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THE INSECT COMMUNITY ASSOCIATED WITH ROSE GALLS OF
DIPLOLEPIS POLITA (CYNIPIDAE, HYMENOPTERA)

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*The single chambered gall of *Diplolepis polita* (Ashmead) (Cynipidae) is initiated in the early spring on immature leaves of *Rosa acicularis* Lindl. (Rosaceae). *D. polita* larvae and succulent gall tissues attract five additional insect species which, by their inter-relationships within the galls constitute a community. Each species appears over a different period so that the community undergoes succession and climax. Life cycles and roles of all members of the community are discussed. Most of the *D. polita* larvae are replaced early in the season by larvae of the inquiline *Periclistus pirata* (Osten Sacken) (Cynipidae). *P. pirata* larvae cause additional cell proliferation and in the process of becoming enclosed in layers of cells, structurally modify their host galls. Galls inhabited by *P. pirata* are larger than galls inhabited by *D. polita*. Larvae of *P. pirata* are the main food source for four entomophagous inhabitants: *Eurytoma longavena* Bugbee (Eurytomidae), *Glyphomerus stigma* (Fabricius) (Torymidae), *Torymus bedeguaris* (Linnaeus) (Torymidae), and *Habrocytus* sp. (Pteromalidae).*

*La Communauté d'Insectes Associés avec des Galles de Rose de *Diplolepis polita* (Cynipidae, Hymenoptère)*

Sommaire

*La galle de *Diplolepis polita* (Ashmead) (Cynipidae) d'une seule chambre s'initie de bonne heure le printemps sur des jeunes feuilles de *Rosa acicularis* Lindl. (Rosaceae). Les larves de *D. polita* et les tissus succulents des galles attirent cinq autres espèces d'insectes, qui par leurs relations constituent une communauté. Chaque espèce se manifeste pendant une période différente de l'année et comme résultat la communauté subit une succession d'habitants et une période d'apogée. Les cycles vitaux et les rôles de tous les membres communautaires sont analysés. La plupart des larves de *D. polita* s'est remplacée tôt dans la saison par des larves de *Periclistus pirata* (Osten Sacken) (Cynipidae). Ces larves de *P. pirata* évoquent une nouvelle prolifération de cellules et pendant le processus de se faire entourer par des couches cellulaires, elles font modifier la structure de la galle-hôte. Les galles habitées par *P. pirata* sont plus grandes que celles habitées par *D. polita*. Les larves de *P. pirata* servent de nourriture principale des quatre habitants entomophages: *Eurytoma longavena* Bugbee (Eurytomidae), *Glyphomerus stigma* (Fabricius) (Torymidae), *Torymus bedeguaris* (Linnaeus) (Torymidae), et *Habrocystus* sp. (Pteromalidae).*

Cecidology, the study of plant galls, has long been of great interest to biologists. Although galls have been mentioned in the literature since ancient times (Hippocrates, 406-377 B. C., wrote on the medicinal properties of galls) it was not until the late eighteenth century that any attempt was made to explain the connection between galls and the insects found in them. Malpighi was probably the first to explain that the stimulus for gall formation was of animal origin (Plumb, 1953). Cosens (1915) reviewed the older gall literature in a paper in which he discussed the founding of cecidology. Plumb (1953) also presented an excellent review of early cecidological literature and explained the development of theories about the source of gall forming stimuli, sites of action, and gall developmental morphology.

Although a great deal of literature on insect galls has been amassed, much of it is only systematic. Most cecidological workers in North America have occupied themselves with the classification of galls and gall insects and have disregarded fundamental problems such as gall initiation, developmental morphology, and the inter-relationships of the inhabitants composing the gall communities. Checklists are prominent in North American cecidological literature and the most popular is by Felt (1940). The most comprehensive treatise of European galls and gall formers is by Buhr (1965).

Insect galls can be defined as atypical growths produced by plants in response to a foreign stimulus. This stimulus, either chemical or physical, or both, can be provided by the larvae or the adult gall former. Gall formers are found in at least 8 insect orders, but the majority are restricted to the families Cecidomyiidae and Cynipidae. Of the approximately 1,450 gall formers in North America (Felt, 1940), about 38% belong to the order Hymenoptera. Of the hymenopterous gall formers, 91% belong to the family Cynipidae, the galls of which are recognized by all students of cecidology as the most remarkable in variety and complexity.

For gall development to occur, the life cycle of the gall former must be synchronized with the optimum galling conditions of the plant. One prime requisite for gall formation is the presence of meristematic tissue. The plant must be in such a condition that the foreign stimulus can alter normal growth patterns. Malyshev (1968) suggested that gall wasps can convert relatively differentiated tissue back into the meristematic state. Wells (1920) suggested that the gall former actually causes the dedifferentiation of host tissue, preventing the normal expression of host characters. Once dedifferentiation has occurred, stimuli from the insects cause the gall to grow into its specific shape. All galls, especially the more complex, have characteristic shapes and structures. The structure of a gall depends upon the genus of insect producing it rather than upon the plant on which it is produced. Kinsey (1920b) suggested that many gall-causing Hymenoptera may be more readily identifiable by their galls than by their own morphological characters.

Although a few gall insects are found on more than one host species, nearly all are specific to a single host genus. Cynipids have found optimal conditions on the oaks since 86% of the known species are associated with this genus. Malyshev (1968) suggested that this can be attributed to the fact that oaks are slow growing and have shoots that stay fresh and susceptible to galling for a long time. Most of the remaining cynipid species are associated with members of Rosaceae and 7% of these are restricted to the genus *Rosa*. A possible explanation for this might be Malyshev's suggestion that primitive Cynipidae caused galls on common ancestors of Rosales and Fagales and the two orders subsequently diverged.

Galls are not evenly distributed on various parts of their host plants. Besides being host specific, gall formers restrict themselves to specific plant organs. Mani (1964) reported that 5% of the known cynipid galls on *Quercus* form on the roots, 22% on branches, 2% on flowers, 4% on acorns, and about 63% on leaves. He also reported that over 80% of the galls on Rosaceae are formed on leaves.

Kuster (1911) distinguished two kinds of galls on the basis of structure. He termed the more primitive galls the kataplasmas and those more complex, the prosoplasmas. Both terms have been widely used. The kataplastic galls (e.g. those caused by aphids) are characterized by a lack of both definitive tissues and constant external shape. Kataplastic galls are composed of homogeneous parenchyma cells, show little differentiation, and are structurally similar to the meristematic tissues from which they develop. Prosoplastic galls are characterized by a definitive size and form. Their tissues, differentiated into well defined zones, are fundamentally different from the normal host tissue. Most cynipid galls are prosoplastic. Wells (1921) presented evidence that prosoplastic galls were phylogenetically derived from kataplastic galls.

Gall structure depends on many factors, including time of oviposition and number of eggs laid in one area. Galls developing with one larva present are termed monothalamous and those containing several larvae are termed polythalamous. In polythalamous galls, each larva is individually surrounded by plant tissue.

Insect galls are often inhabited by numerous species besides the gall former because of the attractiveness of localized concentrations of nutritive plant tissues. The inter-relationships of insect gall inhabitants constitute one of the most important aspects of cecidology. One European gall is reported to have over 75 species of insects associated with it (Mani, 1964).

One of the first tasks in studying inter-relationships of gall insects is to determine the feeding habits of each species. Mani (1964) listed 33 different roles into which gall inhabitants can be classified. I found five insect species associated with the *Diplolepis polita* galls in my study area; they exhibit a variety of feeding habits. Both phytophagous and entomophagous species are present. The gall-forming cynipids are phytophagous for their entire larval stage. One of the inhabitants is also a phytophagous cynipid and although it is unable to initiate galls of its own, it is able to cause further proliferation of gall tissues. Galls inhabited by these insects are not only structurally modified, but also grow much larger. The four remaining species are entomophagous and feed on their hosts either as parasitoids or ectoparasites.

It must be stressed that associating entomophagous species with a particular gall does not give information on host-prey relationships. Great care must be taken in rearing experiments to determine these associations and the present study is one of few where relationships of the entomophagous species in a gall community have been determined.

Little work has been done on the biology of insect galls in Alberta. There has yet to be a checklist compiled for the galls of Alberta and Western Canada. Only the aphid galls have received concentrated attention (Harper, 1959a, 1959b, and 1966; Cumming, 1968). A.C. Kinsey, in several of his works, mentioned receiving galls from Calgary, Alberta. Weld (1926) recorded that a worker in Toronto received galls of *Diplolepis bicolor* (Harris) and *D. multispinosus* (Gillette) from Calgary.

The purpose of this paper is to examine the biology and inter-relationships of each species found in the *D. polita* gall. It is also my objective to show that the associations of species within the gall constitute a community. Each species has its role in the community and the sequence of appearance of each species initiates changes in the community's structure. Because various community attributes such as succession and climax can be examined with relative ease, studying galls may in many ways add to our general knowledge of community ecology.

All species studied in this work are new locality records for Alberta and greatly extend known distributions. Long series of all species discussed have been deposited in the Strickland Memorial Museum, University of Alberta, the University of Saskatchewan Insect Collection, and the Canadian National Collection of Insects in Ottawa.

STUDY AREA

All field work was conducted at the George Lake Field Station of the Department of Entomology, University of Alberta, 40 miles N. W. of Edmonton, Alberta (53° 57' N, 114° 06' W). All galls used in the community inter-relationship studies were found within the one square mile field station situated on the southern margin of the boreal mixed forest subzone (LaRoi, 1968). Fire is an important feature of the boreal mixed forest subzone and has influenced the ecology of George Lake. The forest is otherwise essentially untouched, with

only some isolated logging prior to 1930. *Ledum groenlandicum* Oeder bogs and *Carex* species meadows are found in several places. There are a few open areas which allow bush stratum species to grow densely. Principal trees of the upper stratum are *Populus balsamifera* L. and *P. tremuloides* Michx. Other trees present, but less common, are *Betula papyrifera* March., *Picea glauca* Moench., *Alnus tenuifolia* Nutt., and several species of *Salix*. The bush stratum is more diverse and the dominant species are *Rosa acicularis* Lindl., *Rosa woodsii* Lindl., *Amelanchier alnifolia* Nutt., *Cornus stolonifera* Michx., *Ribes lacustre* Pers., and *Viburnum edule* Michx. Common herbs are *Epilobium angustifolium* L., *Heracleum lanatum* Michx., and several species of *Solidago*.

GENUS *DIPLOLEPIS* GEOFFROY

Dalla Torre and Kieffer (1910) and Weld (1952b, 1957, and 1959) gave excellent descriptions of the family Cynipidae along with keys to the subfamilies and genera. A brief description of the genus *Diplolepis* was included by Dalla Torre and Kieffer. The main character used to distinguish the genus is the plowshare-shaped hypopygium. Kinsey (1920b) gave data on the phylogeny of the cynipid genera and presented biological characters of each. So far as known, *Diplolepis* species form galls only on *Rosa*.

There is considerable confusion in the literature about which generic name should be applied to cynipids forming galls on *Rosa*. *Rhodites* Hartig has been used extensively in cynipid literature, but Rohwer and Fagan (1917) established that *Diplolepis* Geoffroy had priority. Because *Rhodites* and *Diplolepis* are isogenotypic, *Rhodites* disappears in synonymy. Some Europeans still use *Rhodites* as there is sentiment for having it placed on the conservanda list, but Eady and Quinlan (1963) used *Diplolepis* in their key to the British species. Kinsey and Ayres (1922) were the first North Americans to use *Diplolepis*. When Felt (1940) republished his North American checklist of galls, he also changed to *Diplolepis*. There has also been confusion as to whether Geoffroy (1762) or Fourcroy (1785) is the author of *Diplolepis*. Weld (1952a) reviewed the nomenclature problem and recognized Geoffroy.

Diplolepis is Holarctic in distribution. Dalla Torre and Kieffer (1910) and Eady and Quinlan (1963) gave keys to the European species. Dalla Torre and Kieffer also included a number of North American species and provided brief descriptions of each. No inclusive key to North American species has been published. All species descriptions are brief and require extensive elaborations. Males are seldom mentioned in the literature. Undoubtedly new species remain to be described and a complete revision of the genus may show some of the existing names to be synonyms. Felt (1940) recorded 25 species of *Diplolepis*, as well as many varieties, as occurring in North America. There are now about 30 known species and two of these (*D. mayri* Schl. and *D. rosae* L.) have been introduced. Weld (1957 and 1959) listed the species found in various areas of the United States and gave brief descriptions of their galls.

Diplolepis polita Ashmead and its Gall

Diplolepis polita was described by Ashmead (1890) as forming galls on the leaves of *Rosa californica* Cham. and Schlecht. As with other Nearctic *Diplolepis*, the recorded description of *D. polita* is brief and inadequate. One of the key characters used to distinguish the species is its smooth and shiny mesopleura. The mesoscutum, particularly the posterior region, is not as rugose as in other species. Both Ashmead (1890) and Dalla Torre and Kieffer (1910) stated that males and females are entirely black. All females from George Lake have a reddish-brown abdomen as well as reddish-brown legs.

D. polita has been found only in North America. Ashmead (1890) examined specimens from California, Dakota, and Colorado. Weld (1957) recorded *polita* as being found on the Pacific coast but did not mention it (1959) as occurring in Eastern United States. *D. polita* is not mentioned in Eastern North America checklists. Galls of *D. polita* were the most common of the *Diplolepis* galls found at George Lake in 1968 and 1969. I have collected specimens throughout Alberta, but it appears to be most common in central and northern regions. The previous most northern locality recorded was Ashland, Oregon (Bugbee, 1951).

Ashmead (1890) mentioned receiving galls of *D. polita* from Cockerell who had used the manuscript name *spinosellus*. Cockerell (1890) stated that *D. spinosellus* was a new species, but gave no description of the gall former or the gall. Muesebeck *et al.* (1951) declared *spinosellus* Cockerell invalid. Krombein and Burks (1967) again used the name but gave no reference to descriptions of the gall former or the gall. Fullaway (1911) also made brief mention of *D. polita* and its gall. According to Weld (1952a) Fullaway misidentified the *polita* adults and instead considered them *D. bicolor*. Weld examined Fullaway's specimens and found those labelled *D. bicolor* were actually *D. polita*. Beutenmuller (1922) also obtained some of Fullaway's specimens described as *D. bicolor* and realizing they were not *D. bicolor*, proposed the name *D. occidentalis*. Weld (1952a) examined Beutenmuller's *occidentalis* and confirmed its synonymy with *polita*.

The gall of *D. polita* is small (average diameter 4.0 mm), spherical, monothalamous, and is spinulose and sometimes tuberculose. All galls collected were found on the adaxial surface of the leaflets (Figs. 1 and 2), although McCracken and Egbert (1922) stated that they can also be formed on stems. McCracken and Egbert also stated that the gall varies in size from 5 to 10 mm in diameter and often harbours inquiline. Their measurements were probably from inquiline modified galls rather than unmodified *D. polita* galls. *D. polita* galls are usually found in clusters, several galls per leaflet (Fig. 2), although individual galls on a leaf have been found. The largest number of galls found on one leaf was 39. Of all the galled leaves collected, 61% were host to 5 galls or fewer. Galls growing close to one another often coalesce.

Immature galls (Fig. 1) are often smooth or with weakly developed spines. They are soft and composed of large succulent cells, many of which are visible to the naked eye. The *polita* larva is tightly nestled in the interior of the gall where it feeds on the rapidly growing cells. Cells next to the larva often appear much larger than other cells of the gall wall and it is presumed that they play an important role in the larva's nutrition. As the gall matures the walls become brittle and the spines more conspicuous. The spines are easily broken off and as a result galls handled in the laboratory for some time may appear spineless (Figs. 3-6). The mature gall is hollow and smooth on the interior and the last instar larva has an increased amount of space inside the gall (Fig. 3).

Nothing has previously been recorded on the anatomy of the gall other than brief comments. Beutenmuller (1907) mentioned that the gall is thin walled and hollow. McCracken and Egbert (1922) were the first to establish that the gall is monothalamous. My histological studies (Ms. in preparation) show the gall to be prosoplasmic for the wall tissue is composed of four well defined zones.

