

EVOLUTIONARY PATTERNS IN GALL MIDGE — HOST PLANT ASSOCIATIONS (DIPTERA, CECIDOMYIIDAE)

by

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ABSTRACT

Host plant associations of mainly West Palaearctic gall midges have been analyzed to explain some of the radiation of this highly specialized group of endophytophagous insects. Gall midges behave according to some predictions formulated for phytophagous insects in general: woody host plants accumulate more gall midge species than herbaceous ones. In other aspects gall midges seem to be different: taxonomical affinity of host plants might be more important to explain radiation in gall midges than it is for other groups of plant feeders, especially external feeders. Furthermore, gall midges deserve particular attention because the gall inducing feeding mode in this group might be a result of polyphyletical development. Specialization on host plant organs has been analyzed to support this assumption. Finally, various evolutionary processes allied with insect—host plant interactions have been analyzed for gall midges. Sequential evolution could be demonstrated in this group and some examples of apparent parallel cladogenesis, each dealing with a different rank of host plant taxonomy, are treated.

INTRODUCTION

According to recent estimates, about 792,000 species of insects have been described, of which 46% feed upon plants (Southwood, 1978; Price, 1977). Important pioneer work on insect—host plant interactions has been done by Verschaffelt (1910), Dethier (1954) and Fraenkel (1959). The enormous expansion of literature on this subject began with the classic papers by Ehrlich & Raven (1964) on co-evolution, MacArthur & Wilson's (1967) theory of island biogeography and Janzen's (1968) application of the latter theory to insect-host plant interactions. Recent books by Crawley (1983) and Strong et al. (1984) offer a thorough introduction to the literature on this subject. Plant chemistry and, because related plant taxa often share similar compounds, plant taxonomy played an important role in earlier studies. Gradually more host plant traits became involved to explain accumulations of insect species on host plant taxa. Fowler & Lawton (1982), for example, used no less than nine variables, a potpourri of characteristics of host plants, phytophages and natural enemies of phytophages in a multiple regression calculation to explain the species richness of leafminers on British Umbelliferae. In the latter study, host plant taxonomy is not even a significant factor

anymore: 61% of the variation is explained by habitat diversity and leaf form of the host plants. In another study, however, about leaf-miners on British trees, 36% of the variation was caused by taxonomical diversity alone, geographic range being the second trait in importance (Godfray, 1982).

When the literature is subdivided according to the different guilds of phytophagous insects, it is remarkable that papers dealing with external plant feeders (chewing and sucking insects) are abundant, whereas references on endophytophages, such as miners and gall insects are scarce. Nevertheless it is obvious that not only among external plant feeders, but also among endophytophages there are many species with an important impact on host plant development and seed production, in natural situations (e.g., Harnett & Abrahamson, 1979), as well as in pest control (e.g., Bess & Haramoto, 1959) and in agriculture (e.g., Skuhravý et al., 1983). Furthermore, in important aspects endophytophages differ basically from external plant feeders and deserve therefore special attention. Gall insects in particular not only depend on plants for nutriment, but also for shelter, which is constructed by manipulating the defense reactions of the host plants. This very precise tuning of

the insect's needs to the plant's potentials may explain why polyphagous gall insects (species attacking host plants belonging to different families) are extremely scarce, whereas monophagous species are abundant. For this reason ecological opportunists (species shifting to new host plants which are in close proximity to, rather than taxonomically related with, the original ones) may be rare too among this group. A further consequence of the gall inducing feeding mode is that colonization of new resources by these insects, but also by miners, is a substantially slower process (Strong et al., 1984). Therefore, long term processes, playing in "evolutionary time", rather than short term processes, in "ecological" time, seem to be more apparent in interactions between host plants and gall midges.

The present study deals with host plant relations of mainly West Palaearctic gall midges. Compared with other groups of endophytophages, gall midges have some advantages. As a group, they have a broad host plant spectrum, whereas cynipids, another main group of gall insects, are abundant on Fagaceae and Rosaceae only. Agromyzids are also an important group of endophytophages, but are restricted to particular plant organs, mainly leaves.

Until now, it has been impossible to analyze host plant relations of gall midges on a world basis since the detailed knowledge needed for such a study is only available for some parts of the temperate regions. Therefore this study is restricted to data presented by Buhr (1964—1965) and Skuhrová (in press) for the West Palaearctic, extended in some cases, where information from the Nearctic was necessary, to Felt (1940) and Gagné (1969, 1981). Whether the results will hold for other climatic areas must be considered in future.

In the next section some main characteristics will be given of the ecology and taxonomy of gall midges. Which life history traits of gall midges are important in connection to host plant relations and change of host plants? How are the Cecidomyiidae, the family gall midges belong to, subdivided and which group(s) gave rise to gall inducers? Gall midges may be unique among gall insects, because arguments exist for a polyphyletic transition of Cecidomyiidae to the gall inducing feeding mode (Mamaev, 1968). A comparison will be made for subgroups of gall midges to investigate whether specialization to different host plant organs (vegetative or gen-

erative) may contribute evidence for such a polyphyletic shift.

Subsequently, our attention will be focussed on host plant diversity. Because an analysis of evolutionary aspects is our main goal, only taxonomical and some structural diversity of host plants will be considered to explain radiation of gall midges. Taxonomically diverse plant families, including many species, are supposed to support more midge species than less diverse families, because there is more scope for adaptive radiation among phytophages in diverse taxa (Crawley, 1983). Also we will contrast woody against herbaceous host plants, because the first live longer and may be structurally more diverse, and are therefore a more predictable resource offering again more opportunities for adaptive radiation (Lawton, 1983). Other traits of host plants, such as geographical range, local abundance and habitat diversity, important ecological variables indeed, must be omitted because accurate scoring is only possible for some local areas, but not for the West Palaearctic as a whole.

Finally, knowing something about interactions between structural and taxonomical traits of host plants and gall midge diversity, questions rise about the consequences for the evolution of these phytophages. Some interactions resulted in the occurrence of related midge species on related groups of host plants. But how abundant are apparent parallel patterns in the cladogenies of gall midges and host plants and to what extent did they evolve? Are examples of parallel cladogenesis the result of plant — gall midge interaction, or were the host plants changed under influence of other selection factors and did the gall midges follow these changes? We will draw up examples of parallel cladogenesis and discuss the processes.

LIFE HISTORY PATTERNS

Knowledge of life history patterns is essential for evolutionary studies because each mode of speciation needs particular prerequisites of the involved organisms. Speciation processes of gall midges, which are relevant here, are those in which host plants are involved. Modes of sympatric speciation might exist when host plant shifts occur and assortative mating can be demonstrated. Partners are preferred which share the same food plant, or a highly similar food resource, during the larval phase. Therefore, mating site, oviposition site and site of larval de-

velopment have to be coupled by localization on the same host. A transfer to a new host results then not only in a new resource, but channels the gene flow by separating mating and oviposition sites of original and shifted populations (Bush, 1975; Zwölfer & Bush, 1984). On the other hand, modes of allopatric speciation may result from co-evolution, as a reciprocal process between host plants and phytophages or, when the impact of phytophages on host plant changes is doubtful or absent, sequential evolution (Jermý, 1976). Also co-evolution and sequential evolution require a highly coupled niche structure, but host plant shifts are absent. Therefore, cladogenesis of both groups of organisms is characterized by corresponding dichotomies (Regenfuss, 1978). In order to investigate which modes of speciation may occur in gall midges, relevant phases of the gall midge life history are analyzed.

Gall midges¹⁾ alternate a sedentary phase, encapsulated in a gall, with a free-living adult phase, in which dispersion is possible. The free-living phase starts with the emergence of the adults. Males usually emerge some hours earlier than females and periods of activity are species specific (Coutin & Harris, 1968; Jones et al., 1983; Skuhřavý & Skuhřavá, 1982). After a short period of rest males start swarming in search of females; usually they hover in groups in close proximity to galls where emerging females are expected. Males may mate several times (Van Vreden & Arifin, 1977). Females, like males, rest for a while after emergence. During this period the ovipositor is extended in a calling position, emitting sex pheromones (McKay & Hatchett, 1984). Attracted males copulate immediately, without any courtship behaviour. Females mate once, after mating they retract the ovipositor and are not receptive any more.

The mating, or "rendez-vous" site depends on the site where pupation occurs and, consequently, the female emerges. Before pupation, mature larvae either drop onto the soil or remain in the gall. Galls, in their turn, either may be shed from the host plant or may remain connected with it. Fertilized females disperse in search of host plants. Dispersal is mainly passive but females, as well as males, are able to fly against weak wind currents and respond to ol-

factory cues (McKay & Hatchett, 1984; Skuhřavý et al., 1983; Sylven, 1970).

Eggs are usually laid on or close to the site where the neonate larva will penetrate the host plant. There is a considerable variation in clutch-size. The number of eggs may be one per oviposition or up to five. Some species, e.g., *Contarinia pulchripes* (Kieffer), deposit all (up to 150) eggs in one batch (Parnell, 1963). Larvae, eclosed from the same clutch, are gregarious within a gall.

Many midge species produce unisexual families, i.e., the offspring of one female are either all male or all female. This mechanism of sex regulation might be common in gall midges because the sex ratio departs in many cases from 1:1, the ratio expected in obligatory crossbreeding species. The mechanism has been studied by Metcalfe (1935) and Gallun & Hatchett (1969) for the Hessian fly, *Mayetiola destructor* (Say).

Characteristics of the host plant, such as chemical composition and phenology, may have an important impact on gall midge development and, ultimately, on fitness. Host plants that are selected for oviposition may be less suitable, or even unsuitable for larval development. Females of *Dasineura brassicae* (Winnertz), for example, prefer pods of *Brassica napus* and *B. campestris* for oviposition but also lay eggs on *B. juncea* and *B. nigra*. However, the percentage of hatched eggs on the latter pair of host species is lower and larval development less successful, resulting in females with lower egg production (Åhman, 1981 and in press). Females of *Haplodiplosis marginata* (Von Roser) search first for grasses or cereals, but if these are not available, especially during outbreaks, they will lay eggs upon any other plant and even on the soil. However, galls are only induced in grasses belonging to the tribes Triticeae and some Aveneae. Many eggs are laid upon *Avena sativa*, but there is very little survival on this species. For that reason *Avena sativa* is suggested for biological control of *Haplodiplosis* in schemes of crop rotation (Skuhřavý et al., 1983).

