Gramineae.
„ <i>ranunculi</i> Schrank	— <i>Ranunculus</i> .
„ <i>tenella</i> Meigen	— Seeds of <i>Euphrasia</i> .
„ <i>varipes</i> Macquart	— Seeds of <i>Rhinanthus</i> .

Species found in Iceland only.

<i>Cerodontha (Dizygomyza) lindrothi</i> sp. nov.	— Unknown, but probably <i>Carex</i> .
<i>Liriomyza richteri</i> Hering	— Unknown, but probably Gramineae.
<i>Phytomyza angelicae</i> Kaltenbach	— <i>Angelica sylvestris</i> L.
„ <i>hedingi</i> Rydén	— Unknown, but probably in stems or leaf-bases of some genus of Compositae Liguliflorae.

Species found in the Faroes only.

- Agromyza ?nigrociliata* Hendel — Gramineae.
Cerodontha (Dizygomyza) ? caricicola Hering — *Carex*.
Phytomyza archangelicae Hering — *Angelica archangelica* L.
 „ *evanescens* Hendel — Unknown, but probably stems of *Caltha palustris* L.
 „ *taraxacoecis* Hering — Leaf-bases of *Taraxacum*.

The host association of the Gramineae-feeders in Iceland and the Faroes is not established, so that no detailed conclusions can be drawn in this paper. But excluding the Gramineae, it can be seen that there are seven plant genera which have specific Agromyzid parasites — *Caltha* and *Ranunculus* (Ranunculaceae), *Euphrasia* and *Rhinanthus* (Scrophulariaceae), *Angelica* (Umbelliferae), *Taraxacum* (Compositae) and *Carex* (Cyperaceae). Six of these genera — *Rhinanthus*, *Euphrasia*, *Ranunculus*, *Angelica*, *Taraxacum* and *Carex* — include widespread species which are considered by Steindorsson (1962) to be native in Iceland (i. e. to have survived at least one period of glaciation there), a result in accordance with the view that most of the Agromyzid fauna has arrived by land-bridge.

Of the two *Angelica* species, Steindorsson (1962) considers *A. archangelica* L. to be probably native on account of its habitat tolerance, but expresses no view on the origin of *A. sylvestris* L. The situation of *Caltha palustris* L. is also somewhat obscure. Steindorsson classes it as possibly introduced in Iceland, because it is "more or less anthropophilous". The probable parasite — *Phytomyza evanescens* Hendel — has only been found in the Faroes.

The work of Steindorsson and other Icelandic botanists has been based on a detailed analysis of the distribution of plants within and without Iceland. This geographical method works admirably with localised plants, but gives less conclusive results with plants which are common and widespread both in Iceland and outside. More definite conclusions on these widespread species will be reached when parasitological methods are used to supplement distributional studies. The association of host-specific insect species with a plant is strong evidence that that plant is native.

While the above account has been somewhat sketchy, because of the absence of detailed information on host selection in Iceland and the Faroes themselves, it is clear that the occurrence of certain Agromyzids there can provide relevant evidence for as-

sessing the age of immigration of their host-plants. For instance the discovery of *Phytomyza angelicae* Kalténbach in Iceland is evidence in favour of *Angelica sylvestris* L. being native there: this evidence would be further strengthened if the parasite can be found on the Faroes too (as it is implicit in the land-bridge theory that European species have reached Iceland from that direction).

(d) Dispersal.

Lindroth (1931) names four possible methods by which insects may have reached islands without human agency: these are (i) active flight, (ii) air currents, (iii) water currents (including ice), and (iv) by the agency of birds. In the case of the Agromyzidae the last two alternatives cannot apply. It is also incredible that an Agromyzid should entirely by its own efforts fly the hundreds of miles necessary across open sea to reach Iceland or the Faroes. Therefore if a postglacial origin for the Icelandic and Faroese Agromyzid fauna is postulated, there are only two possible means of its arrival — these are (i) by air currents or (ii) by human agency.

I shall consider the first possibility first. Glick (1939) published a detailed account of insects captured at various altitudes over Louisiana, U. S. A., in traps mounted on aeroplanes. The proportion of Diptera was found to be roughly the same at all altitudes being a little over 40% of all the insects taken. Between 200 and 5,000 feet during a total of 1,007 hours of operation of the traps over 7,000 Diptera were taken. Of these over 2,250 were Nematocera of various families, and 2,100 were Chloropidae. Other groups taken frequently were Ephydridae (nearly 730 specimens), Borboridae (538), Dolichopodidae (336), Calyptrata (nearly 370 of which nearly 300 were Anthomyiinae), Syrphidae (251) and Phoridae (121). Agromyzidae came very low on the list with only 18 specimens, of which 15 were Agromyzinae and 3 not identified beyond family.

It is of course unwise to see too much significance in the differences in the numbers, as the relative frequency of the different groups on the ground below is not known. Much of the area was swampy and hence the relative frequency of Ephydridae and Dolichopodidae may be greater than normal. However some broad conclusions may be drawn. The large number of Nematocera in the samples can easily be explained by their weaker flight, but

relatively large surface area, which puts them at the mercy of strong air currents. The same applies to the Dolichopodidae and perhaps to some extent the Anthomyiinae. (The case of the Syrphidae is rather different and outside the present argument — being very active fliers their occurrence high in the air is probably at least in part voluntary, and may be compared with that of Lepidoptera, locusts and other strong fliers).

Turning to the smaller Cyclorrhapha (the so-called Acalypterates) we find that there are only three families which were taken very frequently — the Chloropidae, Ephydriidae and Borboridae. The explanation of this uneven representation should be sought in the relative weight, surface area and power of flight of the insects concerned (see Glick, 1939, pp. 84—87). If the near or complete absence of Phytomyzinae was not fortuitous, the reason may be their tendency to reduced wing-size coupled with greater muscular efficiency (see Nowakowski, 1962, pp. 121-2) by comparison with the Agromyzinae.

Further evidence on the possibility of aerial dispersal of Agromyzids may be deduced from the fauna of Oceanic islands, particularly the numbers of endemic species occurring whose ancestors must have arrived before introduction by human agency was possible. The fauna of Hawaii (Hardy, 1960) contains a profusion of endemic Dolichopodidae and Drosophilidae, but many dipterous families are completely lacking. Out of a total of 14 Agromyzidae 3 are clearly recent introductions through human agency and only 5 may be endemic (Spencer, personal communication). If one compares the fauna of Hawaii with that of the Faroes, the assumption that the Faroese fauna was exterminated during the last glaciation must surely entail that Hawaii has been available to receive its present fauna over a period of time hundreds of times as long as the Faroes. That the Faroes could have received thirteen Agromyzid species by aerial dispersal since the last glaciation thus appears unlikely.

In the case of Iceland the final refutation of the possibility of aerial introduction of the Agromyzid fauna lies in its composition. The affinities of such a fauna would naturally lie with the regions from which the prevailing winds blow. The endemic Dipterous fauna of Hawaii for instance is largely derived from the Pacific area (Hardy, 1960). The prevailing winds over Iceland are westerly, and could only cause the introduction of a

Nearctic fauna (either directly from North America or via Greenland). Conditions which might enable the transport of insects from Europe occur on average only on a few days a year (Lindroth, 1931). Similar considerations apply to the Faroes, although there is admittedly a greater possibility of the transport of insects there from Scotland by south winds.

In view of these considerations I have concluded that the Agromyzid fauna of Iceland and the Faroes cannot be the result of aerial dispersal. The only remaining explanation of post-glacial introduction is human agency. For the Agromyzidae this possibility may be discussed under three headings:

- (i) Accidental transport of adults.
- (ii) Transport of puparia in soil, hay or other dead vegetable material.
- (iii) Transport of eggs, larvae or puparia in living or still fresh plant material.