Two temporally separated groups of *D. polita* galls appeared at George Lake in both 1968 and 1969 seasons. Most galls appeared in the early spring on mature rose plants and in this study are referred to as spring initiated galls. The second group of galls appeared later in the season on new sucker shoots and are referred to here as sucker shoot galls. Sucker shoot galls are somewhat different in appearance from spring initiated galls, often more densely covered with long and hair-like spines. Although sucker shoots probably begin growth in the

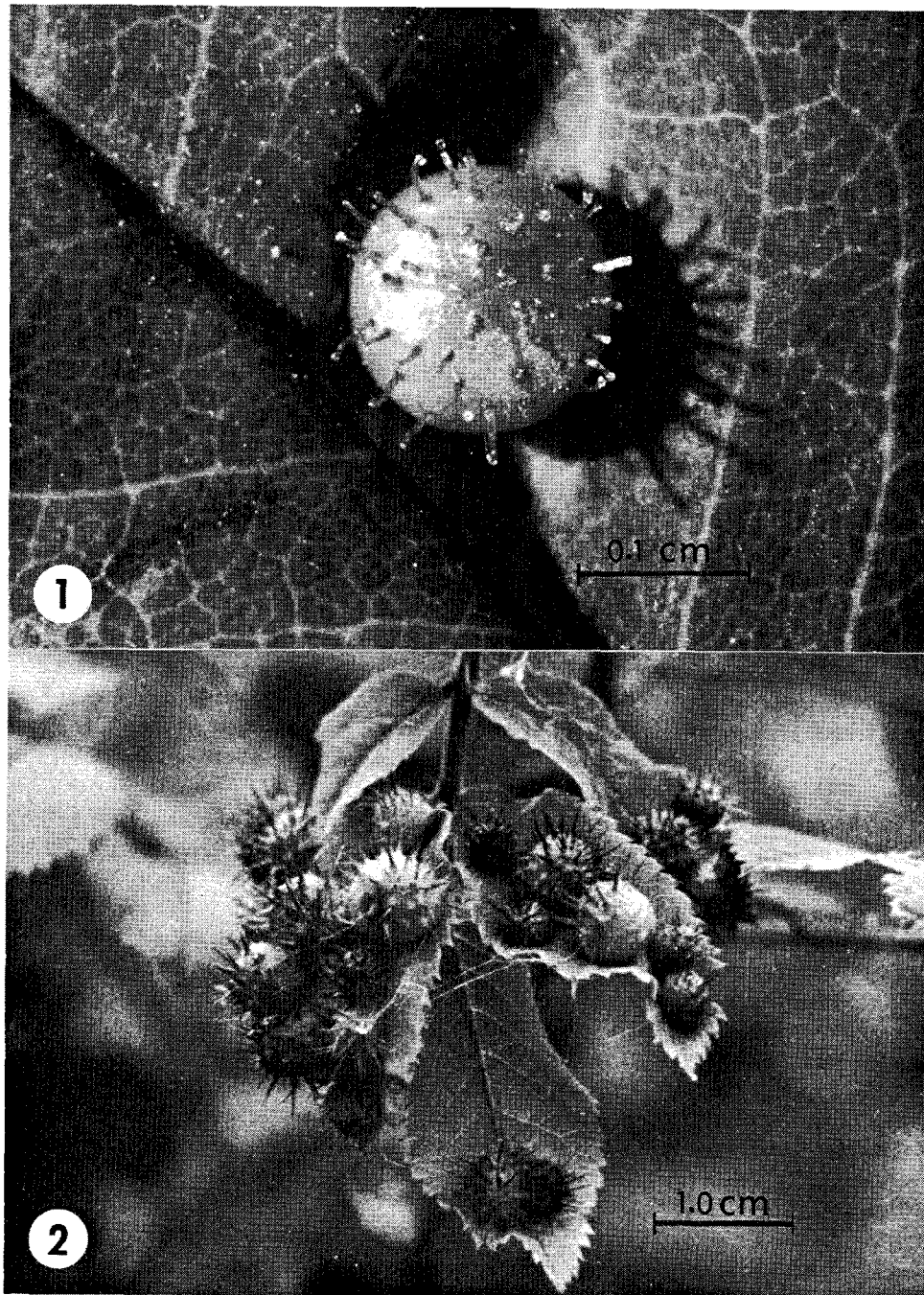


Fig. 1. Immature gall of *Diplolepis polita* on leaflet of *Rosa acicularis* Lindl. George Lake, Alberta. May 20, 1969. Fig. 2. Mature galls of *Diplolepis polita*. George Lake, Alberta. August 10, 1969.

spring, they were first observed near the end of June in both seasons. Sucker shoots are sterile and have larger and more succulent leaves than do older plants. They grow rapidly and most attain a height of 0.9m by the season's end. Their stems are densely spined and the tall thin plants produce few side branches. New sucker shoots were more common around open areas such as *Ledum* bogs and artificial clearings than in the forest.

It has been recorded by several authors that galls growing under various physiological conditions differ in their colorations. Both greenish-yellow and red galls of *D. polita* were found and the amount of sunlight received by the host plant appears to regulate colour. Cosens (1912) stated that galls of *Pontania pomum* Walsh (Family Tenthredinidae) are poorly colored if they grow in deeply shaded areas. *D. polita* galls growing in the shade of *Populus* species are generally a light greenish-yellow. Galls on plants growing in open spaces such as meadows, roadsides, and burned over areas are often bright red, especially when immature. Galls appearing on sucker shoots and those growing in darkly shaded areas may be creamy to pure white in color. Niblett (1943) noted this for the galls of *D. eglanteriae* Htg. and *D. rosarum* Gir. As the *D. polita* galls mature they become brown.

Schröder (1967) found that galls of *D. rosae* were more numerous on roses growing under stress. He reported that plants suffering from a lack of water supported more galls. These plants were small, their yearly growth poor, foliage thin, leaves smaller than normal, and often pale in color. They are unlikely to be the sucker shoot plants described in this paper. Schröder found these plants growing in areas subjected to extreme insolation and although they were common, their growth was poor. He observed ovipositions in both vigorous and weak plants and found that no galls formed on the vigorous plants. He suggested that the osmotic pressure of vigorously growing plants may be responsible for fewer galls. The rarity of *D. rosae* galls on domestic roses also indicates that healthy plants are able to suppress gall formation. *D. polita* galls appeared no more common on plants growing in open spaces such as roadsides than they did on plants growing in shaded areas. Galls occurring in such areas were, however, found to be much more brittle than galls growing in shaded areas.

In any study concerned with insect galls, it is vital that careful attention be paid to the accurate identification of host plants. Although *Diplolepis* species are restricted to *Rosa*, several species can form galls on more than one host species. Niblett (1943) recorded *D. eglanteria* on 7 species of rose. Harrison (1922) exposed 16 species of rose to *D. rosae* and found that oviposition took place only on members of one section. The 3 species of rose found in Alberta are *R. acicularis* Lindl., *R. woodsii* Lindl., and *R. arkansana* Porter, all belonging to section Cinnamomeae. Lewis (1957) emphasized that the genus *Rosa* is one of the most difficult groups to separate into distinct species. Species hybridize with ease giving fertile offspring and the wide variation contributes to identification problems. Of the two species found at George Lake *R. acicularis* is more common than *R. woodsii* and is generally taller, less bushy, and has larger leaflets. *R. woodsii* flowers later in the season and usually has more densely spined stems (both species determined by W. H. Lewis). Galls of *D. polita* were found only on *R. acicularis* at George Lake. Lewis (1959) illustrated the Holarctic and Nearctic distribution of *R. acicularis* and stated that it has the most extended native range of any species in the genus. *R. acicularis* is native to Northern Europe, Asia, and North America.

The *Diplolepis polita* Gall Community

I define an insect gall community as the assemblage of insect populations associated with a collection of galls initiated by the same species of gall former. For the purpose of this paper, the assemblage of insects obtained by making large random collections of galls within

the study area, was considered to constitute the *Diplolepis polita* gall community. Mani (1964) defined climax of gall community succession as being marked by a dominance of entomophagous species. Climax in the *D. polita* gall community can also be defined as being reached when the galls mature and fall to the ground, for once this stage is reached, oviposition and larval feeding activities cease. The periods of emergence and oviposition for all species in the community occur in sequence. Emergence early or late in the season would reduce the reproductive success of that species.

The present study investigates five species found associated with the larvae and galls of *D. polita*. These are *Periclistus pirata* (O.S.) (Cynipidae), *Eurytoma longavena* Bugbee (Eurytomidae), *Glyphomerus stigma* (Fabricius) and *Torymus bedeguaris* (Linnaeus) (Torymidae), and *Habrocytus sp.* (Pteromalidae). Incidentals found associated with a very small percentage of galls were *Eupelmella vesicularis* Retz (Eupelmidae), *Ormyrus sp.* (Ormyridae), and *Tetrastichus rosae* Ashmead (Eulophidae).

Gall inhabitants that feed on gall tissues and do not directly attack the gall former have been termed inquilines. The term inquiline is derived from the Latin 'inquilinus' meaning tenant or guest. According to Askew (1971), inquilinism is a form of commensalism, somewhere between parasitism and symbiosis. An inquiline lives in close spatial relationship with its host, not feeding upon the host, but nevertheless frequently destroying it. In a commensal association all the advantages are to one of the partners and it is common that some commensals do more harm to their hosts than depriving them of some larval food. Though some workers have used inquiline in a somewhat different or broader sense (Triggerson (1914), Malyshev (1968), Lyon (1969)), Askew's definition seems most appropriate.

A close taxonomic relationship between the commensal and its host often exists in inquilinism. Muesebeck et al. (1951) listed the inquiline species of *Periclistus*, *Ceroptres*, *Synergus*, and *Euceroptres* as being guests in insect galls, all being of the family Cynipidae. All species of *Periclistus* are restricted as inquilines of rose gall wasps as are *Synergus* of oak gall wasps. It is probably safe to assume that inquiline cynipids had an ancestor capable of inducing galls. This is indicated by the retention of the ability to induce cell proliferation in many species such as *P. pirata*. Askew (1971) has suggested that inquilinism is on the road to parasitism, demanding only that the inquiline become entomophagous rather than phytophagous.

Some oak galls are inhabited by inquilines that do not interfere with the gall former. Instead they form irregular chambers inside the thick walls of their host gall (Sternlicht, 1968) and do not come in contact with the gall forming larvae. Other oak gall inquilines occupy the central chamber of the gall former (Askew, 1971). Inquilines such as *Periclistus* and *Synergus* species initiate chambers of their own inside galls and in the process obliterate the chamber of the gall former. These species are incapable of initiating gall formation and are completely dependent upon the gall formers for the provision of their larval food.

Osten Sacken (1865) was one of the first to question the inquiline behavior of *Periclistus* species. *Periclistus pirata* was found in nearly all *D. polita* galls and all such galls were modified by the *P. pirata* larvae forming individual chambers. Because *P. pirata* does not feed upon tissues of *D. polita*, it cannot be described as a parasite or predator but instead fits Askew's definition. No galls inhabited by *P. pirata* contained the larva of *D. polita*. It is suggested that the *D. polita* larva is killed when the *P. pirata* oviposits in the immature galls.

There is little uniformity in the literature as to usage of terms associated with entomophagous species inhabiting galls. Common terms such as parasite and predator are often misused. Smith (1916) distinguished parasites and predators on the number of hosts required to complete development. He defined parasitic insects as those which pass their entire larval

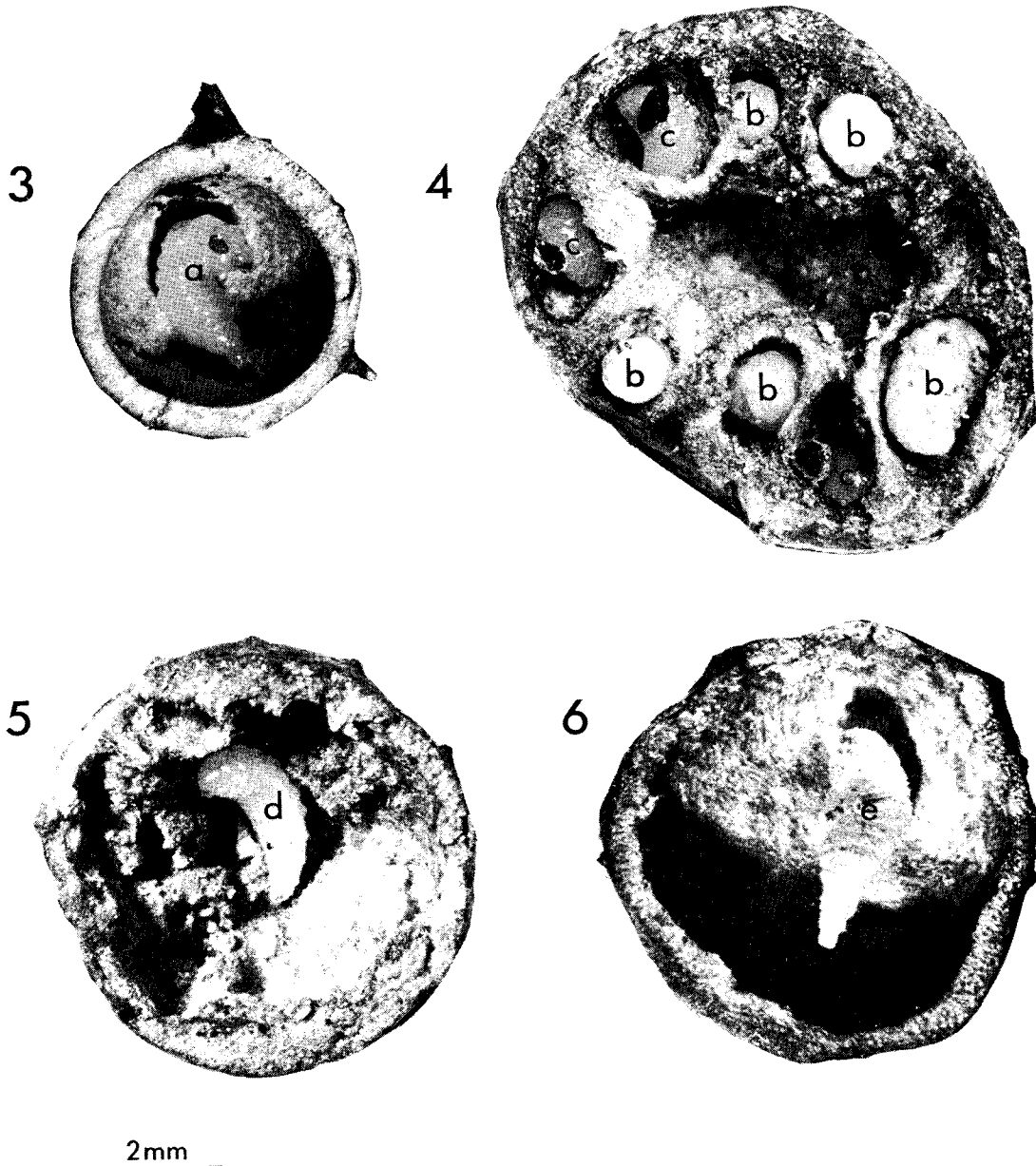
stage within or upon a single host and predacious insects as those which require more than one host to complete development. He also noted that a distinction between parasitism and predation is of limited importance and it is wise to keep in mind that many species are called parasites only because they belong to parasitic groups and not by reason of their behaviour. Many students of galls use the term predator only when referring to birds or mammals which break into galls. There is also a common feeding habit of entomophagous insects intermediate between parasites and predators for which the term parasitoid has been introduced. Parasitoid has been suggested for those insects which destroy their hosts (which are usually insects), are of a relatively large size compared with their hosts, and are parasitic as larvae only (Doutt, 1959). It has not been widely accepted although has received some usage in major works such as Askew,(1971). Its use has merit in gall studies because many of the inhabitants are not true parasites nor can they be considered typical predators. Doutt (1964) discussed the system for classifying entomophagous insects based on host relationships. Parasites attacking a phytophagous host are termed primary parasites. If the primary parasite is attacked, then its enemies are called secondary parasites.

Eurytoma longavena, a common inhabitant of the *D. polita* gall, chews its way from chamber to chamber often consuming two or more *P. pirata* during its development. *Glyphomerus stigma* and *Torymus bedeguaris* may feed ectoparasitically or as parasitoids. Blair (1944) described *G. stigma* and a *Torymus* as ectoparasites. *Habrocytus sp.* was found feeding only on individual larvae of *P. pirata*, that is. as an ectoparasite. Before examining the community inter-relationships of the *D. polita* gall, it is first necessary to examine the biology of each inhabitant species.