Another factor for successful larval development is synchronization of host plant and gall midge phenologies. Winter varieties of wheat and barley are less susceptible for *Haplodiplosis* than summer varieties because neonate larvae are unable to penetrate, at the time of attack, the more mature tissues of earlier planted varieties (Nijveldt & Hulshoff, 1968; Skuhřavý, 1982; Skuhřavý et al., 1983). Phenological synchronization is also important in other gall midge

¹⁾ Gall midges in the strict sense are gall inducers. Among Cecidomyiidae, gall midges sensu lato, some aberrant forms are predators. These are not sedentary.

pests, e.g., *Orseolia oryzae* (Wood-Mason) on rice (Van Vreden & Arifin, 1977), *Thecodiplosis brachyntera* (Schwägrichen) on pine trees (Skuhravý & Hochmut, 1969; Skuhravý, 1970). Hatchett & Gallun (1970) demonstrated a genetic basis for the ability of *Mayetiola destructor* (Say) to survive on different races of wheat. These races of wheat possess genes for resistance against attacks of *Mayetiola*, which on its turn can also be subdivided into races having genes to overcome this resistance. The gene-for-gene interaction between wheat and Hessian fly might have been developed as a reciprocal process (Gallun, 1977).

At the end of this section on life history patterns and host plant suitability we may conclude that variation in life history patterns, relevant for particular modes of speciation, is mainly present during the free-living adult phase. Sometimes a highly coupled niche structure exists indeed: if the pupation site is the gall, and the host plant is long-lived, emerged females may mate and lay eggs on the same host plant. Female dispersal is especially reduced when the eggs are laid in few (or only one) large batches (Weis et al., 1983). However, swarming of males and determination of sex by the mechanism of unisexual families considerably reduces the possibilities of assortative mating and hence sympatric speciation. Furthermore, oviposition on alien host plants occurs under some conditions, but the possibility of larval development may be a considerable hurdle for host plant shifts. Therefore, allopatric models of speciation will prevail in gall midges. Nevertheless, it is hard to imagine that in genera which exhibit extreme resource partitioning, such as the 62 *Stefaniola* species on *Haloxylon*, or the 28 *Rhopalomyia* species, distinguished by Jones et al. (1983) on *Artemisia tridentata*, have exclusively radiated according to an allopatric model of speciation.

TAXONOMY OF GALL MIDGES

Gall midges belong to the nematoceran family Cecidomyiidae (4,300 described species according to estimates of Skuhravý, in press). Within the suborder Nematocera the Cecidomyiidae are a distinct group: wing veins are generally weak and reduced in number, the costal vein is usually continuous around the wing and tibial spurs are absent. The larvae, usually bright yellow, orange or reddish in colour, possess a supernumerary "neck" segment between head and thorax, which allows a great mobility

of the head. On the ventral side of the prothorax a peculiar sclerotized plate, the sternal spatula, is usually present. According to Mamaev (1968) the Cecidomyiidae are closely related to the mycetophagous scavengers Sciaridae, Scaptosidae and Hyperoscelidae.

A generally adopted subdivision of the family is still lacking. Mamaev (1968), following Rüb-saamen & Hedicke (1925—1939) distinguished only two subfamilies: the Lestremiinae, with undifferentiated tarsi and with the ocelli usually present; the Cecidomyiinae with short first tarsomeres and ocelli absent. Möhn (1955), followed by many modern students of the group, proposed a third subfamily Porricondyliinae. However, he was only able to separate this subfamily by larval characters concerning position and shape of the anal aperture. Mamaev, refining Rüb-saamen & Hedicke's system, differentiated the system to the subtribal rank, but many other specialists consider his system tentative and do not use it. The system used by Skuhravý (in press) in her catalogue is compared here with Mamaev's system in table 1. Further differences concerning the Cecidomyiinae deal with taxa that are difficult to place. First, the Stomatosematidi in Skuhravý's system, for example, share various archaic traits, such as wing venation (Rs well developed) and female genitalia (short, not extensile, sometimes even two-segmented cerci) with Porricondyliinae, but differ from this subfamily by the male genitalia, which are reminiscent of those of Lasiopteridi. Gagné (1975), therefore, proposed an independent supertribal status for this taxon. Secondly, Gagné (1976) placed Oligotrophini and Lasiopterini in the supertribus Lasiopteridi because these tribes share derived character states of female genitalia and antennal flagellomeres; these are lacking in their sister-group Ledomyiini, which in its turn is characterized by derived conditions regarding tarsal claws and male genitalia. The relationships of *Brachineura*, *Epimyia* and *Rhizomyia*, placed in separate tribes, are still unclear. These genera are now placed in Lasiopteridi, but may be better regarded as unplaced (Gagné, 1976). Because of the still very uncertain relationships of Gagné's Stomatosematidi and Ledomyiini, we here adopt Mamaev's classification, at least as far as it concerns the tribal subdivisions.

Our special attention is focussed on host plant relations and their importance for the evolution of the gall midges. Therefore we will now analyze the phyletic relations of the tribes in

Table 1. Comparison of systems of Cecidomyiidae according to Mamaev (1968) and Skuhravá (in press, presented with permission from the author). I, inquiline; M, mycetophagous; P, phytophagous and gall inducing; Z, zoophagous.

MAMAEV	SKUHRVÁ	nr. genera	nr. species	feeding mode
LESTREMIINAE 3 tribes, 7 subtribes	LESTREMIINAE 2 supertribes, 8 tribes	36	194	M
CECIDOMYIINAE	PORRICONDYLINAE			
Heteropezini	Heteropezini + Leptosynini	9	13	M
Porricondyliini	Porricondyliini + 7 more tribes	32	265	M
	CECIDOMYIINAE			
Lasiopterini	<u>Lasiopteridi</u>	12	150	PI Z?
6 subtribes	Lasiopterini			
Oligotrophini	no subdivision	63	600	PI
Oligotrophina + 4 more str.	Oligotrophini			
Brachyneurina	Ledomyiini	1	14	MZ
Rhizomyiina	Brachyneurini	5	21	M?
Epimyina	Rhizomyiini	1	8	M
	Epimyini	1	1	M?
Stomatosematina	<u>Stomatosematidi</u>	2	4	M?
Asphondyliini	<u>Asphondyliidi</u>	17	95	P
3 subtribes	4 tribes			
Cecidomyiini	<u>Cecidomyiidi</u>	109	754	GIMZ
13 subtribes	no subdivision			
	unplaced	-	140	-

connection with their feeding modes. All Cecidomyiinae share the absence of ocelli and the shortening of the first tarsal segment of legs, both derived character states. The feeding modes (table 1) in this subfamily are most diverse, ranging from mycetophagy to various forms of phytophagy and zoophagy (Mamaev, 1968). All gall inducing midges, the "true" gall midges, belong to the Cecidomyiinae. Heteropezini and Porricondyliini, with primitive wing venation (R_s usually present) and larval morphology (pattern of setae on the final two abdominal segments and location of the anal aperture), are mycetophagous, as are all Lestremiinae and all forms of the related families Sciaridae, Scatopsidae and Hyperoscelidae. Therefore, feeding on decaying organic material must be regarded as the original feeding mode of Cecidomyiidae (Southwood, 1972; Mamaev, 1968; Roskam, in press). Mycetophagy is also the feeding mode of

oligotrophine Rhizomyiina and some species of *Ledomysia*. Although the larvae of Brachyneurina, Epimyina and Stomatosematina are unknown, these are expected to be mycetophagous too (Mamaev, 1968; Gagné, 1975). Furthermore larvae of the oligotrophine genus *Isogynandromysia* live in the upper layer of forest soil (Spungis, 1981).

Mycetophagy is also common in the tribe Cecidomyiini; it is the feeding mode of *Buhromyiella*, *Camptodiplosis*, *Clinodiplosis*, *Dichaeitia*, *Dichodiplosis*, *Echinella*, *Giardomyia*, *Karshomyia*, *Mycetodiplosis*, *Mycocecis*, *Mycodiplosis*, *Neoisodiplosis* and *Neomycodiplosis*, 59 species together. Some of these genera are closely related, e.g., Möhn's (1955) "*Mycodiplosis* group" and "*Clinodiplosis* group". Mamaev (1968) considered, on morphological criteria, mycetophagous Oligotrophini and Cecidomyiini primitive forms within these two tribes. No