In the case of distant islands the accidental transport of adult Agromyzids may be disregarded as a means of explaining the origin of the fauna, although, now that air traffic is so widespread, it is possible that occasional introductions will occur by this means. Turning to the second alternative, according to Lindroth (1931) there was never traffic in ballast to Iceland, so that the Icelandic fauna is not to be explained by this means. He states however that there has in the past been a considerable traffic in hay to Iceland for feeding animals. It is probable that some grass-feeding Agromyzidae could be introduced by this traffic — but not all. The important distinction lies in the method of pupation. Puparia of species which leave the leaf to pupate in the ground are not likely to be transported with a hay-crop. But puparia which remain in the leaf will easily be transported in this way. Of the grass-feeders in the Icelandic and Faroese fauna the *Agromyza* sp. and *Liriomyza richteri* Hering may be assumed (although this is not yet confirmed) to leave the leaf to pupate, while *Phytomyza nigra* Meigen and *P. milii* Kalténbach are known to pupate *in situ*. The introduction of the latter two species in hay is thus a very reasonable possibility.

There are many examples of the introduction of Agromyzidae associated with crops or garden plants which are to be explained by the transport of the immature stages — whether eggs, larvae or puparia — in living or still fresh plants. For instance *Tylo-*

myza pinguis Fallén can be bred easily from Belgian chicory (*Cichorium endivia* L.) on sale in Britain. The presence of an introduced element associated with cultivated plants in the Icelandic fauna is well-known, and may be expected to contain some Agromyzid species. However all the material before me has been collected in natural habitats mostly far removed from the centres, such as Reykjavík, where such an element is most in evidence. I am consequently unable to give any account of Agromyzidae associated with human cultivation. Of the recorded species one — *Phytomyza atricornis* Meigen — has been widely spread by human agency, and it is consequently difficult to know its original range. However it is generally assumed to be holarctic in origin and may not be introduced in Iceland. A more definite conclusion may be possible when its habitat tolerance and distribution in Iceland are better known.

To summarise, there are thus only three species found in Iceland and the Faroes which may reasonably be thought to be introduced by human agency. These are: *Phytomyza atricornis* Meigen, *P. nigra* Meigen and *P. milii* Kaltenbach. But none of these species seems restricted to man-made habitats, and they may just as likely be indigenous. No convincing explanation can be adduced for the postglacial introduction of the other species recorded from Iceland and the Faroes.

(e) Conclusion.

I have concluded that with the exception of a few species the Icelandic fauna can reasonably be explained only by Lindroth's hypothesis that species which entered Iceland from Europe over a land-bridge during an interglacial period survived there during at least one period of glaciation in an ice-free zone. The Faroes must be considered as a remnant of this land-bridge. For the reasons given in the previous section I believe that any explanation of the fauna of Iceland and the Faroes in terms of postglacial aerial dispersal is untenable and the composition of the fauna is such that it is, to say the least, highly improbable that it can be the result of accidental introduction by man. These conclusions agree with those reached by workers in other groups.

The single Icelandic species thought to be of Greenlandic/American origin may be considered either to have been intro-

duced by the prevailing winds from Greenland, or, alternatively, it may be supposed to have reached Greenland at a time when the land-bridge with Iceland was still unbroken. I am not on present information able to judge between these two hypotheses.

The absence of any obvious morphological differentiation in the Icelandic and Faroese species of European origin suggests that this element in the fauna has not survived in these islands since the tertiary period. This too accords with Lindroth's theory of interglacial arrival.

Appendix I — A new Subspecies in the *Phytomyza milii* Group.

Phytomyza opacella glacialis ssp. nov.

To be compared with *P. opacella opacella* Hendel as follows:

Eye in profile only a little higher than wide (fig. 15 e). Cheeks and orbits clearly visible as an even ring around the eye. The two upper orbitals are of equal length, directed backwards: the first pair of lower orbitals are directed inwards, closely adpressed to the frons (hence not outstanding in profile): second lower orbitals absent (holotype and allotype) or very small (paratype ♂). Orbital setulae long, 5 or 6 in number. 3rd antennal segment short and rounded; arista short, slightly thickened basally.

Acrostichals in 3-4 rows, not reaching beyond the third dorso-central. 2nd costal segment 2.7—3.0 times as long as the 4th.

Colour. Head paler than in related species. Frons mostly ochreous yellow, only a little darkened in its centre above the antennae. Ocellar triangle and vertex contrastingly dark. Face, cheeks and jowls all ochreous yellow. Mesonotum matt, only weakly shining. Legs uniformly dark brown, only the apex of the front femur slightly paler. Wing-base yellow; squamae grey with a dark fringe.

♂ genitalia. Surstyli bearing a dense cluster of short blunt spines (fig. 15 c). Aedeagus (figs. 15 a and 15 b) differing in lateral view from that of the typical subspecies mainly in the shorter paraphalli and the more weakly sclerotised circular sclerite (outer part of hypophallus). In the paratype ♂ the paraphalli form a narrow angle with the distiphallus. In ventral view the hypophallus and paraphalli are similar in appearance to those of *P. milii* Kaltenbach (compare figs. 12 b and 13 b). Ejaculatory bulb (fig. 15 d) minute.

Holotype ♂, Björkliden, Torne Lappmark, Sweden, 12. vii. 54 (Rydén).

Allotype ♀, Docksta, Ångermanland, Sweden, 18. vi. 56 (Rydén).

Paratype ♂, Enontekis, Finnish Lappland (Frey)*.

The holotype and allotype are in Rydén's collection in the Lund University Zoological Institute, Lund, Sweden, and the paratype ♂ in the Naturhistorisches Museum, Wien.

The most important external differences between the new subspecies, *P. opacella opacella* Hd. and *P. milii* Kaltenbach may be summarised as follows:

<i>P. milii</i> Kalt.	<i>P. opacella opacella</i> Hd.	<i>P. opacella glacialis</i> ssp. nov.
Frons all more or less dark.	Frons generally dark at its centre but the orbits and around the sides of the ocellar triangle yellow-brown.	Frons nearly all ochreous yellow.
Two pairs of lower orbital bristles.	Two or sometimes three pairs of lower orbital bristles.	Second pair of lower orbital bristles weak or absent.
3rd antennal segment longer than high with a distinct apical fringe of hairs.	3rd antennal segment more or less round, without an apical fringe.	3rd antennal segment more or less round, without an apical fringe.
Orbits not or barely visible above the eye in profile.	Orbits raised above the eye in profile.	Orbits raised above the eye in profile.
Mesonotum somewhat shining.	Mesonotum matt.	Mesonotum matt.
Surstyli with weak hairs only.	Surstyli with a dense patch of hairs.	Surstyli with a conspicuous patch of blunt black spines.

The principal differences between *P. opacella glacialis* ssp. nov. and the typical subspecies are (i) the spines on the surstyli, (ii) the form of the distal segments of the aedeagus, (iii) the yellow frons and (iv) reduction or loss of the second lower orbital bristle. On present information it is not possible to be certain if the form merits specific or subspecific rank, but, as it appears to be a geographical vicariant of the typical *opacella*, I favour subspecific status.

In the key given by Hendel (1931-6) *P. opacella glacialis* will run to couplet 118. The inclusion of *P. opacella* Hd. in couplet

* Other records of *P. opacella* Hd. from Finland are given by Frey, 1946, Notul. ent., 26: 13-55. I had unfortunately overlooked that paper when writing this account.

119 is probably based on the paratype of subsp. *glacialis* in Hendel's collection, but according to the costal ratio the subspecies is misplaced there. I do not think there is any point in adding to the numerous published amendments of this key, as it is clear that some radical breakdown of the genus *Phytomyza* into the several natural groups which it contains is needed to replace the existing key, which, with its numerous published amendments, has become far too complex. The other species which run to couplet 118 are not at all related and should not be confused with *P. opacella opacella* Hd. or *P. opacella glacialis* ssp. nov.