METHODS

Galls collected in both 1968 and 1969 were used for studying life cycles and the roles played by each species in the community. Most of the galls collected in 1968 were used for associating larvae of the inhabitants with their adults and studying life cycles of each. Galls collected throughout the season were dissected to obtain larvae and determine their feeding behavior. Most larvae were readily distinguished morphologically (Figs. 7-12) and for three species, *P. pirata*, *E. longavena*, and *G. stigma*, the larvae were also identifiable by examining the characteristic damage done to the gall tissues (Figs. 3-6). Eggs of only *P. pirata*, *E. longavena*, and *G. stigma* were easily identified. When mature larvae were found, they were placed in small pin-mounted gelatin capsules as described by Shorthouse (1972). Large numbers of larvae were stored in standard insect specimen boxes where they could be checked for developmental changes. These specimen boxes were stored in a field laboratory under nearly ambient conditions of temperature and humidity to obtain fall emergents. The remaining larvae were then returned to the university, stored at 4°C for 3 months, then incubated at room temperature (approximately 22°C) when a 65% emergence was obtained. Once the larvae pupated, the mandibles were removed from the larval cast skins and mounted on slides. Mandibles of the larvae are structurally dissimilar (Figs. 13-18) and useful for identifications. A correlation among adult, larva, larval mandibles, and feeding behavior was obtained in this manner for each species. Other collections of mature galls made in the fall of 1968 were stored undissected in plastic vials. Fall emergents were removed as they appeared and the galls then subjected to 4°C to break diapause.

Galls collected in the 1969 season were used for observing seasonal changes in the community composition. A total of 27 collections were made. Each collection was made by randomly walking through areas of rose and collecting every gall observed. These walks were



Figs. 3-6. Mature *Diplolepis polita* galls. 3. Gall inhabited by *Diplolepis polita*. 4. Gall modified by *Periclistus pirata*. 5. Gall modified by *Eurytoma longavena*. 6. Gall modified by *Glyphomerus stigma*. (a) *Diplolepis polita* larva; (b) *Periclistus pirata* larva; (c) *Habrocytus sp.* larva; (d) *Eurytoma longavena* larva; (e) *Glyphomerus stigma* larva.

often more than 1,000 metres in length with the result that each collection was composed of samples from numerous rose patches throughout the study area. When a gall or gall-cluster was found, the entire leaf was picked and placed into an 18 ounce 'Whirl-Pak' bag. Size of each collection was roughly governed in the field by collecting two bagfuls of galled leaves. Only 11 of the 27 collections were used for the community study. The first 3 collections were small because of the scarcity of galls in the early spring, but from June 6 until the end of August, galls were sufficiently common that the two bags could be filled within two hours. Because nearly all galls had matured by August 8 (Fig. 28), only one large collection was used for August. Approximately 4,500 galls were collected in this manner. All galls were returned to the laboratory, measured, dissected, and the contents examined, or the galls were fixed in FAA solutions for later examination.

In this study, an empty gall is defined as one which does not contain a live inhabitant and therefore cannot contribute to the community. Galls from which *E. longavena* or *T. bedeguaris* emerged late in the season each had a tiny emergence hole and were considered separately.

LIFE CYCLES OF GALL INHABITANTS

Diplolepis polita (Ashmead)

Few data have been published on the biology of North American *Diplolepis* species and nothing has previously been published on the biology of *Diplolepis polita*. Most North American publications such as Bassett (1890), Beutenmuller (1907), Kinsey and Ayres (1922), McCracken and Egbert (1922), Osten Sacken (1863, 1865) and Weld (1926, 1952a, 1952b, 1957, and 1959) are concerned mainly with species descriptions. Europeans and Asians have contributed much more to our knowledge of *Diplolepis* biology; notable examples being Blair (1944, 1945a), Callan (1940), Kuznetzov-Ugamskij (1930), Niblett (1943, 1947), Schröder (1967), and Yasumatsu and Taketani (1967).

Only 21 adults of *D. polita* were obtained throughout the study. All were reared from galls stored in the laboratory. No adults were collected by sweeping or trapping in 1968 or 1969, nor were any adults observed ovipositing. No adults of other *Diplolepis* species were collected in the study area either and it is assumed that field work began too late in the season. The earliest search for adults began May 7, 1969. Schröder (1967), in his study of *D. rosae* (L.), found that emergence occurred over a period of from 2 to 6 weeks, extending to 8 weeks if the weather was cool. He found that more individuals emerged on warm sunny days than on cool rainy days. He also observed that some females were able to pass a number of days at temperatures below the freezing point without harm. However, Kinsey (1920a) found that most adult cynipids are killed by sudden changes of temperature or humidity and that adults emerging during inclement weather would not oviposit. Niblett (1947) suggested that late frosts are responsible for many casualties and in years when these frosts occur, few galls are to be found. There may be inter-specific as well as generic differences in tolerance of inclement weather conditions.

Yasumatsu and Taketani (1967) observed and described the oviposition of *D. japonica* (Walker) and estimated the time required for initial gall growth to occur after oviposition. It is well established (Mani, 1964) that gall formation is due to larval feeding and if proliferation begins soon after the larva commences feeding, the period between oviposition and hatching can be estimated. Yasumatsu and Taketani estimated that the egg stage of *D. japonica* lasts from 7 to 10 days. Callan (1940) experimented with *D. rosae* and found that the first sign of gall formation was from 12 to 36 days after oviposition. Schröder (1967),

studying the galls of the same species found hatching about 7 days after oviposition and that the gall begins to grow 4 to 5 days later. I found the first *D. polita* galls May 20, 1969 so probably oviposition occurred before May 10 in 1969 and as a result the first visible growth occurred between May 20 and 25. Since no adults were collected when the field search began on May 7, *D. polita* emergence and oviposition probably takes place in late April or early May. Alder and Straton (1894) suggested that adult life is shorter in species of gall wasps which deposited eggs over a short period. *D. polita* adults lived for an average of 4 days in the laboratory which suggests that their eggs are deposited over a short period of time. Kinsey (1920a) found that *Diplolepis* adults live for only a few days and must oviposit soon after emergence.

The eggs of *D. polita* are probably laid in or on the leaf primordia of slightly forced *R. acicularis* buds. Schröder (1967) found that the eggs of *D. rosae* were deposited on the median vein of the pinnules as well as on the developing petioles. He found that the anterior ends of the eggs are inserted into the epidermis of the developing leaflets, leaving the greater part of the egg free between the folded leaves. A similar situation probably occurs with *D. polita*. The eggs of *D. polita* are similar to the stalked eggs of other cynipids described by Berland (1951). *D. polita* females must contain a large number of eggs for although their population is low in the spring (Fig. 21), their galls were one of the most common in the study area. Yasumatsu and Taketani (1967) found that *D. japonica* females contained an average of 331 eggs whereas Schröder (1967) found that 5 to 7 day old *D. rosae* females contained an average of about 780 eggs.

As with all *Diplolepis* species the larvae feed on host tissues and initiate formation of the gall. Little data could be obtained on the time required to complete larval development since this and the time of oviposition depend on factors such as condition of the host plant, which undoubtedly differs from area to area. Hence periodic collections do not clearly indicate the succession of larval instars. *D. polita* larvae have 12 body segments (Fig. 7), lack setae, and undergo an estimated 5 larval instars. Mandibles of the last instar larva are tridentate (Fig. 13). The larvae grow rapidly and continue feeding on succulent gall cells until the gall matures and hardens. Cosens (1912) stated that cynipid larvae feed only on cell contents resulting in the occurrence of collapsed cells around the larva. No fecal material is found inside the gall for the larval gut is blind. When the leaf tissue surrounding the gall matures, the galls fall to the ground where they are protected by snow through the winter. All *Diplolepis* species overwinter as mature larvae. Laboratory reared specimens had a short pupal stage lasting on the average about 10 days. Adults emerge inside the gall and must chew their way through the wall to escape.

When the *D. polita* adults emerge in the early spring, it is assumed that they immediately begin searching for oviposition sites. Callan (1940) found that most males of *D. rosae* appeared before the peak appearance of females. It is well established that parthenogenesis occurs throughout the genus and that males are rare, if found at all. Callan also suggested that some species may exhibit geographic parthenogenesis, that is, males may be more numerous in northern populations. Sex ratio of the 21 specimens I obtained was 0.714 (sex ratio = number of females/ total number of individuals). Kuznetzov-Ugamskij (1930) recorded a *Diplolepis* species from Asia with a sex ratio near 0.500 and in this species parthenogenesis probably does not occur. Although most populations of *D. polita* may be parthenogenetic, the occurrence of a comparatively high number of males indicates that some sexual reproduction occurs. Kinsey (1920a) suggested that in some primitive *Diplolepis* species, normal sexual reproduction may take place, but in the genus as a whole, the male is gradually disappearing and parthenogenesis is becoming the sole means of reproduction. The presence of

males in all collections of *Diplolepis* species found in central Alberta is consistent with the geographic distribution of parthenogenesis as found by Callan (1940) and Schröder (1967).

Periclistus pirata (Osten Sacken)

The genus *Periclistus* Foerster consists of 7 North American species considered by most authors (Muesebeck et al., 1951) to be restricted to an inquiline habit in the galls of *Diplolepis* species. Although the exact relationship between *Periclistus* species and the gall formers are not known, it is accepted that the livelihood of *Periclistus* species depends on the presence of *Diplolepis* galls. *Periclistus* larvae are phytophagous and feed on the same gall tissue as do the gall formers; they cannot initiate galls. There have been no studies concerned with specificity of *Periclistus* species for *Diplolepis* galls. Fullaway (1911) recorded *P. piceus* Fullaway and *P. californicus* Ashmead from galls of *D. polita*. Osten Sacken (1863) described *P. pirata* and obtained the specimens from galls of *D. ignota* (O.S.). This present study is the first record of *P. pirata* from the gall of *D. polita*.

P. pirata was an important occupant of the *D. polita* galls of George Lake in 1968 and 1969. Of the spring initiated galls 88.5% collected June 6, 1969 contained either eggs or larvae of *P. pirata* (Fig. 21). Blair (1944) found that *Periclistus* sp. were present in nearly all the *D. rosae* galls he examined. Although *P. pirata* larvae are phytophagous, in all galls examined in which they were present, the *D. polita* larvae had been destroyed. Fig. 21 shows that as the eggs of *P. pirata* become more abundant in gall collections, the number of galls containing a live *D. polita* larva was reduced. Although the exact mechanism of this replacement is not known, it has been recorded in other *Diplolepis* galls (Blair, 1945a). Because the *D. polita* larva was always found dead in galls containing *P. pirata* eggs, oviposition by *P. pirata* females must kill the immature *D. polita*. Once the *D. polita* larva has been killed, it shrivels and becomes difficult to detect.

P. pirata adults emerged early in the spring, probably two or three weeks after the *D. polita* adults had emerged and oviposited (Fig. 19). The emergence of *P. pirata* is synchronized with the appearance of the immature *D. polita* galls. Male *P. pirata* emerged before the females (Fig. 20). The first males were collected in the field May 16, 1969 the first females May 20, 1969, and the first oviposition was observed May 23, 1969. By June 1, 1969, adults of *P. pirata* were common and 263 were obtained by hand collecting. In the evening the adults rested under the upper leaves of *Rosa* and could be easily dropped into collecting vials. Sex ratio of the adults collected in this manner and from spring rearing experiments was 0.557. It is interesting that an inquiline cynipid species should have a population composed equally of the sexes whereas the gall former populations are dominated by females. Copulation was observed on many occasions both in the field and in the laboratory and it is therefore doubtful that parthenogenesis occurs. Over 300 observations of *P. pirata* ovipositing in immature *D. polita* galls were made (see feature photograph, Ent. Soc. Can. Bull., 1970.2 (4): 102). If both immature and mature galls were present in a cluster, the immature galls would always be chosen for oviposition first. *P. pirata* must have a lengthy emergence period for although most of the population emerges in the spring, adults were found ovipositing in galls up to August 7, 1969. The reappearance of immature galls in July of 1969 (Fig. 25) allowed late emerging females the opportunity for oviposition. The July increase in the number of galls containing *P. pirata* eggs (Fig. 21) is due to the appearance of sucker shoot galls. The mean number of eggs per gall for all collections is given in Table 1. *P. pirata* females oviposited readily in galls that contained eggs from other females. The largest number of eggs found in a spring initiated gall was 23, largest number in a sucker shoot gall 16. This may be

because more *P. pirata* females were present in the spring. The ease with which oviposition could be induced in the laboratory and the observations of oviposition during rainy cool weather, indicated that this species is much more hardy than *Diplolepis* species.

The egg of *P. pirata* is white, of the hymenopteriform type (Clausen, 1940), banana-shaped, and stalked. The stalk, which is as long as the egg, is elastic and has a slight bulge at the distal end. Upon hatching, the larvae distribute themselves around the inner walls of the gall and commence feeding on gall tissues. *P. pirata* larvae initially feed on the same cells as *D. polita* larvae and the area in which they feed is always marked by a layer of empty cells. As the larvae continue feeding, gall tissue surrounds each individual to form an inner chamber (Fig. 4). Blair (1945b) found that *Synergus reinhardi* Mayr (Cynipidae) modified the galls of *Cynips kollari* Hartig (Cynipidae) in a similar manner. Galls containing *P. pirata* chambers appear polythalamous and the original cavity, once containing a single *D. polita* larva, is nearly obliterated (Fig. 4). *P. pirata* larvae (Fig. 8) are easily distinguished from those of *D. polita* by the mandibles (Fig. 14). *P. pirata* larvae are not as active as *D. polita* larvae and do not thrash as violently when disturbed. *P. pirata* inhabited galls fall to the ground and receive the same winter protection under the snow. The seasonal change in the percentage of galls with larvae and the mean number of larvae per gall is shown in Table 1. The pupal stage of laboratory reared specimens lasted about 9 days. Many of the galls collected in the fall of 1969 which overwintered in the laboratory at 4°C and were then moved to 25°C were dissected 4 months after emergence had ceased. About 3% of the *P. pirata* inner chambers contained live larvae. Under normal conditions these larvae may have been destined for emergence later in the season or their presence may indicate that a small percentage of the *P. pirata* population remains in the larval stage throughout the season and emerges the following year.

Eurytoma longavena Bugbee

Eurytomids are one of the most common entomophagous groups associated with *Diplolepis* galls. Bugbee (1967) listed 82 species of North American *Eurytoma* and stated that 33 species attack Hymenoptera. He stated that at least 12 species are known to be phytophagous and listed one species, *E. pachyneuron* Girault, suspected of being both parasitic and phytophagous. Peck (1963) presented a comprehensive bibliography for 72 North American species. Although most gall inhabiting eurytomids are considered parasitic, the lack of detailed life cycle studies hinders such generalizations. Bugbee (1951) discussed 12 species known from *Diplolepis* galls and warned that knowing the associated gall gives little data on actual host relationships. Also in this paper he discussed the phylogeny of the *Eurytoma* species associated with *Diplolepis* galls. He suggested that most *Eurytoma* are restricted to a single species of gall former, but also listed several species known from more than one gall and suggested that further studies will reveal more complex relationships. He pointed out that some species may attack inquilines and other gall inhabitants besides the gall former. Bugbee (1951) also stated that no complete life-histories have been worked out for any of the Nearctic species associated with *Diplolepis* galls.

E. longavena was the most common and influential entomophagous occupant in the 1968 and 1969 *D. polita* gall community. This species was described by Bugbee in 1951 and was found inhabiting *D. bicolor* galls growing on an undetermined species of *Rosa*. *E. longavena* is known only from its type locality of Terrace, British Columbia and according to Bugbee (pers. comm.) nothing is known of its biology. Three species of *Eurytoma* have previously been associated with *D. polita* galls (Bugbee, 1951); these are *E. flavicurensa* Bugbee, *E. incerta* Fullaway, and *E. terrea* Bugbee. *E. longavena* has not been previously recorded from the *D. polita* gall.