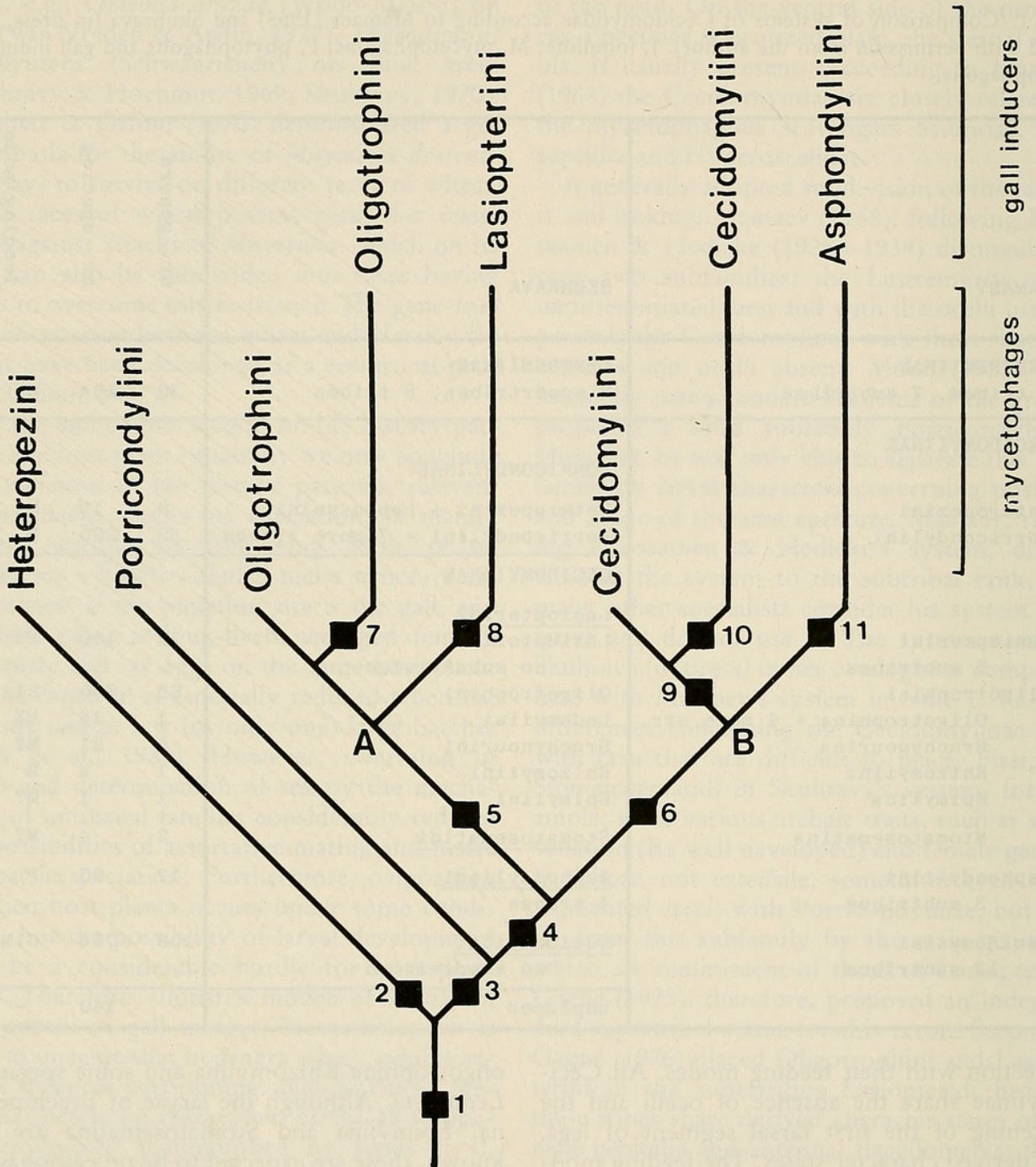


Fig. 1. Phylogenetic relations of the Cecidomyiinae tribes. Black squares indicate synapomorphic conditions. 1, ocelli absent, shortened first tarsomeres; 2, paedogenesis; 3, larval anus shifted into ventral position and slit-like; 4, reduction in number of Malpighian tubes of larval digestive tract, reduced number of dorsal and ventral papillae on the larval eighth abdominal segment; 5, substitution of parameres in male genitalia by mediobasal outgrowths of basimeres sheathing aedeagus, retractile ovipositor with fused cerci; 6, mediobasal outgrowths of male genitalia absent, number of adult antennal segments basically fixed, 2 + 12; 7, constriction in larval mid-gut shifted proximally; 8, wing vein R_5 closely adjacent to R_1 and C, reduced in length, antennal segments not or barely sexually dimorphic and barrel-shaped, characteristic ovipositor with hooks and spines adapted to abrade plant tissue; 9, binodal male antennal segments with looped circumfila, reduction of the eighth tergite of the female abdomen; 10, loss of the constriction in the larval mid-gut; 11, necks of antennal segments reduced in length with reticulate, closely appressed circumfila, retractile needle-like ovipositor with fused (reduced?) cerci. For further explanation see text.

mycetophagous representatives are known of Asphondyliini and Lasiopterini.

Zoophagy is mainly restricted to Cecidomyiini. Four genera are known as predators of

mites, six predate on aphids, five on coccids and two attack other cecidomyiids. Three genera are endoparasitoids of aphids and psyllids. Some of these zoophages are important agents in biolog-

Table 2. Tribal preference for vegetative (veg.) and generative (gen.) host plant tissues. Gall midges belonging to the "mixed" category attack both types of tissues. Data are from an analysis of keys on plant galls by Buhr (1964—1965), only described gall midge species included and inquiline excluded. Expected values according to "chi-square" calculation (in brackets).

	sp.nr.	veg.	gen.	mixed
TRIBUS 1. LASIOPTERINI				
Lasioptera	11	9	2	0
Ozirhincus	5	0	5	0
Stefaniella	2	2	0	0
3 monotypic genera	3	3	0	0
TOTAL	21	14 (13.4)	7 (6.2)	0 (1.4)
TRIBUS 2. OLIGOTROPHINI				
Arnoldiella	3	2	1	0
Bayeria	5	5	0	0
Cystiphora	6	6	0	0
Dasineura	110	74	33	3
Geocrypta	5	4	0	1
Iteomyia	2	2	0	0
Jaapiella	21	17	8	3
Janetia	5	5	0	0
Janetiella	6	5	0	1
Lathyromyza	2	1	1	0
Macrolabis	14	12	2	0
Mayetiola	13	13	0	0
Misospatha	5	1	1	3
Neomikiella	2	2	0	0
Oligotrophus	4	4	0	0
Physemocercis	2	2	0	0
Rabdophaga	37	36	0	1
Rhopalomyia	14	3	4	7
Wachtliella	7	4	1	2
21 monotypic genera	21	18	3	0
TOTAL	291	216 (186.3)	54 (85.7)	21 (19.0)
TRIBUS 3. ASPHONDYLIINI				
Asphondylia	28	6	19	3
Placochela	2	0	2	0
Polystepha	2	2	0	0
2 monotypic genera	2	0	2	0
TOTAL	34	8 (21.8)	23 (10.0)	3 (2.2)
TRIBUS 4. CECIDOMYIINI				
Ametrodiplosis	5	2	3	0
Antichiridium	2	2	0	0
Contarinia	85	26	52	7
Diodaulus	2	0	2	0
Harmandia	4	4	0	0
Loewiella	2	2	0	0
Macrodiplosis	2	2	0	0
Massalongia	2	2	0	0
Planetella	13	13	0	0
Plemeliella	2	2	0	0
Thurauia	2	2	0	0
Tricholaba	4	3	1	0
18 monotypic genera	18	15	2	1
TOTAL	143	75 (91.5)	60 (42.1)	8 (9.4)

ical control. Apart from the Cecidomyiini, some species of *Trotteria* (*T. galii* Rübsaamen and *T. ligustri* Barnes), Lasiopterini, and of *Ledomysia* (*L. acariphaga* Marikovskij, *L. acerina* Giraud and *L. cardui* Kieffer), Oligotrophini, are supposed to be predators. Other forms of both genera are inquilines, and are regarded as early offshoots within their respective tribes (Mamaev, 1968; Möhn, 1966). No conclusion is possible about the origin and evolution of the zoophagous Cecidomyiini. They may have evolved polyphyletically from either mycetophagous or phytophagous ancestors. Möhn (1955) indicated three groups of related genera, namely, the *Lestodiplosis* group (e.g., *Lestodiplosis*, *Feltiella* and *Therodiplosis*, predators of gall midges, aphids and mites), the *Phaenobremia* group (e.g., *Phaenobremia*, *Aphidoletes* and *Monobremia*, on aphids) and the mutually close endoparasitoids *Endaphis* and *Endopsylla*.

A cladogram of Mamaev's tribal division of the Cecidomyiinae is presented in fig. 1. The synapomorphies (shared derived character states) 5 and 6, concerning male genitalia and antennae of both sexes, validate the two complexes of Oligotrophini-Lasiopterini and Cecidomyiini-Asphondyliini. At dichotomy A, a lasiopterine form adopted phytophagy and separated from the Oligotrophini. Then, at a further dichotomy an oligotrophine form, becoming phytophagous too, separated from the remaining mycetophagous Oligotrophini. A similar process, starting at B, subsequently gave rise to phytophagous Asphondyliini and Cecidomyiini. Hence, unless mycetophagy in Oligotrophini and Cecidomyiini is a derived feeding mode, the transition to phytophagy, culminating in gall inducing, occurred several times in a parallel way. Morphological arguments (fig. 1, the synapomorphies 7, 8, 10 and 11) as well as arguments emerging from gall midge parasitoids make a secondary transition to mycetophagy highly improbable. Mycetophagous and phytophagous cecidomyiids both have scelionid parasitoids. Chalcidoid parasitoids, however, are abundant on phytophages but do not attack mycetophages. If mycetophages have evolved from phytophages, undoubtedly some chalcidoid parasitoids would have followed their hosts and would now be present on mycetophages (Mamaev, 1968).

SPECIALIZATION ON HOST PLANT ORGANS

The transition from mycetophagy to phytophagy is supposed to coincide with the expan-

sion of the angiosperms during the Upper Cretaceous, about 65 million years ago (Klausnitzer, 1977; Mamaev, 1968; Zwölfer, 1978). In Upper Miocene formations, 30 million years ago, all gall midge tribes were well represented (Gagné, 1973). Two prerequisites presumably were responsible for angiosperm expansion, namely, the progressive development of the conducting system ensuring intensive movements of sap and rapid progress in the development of the flower as an adaptation to insect pollination (Takhtajan, 1954). If the earlier assertion of a polyphyletic transition to phytophagy is true, it might be reflected in different specializations of the phytophagous members of the various tribes to the different progressive developments of their host plants. In other words, some tribes might basically be adapted to exploit the conducting system of their host plants, subsequently colonizing other organs, such as leaves, whereas other tribes might be primarily adapted to generative structures, such as flowers, compact inflorescences as heads of Asteraceae and fruits.

With the help of table 2 we can investigate whether differences exist at the tribal rank in the specialization of gall midge species on tissues of their host plants. The species, compiled from Buhr (1964—1965), are subdivided into three categories: those causing deformations of vegetative structures, of generative structures and those with a "mixed" strategy, attacking both vegetative and generative structures. The data have been submitted to a chi square-test. The null hypothesis, i.e., no significant differences exist between tribes regarding specialization for organs of host plants, has to be rejected ($\chi^2 = 54.8$, DF = 6, $P < 0.001$).

The frequencies of Lasiopterini accord with the expected ones (in brackets), although the species of this tribe have ovipositors which are primarily adapted to abrade stems and to insert eggs into them. *Ozirhincus*, although sharing these morphological features, is aberrant, galling generative instead of vegetative tissues. In North America, where the Lasiopterini are well represented, most species are stem feeders since only six out of 70 species belong to the "generative" or "mixed" category (Felt, 1940; Gagné, 1969). Oligotrophini have a distinct preference for vegetative organs. Aberrant oligotrophine genera are *Gephyraulus*, *Kaltenbachiola* and *Semudobia*; aberrant species are found in most larger genera, viz., *Dasineura*, *Jaapiella*, *Macrolabis*, *Misopatha*, *Rhopalomyia* and *Wachtliel-*

Table 3. Distribution of gall midge species among orders of vascular plants. Only orders with West Palaearctic representatives have been considered and are subdivided into a fundamentally woody (+) category and a fundamentally herbaceous one (Hutchinson, 1969). The numbers of the orders refer to Takhtajan (1980), the numbers of plant species are taken from Rothmaler (1972), those of gall midge species from Buhr (1964—1965). (1) = Hutchinson's Brassicales; (2) = Hutchinson's Umbellales.