Phytomyza luzulae Hering (genitalia at figs. 16 a-c) also belongs to the *mili* group, but will not be confused with the above species by reason of its paler coloration — the tips of all the femora are broadly yellow, the first and the second antennal segments red-brown and the squamae and squamal fringe are pale.

Appendix II — The Genital Characters of the *Phytomyza robustella* Group.

The first species described in this group were *Phytomyza penicilla* Hendel and *P. robustella* Hendel (Hendel, 1931-6). The latter species is described in the text as "*Phytomyza robusta* sp. nov.", but the new name *robustella* is substituted in the index, after Hendel had discovered that the name *robusta* was preoccupied.

The first breeding record of a species of this group was of *Phytomyza cecidonomia* Hering, bred from "gall-mines" in the leaf-bases of *Hypochaeris radicata* L. (Hering, 1937). Subsequently he and Dr. H. Buhr bred further species which were described as *P. crepidocecis* Hg. from *Crepis biennis* L. and *P. taraxacocecis* Hg. from *Taraxacum officinale* agg. (Hering, 1949), *P. picridocecis* Hg. from *Picris hieracioides* L. (Hering, 1957) and finally *P. aracioccecis* Hg. from *Crepis paludosa* (L.) Moench (Hering, 1958). Buhr (1955) also established that *P. penicilla* Hendel breeds in *Lactuca serriola* L.

However of the bred species only *P. penicilla* Hd. has hitherto been recognised in caught material, because of its characteristic antennae. The other species of the group have been recorded indiscriminately as *P. robustella* Hd. Hering (1957) made a brave attempt to construct a key based on external characters,

but the differences observed are not sufficiently clear-cut to allow accurate determination of caught material. While studying the Faroese species (*P. taraxacocecis* Hg.) I examined the genitalia of all the above species and found that there are striking and obvious differences in the aedeagus, which should allow certain identification of caught males. I have illustrated these differences in the hope that my figures will enable more accurate determination of caught material in the future. For the biology of these species reference should be made to Hering (1949 and 1958) and Buhr (1955).

Phytomyza robustella Hendel, 1936, Flieg. pal. Reg., 59: 567.
(nomen novum for *Phytomyza robusta* Hendel *loc. cit.*: 470, nec Meunier, 1905)

Phytomyza crepidocecis Hering, 1949, Notul. Ent., 29: 28—29. **Syn. nov.**

Distiphallus (figs. 17 a, 17 b) consisting of two very elongate tubules, which extend laterally, and then curve downwards. Ejaculatory bulb (fig. 17 c) relatively small.

The genitalia of three specimens have been examined. That figured belongs to one of Hendel's specimens from Langenzersdorf, Austria (in the Naturhistorisches Museum, Wien). Hendel obtained a series of six specimens from this locality and, although the mount labelled as "type" supports two females, the six specimens clearly form a homogeneous series, and there is no difficulty about using the male figured to characterise the species. The male of *P. crepidocecis* Hg. from *Crepis biennis* L. (Mühlhausen, Thuringia, emerged 18. vi. 55) which Professor Hering has kindly lent me is clearly identical. A further male in Professor Hering's collection bred from the stem of *Crepis biennis* L. (Kyffhäuser, Thuringia, emerged 23. ix. 62) is also the same species.

Previous published records of this species all require revision, as many of them will refer to related species (particularly *P. taraxacocecis* Hg.).

Phytomyza taraxacocecis Hering, 1949, Notul. Ent., 29: 29—30.

Tubules of the distiphallus (figs. 18 a, 18 b) closely approximated, rather hook-shaped. Ejaculatory bulb (fig. 18 c) very small. See above on page 410.

The genitalia of six specimens have been examined. The ex-

ample from the Faroes is referred to on page 410; the data of the other five examples is as follows:

Holotype ♂ bred from *Taraxacum officinale* agg., Mönkveden, Mecklenburg, Germany, emerged 25. v. 48 (in the Humboldt University Museum, Berlin).

Berlin, 28. v. 29 (Hering).

Wieslock, Mühlhausen, Thuringia, 5. vi. 58 (K. A. Spencer).

Berlin, Dahlem, 2. vi. 55 (Hering).

From puparia in *Taraxacum* sp., 5. v. 63, on the lawn in my garden at East Barnet, Herts., emerged 29. v.

This appears to be one of the commonest species in the *robustella* group.

Phytomyza picridoecis Hering, 1957, Bestimmungstab.,
Bd. III: 20—21.

The tubules of the distiphallus (figs. 19 a, 19 b) are closely approximated, but differently shaped from *taraxacoecis*. Ejaculatory bulb not examined.

The figure is of Hering's holotype, bred from *Picris hieracioides* L., Mühlhausen, Thuringia, emerged 27. vi. 55, which was the only specimen seen.

Phytomyza aracioecis Hering, 1958, Deutsch. ent. Z., 5: 390-1.

Distiphallus (fig. 20 a, 20 b) forked. Ejaculatory bulb (fig. 20 c) large, heavily sclerotised about its base.

The figure is of Hering's holotype bred from *Crepis paludosa* (L.) Moench, Mühlhausen, Thuringia, emerged 1. vi. 57, which was the only specimen seen.

Phytomyza penicilla Hendel, 1936, Flieg. pal. Reg., 59: 452.

The genitalia of this species have not been figured separately, as they are extremely close to those of *P. aracioecis* Hg. The ejaculatory bulb is not heavily sclerotised about its base, as in the *aracioecis* holotype, but apart from this feature the differences are trivial.

It is fortunate that the two species of the group which are not obviously different from their genitalia can be distinguished on external characters. The long hairs on the third antennal segment of *P. penicilla* Hd. appear to be a constant character, and in view of this feature and the different host I do not doubt that this species and *P. aracioecis* Hg. are distinct. A forked distiphallus is found in other unrelated *Phytomyza* spp. and may possibly be a plesiomorph feature.

The genitalia of two males have been examined, both bred from *Lactuca serriola* L., one from La Baule, Loire, France, emerged 14. iv. 43, and the other from Mühlhausen, Thuringia, Germany, emerged 3. ix. 61 (both collected by Buhr but now in K. A. Spencer's collection).

Phytomyza hedingi Rydén, 1953, Ent. Medd., 26: 467-8.

Male unknown. Doubtfully distinct from *P. penicilla* Hd. (see above on page 404).

Phytomyza cecidonomia Hering, 1937, Blattminen N.- u. M.-Europas: 583.

Tubules of distiphallus (figs. 21 a, 21 b) short and straight. Ejaculatory bulb (figs. 21 c) very small.

Three preparations have been examined; that figured is of a male caught at Kunnersdorf, near Görlitz, vii. 55; one was a paratype bred from *Hypochoeris radicata* L. at Körkwitz, Mecklenburg, emerged 1. vii. 36 (leg. Buhr but now in the author's collection); the other was a paratype of ssp. *britannica* Griffiths, 1956, bred from puparia taken 22. v. 55 in *Hypochoeris radicata* L. at Chiddingfold, Surrey, England, emerged 21. vi. 55.

Although the distiphallus is more or less constant in all three preparations the paraphallic complex is variable, and more material is needed to clarify the significance of this variation.

Phytomyza rhabdophora sp. nov.

Tubules of distiphallus (figs. 22 a, 22 b) widely separated, characteristically club-shaped. Hypophallus short. Ejaculatory bulb (fig. 22 c) larger than in related species.

External morphology. Frons in dorsal view about twice as wide as an eye. In profile the eyes are about 4 times as high as the jowls; orbits only narrowly visible above the eyes. 4 orbital bristles: about 7 orbital setulae. 3rd antennal segment with short upturned pubescence. 6-7 pairs of acrostichals reaching to the fourth dorsocentral. Wing. 2nd costal segment about 2.4 times as long as the 4th.