Table 1. Incidence of *Periclistus pirata* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs	Mean no. of eggs per gall \pm S.D.*	% of galls with larvae	Mean no. of larvae per gall \pm S.D.*
20-V	4	0	0	0	0
25-V	55	38.1	6.2 \pm 3.9	0	0
28-V	54	83.5	10.1 6.8	0	0
6-VI	166	43.6	5.4 4.8	71.0	6.9 \pm 5.5
12-VI	156	13.0	3.0 1.8	62.3	5.7 3.7
20-VI	176	8.1	2.5 1.5	37.0	4.1 3.6
27-VI	127	2.1	—	35.4	4.2 3.8
5-VII	119	0	0	25.2	3.6 3.3
14-VII	156	0	0	20.0	3.7 2.9
spring					
14-VII	21	80.9	5.0 4.1	9.5	5.0 4.1
sucker					
23-VII	190	0	0	17.2	3.9 3.6
spring					
23-VII	106	9.4	4.9 4.1	50.0	5.2 4.2
sucker					
22-VIII	275	0	0	8.1	3.5 3.2

*means are calculated exclusive of galls without eggs or larvae

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Larvae of *E. longavena* were found in 17% of the mature galls collected August 17-23, 1968 and in 32% of the galls collected August 22, 1969 (Fig. 21). Most of the empty galls found in 1968 and 1969 were also a result of *E. longavena* activities. Gall collections described under methods were used in tabulating incidence of *E. longavena* eggs, larvae, and pupae in the galls of the 1969 season (Table 2). *E. longavena* has two generations per year in the study area, although only a small percentage of the total population is derived from the second generation. From a large collection of 1969 spring initiated galls, 12.3% of the *E. longavena* population emerged the same season and the remainder emerged the following spring. Adults that emerged in the fall of the same season were able to oviposit in sucker shoot galls. The *E. longavena* population found in sucker shoot galls emerges the following spring. Clausen (1940) stated that the number of generations of *Eurytoma* per year is dependent upon the hosts attacked and mentioned that *E. monemae* Ruschka may have three generations per year.

Bugbee (1951) stated that the sex ratios for several species he studied were approximately equal although females are usually more numerous. A total of 423 *E. longavena* adults were

obtained in this study and the sex ratio was 0.912. The fall populations of *E. longavena* consisted of females only and the sex ratio of all individuals collected, exclusive of fall emergents, was 0.892. Niblett (1947) found that a small percentage of the *E. rosae* Nees populations emerged in the first year and that the sexes were in equal numbers. *E. longavena* females emerged late in the season from 5% of the mature galls collected in 1968 and from 7% of the mature galls in 1969.

Fig. 20 indicates that *E. longavena* adults begin to emerge about the same time as *P. pirata* and are probably present when the first *D. polita* galls appear. The first eggs were found in galls collected May 25, 1969, although the earliest of 53 ovipositions observed in 1969 was June 5, 1969 (Fig. 19). Spring adults emerge over a long period of time as indicated in Fig. 20, and may overlap the fall population. The last ovipositing female observed, August 9, 1969, thus may have been from either the spring or fall population. This extended activity period is also shown by the presence of eggs in sucker shoot galls (Table 2). These eggs could have been deposited by either late spring emergents or fall emergents. The mean number of eggs laid per gall is also shown in Table 2. Dates without data were due to difficulties in locating eggs amongst *P. pirata* chambers and uneaten gall tissues. As with *P. pirata*, *E. longavena* would readily oviposit in galls containing eggs from previous females.

E. longavena eggs are similar in appearance to other *Eurytoma* eggs described by Clausen (1940) and Phillips (1927). They are brown and have a small curled stalk at one end. The stalk is about one-third as long as the egg. The eggs are white immediately after oviposition but turn brown within 24 hours. Several *E. longavena* females were dissected and all contained 6 eggs or less. The largest number of eggs found in a spring initiated gall was 11 and the largest number in a sucker shoot gall was 4. *E. longavena* eggs were found only in immature galls containing eggs or larvae of *P. pirata*. No eggs were found in galls containing a *D. polita* larva, which indicates that the females can distinguish gall contents. Eggs were deposited along the inner walls of the gall and upon hatching the larvae immediately began feeding on the eggs or larvae of *P. pirata* and later fed on any gall inhabitants they encountered. Because *P. pirata* was the most abundant species in the gall community, it was the chief host of *E. longavena*. I observed several *E. longavena* larvae feeding even before they were completely free of their egg shells. Later in the season *E. longavena* larvae were also found consuming immature larvae of *Glyphomerus stigma*, *Torymus bedeguaris*, and *Labrocytus* sp. *E. longavena* are also cannibalistic and though most galls attacked by this species contained several eggs (Table 2), only one larva usually survived. Of the galls containing *E. longavena* 94% produced a single adult. Galls producing two adults were large. Caltagirone (1964) stated that when more than two *Eurytoma* sp. eggs were present in the *Pontania* gall he studied, the larva that hatched first killed the remaining eggs.

E. longavena larvae are both entomophagous and phytophagous but they must feed on insect tissue before they feed on plant tissue. This is shown by the fact that larvae often do not survive if hatched in galls with completed *P. pirata* chambers. *E. longavena* larvae must consume free host material before they are capable of chewing through chamber walls. Once the larvae have reached a certain stage in their development, they are capable of feeding on either plant tissues or insect tissues found inside the *P. pirata* chambers. Once the *P. pirata* larvae are enclosed by gall tissues, the *E. longavena* larvae must chew through chamber walls if more insect tissue is required. If the combined feeding activities of several *E. longavena* larvae consume all insect host material before they are capable of phytophagous feeding, all will perish and an empty gall results. Most galls contained sufficient immature *P. pirata* to supply the *E. longavena* with food and also allow some *P. pirata* to escape and form chambers. It is pertinent that the hosts are not killed at the time of oviposition, for the presence

of *P. pirata* larvae provide the *E. longavena* larvae with access to succulent parenchyma cells and to other entomophagous species attracted to the chambers. Moser (1965), Caltagirone (1964), and Malyshev (1968) reported that the gall inhabiting *Eurytoma* they studied stung and paralysed the hosts at the time of oviposition. Blair (1944 and 1945a) suggested that *E. rosae* found in galls of *D. rosae* were predators, but Niblett (1947) and Askew (1961) disagreed.

When *E. longavena* larvae chew from chamber to chamber, uneaten plant tissues accumulate inside the gall and this condition is characteristic of *Eurytoma* damage (Fig. 5). Although the presence of this tissue suggests that the larvae tear through chamber walls, I observed many individuals ingesting plant cells, thus confirming that the species is phytophagous. Varley (1937) recorded the same behavior for the larvae of *E. robusta* Mayr. Blair (1954a) stated that the larvae of *E. rosae* feed on *Periclistus* larvae and chew into gall tissues but did not record a phytophagous habit. Malyshev (1968) listed several other eurytomids that initially feed on eggs and host larvae and then feed on gall tissues. It appears that once a *E. longavena* larva consumes a certain amount of entomophagous material, it is capable of continued development on gall tissues. Phillips (1927) in his study of *E. parva* (Girault), suggested that this species, similar to *E. longavena*, is gradually breaking away from the entomophagous habit and is becoming phytophagous. Blair (1945a) suggested the same for *E. rosae*.

Mature *E. longavena* larvae are recognized by their distinct segmentation, abdominal protrusions, and anterior sensory setae (Fig. 9). The larval mandibles (Fig. 15) are heavily sclerotized, triangular in outline, and each has one large denticle on the inner margin. *E. longavena* larvae, except for the fall emergents, overwinter inside the gall and pupate the following spring. The pupal stage of laboratory reared specimens lasted about 12 days.

Glyphomerus stigma (Fabricius)

The genus *Glyphomerus* is monobasic containing the single species *G. stigma*. This species, described in 1793 by Fabricius, has a Holarctic distribution and is known mainly as an ectoparasite of gall inhabitants. Viereck (1916) recorded it from the gall of *D. rosae* and Hoffmeyer (1930) from the gall of *D. polita*. Peck (1963) presented a bibliography of North American records and Fulmek (1968) listed it as associated with 6 of the 7 European species of *Diplolepis*. *G. stigma* is therefore not host specific for it has been recorded from 3 Nearctic galls (Peck, 1963) and 9 Palearctic galls (Fulmek, 1968). Blair (1945a) found the species attacking *Periclistus brandtii* Er. in the galls of *D. rosae*. Other than these host records, very little is known of its biology.

The same gall collections mentioned previously were used in tabulating the incidence of *G. stigma* eggs and larvae in the *D. polita* galls collected in 1969 (Table 3). Larvae of *G. stigma* were found in 21% of the mature galls collected August 17-23, 1968 and in 12.5% of the mature galls collected August 22, 1969 (Fig. 21). *G. stigma* at George Lake is univoltine, although Niblett (1947) found that a few adults associated with British galls emerged in the fall of the first season. Fig. 20 indicates that the George Lake males emerge before females and this was confirmed by field collections. Females are rapid fliers and unless they are found with their ovipositors inserted deep into a gall, they are exceedingly difficult to capture. From gall emergence studies 139 adults were obtained and the sex ratio was 0.561. *G. stigma* has a lengthy period of emergence as indicated by the 42 oviposition observations in Fig. 19 and the presence of eggs both in galls collected in spring and in sucker shoot galls (Table 3). Niblett (1947) found that July and August was the normal emergence period for British populations associated with *D. rosae* galls. I recorded the first oviposition May 23,

Table 2. Incidence of *Eurytoma longavena* eggs, larvae, and pupae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs (hatched & unhatched)	Mean no. of eggs per gall \pm S.D.*	% of eggs hatched	% of galls with larvae	% of galls with pupae
20-V	4	0	0	0	0	0
25-V	55	3.4	1 \pm	0	0	0
28-V	54	33.8	1.1 0.4	0	0	0
6-VI	166	78.3	2.1 1.3	38.7	16.0	0
12-VI	156	87.1	2.7 1.3	48.0	44.8	0
20-VI	176	89.2	3.1 2.0	61.0	52.8	0
27-VI	127	85.8	2.2 1.3	80.4	51.1	0
5-VII	119	90.7	2.4 1.6	92.0	63.8	0
14-VII spring	156	—	—	—	47.5	5.0
14-VII sucker	21	26.6	2.5 1.6	0	0	0
23-VII spring	190	—	—	100**	38.2	0
23-VII sucker	106	81.1	2.1 1.2	44.0	41.5	0
22-VIII	275	—	—	100**	32.1	0

* means are calculated exclusive of galls without eggs

** estimate

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

1969 although the first eggs were not found until June 6, 1969 (Table 3). Laboratory emergence studies (Fig. 20) indicated that the peak emergence occurs after that of *P. pirata* and *E. longavena*.

G. stigma eggs are white to transparent and are banana-shaped with one end slightly thicker than the other. The thicker end also has a small knob at the tip. The long ovipositor of the adult enables it to deposit eggs in large, thicker walled galls unavailable to *E. longavena*. The eggs are laid on the inside surface of the gall cavity or directly on the host larvae. Once the eggs hatch, the shells are almost impossible to detect and therefore Table 3 includes only unhatched eggs. Some of the unhatched eggs may have been missed and this could be one explanation for the sudden increase of galls containing larvae in the August 22, 1969 collection (Table 3). Of the 1969 attacked galls 80% contained a single egg and the remainder contained two eggs. The larvae are cannibalistic and the first hatched consumes other eggs pre-

Table 3. Incidence of *Glyphomerus stigma* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	Sample size	% of galls with eggs (unhatched)	% of galls with larva
20-V	4	0	0
25-V	55	0	0
28-V	54	0	0
6-VI	166	9.0	0
12-VI	156	11.5	0
20-VI	176	22.1	0
27-VI	127	13.0	1.0
5-VII	119	3.8	3.4
14-VII spring	156	0	4.5
14-VII sucker	21	5.0	0
23-VII spring	190	0	5.4
23-VII sucker	106	5.6	0
22-VIII	275	0	12.5

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

sent, with the result that no more than one *G. stigma* larva was ever found per gall. Because this species consumes all inhabitants of the *D. polita* galls in which they occur, it plays an important role in the gall community. *G. stigma* larvae were found preying upon the larvae of *D. polita*, *P. pirata*, *E. longavena*, *T. bedeguaris*, and *Habrocytus sp.*, with *P. pirata* the most important prey. Chamber wall tissue was consumed when the attacked gall contained *P. pirata*, indicating that the species is phytophagous as well as entomophagous. Larvae of *E. longavena* and *Habrocytus sp.* were consumed if they were found inside *P. pirata* chambers. Galls attacked by *G. stigma* larvae have their interiors hollowed and other than being larger (Fig. 6), are similar in appearance to normal galls containing only a *D. polita* larva. The larvae consume most of the inner, more succulent tissues of the gall and as a result the damaged gall has an interior lined with several layers of cell particles.

Blair (1945a) gave a brief description of the *G. stigma* larva. The mature larva is white, tapers towards the anterior end and is clothed with long soft hairs (Fig. 10). The head is cordiform and has two deep, elongated fossae that turn dark brown as the larva matures. Mandibles of the mature larva are slender and curved with a denticle on the inner side some distance before the apex (Fig. 16). Larvae overwinter inside the gall and pupate the following season. The pupal stage of laboratory reared specimens lasted about 20 days.

Torymus bedeguaris (Linnaeus)

The genus *Torymus* includes both phytophagous and entomophagous species, the latter mainly attacking gall makers and gall inhabitants. According to Huber (1927), genus *Torymus* in North America is known to include 40 species that attack immature stages of Cynipoidea. Of the 106 Nearctic torymids listed by Peck (1963), 7 are recorded from *Diptolepis* galls. Fulmek (1968) listed 103 European species associated with insect galls and recorded 6 of the 7 European *Diptolepis* as hosts. He recorded one *Diptolepis* species known as the host for 10 *Torymus* species. *T. bedeguaris*, a Holarctic species, was found associated with George Lake *D. polita* galls but it was not a common species in the community. Peck (1963) listed three species of *Diptolepis* known as hosts of *T. bedeguaris* and Fulmek (1968) listed 9 European gall formers as hosts. *T. bedeguaris* has not been previously recorded from *D. polita* galls.

Only 132 *T. bedeguaris* adults were obtained in the two years and the sex ratio for the series was 0.404. Clausen (1940) stated that there is a preponderance of females for all species in which sex ratios are known. In the fall of 1968 39 adults emerged from galls collected that spring and the sex ratio of these specimens was 0.435. No adults emerged in the fall of 1969 from galls collected that season, although 44 were obtained once diapause was broken. Sex ratio of these specimens was 0.388.

All *T. bedeguaris* that emerged in the fall of 1968 did so in late August or early September. Emerging at this time, the adults would find sucker shoot galls available for oviposition. Three *T. bedeguaris* were observed ovipositing in sucker shoot galls in 1968 and one in 1969. Eight other females were collected in the field in July and August of 1969, which indicates that the species is active later in the season than other members of the community (Fig. 19). Only 4 adults emerged from the 300 galls used in the spring emergence study (Fig. 20) and their emergence period was after that of most other species. Varley (1941) stated that temperature influenced the fall emergence of *T. cyanimus* Boh., an ectoparasite of *Urophora jaceana* Hering (Tephritidae). Varley (1937) stated that the larvae of *T. cyanimus* attacked the full grown host larvae in August. He found some adults emerging in the fall, but the majority passed the winter in the larval stage and emerged the following spring. In 1947 he reported that although most *T. cyanimus* adults emerged in May, no eggs or larvae were found until August. As an explanation, he suggested that *T. cyanimus* may have an alternative host or the adults may wait from May until August before the eggs are matured and laid. Moser (1965) reported that *T. vesiculus* Moser, an ectoparasite of *Pachyphylla celtidivesicula* Riley (Psyllidae, Homoptera), has two generations per year with some of the first and all of the second generation overwintering as mature larvae inside the gall. Although it is strange that some *T. bedeguaris* emerged in the fall of 1968 and none emerged in the fall of 1969, the fact that so few specimens were obtained makes it difficult to discuss population trends with any degree of confidence. *T. bedeguaris* may have two generations per year under certain conditions. Their populations may have been high in the spring of 1968, and ensuing conditions may have allowed many of them to emerge in the fall.