(sub)class	order	plant species	midge species
Lycopsida	Lycopodiales	6	-
	Selaginellales	2	-
	Isoetales	2	-
Sphenopsida	Equisetales	10	-
Pteropsida	Ophioglossales	6	-
	Osmundales	1	-
	Polypodiales	46	2
	Marsileales	2	-
	Salviniales	2	-
Ginkgoopsida	+ Ginkgoales	1	-
Taxopsida	+ Taxales	1	1
Coniferopsida	+ Pinales	33	6
Magnoliidae	5 Aristolochiales	3	-
	7 Nymphaeales	6	-
Ranunculidae	9 Ranunculales	81	12
	10 Papaverales	27	1
Hamamelidae	16 + Hamamelidales	1	-
	18 + Urticales	15	6
	21 + Fagales	18	40
	24 + Myricales	1	-
	25 + Juglandales	2	-
Caryophyllidae	26 Caryophyllales	184	26
	27 Polygonales	41	8
	28 Plumbaginales	3	-
Dilleniidae	30 + Paeoniales	2	-
	31 + Theales	13	3
	32 + Violales	38	7
	34 Capparales 1)	153	17
	35 + Tamaricales	1	-
	36 + Salicales	34	46
	37 + Ericales	31	5
	39 Primulales	35	1
	40 + Malvales	15	5
	41 + Euphorbiales	24	7
	42 + Thymelaeales	8	2
Rosidae	43 Saxifragales	61	5
	44 + Rosales	154	27
	45 + Fabales	139	69
	49 + Myrtales	33	3
	50 + Rutales	6	1
	51 + Sapindales	14	7
	52 Geraniales	32	3
	53 + Polygalales	9	1
	54 + Cornales	4	1
	55 Araliales 2)	96	21
	56 + Celastrales	3	-
Asteridae	57 + Santalales	9	-
	59 + Rhamnales	7	4
	62 Gentianales	64	17
	63 + Oleales	6	5
	64 Dipsacales	43	15
	66 Polemoniales	62	9
	67 Lamiales	90	28
	68 Scrophulariales	163	15
Alismidae	69 Campanulales	34	7
	72 Asterales	317	70
	1 Alismatales	14	-
	2 Najadales	33	-
Liliidae	4 Liliales	89	6
	7 Orchidales	56	-
	9 Juncals	42	-
	10 Cyperales	145	18
	15 Poales	206	29
Arecidae	20 Typhales	9	-
	21 Arales	8	-
TOTALS	+ woody orders	622	246
	herbaceous orders	2174	310

la. Asphondyliini occur predominantly on generative structures. However, *Polystepha* is aberrant as are nine out of 28 *Asphondylia* species. The situation is rather complex in Cecidomyiini. Although almost half of the species induce galls in vegetative tissues, a substantially larger portion is predicted. *Contarinia*, by far the largest genus of Cecidomyiini, is almost completely responsible for deviations of this tribe from the expected value.

The ambiguous preference of Cecidomyiini does not allow drawing conclusions about the original specialization of the group. Two alternative ways of radiation might be possible. First, as in Oligotrophini, a phytophagous behaviour started on vegetative parts and differentiation at the generic level coincided with a shift to generative parts. The radiation of *Contarinia* has than to be regarded in connection with this shift from vegetative to generative organs. Secondly, as in Asphondyliini, the preference of *Contarinia* for generative organs should

be regarded as original. Specialists of vegetative tissues, belonging to *Contarinia* as well as to other genera, then have ancestors on generative parts. Synapomorphic conditions of male genitalia and antennae in Cecidomyiini and Asphondyliini (fig. 1: 6) support the second alternative, but a further phylogenetic study (according to current opinion *Contarinia* is not monophyletic!) is needed to solve this problem.

SPECIES RICHNESS AND HOST PLANT DIVERSITY

A further consequence of the assumed coincident radiation of gall midges and host plants is that these ecologically linked groups of organisms are expected to illustrate Eichler's rule (Eichler, 1948; Price, 1977): host plant taxa with many species will support more midge species than taxa which are less diverse, because there is more scope for radiation among the midges. In table 3 the accumulations of gall midge species are given for all orders of West Palearctic vascular plants. All dicotyledonous

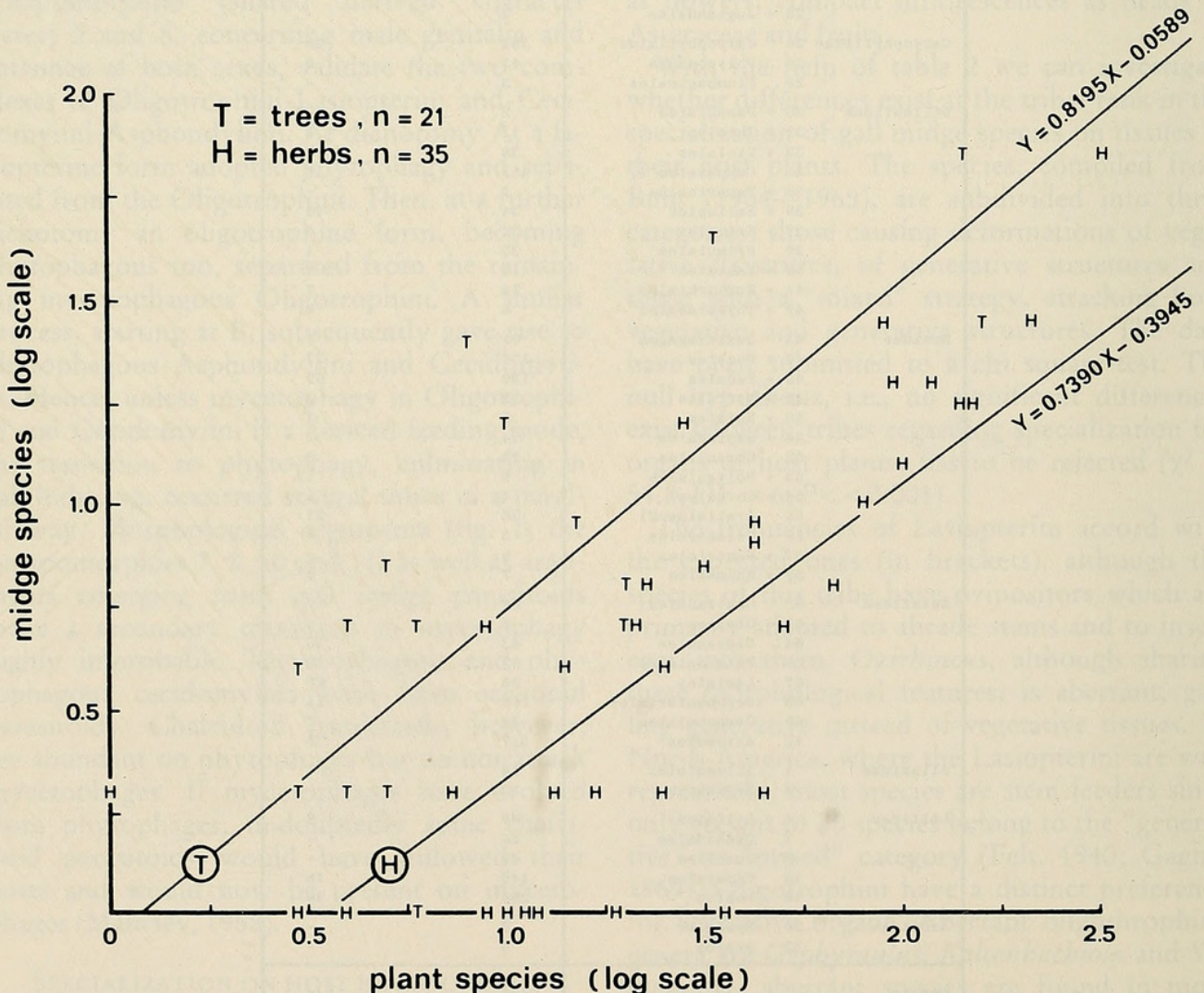


Fig. 2. Interdependence of numbers of plant and gall midge species per plant family. Midge species according to Buhr (1964—1965), plant species according to Rothmaler (1972).

orders which include ten species or more have host plants attacked by gall midges. Fagales, Salicales and Fabales (Leguminosae) in particular have host plants which shelter numerous gall midge species. Large monocotyledonous orders, such as Juncales and Orchidales, as well as most ferns and gymnosperms, lack gall midges. Poales and Cyperales, however, have many representatives with gall midges.

In fig. 2 the interdependence between the number of gall midge and host plant species per plant family is analyzed. Contrary to earlier students of insect species richness (e.g., Lawton & Price, 1979; Fowler & Lawton, 1982), we used the plant family and not the plant genus as the variate for "taxonomic diversity" (= taxonomic isolation) of host plants. This is because the present study involves many host plant families, whereas Lawton, Price and Fowler only dealt with one family, Umbelliferae. Furthermore, in different families different criteria are used to delimit genera, which makes genera unsuitable for comparison when more families are involved. For logarithmic transformed data taxonomical interdependence alone explains 52.5% ($r = 0.72$) of the variation in gall midge species richness on host plants, and is therefore a very important factor. When host plants are subdivided into woody and herbaceous categories the percentages are even higher, namely, 66.1% ($r = 0.81$) for woody and 63.3% ($r = 0.80$) for herbaceous host plants. These high percentages mean that taxonomic diversity, reflecting diversity of host plant chemistry (Hegnauer, 1962—1973) is not the only but apparently a major factor determining accumulation of gall midge species on host plants. Similar suggestions were made by Claridge & Wilson (1981), dealing with mesophyll-feeding leafhoppers. Price (1977) observed a similar interdependence for another group of endophytophages: Agromyzidae. In his calculation 50.4% of the variation of leafminer species per host plant family was explained by the number of plant species in that family ($r = 0.71$).

The regression lines for woody and herbaceous host plants do not differ significantly by slope, only by intercept. Hence, gall midge species are more numerous in plant families with woody representatives than in those with herbaceous ones: the "high apparency" of long-lived woody host plants (Fox, 1981; Lawton, 1983; Lawton & Schröder, 1977; Klausnitzer, 1977) also works positively out for gall midges.

When the gall midges are subdivided into

Table 4. Tribal preference with respect to the life form of host plants. Data after an analysis of the keys by Buhr (1964—1965).

	species number	percentage of life form			
		annual/ biennial	perennial herbs	shrubs/ trees	
Lasiopterini	21	28.6	52.4	19.0	
Oligotrophini	291	8.9	54.3	36.8	
Asphondyliini	34	7.9	63.3	28.9	
Cecidomyiini	143	4.7	61.7	33.6	

tribes and host plants categories according to their life form (table 4), most gall midges of all tribes occur on perennial herbs, whereas short-lived herbs are poorly represented. The high score of Lasiopterini for short-lived herbs is mainly caused by one species, *Lasioptera carophila* F. Loew, which attacks many short-lived umbellifers. When analyzing the life form preference of Lasiopterini for North America, where *L. carophila* is absent (compilation of Felt, 1940, and Gagné, 1969), 7.1% of 70 species occur on annual and biennial host plants, 67.1% on perennial herbs and 25.7% on shrubs and trees, values conforming to those of tribes other than Lasiopterini in Europe.