Otherwise as for *P. robustella* Hendel.

Colour. As in *P. robustella* Hd. except that the rear eye-margins are darkened on their upper half as far as the inner vertical bristles.

Holotype ♂, Lausitz, Rotstein, 27. vi. 55 (Hering 6091), retained in Professor Hering's collection (Berlin, Dahlem, Reichensteiner Weg, 21).

The above account has only dealt with the species attacking Compositae Liguliflorae. I have not made any search to see if other species should be associated with this group, but certainly *Phytomyza cardui* Hering (bred from *Carduus* and *Cirsium*) is rather closely related to the above species and may be included with them in the *robustella* group.

Acknowledgements.

My thanks are due to the following for the loan of material from Iceland and the Faroes: Mr. Leif Lyneborg and Mr. Jens Böcher of the Zoological Museum, Copenhagen; Mr. Hugo Andersson of the Zoological Institute at Lund University; Mr. H. W. Waldén of the Göteborg Natural History Museum. Type material for establishing the absolute identity of the species recorded was kindly made available by: Professor E. M. Hering; Dr. H. J. Hannemann of the Humboldt University Museum, Berlin; Dr. M. Beier of the Naturhistorisches Museum, Wien; Mr. Hugo Andersson of the Zoological Institute at Lund University; Mr. K. A. Spencer; Mr. Carl-Johan Hedqvist of the Naturhistoriska Riksmuseet, Stockholm. Were it not for their liberal attitude reliable identification of some of the species would have been impossible.

Professor C. H. Lindroth was kind enough to look through the manuscript. Mr. Andersson provided me with ecological notes on the material collected by the Lund University Expedition to Iceland, which help was particularly valuable as I am not personally acquainted with the island. These notes form the basis of the paragraphs on ecology in this paper. Mr. Leif Lyneborg and Dr. S. L. Tuxen also deserve especial thanks for checking the orthography of the place-names.

Dr. J. T. Nowakowski gave valuable assistance in interpreting the *Cerodontha* species.

Summary.

1. The author has examined all material of Agromyzidae (Diptera) found on Iceland and the Faroes which is known to him. The results of this examination are that the following species are recorded for both regions:

Phytomyza atricornis Meigen, *P. fallaciosa* Brischke, *P. milii* Kaltenbach, *P. nigra* Meigen, *P. opacella opacella* Hendel, *P. ranunculi* Schrank, *P. tenella* Meigen, *P. varipes* Macquart.

The following three species are recorded for Iceland only:

Cerodontha (Dizygomyza) lindrothi sp. nov., *Liriomyza riecherti* Hering, *Phytomyza angelicae* Kaltenbach.

The following three species are recorded for the Faroes only:

Phytomyza archangelicae Hering, *P. evanescens* Hendel, *P. taraxacocecis* Hering.

In addition there are four species whose identity has not been established because of inadequate material. These are an *Agromyza* sp. and a *Cerodontha (Dizygomomyza)* sp. from the Faroes and two *Phytomyza* spp. from Iceland.

2. *Cerodontha (Dizygomomyza) lindrothi* sp. nov. is described from Greenlandic and Icelandic material. This is the only Agromyzid in the Icelandic fauna which is confirmed not to be of European origin.

3. Excluding the four species of doubtful identity, it is shown that the Faroese fauna consists of 11 species, all of European origin, of which 8 reach Iceland and 3 also Greenland. In Iceland there are 9 species of European origin (of which only one has not been found in the Faroes) and one species, the new *Cerodontha*, which probably represents a Greenlandic/American element. In addition *Liriomyza richteri* Hering is very tentatively classified as Arctic, but its distribution is not yet adequately known.

4. The author comments on the distribution of the species within Iceland and the Faroes and their host-plant association, although the information available is very inadequate.

5. The author considers the implications of his studies on the Agromyzid fauna for Prof. C. H. Lindroth's theory that most of the Icelandic fauna has reached the island by a land-bridge from Europe during an interglacial period. Consideration of the composition of the fauna and the means of dispersal of Agromyzid species lead him to the conclusion that post-glacial overseas introduction of the entire Agromyzid fauna, whether by air currents or human agency, is incredible (only for three species does introduction by human agency seem possible) and Lindroth's land-bridge theory provides the only acceptable explanation for the present fauna. The close relationship of the Faroese to the Icelandic fauna is explained by those islands being a remnant of such a bridge.

6. In Appendix I a new subspecies of *Phytomyza opacella* Hendel from Lappland is described. Appendix II summarises the results of an examination of the genitalia characters of European species of the *Phytomyza robustella* group, including the description of a new species.

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Note on figures. Scale 0.1 mm. All lateral and ventral view figures are drawn from the left side (i. e. the head of the insect should be imagined as facing the left-hand margin of the page).

Fig. 1. *Liriomyza richteri* Hering lectotype. a, aedeagus in lateral view; b, distiphallus in ventral view; c, ejaculatory bulb.

Fig. 2. *Phytomyza angelicae* Kaltenbach bred from *Angelica sylvestris* L., Iceland. a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb.

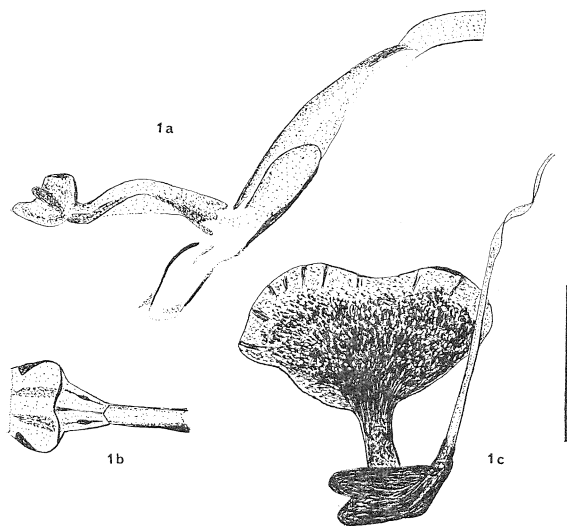


Fig. 1.

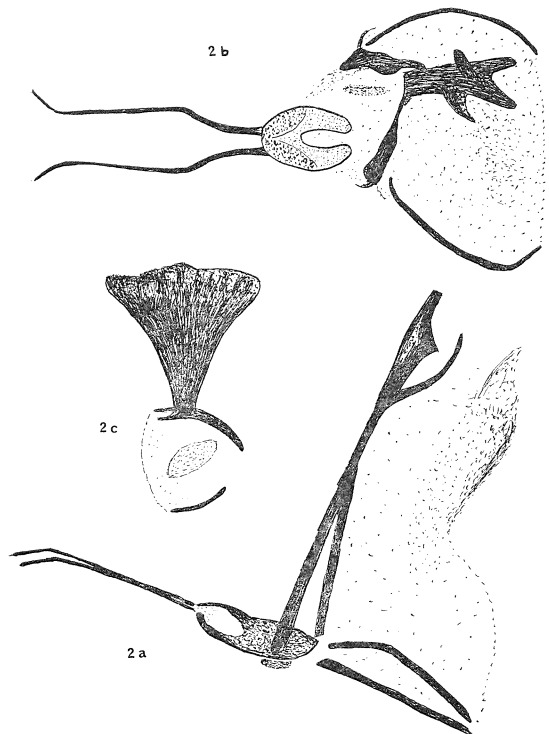


Fig. 2.