No *T. bedeguaris* eggs were identified in any of the 1968 or 1969 gall collections, although they may have been confused with *G. stigma* eggs. Varley (1947) reported that *T. cyanimus* often laid eggs in groups and although several larvae may be found feeding on the same host, only one larva matured. Only four *T. bedeguaris* larvae were found in the August 22, 1969 collection (Fig. 21) and two of these were reared to adults. Ten other adults were obtained from rearing larvae in gelatin capsules. Eight of these were found as first or second instar larvae attached to paralysed larvae of either *D. polita*, *P. pirata*, *G. stigma*, or *E. longavena*. The occurrence of first and second instar larvae late in August indicated that the species may be capable of overwintering as an immature larva and continuing its development

the following season. Hosts of *T. bedeguaris* are completely consumed leaving only an empty cast skin. *T. bedeguaris* matures on a single host.

The mature larva of *T. bedeguaris* (Fig. 22) is white and clothed with more long hairs than the larva of *G. stigma*. It bears both heavy and long sensory hairs and several rows of long integumentary hairs in a band encircling each segment, giving it a distinctly hairy appearance. The posterior end does not taper abruptly as does the larva of *G. stigma*, nor does it have the sunken fossae. The mandibles (Fig. 17) are narrow and acute without denticles and are difficult to locate in the larval cast skins.

Habrocytus sp. (indet.)

The Pteromalidae contains some of the most common of the Chalcidoidea and many of the species are known to attack larvae of Hymenoptera. The biology of most species remains unknown and Peck (pers. comm.) stated that the entire genus *Habrocytus* requires revision. Specific characters have yet to be worked out. Peck (1963) listed 31 species of *Habrocytus* and recorded 3 associated with *Diplolepis* galls. Fulmek (1968) recorded 15 European species and listed 4 associated with *Diplolepis* galls. The present study is the first record of a *Habrocytus* species from a gall of *D. polita*.

Habrocytus sp. larvae were found attacking only larvae of *P. pirata*, although I suspect they attack *D. polita* larvae along with other inhabitants. *P. pirata* chambers are probably completed and the larvae matured before *Habrocytus* sp. oviposits. Varley (1937) suggested that *H. trypetae* Thoms. was not specific in its choice of hosts and would attack other parasites encountered. Blair (1944) found that *H. bedeguaris* Thoms. attacked full grown larvae and pupae of *Diplolepis* and *Periclistus* and that cannibalism often occurred. Callan (1944) suggested that *Habrocytus periclisti* Callan was restricted to *Periclistus brandti* Ratzb., an inquiline in the galls of *D. rosae*. No eggs of *Habrocytus* sp. were found and the first larvae were observed July 5, 1969 (Table 4) crawling over paralyzed *P. pirata* larvae. Only a single larva was found per host and the number of larvae per gall is dependent upon the number of *P. pirata* larva present (Table 4), the maximum recorded was 11. Superparasitism, as Varley (1947) recorded for *H. trypetae*, was not observed, although if several eggs had been laid per host, the first hatched could easily have consumed other eggs or larvae present. Urbahns (1916) in his study of *H. medicaginis* Gahan also found only a single larva was able to develop per host. They destroy their hosts quickly and only a round, black, pellet remains. This pellet is readily visible in dissected galls (Fig. 4) and was used as the species indicator. Urbahns (1916) stated that the larva of *H. medicaginis* can become fully developed in 6 days after its first meal. *Habrocytus* sp. overwintered in the larval stage inside the gall.

Approximately 300 adults were obtained in this study and the sex ratio was 0.491. Callan (1944) reported examining a series of *H. bedeguaris* reared from galls of *D. rosae*, in which the sex ratio was 0.360 and a series of *H. periclisti* in which the sex ratio was 0.490. *Habrocytus* sp. adults emerged late in the season and were the last species in the *D. polita* gall community to emerge under laboratory conditions (Fig. 20). Forty-two observations of oviposition were made, the earliest was June 22, 1969 and the last was August 20, 1969 (Fig. 19). Only two adults were observed ovipositing in sucker shoot galls. Sucker shoot galls may not be readily attacked by *Habrocytus* sp. because few *P. pirata* larvae are able to form inner chambers.

Table 4. Incidence of *Habrocytus sp.* larvae in the galls of *Diplolepis polita*. George Lake, Alberta, 1969

Date	Sample size	% of galls with larvae	Mean no. of larvae per gall	
			S.D.	*
20-V	4	0	0	
25-V	55	0	0	
28-V	54	0	0	
6-VI	166	0	0	
12-VI	156	0	0	
20-VI	176	0	0	
27-VI	127	0	0	
5-VII	119	1.0	1.0 ± 0	
14-VII spring	156	5.0	1.0	0.3
14-VII sucker	21	0	0	
23-VII spring	190	23.0	2.7	2.4
23-VII sucker	106	0	0	
22-VIII	275	8.1	3.0	1.9

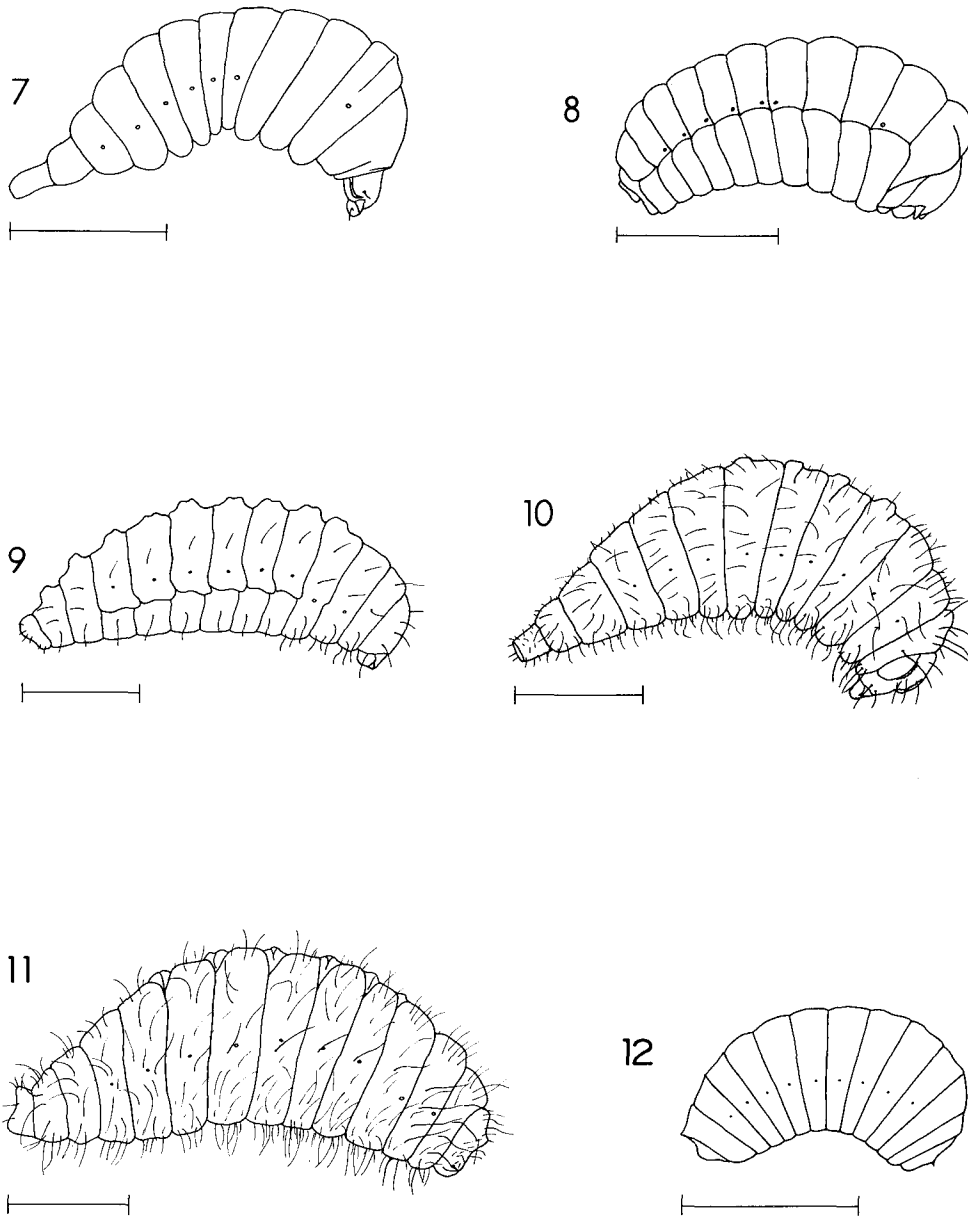
* means are calculated exclusive of galls without larvae

spring = galls initiated in the spring only

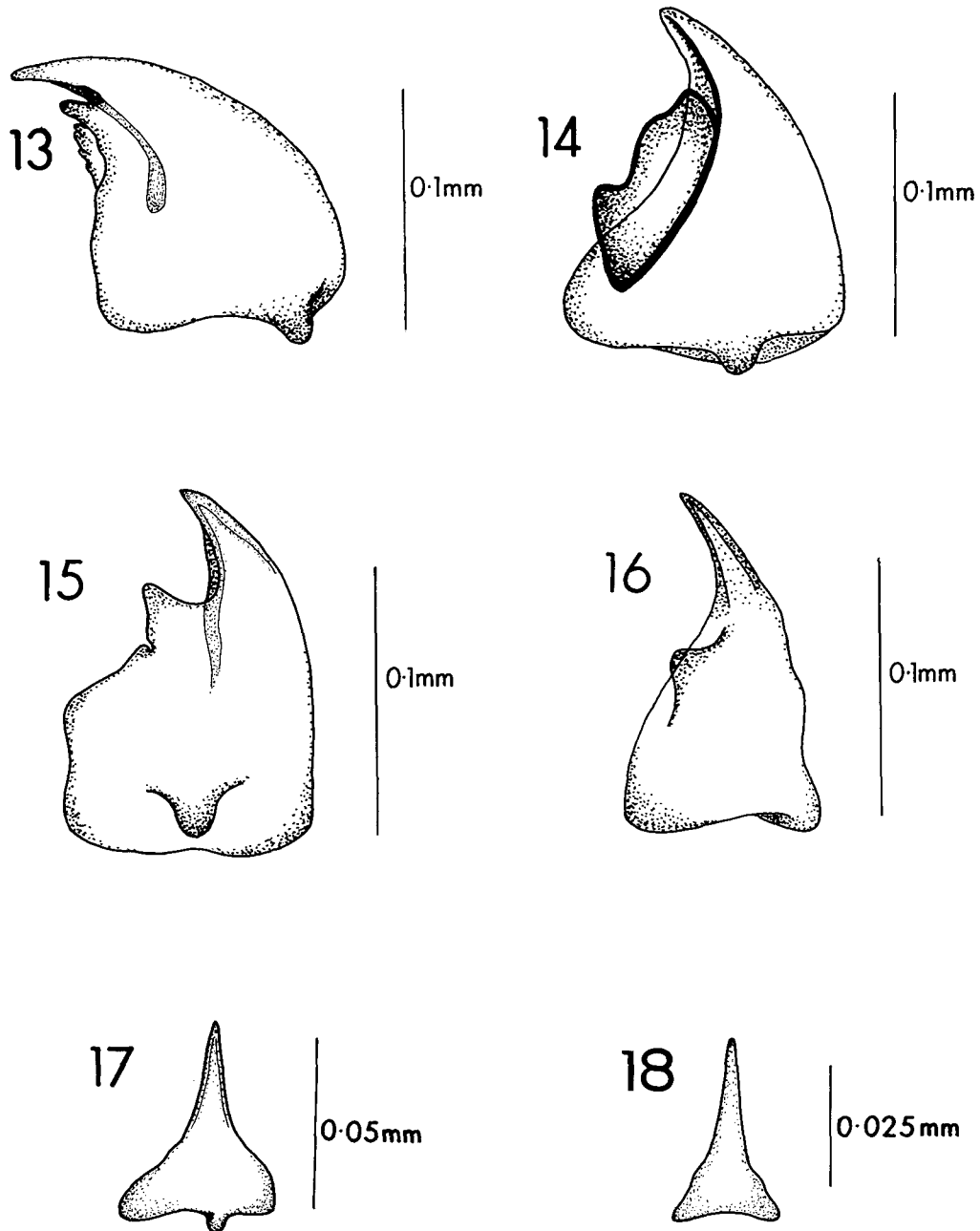
sucker = galls initiated on sucker shoots only

Habrocytus sp. is almost entirely univoltine and the adults emerge the following season. Only six fall emergents were obtained in the two years and it is not known whether they oviposited. Niblett (1947) found that a few adults of *H. bedeguaris* emerged in the fall of the first year, but the majority emerged in July and August of the second year. Several mature galls incubated after exposure to 4°C for 3 months were dissected 4 months after inhabitants had stopped emerging. Live *Habrocytus sp.* larvae were found in a few of the *P. pirata* chambers indicating that the species may be capable of an extended larval stage and emergence two seasons later. Many *Habrocytus sp.* larvae are probably consumed by larvae of *E. longavena*, *G. stigma*, and *T. bedeguaris*. The decrease in percentage of galls containing *Habrocytus sp.* larvae on August 22, 1969 (Table 4) is partly due to the feeding of these insects. The inclusion of sucker shoot galls, which contain few if any *Habrocytus sp.* larvae, in the August 22, 1969 collection, also decreased the percentage of galls with larvae.

The mature grub-like *Habrocytus sp.* larva lacks distinguishing features and has weak segmentation (Fig. 12). The integument is smooth and sensory setae are reduced. The tiny mandibles are simple and lack denticles (Fig. 18).



Figs. 7-12. Mature larvae of *Diplolepis polita* gall inhabitants. 7. *Diplolepis polita*. 8. *Periclistus pirata*. 9. *Eurytoma longavena*. 10. *Glyptomenus stigma*. 11. *Torymus bedeguaris*. 12. *Habrocytus* sp. Scale lines all 1.0 mm.



Figs. 13-18. Mandibles of mature larvae found in galls of *Diplolepis polita*. 13. *Diplolepis polita*. 14. *Periclistus pirata*. 15. *Eurytoma longavena*. 16. *Glyphomerus stigma*. 17. *Torymus bedeguaris*. 18. *Habrocytus* sp.

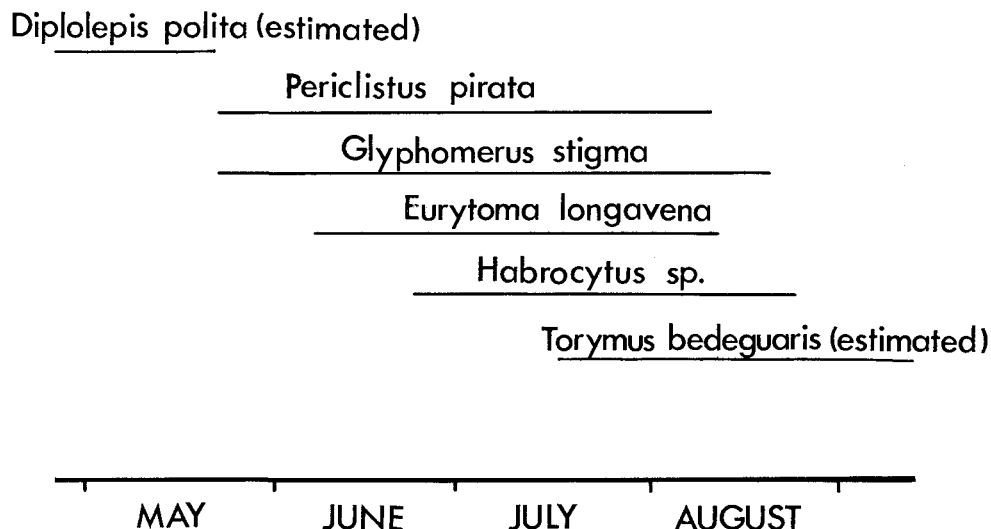


Fig. 19. Oviposition periods recorded for species associated with galls of *Diplolepis polita*. George Lake, Alberta, 1969.