The short-lived host plants need a further analysis. Many of these plants are characterized by conspicuous chemicals as furanocoumarins (Apiaceae) or mustard oil glucosides (Brassicaceae). Short-lived Apiaceae are hosts for two polyphagous species, viz., *Lasioptera carophila* F. Loew and *Kiefferia pimpinellae* (F. Loew). Short-lived Brassicaceae harbour polyphagous *Contarinia nasturtii* (Kieffer). *Dasineura brassicae* (Winnertz) and *D. sisymbrii* (Schrank) and *Gephyraulus raphanistri* (Kieffer). *Mayetiola destructor* (Say), *Haplodiplosis marginata* (Von Roser) and *Hybolasioptera cerealis* (Lindeman) have many annual cereals in their host ranges. These cereals occur in high densities, in "flocks", and germinate not far from the place where the previous generation lived. In this way they are "predictable" resources and resemble perennials. Finally, short-lived host plants are present among Chenopodiaceae (*Haloxylon*), Asteraceae (e.g., *Senecio*, *Sonchus*, *Cirsium* and *Carduus*) and Leguminosae (e.g., *Lathyrus*,

Lens, *Medicago*, *Melilotus*, *Pisum* and *Vicia*). These host plants either occur under natural conditions in dense populations, or are also cultivated.

PARALLEL PATTERNS IN GALL MIDGE AND HOST PLANT EVOLUTION

If related parasites live on related hosts, allopatric speciation patterns in both groups of organisms may have evolved along parallel lines: dichotomies in host cladograms then have corresponding dichotomies in cladograms of parasites. Corresponding dichotomies or co-cladogeneses may be the result of a reciprocal process between hosts and parasites: parasite attack, reducing fitness of the host, provokes the host to develop defense or avoiding mechanisms. Parasites, on their turn, try to overcome host defenses by counter adaptations and so on. However, long term reciprocal interactions (defined by Janzen (1980) as co-evolution) are not the only process resulting in parallel patterns. Moreover, when they do so, they may be difficult to measure. Parasites usually share their host plants with many other parasites, each possessing different trophic links with their hosts (Klausnitzer, 1977). A change of a host, to avoid one parasite, might be advantageous for another. The complexity of interactions reduces the profits of that change (Fox, 1981). Changes in the host plant may also, and more frequently, be the result of responses to abiotic changes of the host plant habitat. Parasites may follow the changes of their hosts for their own benefit. This type of parallel evolution has been defined by Jermy (1976) as sequential evolution. Finally, speciation processes in host plants and parasites may coincide, but as independent responses to the same abiotic factor. Vicariance, caused by the same geographic isolation in subgroups of hosts and parasites, may so cause a parallel pattern in the phylogenies of both groups (e.g., Roskam, 1979).

Parallel patterns need not necessarily be strict because phytophages, unlike many parasites of vertebrates, have a free phase during their life-cycle. While dispersion of vertebrate parasites usually occurs by conspecific contacts of their hosts, dispersion of phytophages, at least in gall midges is possible during a free-living phase, as was reported in the above. They may shift to other, usually related, host species during that phase, causing disturbances of parallel patterns (Regenfuss, 1978).

Whereas the host range of zoophagous and

saprophagous cecidomyiids is relatively wide (Nijveldt, 1969; Skuhravá, 1973), most gall inducing and inquiline species have only narrow host plant ranges. They usually attack some related species belonging to the same genus, or species belonging to closely related genera. Exceptions are, e.g., *Lasioptera carophila* F. Loew and *Kiefferia pimpinellae* (F. Loew) on Apiaceae; *Dasineura sisymbrii* (Schrank), *D. brassicae* (Winnertz) and *Gephyraulus raphanistri* (Kieffer) on Brassicaceae. Both host plant families are distinct by chemical compounds, furanocoumarins and mustard oil glucosides, respectively. Some *Asphondylia* species alternate host plants during their life-cycle, as do aphids. According to Orphanides (1975), the winter generation of the carob gall midge, *Asphondylia* sp., induces galls in pods of carobs, *Ceratonia siliqua*. Summer generations, however, attack various, not related, plant species, viz., *Capsicum* and *Solanum* (Solanaceae), *Capparis* (Capparidaceae), *Eruca* and *Sinapis* (Brassicaceae), *Hypericum* (Hypericaceae), *Verbascum* (Scrophulariaceae), *Sesamum* (Pedaliaceae) and even monocots, viz., *Urginea* and *Asphodelus* (Liliaceae). It is still uncertain whether midges reared from these plants will be conspecific. Some, however, certainly are. A similar situation seems to exist in the soybean gall midge, *Asphondylia* sp., overwintering in soybean pods but with unknown summer hosts (Yukawa et al., 1983).

Among gall midge genera large differences exist regarding the breadth of their host plant spectrum. In table 5 gall inducing midge genera are subdivided into three categories, namely, monophagous, oligophagous and polyphagous genera. Genera with eight species or more are listed, whereas smaller genera only are indicated by their number of species. The large genera *Dasineura*, *Contarinia*, *Jaapiella* and *Macrolabis*, but also the smaller *Wachtliella*, are presented in brackets, because they are highly artificial and therefore do not allow conclusions about the affinities of their host plants. Interdependence between gall midge species diversity and breadth of the host plant spectrum seems to be absent: not only large genera as *Asphondylia*, *Rhopalomyia* and *Lasioptera* are polyphagous, but also many small genera consist of species which occur on host plants belonging to different families. Monotypic polyphagous genera are absent.

Lasioptera and *Neolasioptera* are two large genera which are thought to be natural. Gagné

Table 5. Host plant spectrum of gall midge genera. M, monophagous genera, all host plants belong to only one genus; O, oligophagous genera, host plants belong to one family; P, polyphagous genera, host plants belonging to several families. Data from Skuhravá (in press, with permission from the author). For further explanation, see text.

genus	nr. of species	M	O	P
<i>Dasineura</i>	257			(1)
<i>Contarinia</i>	151			(1)
<i>Stefaniola</i>	69	1		
<i>Asphondylia</i>	54			1
<i>Rhopalomyia</i>	49			1
<i>Lasioptera</i>	45			1
<i>Rabdophaga</i>	38		1	
<i>Halodiplosis</i>	37		1	
<i>Jaapiella</i>	31			(1)
<i>Macrolabis</i>	31			(1)
<i>Planetella</i>	26	1		
<i>Mayetiola</i>	25		1	
<i>Baldratia</i>	23		1	
<i>Janetiella</i>	15			1
<i>Ametrodiplosis</i>	13			1
<i>Oligotrophus</i>	10			1
<i>Arnoldiella</i>	8	1		
<i>Wachtliella</i>	8			(1)
2 genera	7	1		1
4 genera	6	2	2	
5 genera	5	1	1	3
3 genera	4	2	1	
15 genera	3	8	4	3
18 genera	2	7	2	9
total natural genera with more than one species		24	14	22
71 genera	1	68	3	

(1969) revised the Nearctic species, of which Felt (1940) presented the host plants. Both genera are well represented on host plants belonging to the subclasses Rosidae (orders: Rosales, Fabales, Cornales and Rhamnales) and Asteridae (orders: Lamiales, Scrophulariales and Asterales). They are absent from Monocotyledonae; two species of *Lasioptera* occur on *Ephedra* (Gymnospermae, Gnetales). *Lasioptera* has five species on host plants of the subclass Hamamelidae (*Humulus* and *Quercus*), from which subclass *Neolasioptera* is absent. On the other hand, *Neolasioptera* is represented in the subclasses Magnoliidae (Lauraceae: *Benzoin*) and Ranunculidae (Ranunculaceae: *Clematis*) where *Lasioptera* is absent. Although both genera have accumulations of species on Rosidae and Asteridae, apparent parallel patterns with the phylo-

geny of host plants belonging to these subclasses are still lacking.

Some smaller genera also have species attacking hosts belonging to unrelated families or even have species with a non-ecidogenic feeding mode. *Janetiella*, for example, occurs on hosts belonging to Pinaceae, Cupressaceae, Fagaceae, Ulmaceae, Chenopodiaceae, Brassicaceae, Leguminosae, Vitaceae, Euphorbiaceae, Labiatae and Asteraceae. Host plants of *Ametrodiplosis* belong to ten families; two species are inquilines. Even among genera with only two included species, nine occur on host plants which are taxonomically distant. *Physemocercis hartigi* (Liebel) causes galls on *Tilia* (Tiliaceae), whereas *P. ulmi* (Kieffer) occurs on *Ulmus* (Ulmaceae). *Antichiridium caricis* Kieffer and *A. striatum* (Rübsaamen) cause galls on *Carex* (Cyper-

raceae) and *Molinia* (Poaceae), respectively. *Plemyella abietina* Seitner and *P. betulicola* (Kieffer) have *Abies* (Pinaceae) and *Betula* (Betulaceae), respectively, as host plants. These genera may involve examples of ecological opportunists because the host plants on which their species occur share the same habitat. Other genera with two species, however, occur on host plants which have neither taxonomical, nor apparent ecological connections, e.g., *Dicthyomyia navasiana* Tavares and *D. salsolae* Tavares on *Santolina* (Asteraceae) and *Salsola* (Chenopodiaceae), *Schizomyia galiorum* Kieffer and *S. tami* Kieffer on *Galium* (Rubiaceae) and *Tamus* (Dioscoreaceae).

On the other hand, some larger genera radiated on closely related host plants. *Stefaniola* and *Planetella* have host plants belonging to only one genus, *Haloxylon* and *Carex*, respectively. *Rabdophaga* occurs on Salicaceae (mainly on *Salix*) and *Mayetiola* on grasses. *Baldratia* and *Halodiplosis* exclusively occur on Chenopodiaceae. When apparently monophyletic genera are taken together no less than 63% (38 out of 60 genera) radiated on host plants which are taxonomically close.

Examples of parallel cladogenesis in gall midges and host plants will primarily be found in genera that radiated on taxonomically related host plants. In the next paragraph of this section some of these examples will be treated. The examples are arranged according to the taxonomical rank of the host plants at which the radiation occurred.

A. Host plant family

Host plants of *Asphondylia* mainly belong to two families which are phylogenetically distant, namely, Leguminosae and Labiatae. Correlated with the taxonomic position of the host plants there is a specialization with respect to the host plant tissue. Out of 28 species mentioned in Buhr (1964–1965), all species on Labiatae (6) make flower galls, whereas 18 species on Leguminosae are specialized on pods (11) or vegetative parts (6); *A. sarothamni* H. Loew on *Sarothamnus* causes galls in pods, flowers and shoots. Hence, species causing flower galls on Labiatae and fruit galls (and later in evolutionary time, shoot galls?) on Leguminosae may represent two different evolutionary lines in this polyphagous genus.