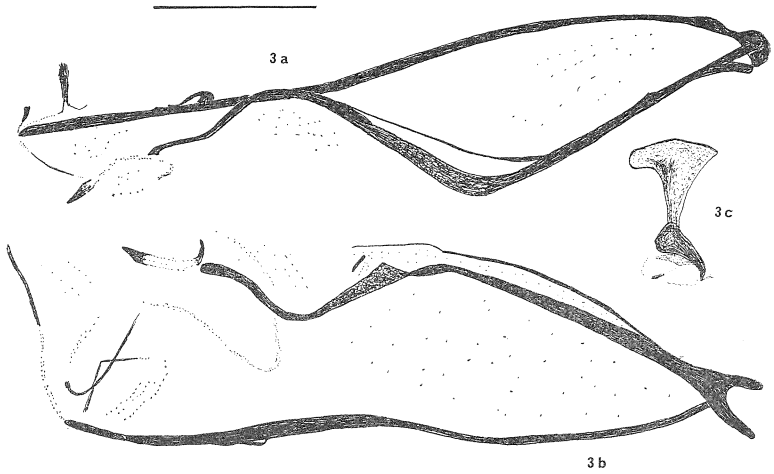


Fig. 3. *Phytomyza archangelicae* Hering, Faroes. a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb.

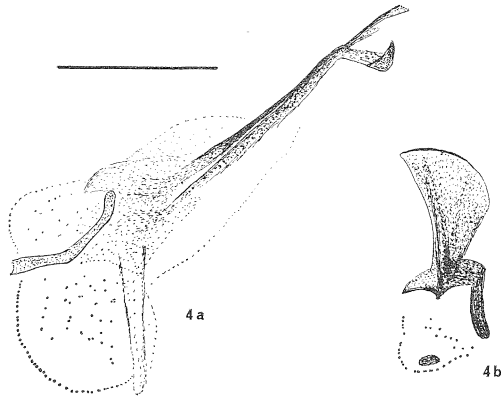


Fig. 4. *Phytomyza atricornis* Meigen, Iceland (Bæjarstaðaskógur). a, aedeagus in lateral view; b, ejaculatory bulb.

Fig. 5 a-f. *Phytomyza evanescens* Hendel, Faroes (Tórshavn). a, aedeagus, postgonite, aedeagal hood and part of aedeagal apodeme (lateral view); b, aedeagus in ventral view; c, ejaculatory bulb; d, 9th sternite and hypandrial apodeme (ventral view); e, abdominal segments 2-8 in lateral view (with tergites numbered); f, 9th tergite and surstylus in lateral view.

Fig. 5 g. *Phytomyza evanescens* Hendel holotype; surstylus in lateral view.

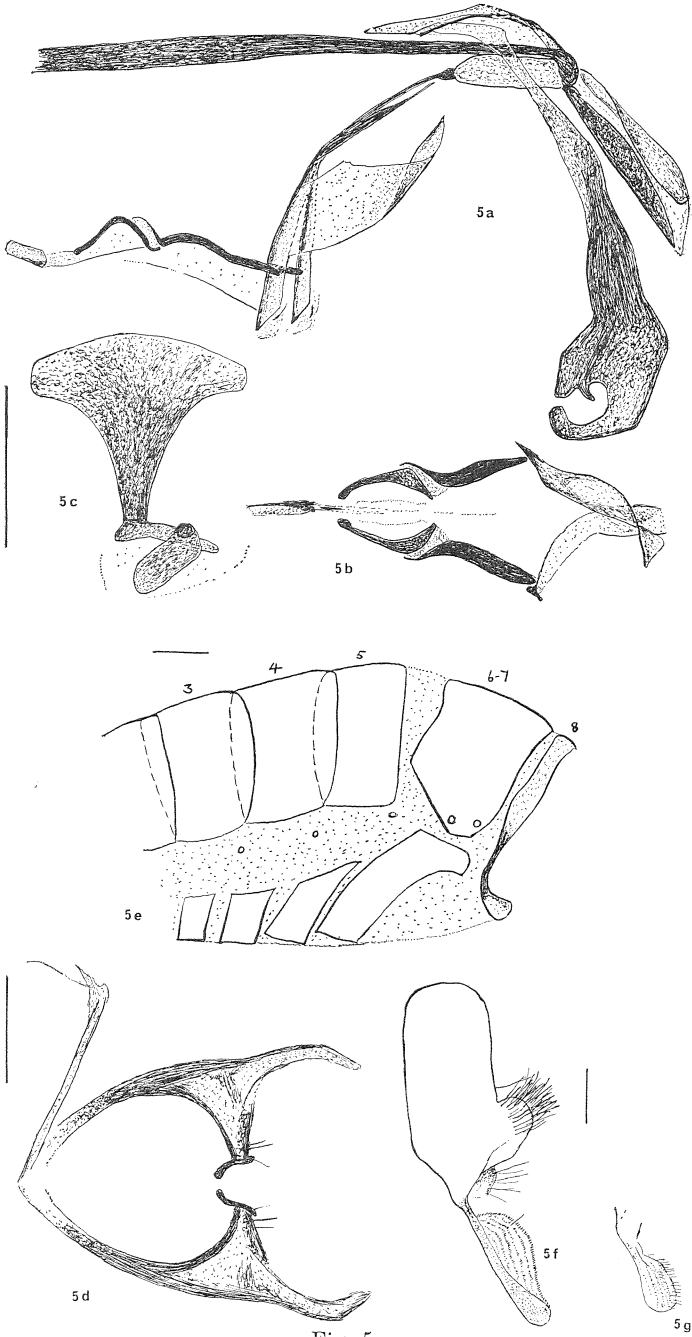


Fig. 5.

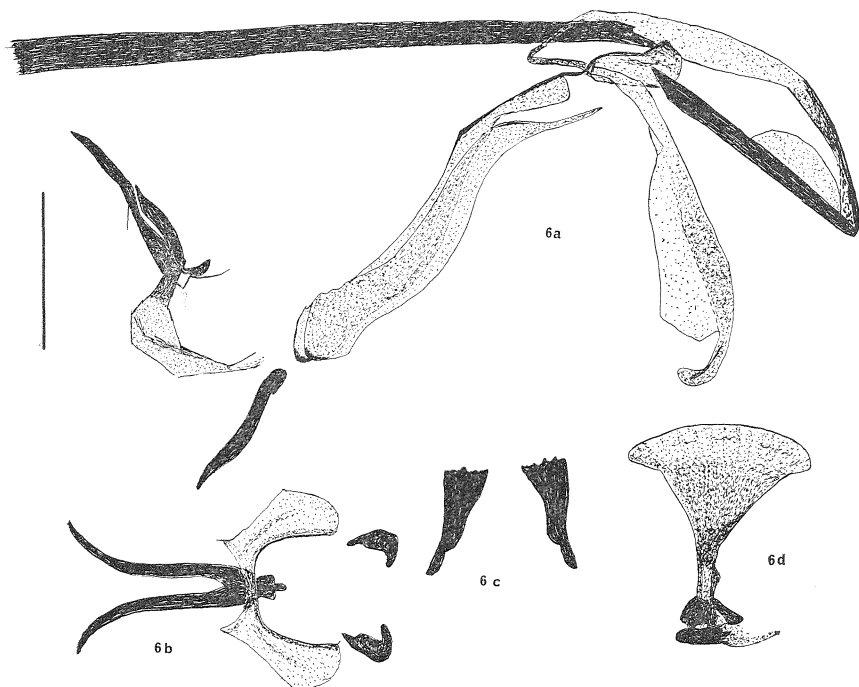


Fig. 6. *Phytomyza fallaciosa* Brischke, Faroes. a, aedeagus, postgonite, aedeagal hood, and part of aedeagal apodeme (lateral view); b, distiphallus, paraphalli and hypophallus in ventral view; c, hypophallus in posterior view; d, ejaculatory bulb.