SUCCESSION AND CLIMAX IN THE *DIPLOLEPIS POLITA* GALL COMMUNITY: FATE OF MEMBER SPECIES

Mani (1964) briefly introduced the study of plant gall communities. He emphasized that the predator-parasite complex of galls is often considerably larger than that of inquiline and while some galls lack inquilines few, if any, are free from entomophagous inhabitants. The classic paper on this subject is by Varley (1947) in which he discussed factors controlling population density of the knapweed gall-fly. Although there are many factors regulating the gall former population, such as weather and availability of oviposition sites, it is the objective of this section to examine the roles played by each member species in the gall community.

D. polita is the central species in the gall community for it causes gall formation and without the gall none of the subsequent species could exist. When the galls first appeared in the spring, *D. polita* predominated. The first three collections in 1969 contained only larvae of *D. polita* (Figs. 21 and 23). The *D. polita* larval population decreased once the eggs of *P. pirata* appeared. By May 28, 1969, only 18.5% of the galls contained a live *D. polita* larva, although only the eggs of *P. pirata* and *E. longavena* were present in the remaining galls (Fig. 21). If *E. longavena* occurred in galls without *P. pirata*, it would undoubtedly devour the *D. polita* larva resulting in a further decrease in the *D. polita* population. The largest population of *P. pirata* larvae was found early in the season (Fig. 23) and because they formed the main food source of the entomophagous species, their dominance soon began to decline. *E. longavena* had the greatest influence on the *P. pirata* population and the number of galls containing the former species had risen substantially by June 20 (Fig. 21). Varley (1947) found that *E. curta* Walker was chiefly responsible for controlling the population density of the knapweed gall-fly. Cannibalistic activities of *E. longavena* probably prevented a major

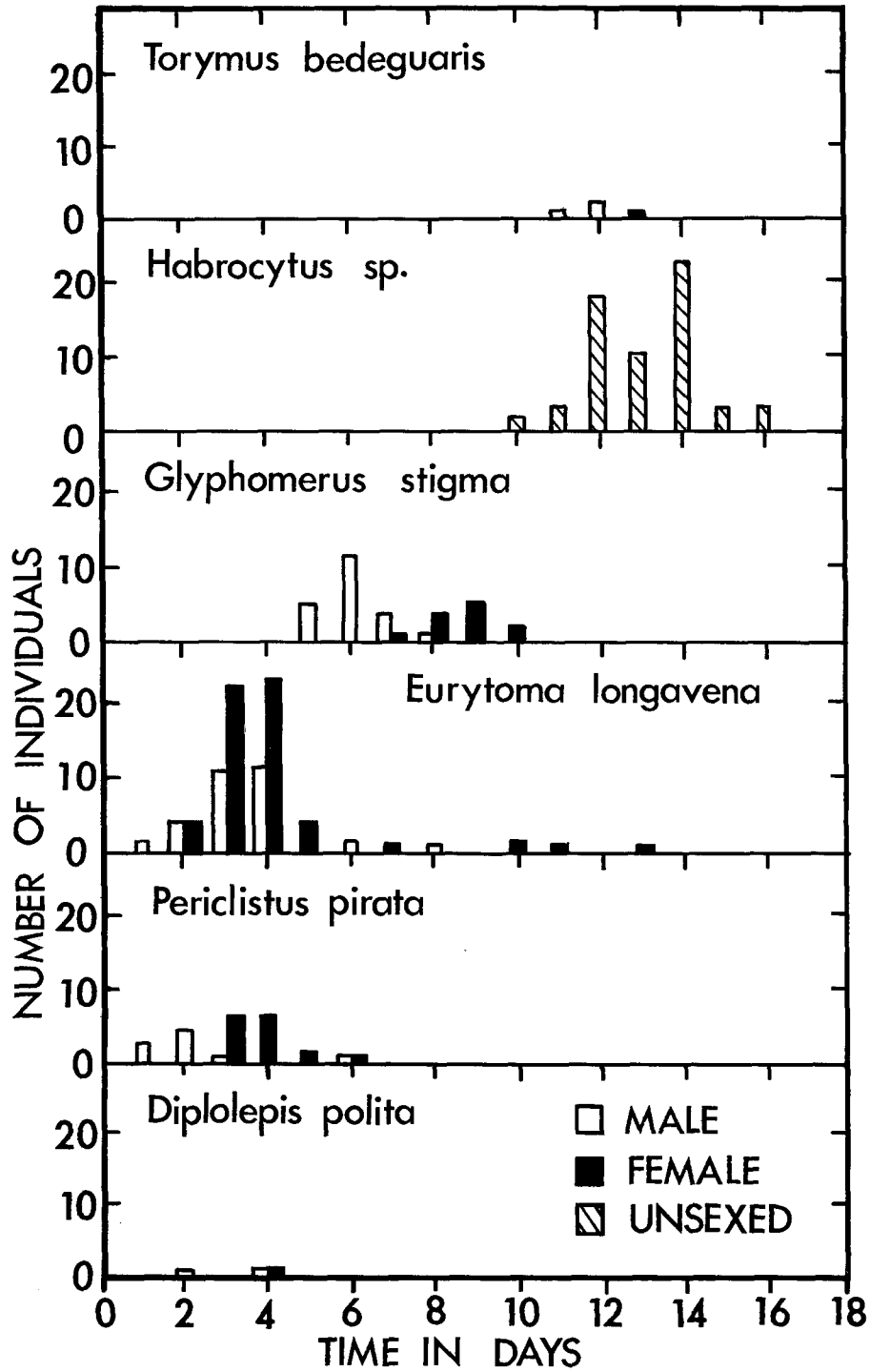


Fig. 20. Spring emergence from 300 galls of *Diptolepis polita* stored at 3°C for 3 months then transferred to 22°. The day of first emergence is day 1. Galls collected at George Lake, Alberta, 1969.

change in the proportion of *E. longavena* to *P. pirata* between June 12 and June 27 (Fig. 23). As the season advanced, feeding activities of *E. longavena* continued to reduce both the *P. pirata* population (Fig. 23) and the number of galls containing *P. pirata* (Fig. 21). Once all *P. pirata* in a gall were consumed, there was an increase in the percentage of galls containing only *E. longavena* (Fig. 21, July 5). *E. longavena* larvae perished if they did not obtain sufficient food before the supply of *P. pirata* was depleted. This was indicated by a decrease in percentage of galls containing *E. longavena* between July 5 and July 14 (Fig. 21). The first larvae of *G. stigma* appeared June 27 although this species was not abundant until later in the season. Larvae of *Habrocytus sp.* had only a slight influence on the *P. pirata* population in the first few collections in which they appeared (Fig. 23).

The occurrence of sucker shoot galls is shown by the reappearance of *P. pirata* and *E. longavena* eggs in the July 14 collection (Fig. 21). *P. pirata* was as detrimental to *D. polita* in sucker shoot galls as in spring initiated galls. The presence of sucker shoot galls did little to increase the *D. polita* population, although it was beneficial to both *P. pirata* and *E. longavena* (Fig. 21). Only 6 galls containing a *D. polita* larva were found in the 107 sucker shoot galls collected July 23. Fall emergence of *E. longavena* enabled this species to oviposit in a large percentage of the sucker shoot galls and as a result the sucker shoot population of *P. pirata* was reduced. Because *G. stigma* larvae consumed all occupants of the galls they inhabited, their presence in 5% of the July 14 galls represented a substantial decrease in the numbers of other larvae. No *G. stigma* larvae were found in sucker shoot galls and therefore the inclusion of sucker shoot galls in the July 23 collection lowers the percentage of galls containing this species (Fig. 21). The presence of *E. longavena* and *P. pirata* in sucker shoot galls increased the relative abundance of these species in the July 23 collection. Had these additional larvae not been present in sucker shoot galls, the proportion of *G. stigma* and *Habrocytus sp.* would have been higher. Most of the *P. pirata* larvae in sucker shoot galls were consumed by mid-August and this also explains the further decrease in the numbers of this species (Fig. 23). Because each *Habrocytus sp.* requires one *P. pirata* larva, their presence helped decrease the number of *P. pirata* in the July 23 and August 22 collections (Figs. 21 and 23).

Fig. 24 shows the inter-relationships of all species composing the *D. polita* gall community. Although *D. polita* was the key species in the community, later in the season *P. pirata* took over the central position of the food web. *P. pirata* had the greatest influence on the *D. polita* population and the presence of this species greatly increased biomass in the community. The remaining entomophagous species depended upon *P. pirata* as their chief source of food. *Habrocytus sp.* larvae were second to those of *E. longavena* as the chief destroyers of *P. pirata*. *G. stigma* and *T. bedeguaris* did not restrict their attack to any one species. Their importance in the community is therefore dependent upon the number of inhabitants in each gall attacked.

The most common cause of empty galls in 1968 and 1969 was food shortage. *E. longavena* and *G. stigma* perished if the galls they inhabited did not contain adequate food for their development. This was less likely for *T. bedeguaris* because they oviposited later in the season when competition between entomophagous species was nearing its climax. The interior of empty galls often contained remains and particles of gall tissue. From the two seasons 8% of the empty galls contained only the remains of first instar larvae of *P. pirata* and had no internal chamber development. Abnormal environmental conditions in the gall cavity or some unusual physiological condition of the plant tissue may have had a toxic effect which killed the gall inhabitants. Sometimes *P. pirata* females may have killed the immature *D. polita* larva and then failed to oviposit. About 15% of the empty galls in the August 22 collection contained fungus. This fungus may have initially attacked plant tissues resulting in the

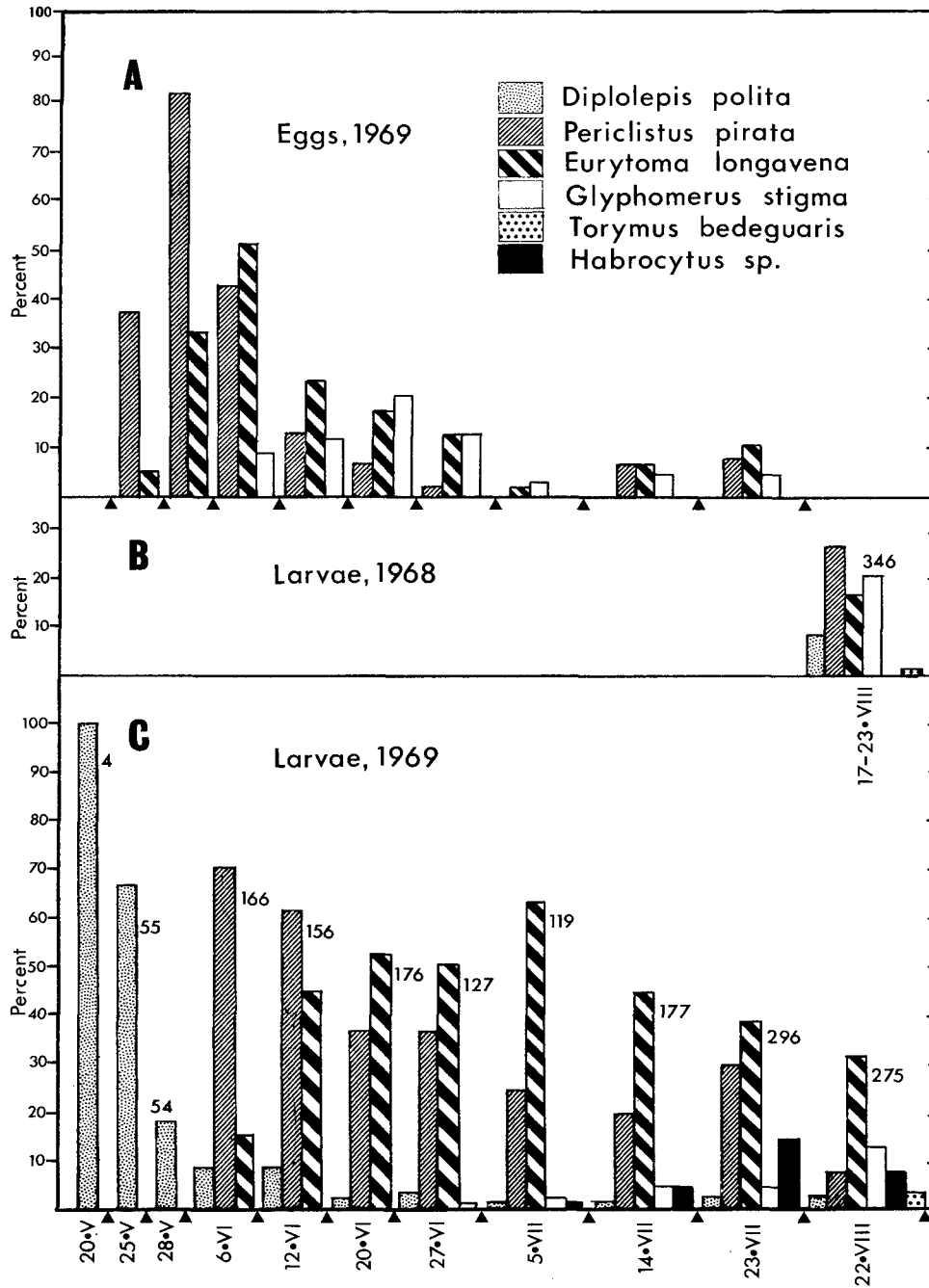


Fig. 21. Percentages of galls containing members of the *Diptolepis polita* gall community. Number of galls in each collection is indicated. George Lake, Alberta, 1968 and 1969. A. Eggs found in galls collected May to August, 1969. B. Larvae found in mature galls collected August 17-23, 1968. C. Larvae found in galls collected May to August, 1969.

death of the inhabitants or it may have developed on dead inhabitants and subsequently spread throughout the gall interior. Disease undoubtedly killed some inhabitants.

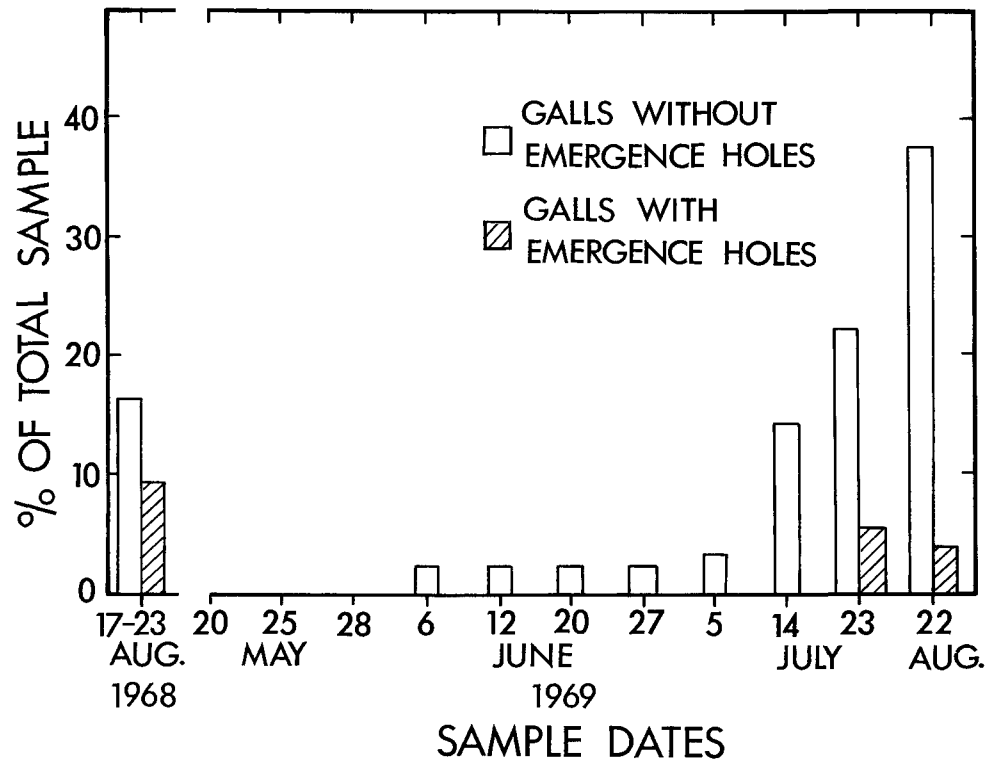


Fig. 22. Incidence of empty *Diplolepis polita* galls. George Lake, Alberta, 1968 and 1969.