Three genera, *Mayetiola* (Oligotrophini), *Haplodiplosis* (Cecidomyiini) and *Hybolasiop-tera* (Lasiopterini), of which the latter two are

monotypic, induce galls in culms and shoots of Poaceae. As a rule, they attack many wild grasses. Some species, however, are extremely important pests of cereals. *Mayetiola destructor* (Say), the Hessian fly, is the most important gall midge species damaging cereals. Wild grasses from which the species has been reported belong to *Cynodon* (Poaceae-Eragrostideae), *Phleum*, *Aegilops*, and *Agropyron* (Poideae). Other *Mayetiola* species, usually one per plant genus, induce galls in culms and shoots of *Avena*, *Brachypodium*, *Calamagrostis* (various *Mayetiola* species occur in this genus), *Dactylus*, *Holcus*, *Molinia*, *Phalaris*, *Poa* and *Secale* (all Pooideae). *Giraudiella*, one species, closely related to *Mayetiola*, induces galls on *Phragmites* (Pooideae). Hence, most host plants belong to the subfamily Pooideae, but at a lower level apparent patterns are absent.

B. Host plant tribe

Four clusters of oligophagous genera, restricted to Asteraceae, are of particular interest with respect to parallel cladogenesis (table 6). All five species of *Ozirhincus* (Lasiopterini) induce fruit galls in host plants belonging to Asteroideae-Anthemidae, as does *Lasioptera* (*Pro-lasioptera*) *niveocincta* (Kieffer). The Nearctic genus *Asteromyia* (Lasiopterini), with 20 species, only induces galls in members of the tribe Asteraceae. Two related Oligotrophini genera, namely, *Rhopalomyia* (49 spp.), of which 14 are mentioned in Buhr, and *Misospatha* (5 spp.), are present in Anthemidae too. *Cystiphora* (6 spp.), which also belongs to the Oligotrophini, only causes galls in members of the subfamily Cichorioideae. In *Cystiphora*, there is host specificity below the genus level: *C. hieracii* (F. Löw) and *C. pilosellae* Kieffer are restricted to the *Archie-racium* and *Pilosella* groups of species, respectively. In Asteroideae-Cardueae both species of *Loewiola* (Cecidomyiini) induce leaf galls in *Centaurea* and *Serratula*, whereas *Acodiplosis* (1 sp.), close to *Loewiola*, is present on *Inula* (Inuleae). We may conclude that, contrary to gall midges occurring on grasses, midge genera on Asteraceae exhibit specificity at the tribal rank.

C. Host plant genus

Many gall midge genera are restricted to only one host plant genus. Sometimes, related midge genera have related host plants. *Dryomyia*, for example, with four species, is reported from leaves of *Quercus*, whereas its relative, *Harti-giola*, with one species, causes galls in leaves of

Table 6. Gall midge genera associated with Asteraceae. Subdivision of Asteraceae according to Engler (1964).

subfamily	tribe	genus	Cecido- myiini	Oligo- trophini	Lasio- pterini
			Loewiola Acodiplosis	Rhopalomyia Misospatha Cystiphora	Ozirhincus L. (Prolasioptera) Asteromyia
Asteroideae	Eupatorieae	-			
		Senecioneae			
		Calenduleae			
	Anthemideae	Anthemis		+	+
		Achillea		+	+
		Matricaria		+	+
		Chrysanthemum		+	+
		Tanacetum		+	+
		Artemisia		+	
		Erigeron		+	+
	Astereae	Aster			+
		Solidago			+
		Bigelowia			+
	Inuleae	Inula	+		
	Cynareae	Serratula	+		
		Centaurea	+		
Cichorioideae	Cichorieae	Hypochoeris		+	
		Leontodon		+	
		Scorzonera		+	
		Chondrilla		+	
		Taraxacum		+	
		Sonchus		+	
		Crepis		+	
		Hieracium		+	

Fagus. *Semudobia*, with three Palaearctic species, occurs on *Betula*, whereas its relative *Mikomyia*, with one species, causes galls in *Corylus*. Within this category three examples have been selected, viz., *Rabdophaga* (Oligotrophini), with 38 species on *Salix*, *Planetella* (Cecidomyiini), with 26 species on *Carex*, and *Semudobia* (Oligotrophini) in fruit catkins of *Betula*.

One species of *Rabdophaga* is known from twigs of *Populus*, the other species cause galls in shoots, twigs and catkins of *Salix*. Within *Salix*, there seem to be three levels of specialization that coincide with the division of *Salix* into subgenera. Infections are absent from the subgenus *Chaematia* Dumortier, all prostrate, small shrubs. Some *Rabdophaga* species occur in both remaining subgenera: *Salix* s.s. (trees and large shrubs) and *Caprisalix* Dumortier (shrubs). *R. terminalis* Kieffer, for instance, occurs in shoots and leaves, *R. rosaria* (H. Loew) in shoots, *R. deletrix* (Rübsaamen) in buds and *R. nervorum* (Kieffer) in leaves. However, a number of species exclusively attack willows of the subgenus *Salix*: *R. saliciperda* (Dufour) in twigs, *R. triandraperda* Barnes in twigs, *R. heterobia* (H. Loew) in shoots and in male catkins. The majority of *Rabdophaga* species are restricted to the large genus *Caprisalix*.

Table 7 presents the host plant relations of 13 *Planetella* species which are recorded in Buhr (1964—1965). Two groups of species are distinct, namely, the species which cause galls in sedges belonging to both sections *Vignea* (Beauvois) Kükenthal and *Carex*, and those which are restricted to the section *Carex*. Records are absent from the remaining subgenera *Indocarex* Baillon and *Primocarex* Kükenthal. When analyzing Rübsaamen & Hedicke's (1925—1939) keys, there is a parallel situation in gall midges and host plants with respect to the state of derivativeness of some characters: the species which exhibit apomorphic character states in the shape of the adult thorax and/or number of male flagellomeres, viz., *Planetella tarda* (Rübsaamen), *rosenhaueri* (Rübsaamen), *fischeri* (Frauenfeld), *tumorifica* (Rübsaamen) and *cornifex* (Kieffer), only occur on sedges which in their turn share synapomorphies with respect to the differentiation of their inflorescences in male and female spikes. Unfortunately, the two poorly known species *P. kneuckeri* (Kieffer) and *P. subterranea* (Kieffer & Trotter), which were only reported from sedges belonging to the section *Vignea*, are not mentioned in Rübsaamen & Hedicke.

Table 7. Species of *Planetella* associated with subgenera of *Carex*. Subdivision of *Carex* according to Chater (1980).

	Vignea	Carex
caricis	+	+
baudisi	+	+
granifex	+	+
arenaria	+	+
subterranea	+	-
gallarum	+	+
fireni	+	+
kneuckeri	+	-
tarda	-	+
cornifex	-	+
rosenhaueri	-	+
fischeri	-	+
tumorificus	-	+

Cladograms of gall midges and host plants have been provided by Roskam (1979) for *Semudobia* (five spp.), including two Nearctic species, and *Betula* (about 40 spp.) (fig. 3). Four dichotomies, or events of speciation, in *Semudobia* have corresponding branchings in *Betula*. First, *S. skuhravae* Roskam induces galls in the bracts of fruit catkins, whereas *S. betulae* (Winertz), *S. tarda* Roskam, *S. brevipalpis* Roskam and *S. steenisi* Roskam, sharing apomorphies of larval and adult morphology, make galls in fruits. This dichotomy 1 is reflected in *Betula* at the section level. Whereas birches belonging to the sections *Costatae* (Regel) and *Humiles* (Koch) have erect catkins with fruits overwintering in the trees, birches of the sections *Excelsae* (Koch) and *Acuminatae* (Regel) bear pendent catkins and disperse their fruits in the autumn of the year of flowering, an apomorphic condition. Acuminate birches lack *Semudobia* galls. *S. skuhravae* causes galls in birches of all remaining sections, but the fruit galling midges are only present on birches of the section *Excelsae*. The structure of the catkins in the latter