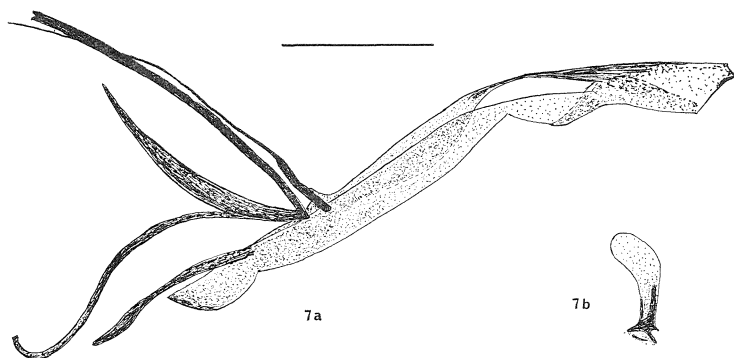


Fig. 7. *Phytomyza nigra* Meigen, Faroes. a, aedeagus in lateral view; b, ejaculatory bulb.

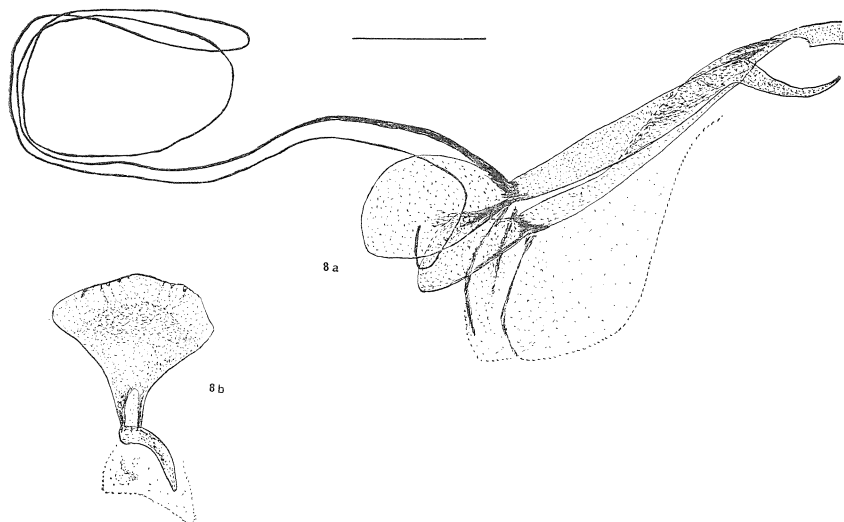


Fig. 8. *Phytomyza ranunculi* Schrank, Faroes (leg. Hansen). a, aedeagus in lateral view; b, ejaculatory bulb.

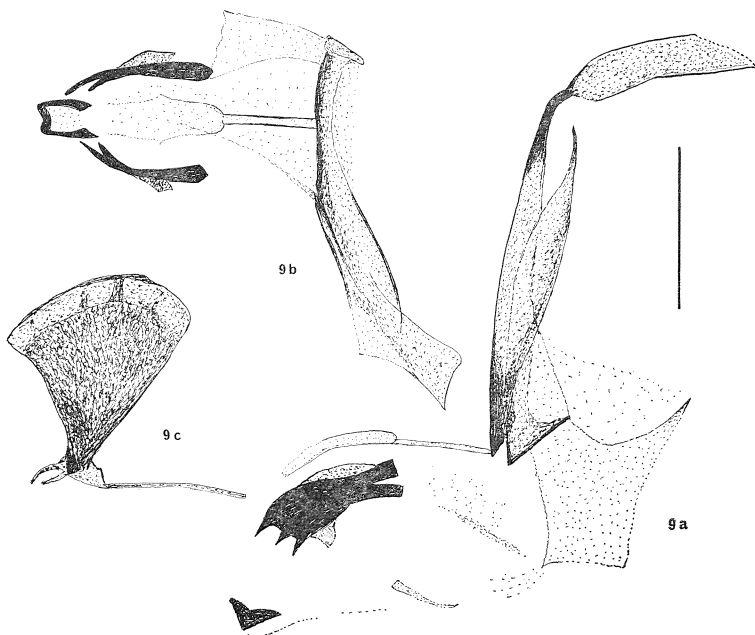


Fig. 9. *Phytomyza tenella* Meigen, presumed holotype from the Winthem collection. a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb.

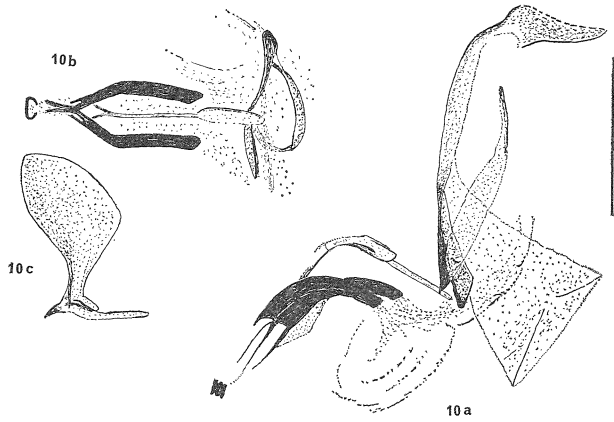


Fig. 10. *Phytomyza tenella* Meigen, Faroes. a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb.

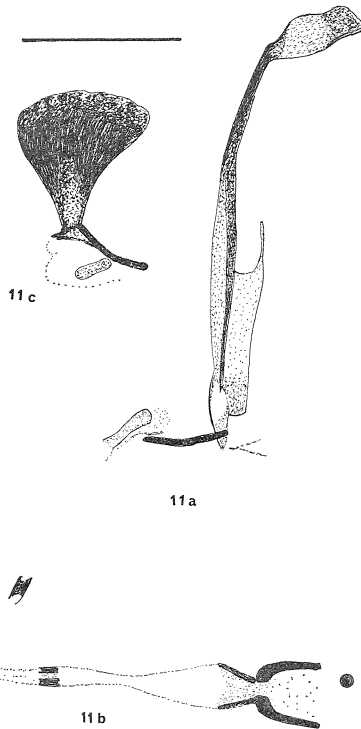


Fig. 11. *Phytomyza varipes* Macquart, Iceland (Skaftafell). a, aedeagus in lateral view; b, distiphallus and paraphalli in ventral view; c, ejaculatory bulb.

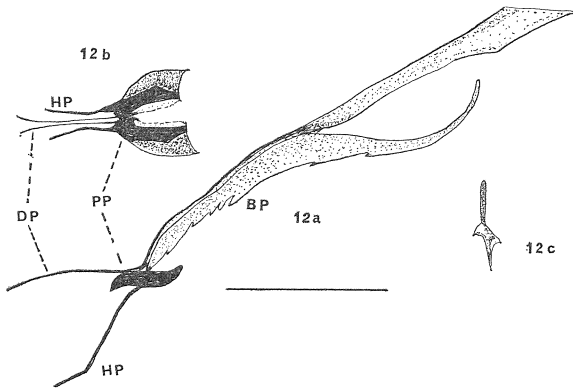


Fig. 12. *Phytomyza milii* Kaltenbach bred from *Milium effusum* L., England. a, aedeagus in lateral view; b, distiphallus, paraphalli and hypophallus in ventral view; c, ejaculatory bulb. BP basiphallus, HP hypophallus, PP paraphalli, DP distiphallus.

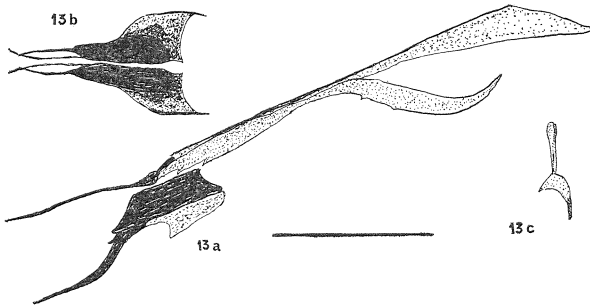


Fig. 13. *Phytomyza milii* Kaltenbach, Faroes. a, aedeagus in lateral view; b, distiphallus, paraphalli and hypophallus in ventral view; c, ejaculatory bulb.