Once the galls matured and fell to the ground, no further population additions took place and by analysing collections of these galls, climax of the succession was fixed. Also, after analysing the percentage of galls containing each species (Fig. 21) and the relative abundance of each species (Fig. 23), one can predict population trends for the following season. Predictions of this nature are dependent upon many factors, such as weather, which may have varying effects on the emergence of each species. It was obvious that the occurrence of *D. polita* in 9% of the 1968 mature galls was sufficient to allow for an abundance of galls in 1969. This indicates that the *D. polita* gall community is constructed to tolerate low numbers of the gall former. Several authors have found the same for other galls (Askew, 1961,

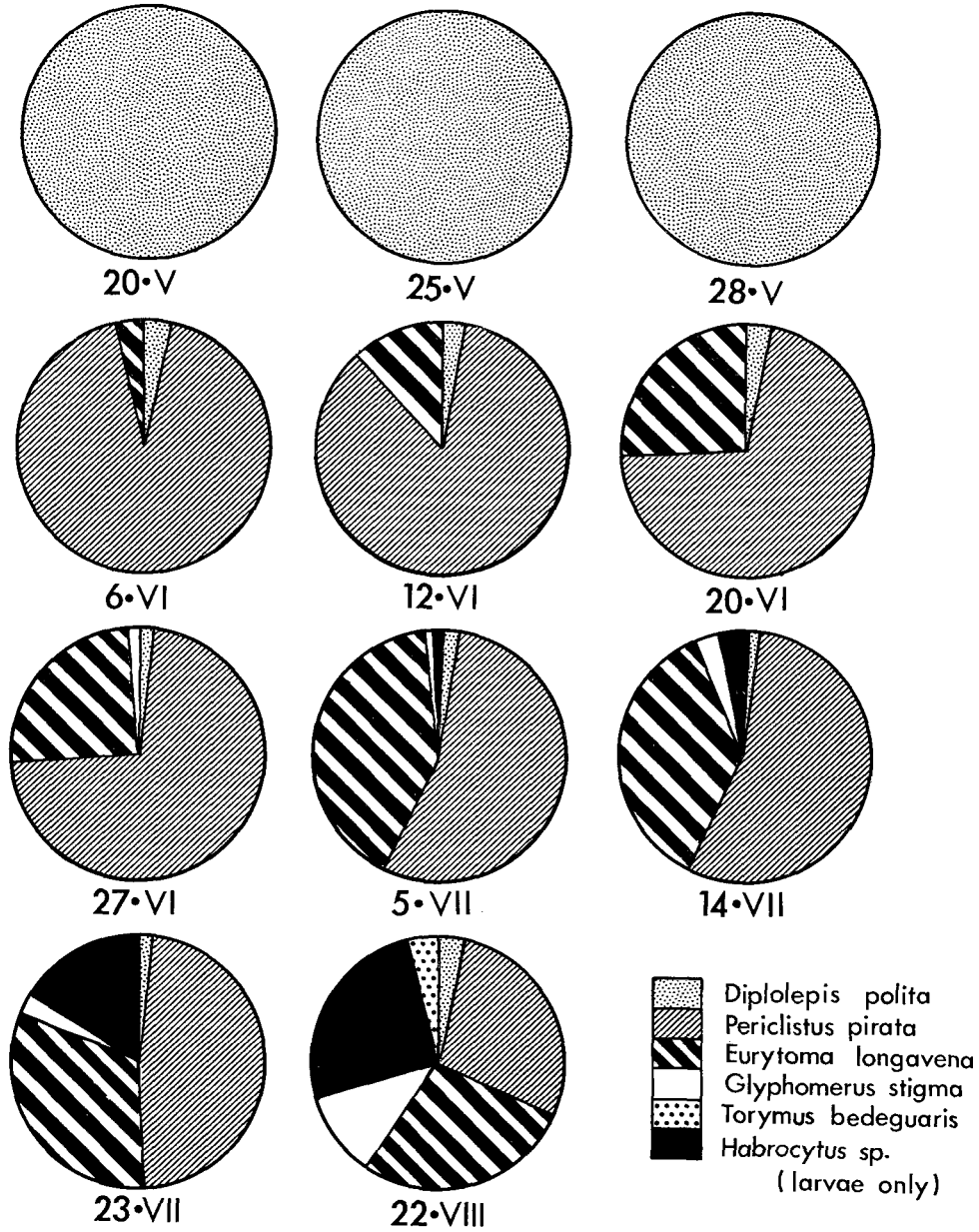


Fig. 23. Incidence of species in the *Diplolepis polita* gall community expressed as percentage of the total populations of gall inhabitants. George Lake, Alberta, 1969.

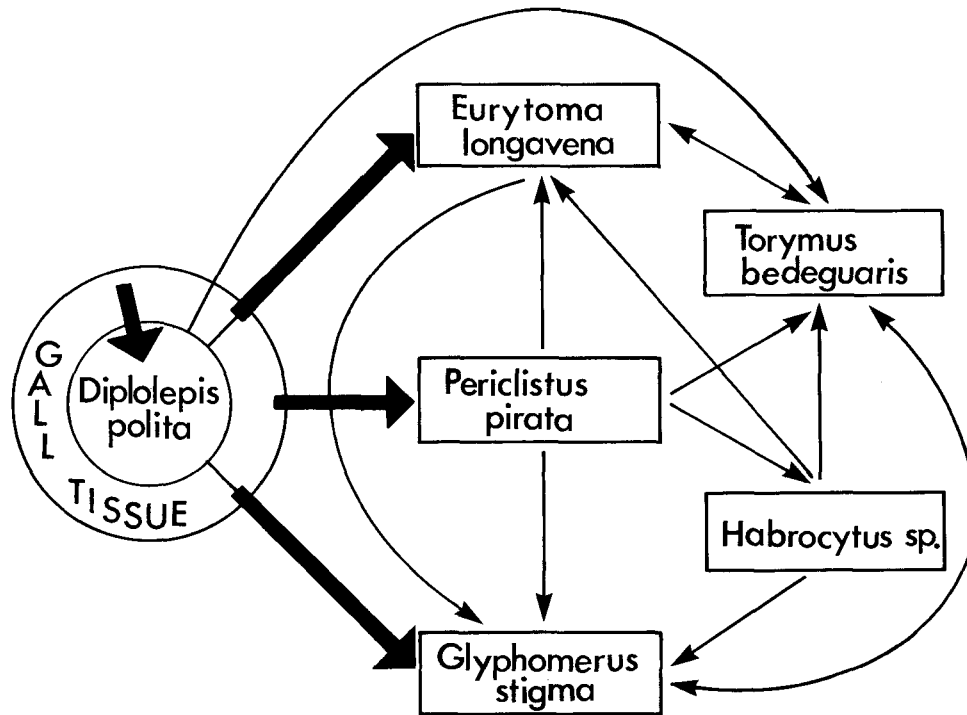


Fig. 24. Food web of species of the *Diplolepis polita* gall community. George Lake, Alberta, 1968 and 1969. Heavy lines represent phytophagous habit, narrow lines represent entomophagous habit.

Evans, 1967; and Gordinier, pers. comm.). By the end of 1969, the *D. polita* population was reduced and initial field observations in 1970 indicated that the galls were less common than in 1969. The occurrence of *P. pirata* larvae in 27% of the 1968 mature galls was chiefly responsible for the decrease in the *D. polita* population by the end of 1969. The availability of *P. pirata* larvae allowed an increase in the *E. longavena* population which in turn was partially responsible for the increase in empty galls. Few *Habrocytus sp.* larvae were found in 1968 mature galls and their abundance in 1969 was probably due to the increase in the *P. pirata* population. The decrease in numbers of *G. stigma* from 1968 to 1969 may be due to some unknown factor affecting only the biology of this species. For the 1970 community structure, I predict a large increase in *D. polita*, because of a decrease in the abundance of *P. pirata*. A decrease in *P. pirata* larvae would also cause a decrease in all entomophagous species and this again would reflect the importance of *P. pirata* in the gall community. This reduction of entomophagous species would allow for a 1971 increase in the *P. pirata* population

which in turn would decrease the *D. polita* population again.

GROWTH OF *DIPLOLEPIS POLITA* GALLS

The objective of this section is to correlate seasonal changes in gall dimensions with gall contents. In this section the growth rate of galls inhabited by a single *D. polita* larva is compared with the growth rate of galls inhabited by *P. pirata* eggs and larvae.

All studies on gall growth were made in 1969 and the field search for both galls and adults began May 7, 1969. No leaves of *R. acicularis* were out at this date, although those of *Populus* and *Salix* were just appearing. The first *R. acicularis* leaves were found May 8, 1969, in areas of greatest insolation; by May 11, 1969, immature leaves were present on nearly all rose plants. The first *D. polita* galls, 2 leaves with 2 galls on each, were collected May 20, 1969. From May 25, 1969 on, galls were much more common. The diameters of all galls in the 11 random collections described previously were recorded and correlated with gall contents. The mean sizes of galls containing either a *D. polita* larva or *P. pirata* eggs or larvae, for all collection dates, are presented in Tables 5 and 6. In another study, 80 one square metre quadrats were randomly marked off in 4 different rose patches. A total of 134 galls on 30 leaves were found within these quadrats. Each gall was examined and measured approximately every 7 days and data were obtained on their growth rate, shrinkage, senescence, and leaf abscission. Once the galls had fallen, they were returned to the laboratory for dissection. Unfortunately none of these galls contained a larva of *D. polita*.

Growth of Galls Inhabited by larvae of *Diplolepis polita* only

The mean diameter of 44 mature galls (Fig. 26) collected in 1968 and containing only a single *D. polita* larva was 3.8 mm (S.D. 0.47). An estimate of the growth curve for normal galls collected in 1969 containing a *D. polita* larva is shown in Fig. 26. By studying growth curves of individual plot galls, it was estimated that the maximum size of normal *D. polita* galls occurred around the middle of July. After this date there was shrinkage and the final size due to gall maturation was reached by the middle of August. The average amount of shrinkage in gall diameter for the 134 plot galls was 0.82 mm (S.D. 0.57) indicating that some of the mature *D. polita* galls collected August 22, 1969 (Table 5) could have been as large as 5.1 mm in diameter. Undoubtedly growth rate and condition of the host plant affects growth rates of attached galls. Factors such as soil condition and availability of light and water affects plant growth rates and must also influence growth rates of galls. Ovipositing in buds not in an optimum condition for galling could affect gall size. Positioning of the gall on the leaflets, the number of leaflets per leaf, and the number of galls per leaflet and leaf, could also influence gall size. Galls growing on older plants may have a different growth rate and final size compared to galls growing on younger plants and sucker shoots.

The first immature sucker shoot galls, all less than 2.9 mm in diameter, were found July 14, 1969. As the season advanced, immature galls on these shoots became more abundant and several collections were made up to August 13. Fig. 25 shows an increase in the number of immature galls less than 4.0 mm in diameter on July 14. Each successive collection contained a decreasing number of immature galls less than 4.0 mm in diameter as maturation processes began (Fig. 25), but the July 14 collection, and the three that followed, showed an increase in the number of immature galls. This increase illustrates the appearance of sucker shoot galls. In the July 23 collection, 106 of the 296 galls were from sucker shoots and 6 of these contained a *D. polita* larva (Table 5). Sucker shoot galls less than 4.0 mm in diameter from two further collections (July 28, 1969 and August 13, 1969) are included in Fig. 25, but their contents are unknown. All galls in the August 22, 1969 collection were

mature and the sucker shoot galls in this collection were combined with spring initiated galls (Fig. 21).

Table 5. Mean diameters of galls containing one larva of *Diplolepis polita*. George Lake, Alberta, 1969.

Date	No. of galls in collection	No. of galls containing <i>D. polita</i>	Mean size of galls containing <i>D. polita</i> larva \pm S.D.
20-V	4	4	0.8 \pm 0.05
25-V	55	35	0.9 0.4
28-V	54	10	1.9 0.6
6-VI	166	15	2.4 1.0
12-VI	156	13	3.2 1.3
20-VI	176	9	3.3 1.2
27-VI	127	4	3.7 1.1
5-VII	119	4	3.4 0.7
14-VII spring	156	2	—
14-VII sucker	21	-	—
23-VII spring	190	2	—
23-VII sucker	106	6	1.7 0.3
22-VIII	275	7	4.3 0.6

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Immature galls appearing on sucker shoots in July could be due to a delayed hatching mechanism, as mentioned by Yasumatsu and Taketani (1967). They found that *D. japonica* has two periods of gall formation, each appearance of the galls being dependent on the length of time before hatching. They reported that the first group of galls began developing 7 to 10 days after oviposition and the second group began developing 40 days after oviposition. It is possible that the increase in number of immature *D. polita* galls near the middle of July is a result of such a delay. If all *D. polita* eggs were laid around May 1, this second group of immature galls would be developing after approximately 70 days' hatching delay. Although all 13 immature galls collected July 14 contained *P. pirata* eggs, the remains of a *D. polita* larva were found in 5 of them. It appears that hatching of the eggs laid in the buds of sucker shoots is more delayed than in buds of older plants, perhaps because of some physiological condition within the host plant.

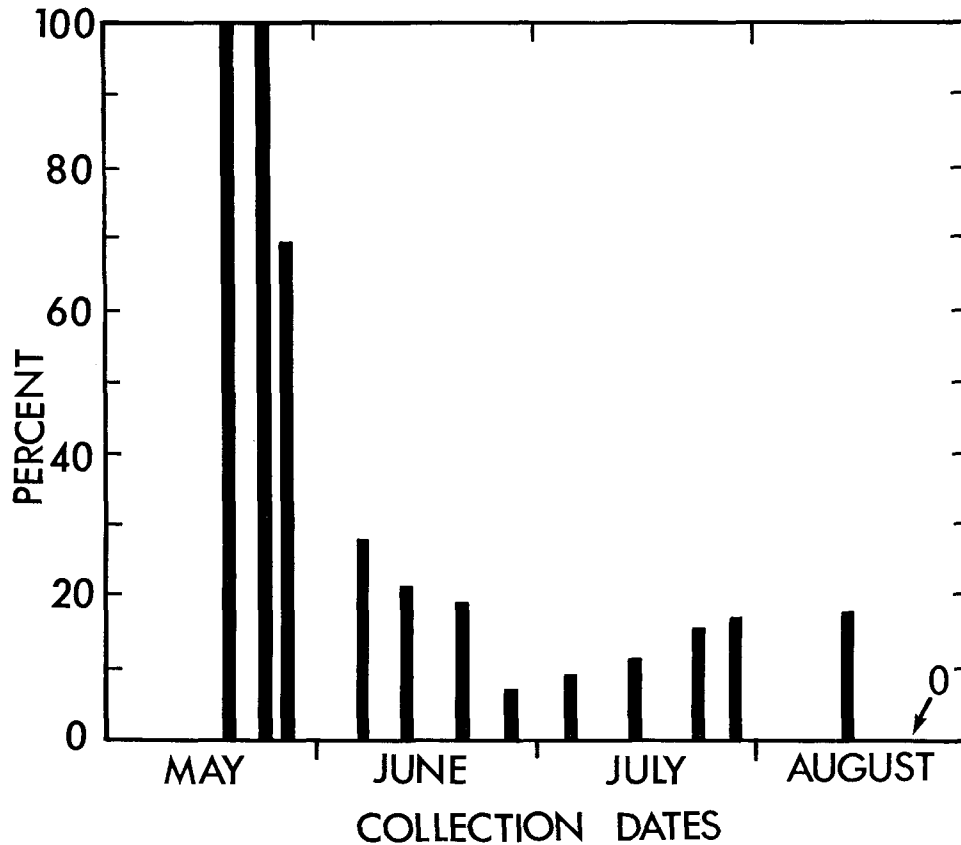


Fig. 25. Seasonal change in the numbers of immature *Diplolepis polita* galls less than 4.0 mm in diameter, expressed as a percentage of each gall collection. George Lake, Alberta, 1969.

Growth of Galls Inhabited by *Periclistus pirata*

Although many authors have discussed the position of 'inquilines' in gall communities, few have mentioned their ability to increase gall size. Niblett (1947) was one of the few to show this and stated that the *Diplolepis* gall he was studying showed a great variation in size when inhabited by *Periclistus* larvae. Blair (1945) maintained the opposite for the inquiline *Synergus reinhardi* Mayr in the galls of *Cynips kollari* Hartig, suggesting that inquiline larvae may inhibit gall growth. Evans (1967) stated that if the *Besbicus mirabilis* (Kinsey) gall is inhabited by the inquiline *Ceroptres* species, the immature gall ceases to grow and becomes hard and brittle. Yasumatsu and Taketani (1967) found that galls of *D. japonica* attacked by *Periclistus* sp. were irregular in shape, but they made no mention of size changes.