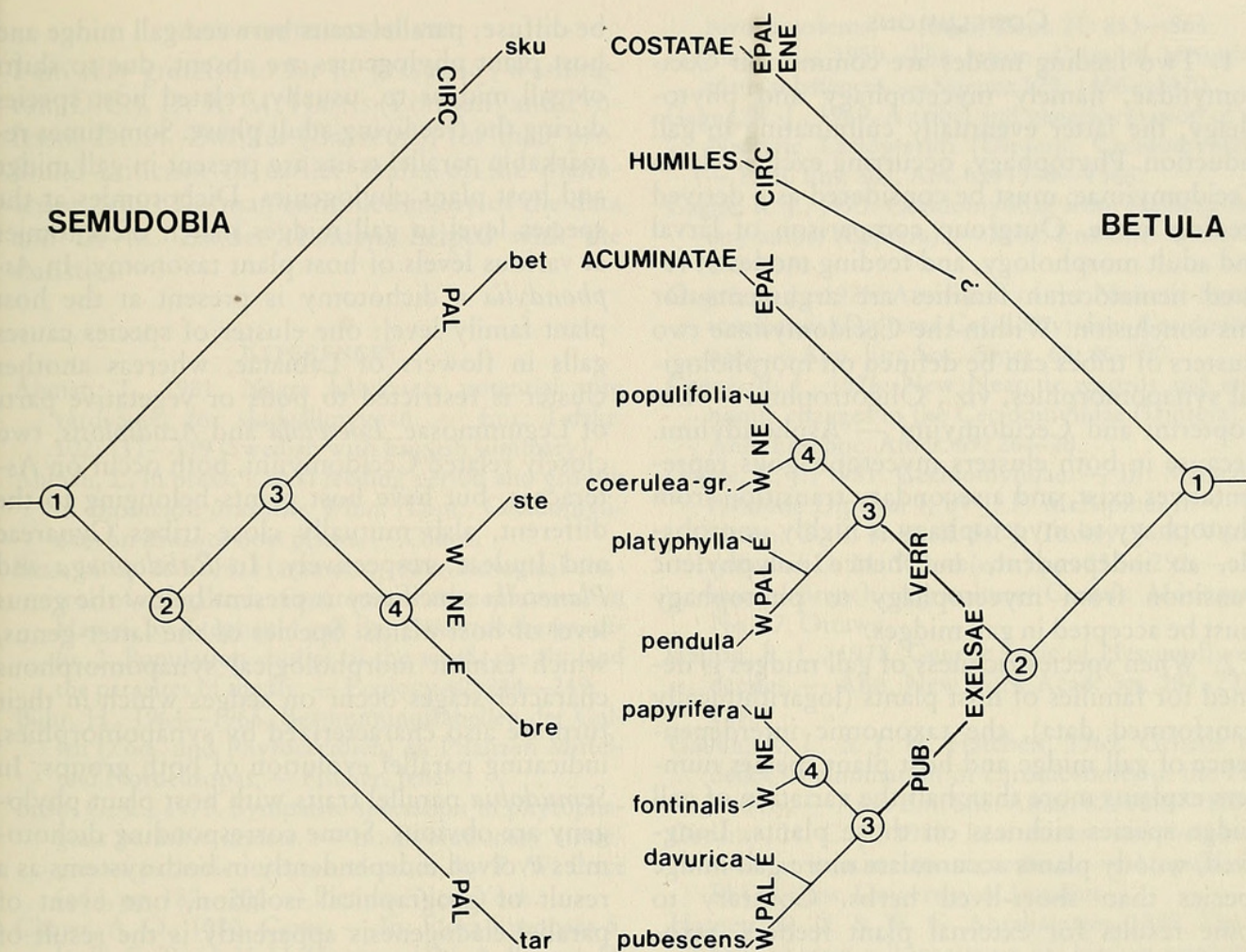


Fig. 3. Parallel cladogenesis in *Betula* and *Semudobia*. The numbers refer to corresponding dichotomies in the cladograms. The branch which is not supported by apomorphies is indicated by a question mark. CIRC, Circumboreal; NE, Nearctic; PAL, Palearctic; PUB, *Pubescentes*; VERR, *Verrucosae*; bet, *Semudobia betulae*; bre, *S. brevipalpis*; sku, *S. skuhravae*; ste, *S. steenisi*; tar, *S. tarda*.

section allows fruit galling *Semudobia* species to hibernate in the soil, which is a favourable condition (Möhn, 1961).

Dichotomy 2 in *Semudobia* is paralleled by *Betula* at the series level: *S. tarda* is common in birches of the series *Pubescentes* Sukaczew of *Excelsae*, whereas *S. betulae* predominates in birches belonging to the series *Verrucosae* Sukaczew. This branching separates birches of different habitat conditions and apparently evolved under allopatric conditions. However, the recent birches of both series may occur sympatrically, as do *S. betulae* and *S. tarda*. Both midge species are able to induce galls in birches belonging to both series, but their preference is different, reminiscent to the original, allopatric situation (Roskam & Van Uffelen, 1981).

Finally, there is a correspondence regarding the third and fourth branchings, as a result of geographical vicariance. In both series of the section *Excelsae* different species occur in the

western and eastern part of both Palaearctic and Nearctic. In the "betulae group" of *Semudobia* species, viz., *S. betulae*, *S. brevipalpis* and *S. steenisi*, this vicariance is incompletely paralleled: *S. brevipalpis* and *S. steenisi* being restricted to the East and West Nearctic, respectively, and *S. betulae* occurring in the whole Palaearctic (Roskam, 1979).

We must conclude, as was expected in phytophages, that parallel branchings in *Betula* and *Semudobia* are not complete. Moreover, fruit-galling *Semudobia* species were able to shift to other phyletic lines of birches under circumstances of secondary sympatry. Real reciprocal adaptations are absent. The first dichotomy is an example of sequential evolution: a change in the construction of the catkin, in favour of dispersal of the birch fruits, is exploited by the fruit-galling midges to improve their conditions for hibernation. All other branchings evolved simultaneously in plants and midges under conditions of allopatry.

CONCLUSIONS

1. Two feeding modes are common in Cecidomyiidae, namely mycetophagy and phytophagy, the latter eventually culminating in gall induction. Phytophagy, occurring exclusively in Cecidomyiinae, must be considered as a derived feeding mode. Outgroup comparison of larval and adult morphology, and feeding modes of related nematoceran families are arguments for this conclusion. Within the Cecidomyiinae two clusters of tribes can be defined on morphological synapomorphies, viz., Oligotrophini — Lasiopterini and Cecidomyiini — Asphondyliini. Because in both clusters mycetophagous representatives exist, and a secondary transition from phytophagy to mycetophagy is highly improbable, an independent, and hence polyphyletic transition from mycetophagy to phytophagy must be accepted in gall midges.

2. When species richness of gall midges is defined for families of host plants (logarithmically transformed data), the taxonomic interdependence of gall midge and host plant species numbers explains more than half the variation of gall midge species richness on those plants. Long-lived, woody plants accumulate more gall midge species than short-lived herbs. Contrary to some results for external plant feeders, taxonomical diversity of host plants is an important variate for this group of endophytophages to explain their radiation.

3. At the tribal rank gall inducing Cecidomyiidae are differently adapted to structures of their host plants. In Lasiopterini and Oligotrophini significantly more species are adapted to vegetative organs, such as stems, vegetative shoots and leaves, whereas in Asphondyliini and Cecidomyiini more species are adapted to generative organs, such as flowers, inflorescences and fruits. If the preference for generative tissues in *Contarinia* is original for Cecidomyiini, the different preference of gall midge tribes for host plant organs may function as evidence for a polyphyletic transition to phytophagy.

4. Most gall inducing midge species have narrow host plant spectra. Limits at the gall midge genus level are usually narrow too: species of the same genus have host plants which are also congeneric or belong to some closely related genera. Although examples of ecological opportunists are in the minority, they also exist in gall midges. Gall midge — host plant relations may

be diffuse: parallel traits between gall midge and host plant phylogenies are absent, due to shifts of gall midges to, usually, related host species during the free living adult phase. Sometimes remarkable parallel traits are present in gall midge and host plant phylogenies. Dichotomies at the species level in gall midges match dichotomies at various levels of host plant taxonomy. In *Asphondylia* a dichotomy is present at the host plant family level: one cluster of species causes galls in flowers of Labiatae, whereas another cluster is restricted to pods or vegetative parts of Leguminosae. *Loewiola* and *Acodiplosis*, two closely related Cecidomyiini, both occur on Asteraceae, but have host plants belonging to the different, also mutually close tribes Cynareae and Inuleae, respectively. In *Rabdophaga* and *Planetella* specificity is present below the genus level of host plants. Species of the latter genus, which exhibit morphological synapomorphous character stages occur on sedges which in their turn are also characterized by synapomorphies, indicating parallel evolution of both groups. In *Semudobia* parallel traits with host plant phylogeny are obvious. Some corresponding dichotomies evolved independently in both systems as a result of geographical isolation, one event of parallel cladogenesis apparently is the result of sequential evolution.

5. Prerequisites for sympatric speciation are present in gall midges which live in perennial plants, hibernating and pupating in the galls; mating and oviposition then occurs in close proximity to the gall. However, assortative mating, another prerequisite, is unlikely in many instances because of the production of unisexual families by females and swarming flights of virgin males. Furthermore, in cases of host shifts, even to closely related plant taxa, a considerable reduction of fitness can be observed. Nevertheless, analysis of life-history traits offers a few examples in which gall midges possess a niche structure appropriate for sympatric speciation, e.g., Nearctic *Rhopalomyia* species on *Artemisia*.

Finally, we must be aware that in a group of phytophages, where so many related taxa share related host plants, many more parallel events will be discovered. Only when monographic work is combined with a detailed study of host plant relations, the major processes responsible for the present gall midge diversity will become understood.

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REFERENCES

- Åhman, I., 1981. Några kälväxters potential som värdväxter för skidgallmygga. — Ent. Tidskr. 102: 111—119 (Swedish with English summary).
- Åhman, I., in press. Larval feeding period and growth of *Dasineura brassicae* Winn. (Dipt., Cecidomyiidae) on *Brassica* host plants. — Oikos.
- Bess, H. A. & F. H. Haramoto, 1959. Biological control of pamakani, *Eupatorium adenophorum*, in Hawaii by a tephritid gall fly, *Procecidochares utilis*. 2. Population studies of the weed, the fly, and the parasites of the fly. — Ecology 40: 244—249.
- Buhr, H., 1964—1965. Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen Mittel- und Nordeuropas. — Fischer, Jena.
- Bush, G. L., 1975. Sympatric speciation in phytophagous parasitic insects. — In: Evolutionary strategies of parasitic insects and mites, by P. W. Price (ed.), pp. 187—206. — Plenum, New York.
- Chater, A. O., 1980. *Carex*. — In: Flora Europaea 5, by T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters and D. A. Webb (eds.), pp. 290—323. — Cambridge University Press, Cambridge.
- Claridge, M. F. & M. R. Wilson, 1981. Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. — Ecol. Entomol. 6: 217—238.
- Coutin, R. & K. M. Harris, 1968. The taxonomy, distribution, biology and economic importance of the millet grain midge, *Geromyia penniseti* (Felt), gen.n., comb.n. (Dipt., Cecidomyiidae). — Bull. ent. Res. 59: 259—273.
- Crawley, M., 1983. Herbivory: the dynamics of animal-plant interaction. — Blackwell, Oxford.
- Dethier, V. G., 1954. Evolution of feeding preferences in phytophagous insects. — Evolution 8: 33—54.
- Ehrlich, P. R. & P. H. Raven, 1964. Butterflies and plants: a study in coevolution. — Evolution 18: 586—608.
- Eichler, W., 1948. Some rules in ectoparasitism. — Ann. Mag. Nat. Hist. Ser. 12 (1): 588—598.
- Engler, A., 1964. Syllabus der Pflanzenfamilien, 2nd part. — Borntraeger, Berlin.
- Felt, E. P., 1940. Plant galls and gall makers. — Hafner, New York.
- Fowler, S. V. & J. H. Lawton, 1982. The effects of host-plant distribution and local abundance on the species richness of agromyzid flies attacking British umbellifers. — Ecol. Entomol. 7: 257—265.
- Fox, L. R., 1981. Defense and dynamics in plant herbivore systems. — Amer. Zool. 21: 853—864.
- Fraenkel, G., 1959. The raison d'être of secondary plant substances. — Science 129: 1466—1470.
- Gagné, R. J., 1969. A tribal and generic revision of the Nearctic Lasipteridi (Diptera: Cecidomyiidae). — Ann. Ent. Soc. Am. 62: 1348—1364.
- Gagné, R. J., 1973. Cecidomyiidae from Mexican tertiary amber (Diptera). — Proc. Ent. Soc. Wash. 75: 169—171.
- Gagné, R. J., 1975. A revision of the Nearctic Stomatosematidi (Diptera: Cecidomyiidae: Cecidomyiinae). — Ann. Ent. Soc. Amer. 68: 86—90.
- Gagné, R. J., 1976. New Nearctic records and taxonomic changes in the Cecidomyiidae (Diptera). — Ann. Ent. Soc. Amer. 69: 26—28.
- Gagné, R. J., 1981. Cecidomyiidae. — In: Manual of Nearctic Diptera. I, by J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth and D. M. Wood (eds.) pp. 257—292. — Research Branch Agriculture Canada Monograph No. 27, Ottawa.
- Gallun, R. L., 1977. Genetic basis of Hessian fly epidemics. — Ann. New York Acad. Sci. 287: 223—229.
- Gallun, R. L. & J. H. Hatchett, 1969. Genetic evidence of elimination of chromosomes in the Hessian fly. — Ann. Ent. Soc. Amer. 62: 1095—1101.
- Godfray, H. C. J., 1982. Leaf miners and their parasites in relation to succession. — Unpublished PhD Thesis, University of London.
- Harnett, D. C. & W. G. Abrahamson, 1979. The effects of stem gall insects on life history patterns in *Solidago canadensis*. — Ecology 60: 910—917.
- Hatchett, J. H. & R. L. Gallun, 1970. Genetics of the ability of the Hessian fly, *Mayetiola destructor*, to survive on wheats having different genes for resistance. — Ann. Ent. Soc. Amer. 63: 1400—1407.
- Hegnauer, R., 1962—1973. Chemotaxonomie der Pflanzen. I—VI. — Birkhauser, Basel.
- Hutchinson, J., 1969. Evolution and phylogeny of flowering plants. Dicotyledons: facts and theory. — Academic Press, London.
- Janzen, D. H., 1968. Host plants as islands in evolutionary and contemporary time. — Amer. Nat. 102: 592—595.
- Janzen, D. H., 1980. When is it coevolution? — Evolution 34: 611—612.
- Jermey, T., 1976. Insect-host plant relationship: coevolution or sequential evolution? — Symp. Biol. Hung. 16: 109—113.
- Jones, R. G., R. J. Gagné & W. F. Barr, 1983. Biology and taxonomy of the *Rhopalomyia* gall midges (Diptera: Cecidomyiidae) of *Artemisia tridentata* Nuttall (Compositae) in Idaho. — Contrib. Amer. Ent. Inst. 21: 1—90.
- Klausnitzer, B., 1977. Evolution der Insekten als Einmischungsprozess bei Angiospermen. — Biol. Rundschau 15: 366—377.
- Lawton, J. H., 1983. Plant architecture and the diversity of phytophagous insects. — Ann. Rev. Ent. 28: 23—39.
- Lawton, J. H. & P. W. Price, 1979. Species richness of