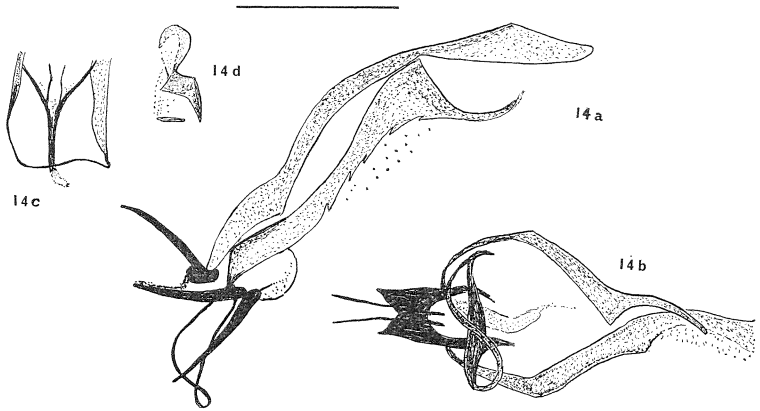


Fig. 14. *Phytomyza opacella opacella* Hendel, Faroes. a, aedeagus in lateral view; b, aedeagus in ventral view; c, posterior view of hypophallus; d, ejaculatory bulb.

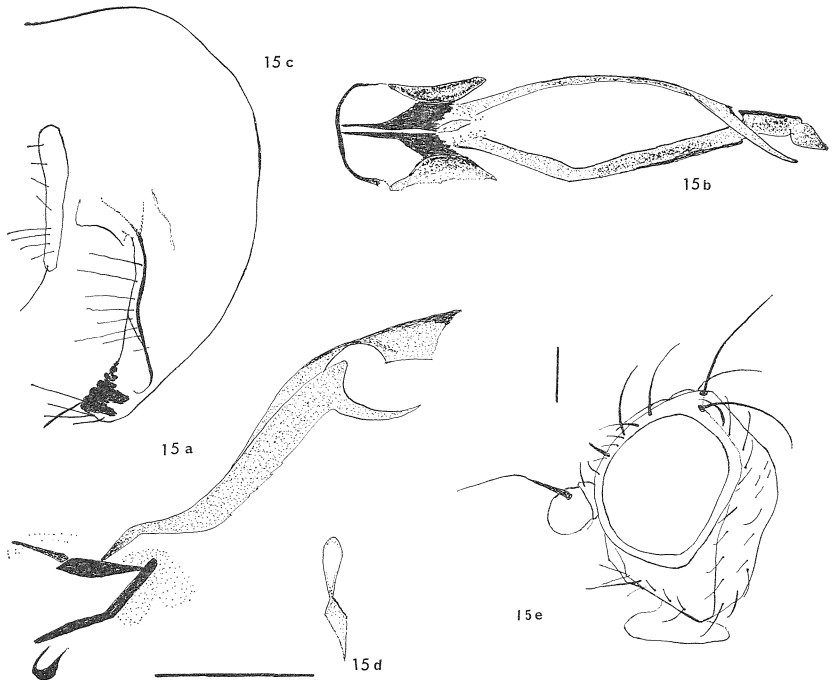


Fig. 15. *Phytomyza opacella glacialis* ssp. nov. holotype. a, aedeagus in lateral view; b, aedeagus in ventral view; c, part of 9th tergite with surstylus (posteroventral view); d, ejaculatory bulb; e, head in lateral view.

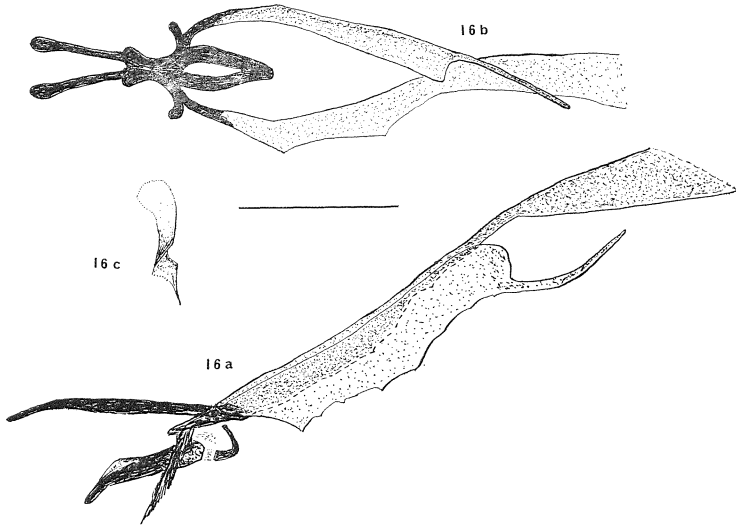


Fig. 16. *Phytomyza luzulae* Hering bred from *Luzula* sp., Germany (Stuttgart). a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb.

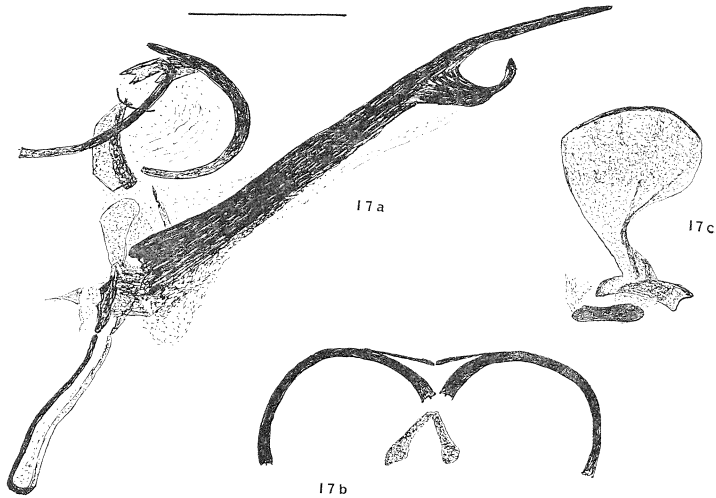


Fig. 17. *Phytomyza robustella* Hendel (from series containing the types). a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view; c, ejaculatory bulb.

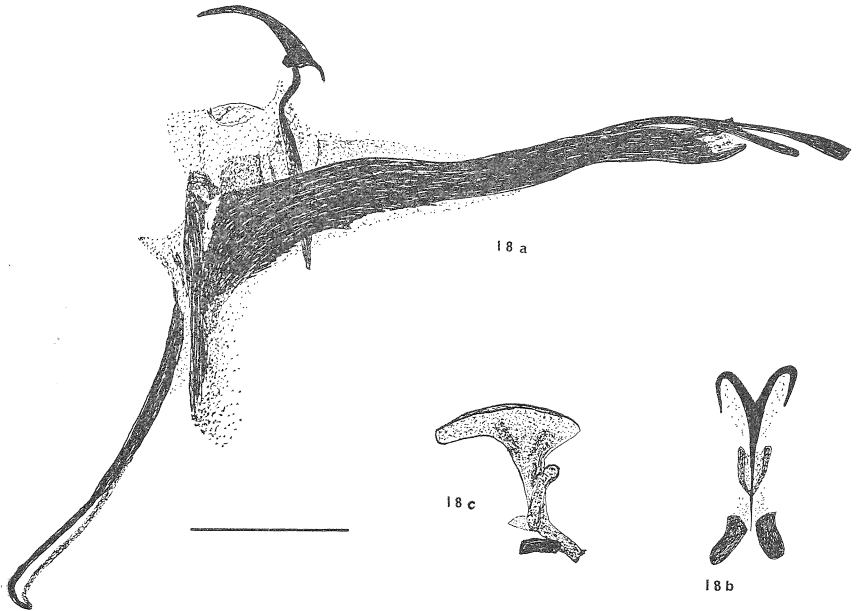


Fig. 18. *Phytomyza taraxacoecis* Hering, Faroes. a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view; c, ejaculatory bulb.

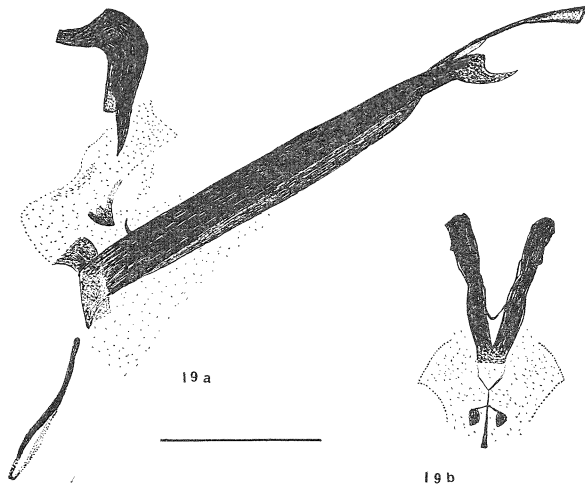


Fig. 19. *Phytomyza picridoecis* Hering holotype. a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view.

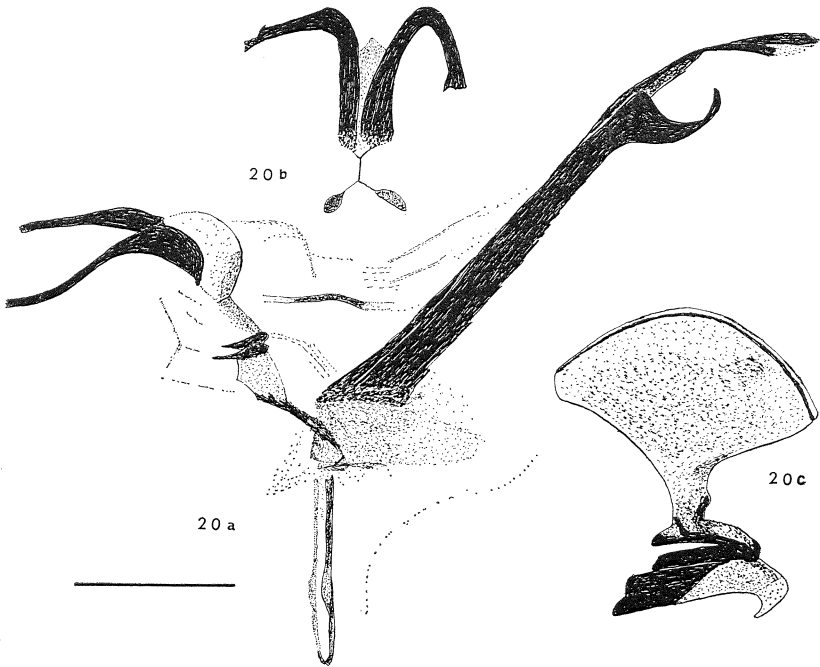


Fig. 20. *Phytomyza araciocecis* Hering holotype. a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view; c, ejaculatory bulb.

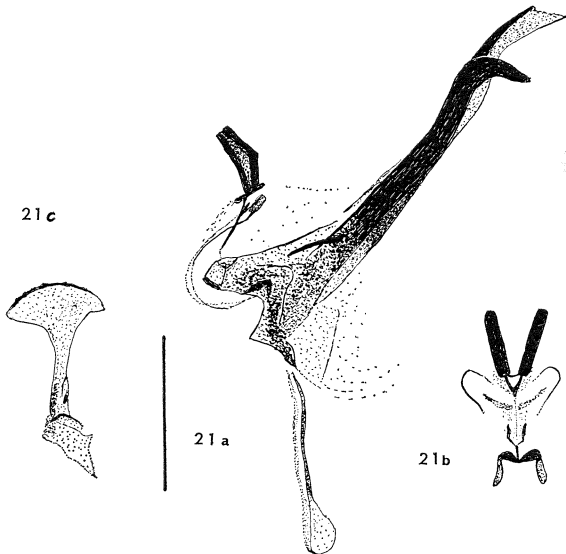


Fig. 21. *Phytomyza cecidonomia* Hering, Germany (Görlitz). a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view; c, ejaculatory bulb.

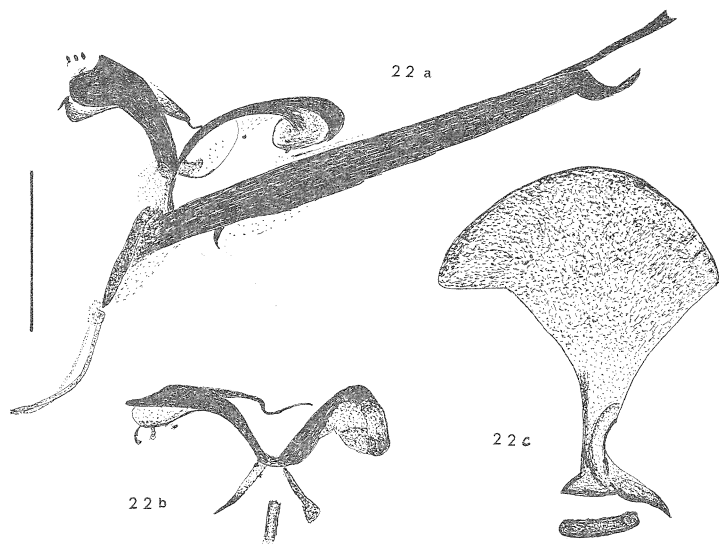


Fig. 22. *Phytomyza rhabdophora* sp. nov. holotype. a, aedeagus in lateral view; b, distiphallus and associated sclerites in anterior view; c, ejaculatory bulb.

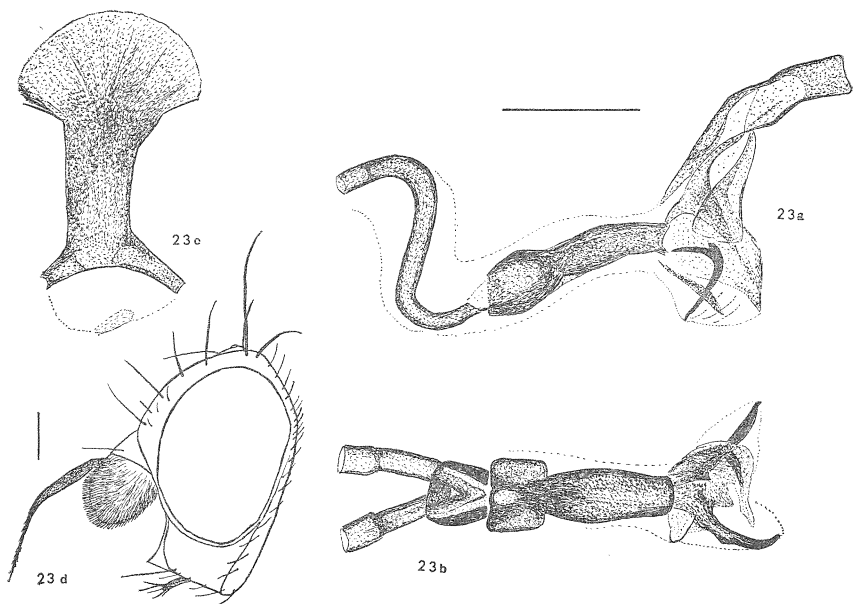


Fig. 23. *Cerodontha (Dizygomyza) lindrothi* sp. nov. a-c, holotype. a, aedeagus in lateral view; b, aedeagus in ventral view; c, ejaculatory bulb. d, paratype ♂, Iceland, Mælifell; head in lateral view.