- parasites on hosts: agromyzid flies on the British Umbelliferae. — J. Anim. Ecol. 48: 619—637.
- Lawton, J. H. & D. Schröder, 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. — Nature 265: 137—140.
- MacArthur, R. H. & E. O. Wilson, 1967. The theory of island biogeography. — Princeton University Press, Princeton, N.J.
- McKay, P. A. & J. H. Hatchett, 1984. Mating behavior and evidence of a female sex pheromone in the Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae). — Ann. Ent. Soc. Amer. 77: 616—620.
- Mamaev, B. M., 1968. Evolution of gall forming insects — gall midges. — British Library Lending Division, Boston Spa, Wetherby, translated by A. Crozy (1975).
- Metcalfe, M. E., 1935. The germ cell cycle in *Phytophaga destructor* (Say). — Q. J. Microsc. Sci. 77: 585—604.
- Möhn, E., 1955. Neue freilebende Gallmücken — Gattungen. — Deut. Ent. Zeitschr. NF 2: 127—151.
- Möhn, E., 1961. Gallmücken (Diptera, Itonidae) aus El Salvador. 4. Zur Phylogenie der neotropischen und holarktischen Region. — Senck. Biol. 42: 131—330.
- Möhn, E., 1966. 6.L. Cecidomyiidae = (Itonidae). — In: Die Fliegen der palaearktischen Region, bij E. Lindner (ed.), pp. 1—41. — Schweizerbart, Stuttgart.
- Nijveldt, W. [C.], 1969. Gall midges of economic importance. VIII. — Crosby Lockwood & Son, London.
- Nijveldt, W. C. & A. J. A. Hulshoff, 1968. Waarnemingen inzake de tarwestengelgalmug (*Haplodiplosis equestris* Wagner) in Nederland. — Inst. Plantenziektkundig Onderzoek, Med. 459: 1—77 (Dutch with English summary).
- Orphanides, G. M., 1975. Biology of the carob midge complex, *Asphondylia* spp. (Diptera, Cecidomyiidae), in Cyprus. — Bull. ent. Res. 65: 381—390.
- Parnell, J. R., 1963. Three gall midges (Diptera: Cecidomyiidae) and their parasites found in the pods of broom (*Sarothamnus scoparius* (L.) Wimmer). — Trans. R. Ent. Soc. Lond. 115: 261—275.
- Price, P. W., 1977. General concepts on the evolutionary biology of parasites. — Evolution 31: 405—420.
- Regenfuss, H., 1978. Ursachen und Konsequenzen einer parallelen phylogenetischen Aufspaltung von Parasiten und Wirten. — Sonderbd. naturwiss. Ver. Hamburg 2: 83—99.
- Roskam, J. C., 1979. Biosystematics of insects living in female birch catkins. II. Inquiline and predaceous gall midges belonging to various genera. — Neth. J. Zool. 29: 283—351.
- Roskam, J. C., in press. Evolution of the gall inducing guild. — In: Biology of insect and acarina induced galls, by J. D. Shorthouse & O. Rohfritsch (eds). — Praeger, New York.
- Roskam, J. C. & G. van Uffelen, 1981. Biosystematics of insects living in female birch catkins. III. Plant — insect relation between white birches, *Betula* L., section *Excelsae* (Koch) and gall midges of the genus *Semudobia* Kieffer (Diptera, Cecidomyiidae). — Neth. J. Zool. 31: 533—553.
- Rothmaler, W., 1972. Exkursionsflora für die Gebiete der DDR und der BDR. Gefäßpflanzen. — Volk und Wissen, Berlin.
- Rübsaamen, E. H. & H. Hedicke, 1925—1939. Die Zoocecidien, durch Tiere erzeugte Pflanzengallen Deutschlands und ihre Bewohner. — Zoologica 29: 1—350.
- Skuhrová, M., 1973. Monographie der Gallmückengattung *Clinodiplosis* Kieffer, 1894 (Cecidomyiidae, Diptera). — Studie ČSAV 17: 1—80.
- Skuhrová, M., in press. Family Cecidomyiidae. — In: Catalogue of Palaearctic Diptera, by A. Soós & L. Papp (eds). — Elsevier, Amsterdam.
- Skuhrová, V., 1970. Das Schadbild der Kiefernadelgallmücke *Thecodiplosis brachyntera* (Schwägr.) (Diptera, Itonididae) an Nadeln einiger *Pinus*-arten. — Marcellia 36: 229—241.
- Skuhrová, V., 1982. The saddle gall midge *Haplodiplosis marginata* (Von Roser) (Diptera, Cecidomyiidae), an important pest of wheat and barley in Czechoslovakia. — Folia Fac. Sci. Nat. Univ. Purkynianae Brunensis 23: 133—135.
- Skuhrová, V. & R. Hochmut, 1969. Befallsdichte der Kiefernadelgallmücke *Thecodiplosis brachyntera* (Schwägr.) an *Pinus silvestris* L. verschiedener Provenienz. — Anz. Schädlingssk. u. Pflanzensch. 42: 165—169.
- Skuhrová, V. & M. Skuhrová, 1982. Flugaktivität und Wirtspflanzenkreis der Sattelmücke, *Haplodiplosis marginata* (Von Roser) (Cecidomyiidae, Diptera). — Wiss. Beitr. Martin Luther Univ. Halle-Wittenberg 17: 263—271.
- Skuhrová, V., M. Skuhrová & J. W. Brewer, 1983. Ecology of the saddle gall midge *Haplodiplosis marginata* (Von Roser) (Diptera, Cecidomyiidae). — Zeitschr. angew. Ent. 96: 476—490.
- Southwood, T. R. E., 1972. The insect/plant relationship — an evolutionary perspective. — In: Insect/plant relationships, by H. F. van Emden (ed.), pp. 3—30. — Blackwell, Oxford.
- Southwood, T. R. E., 1978. The components of diversity. — Symp. R. Ent. Soc. Lond. 9: 19—40.
- Spungis, V., 1981. New species of gall midges from the tribes Oligotrophini and Porricondyliini. V. — Latvijas Entomologs 24: 43—55 (Russian with English summary).
- Strong, D. R., J. H. Lawton & Sir Richard Southwood, 1984. Insects on plants. — Blackwell, Oxford.
- Sylvén, E., 1970. Field movement of radioactively labelled adults of *Dasyneura brassicae* Winn. (Dipt., Cecidomyiidae). — Ent. Scand. 1: 161—187.
- Takhtajan, A. L., 1954. Origin of angiospermous plants. — Amer. Inst. Biol. Sci., Washington, translated by O. H. Gankin (1958).
- Takhtajan, A. L., 1980. Outlines of the classification

- of flowering plants (Magnoliophyta). — Bot. Rev. 46: 225—359.
- Van Vreden, G. & K. Arifin, 1977. Bionomics of the rice gall midge *Orseolia oryzae* (Wood-Mason) with emphasis on insect — plant relationship. — Contr. Centr. Res. Inst. Agric. Bogor 27: 1—18.
- Verschaffelt, E., 1910. The cause determining the selection of food in some herbivorous insects. — Proc. Acad. Sci., Amsterdam 13: 536—542.
- Weis, A. E., P. W. Price & M. Lynch, 1983. Selective pressures on clutch size in gall maker *Asteromyia carbonifera*. — Ecology 64: 688—695.
- Yukawa, J., T. Ohtani & Y. Yazawa, 1983. Host-change experiments from wild plants to soybean in *Asphondylia* species (Diptera, Cecidomyiidae). — Proc. Assoc. Pl. Prot. Kyushu 29: 115—117 (Japanese with English summary).
- Zwölfer, H., 1978. Mechanismen und Ergebnisse der Co-evolution von phytophagen und entomophagen Insekten und höheren Pflanzen. — Sonderbd. naturwiss. Ver. Hamburg 2: 7—50.
- Zwölfer, H. & G. Bush, 1984. Sympatrische und parapatrische Artbildung. — Zeitschr. Zool. Syst. Evol.-forsch. 22: 211—233.



Roskam, J C. 1985. "Evolutionary patterns in gall midge - host plant associations (Diptera, Cecidomyiidae)." *Tijdschrift voor entomologie* 128, 193–213.

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