Eighteen of the 55 *D. polita* galls collected May 25, 1969, contained eggs of *P. pirata* and

in all 18 the larva of *D. polita* had been killed. In the May 28 collection, 44 of 54 galls contained *P. pirata* eggs and their mean size was greater than that of the 10 remaining (Fig. 26). Initiation of inner chamber development by the *P. pirata* larvae was first observed June 20, 1969 and by July 14, chambers were completed in 82% of the galls containing *P. pirata* larvae. The largest spring initiated gall containing *P. pirata* was found July 5, 1969 and was 12.4 mm in diameter.

The increased size of galls containing *P. pirata* eggs (Table 6) results from additional cell proliferation. Substances that cause the proliferation could be injected into gall tissue at the time of oviposition or the eggs may secrete activating substances. Once hatched, larval feeding activities also contribute to the increase in gall size. Even though predators may destroy all gall inhabitants, gall size has usually already been influenced by the *P. pirata* larvae. Predation after *P. pirata* had influenced gall size, results in many large galls without *P. pirata* chambers. Similar findings were also recorded by Niblett (1947).

Table 6. Mean diameters of *Diplolepis polita* galls containing eggs or larvae of *Periclistus pirata*. George Lake, Alberta, 1969

Date	No. of galls in collection	No. of galls containing eggs or larvae	Mean size of galls containing eggs or larvae \pm S.D.	
20-V	4	0	-	-
25-V	55	18 (eggs)	1.6 \pm	0.7
28-V	54	44 (eggs)	3.5	0.8
6-VI	166	119 (larvae)	5.0	1.4
12-VI	156	96 (larvae)	6.4	1.5
20-VI	176	64 (larvae)	6.4	1.7
27-VI	127	45 (larvae)	6.5	1.6
5-VII	119	29 (larvae)	7.0	2.0
14-VII spring	156	35 (larvae)	6.9	1.9
14-VII sucker	21	17 (eggs & larvae)	3.2	1.3
23-VII spring	190	33 (larvae)	8.1	1.6
23-VII sucker	106	53 (larvae)	4.6	1.0
22-VIII	275	21 (larvae)	7.2	1.9

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

Galls formed on sucker shoots later in the season are also attacked by *P. pirata*. Another characteristic of sucker shoot galls is that they do not attain the size of *P. pirata* enlarged galls initiated in the spring. The largest sucker shoot gall found was 6.4 mm in diameter. Of the 106 sucker shoot galls found July 23, 1969, 50% contained larvae of *P. pirata*, but 94% of these galls had no inner chamber development. Mean size of these 53 galls was 4.6 mm (S.D. 1.0), significantly smaller than the mean of 8.1 mm (S.D. 1.6) for spring initiated galls (Fig. 26).

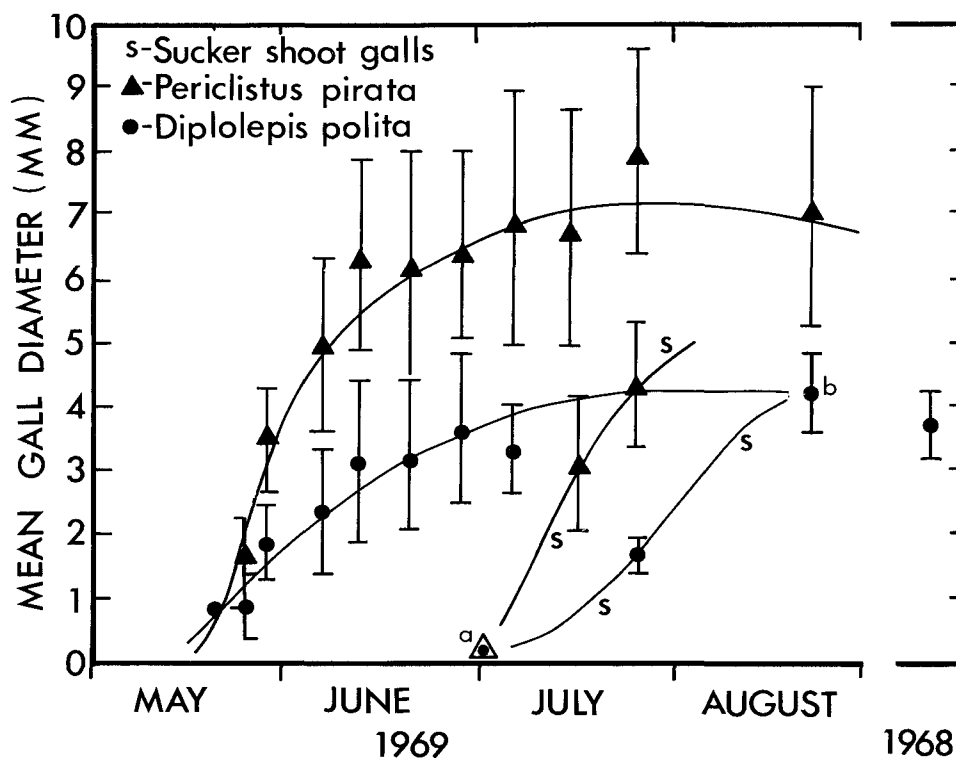


Fig. 26. Seasonal change in the mean size of galls containing a single *Diplolepis polita* larva (solid lines) compared to galls containing *Periclistus pirata* eggs or larvae only (broken lines). Vertical lines indicate one standard deviation each side of the mean. George Lake, Alberta, 1968 and 1969.

Gall Senescence and Abscission

Maturation of gall tissue affects nearly all the insects associated with a gall community. Most of the phytophagous larvae are only capable of feeding as long as plant cells remain soft and succulent. All feeding activities of *D. polita* and *P. pirata* larvae are terminated once gall tissues mature. Gall maturation also offers gall inhabitants some protection from predators and parasites. Oviposition activities of predators and parasites are influenced by the degree of tissue maturation. Askew (1961) found that as a gall matured, there was an increase

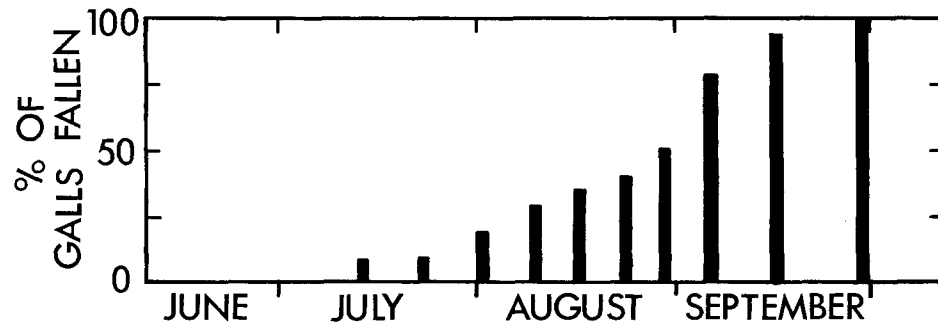
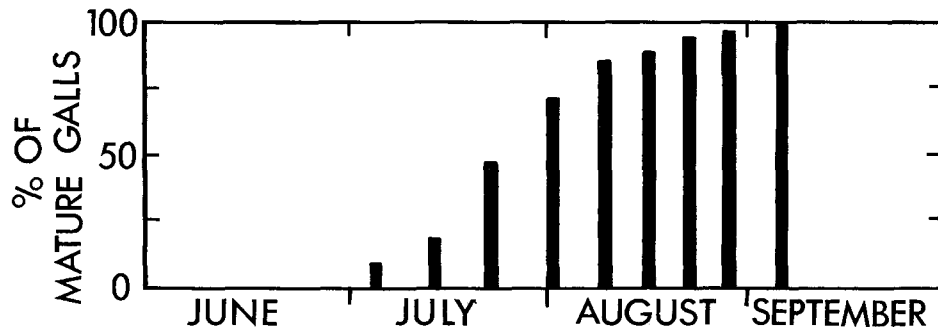
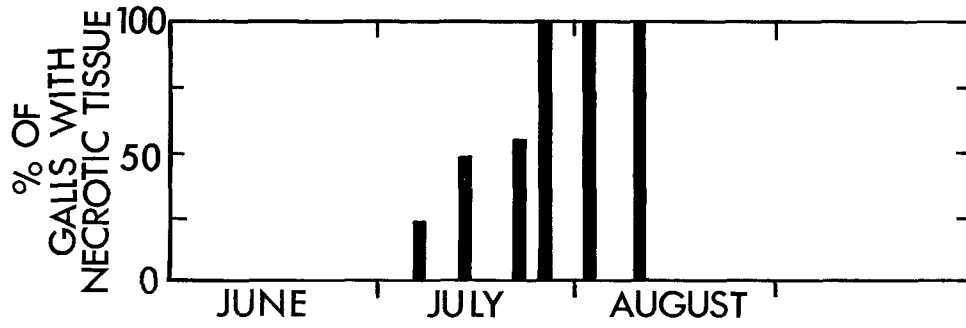


Fig. 27. Percentage of galled leaves with necrotic tissue in collections of spring initiated *Diplolepis polita* galls. George Lake, Alberta. 1969. Fig. 28. Rate of gall maturation of spring initiated *Diplolepis polita* galls found in 80 random plots. George Lake, Alberta. 1969. Fig. 29. Rate of gall abscission of spring initiated *Diplolepis polita* galls in 80 random plots. George Lake, Alberta. 1969.

in the time taken for a parasite to pierce the gall wall. He also measured gall hardness and found that the walls of mature galls of *Cynips divisa* Htg. were 200 times more resistant to crushing than were the walls of immature galls.

Ignoffo and Granovsky (1961) defined gall senescence as the process of turning brown due to tissue necrosis. They considered a gall necrotic when seven-eighths of the surface was brown. Mani (1964) stated that the nutritional deficiency of a leaf beyond the gall is first observed when the gall begins to mature. Early maturation of a galled organ is one of the affects of gall formation on the host and was observed in galled *R. acicularis* leaflets in the present study. The percentage of galled leaves with necrotic tissue, found in the 11 major collections of 1969, is shown in Fig. 27. Only the spring initiated galls are represented in this graph. All galled leaves had necrotic tissues by July 28, 1969, whereas the first discoloration of normal leaves was seen in the last week of August.

D. polita galls were considered mature when at least 75% of the gall tissue was dark brown. The rate of gall maturation was determined by examining the 134 galls found in the random plots described previously (Fig. 28). The first mature gall was observed June 28, 1969 and all were mature by September 6, 1969.

Once a mature gall has fallen to the ground, it can be considered immune to attack by most predators and parasites though rodents undoubtedly consume some fallen galls. The rate of gall abscission was also determined by examining the 134 plot galls. The first plot gall had fallen by July 14, 1969 and all had fallen by September 28, 1969 (Fig. 29). Galls growing in large clusters probably fall before galls growing singly because of their combined weight. Large gall clusters often cause the entire leaf to hang vertically (Fig. 2). Galls with their weight increased by *P. pirata* larvae probably fall before galls containing a single *D. polita* larva. Ignoffo and Granovsky (1961) found that the gall of *Mordwilkoja vagabunda* Walsh (Aphididae) prevented the formation of an abscission layer and the gall may remain on the host for 3 years. Yasumatsu and Taketani (1967) found the first galls of *D. japonica* began falling 39 days after initiation. If the average initiation date for the *D. polita* galls can be considered about the middle of May, then the first galls fell approximately 60-70 days after initiation. *D. polita* galls overwinter on the ground and because they fall before normal leaf abscission occurs, their subsequent covering by the autumn complement of leaves helps to protect the gall inhabitants against winter.

DISCUSSION

This investigation of the *Diptolepis polita* gall and its inhabitants has revealed many basic features of cynipid gall ecology. It is apparent that by studying cynipid galls, one has the opportunity of gaining new information on such basic concepts of biology as community ecology, insect-plant specificity, plant developmental morphology, and the evolution of specialized insect groups.

D. polita is the central character in the gall community although as the season advances its dominance in terms of biomass is soon lost to other gall inhabitants. *Periclistus pirata* is mainly responsible for the rapid decline in the *D. polita* population. The entomophagous inhabitants that subsequently invade the galls depend more on the larvae of *P. pirata* as their source of food than they do on *D. polita* larvae. It therefore can be shown that the gall former prepares requisite conditions for the inquiline, which in turn provides requisite conditions for the entomophagous species. By the end of the season, the community consists of much larger proportions of inhabitants other than the gall former and it is the relative proportions of these inhabitants that determines community structure the following season.

The *Diplolepis* species complex has received little attention and the entire genus is in need of taxonomic revision. Several of the names in use are incorrect. Species have been distinguished mainly by their external morphology and because the species exhibit limited variation, use of many of these characters may have led to the taxonomic problems.

A great deal has yet to be learned about the biology of *D. polita* and for that matter, all *Diplolepis* species. Adult *D. polita* can undoubtedly be observed in the field if the researcher is at the right place at the right time. Condition of the host plant at the time of oviposition and gall initiation should be easily delineated. Surprisingly little is known about the induction of cynipid galls. Plant biochemists and morphologists would undoubtedly be interested in learning of the chemical stimuli these insects have evolved to cause cell hypertrophy and hyperplasy. The various stages of gall development from the time of oviposition to gall maturity may reveal structural features that influence activities of the associated insects. The presence of males in the *D. polita* population indicates that normal sexual reproduction occurs and in light of theories of north-south gradations in parthenogenesis, larger populations of all northern species should be examined. The appearance of sucker shoot galls also requires further investigation. If ovipositing females can be handled in the field, controlled ovipositions in both spring and sucker shoot host plants and subsequent observations of gall development should reveal whether there is a delay mechanism in initiation of sucker shoot galls.

From the data obtained on the biology of *Periclistus pirata*, it is apparent that inquilines have an important role in cynipid gall ecology. They take an important position in the community and grossly modify the normal gall structure. Exactly how *Periclistus* disposes of the *Diplolepis* larvae requires further investigation. Because *D. polita* galls were observed to enlarge even before the *Periclistus* eggs hatched, it appears that substances inducing further cell hypertrophy come from either the ovipositing females or the unhatched eggs. *Periclistus* larvae may exhibit cannibalism, but this has yet to be determined. It would be interesting to compare the manners in which *Diplolepis* and *Periclistus* stimulate and modify the plant tissues with which they are in contact. From observations of immature *D. polita* galls it appears that the immature *Diplolepis* larva is surrounded by plant tissues when it hatches and subsequent feeding causes cellular hypertrophy and hyperplasy in all directions from the larva. When *Periclistus* larvae feed, the plant cells are stimulated in such a manner that the tissues grow up and around the individual larva. It will be interesting to determine whether other *Diplolepis* galls are modified by *Periclistus* in a similar manner. If the structure of other galls can be modified as extensively as those of *D. polita*, then many of the gall descriptions and illustrations now in the literature for *Diplolepis* may be inaccurate.

Plant morphologists may benefit from studies of cynipid gall developmental morphology. How these insects gain control of morphogenetic potentialities of host organs remains unknown. Galls cannot be regarded as organs, but they are more than tissue abnormalities for they have constant size and structure. An interesting problem for the morphologist would be to determine whether galls and the tissues composing them can be regarded as 'new' structures, morphologically different from familiar structures. Galls of *Diplolepis* have cells and tissues unlike those normally found in the host plant. We require more information on the mechanisms that induce gall cells to divide without reference to the morphogenetic character of the host organ. It may even be easier for morphologists to study processes of form determination in galls than in normal developmental processes in plants. In galls the inducing agent is not part of the physiological mechanism of the plant, but rather is introduced into the plant.

Insect galls afford numerous opportunities for studying insect-plant host specificity and specificity of the inhabitants. It is now known how certain insects are attracted and restrict-

ed to either one or several closely related hosts, but little, if any, attention has been given to why a species is restricted to one organ of the host plant. Why, for example, is *D. polita* restricted to leaves? Would gall tissue develop if immature larvae were transplanted into meristematic tissues of stems or roots? *D. polita* was found only on *R. acicularis*, although *R. woodsii* often grows alongside. Is *D. polita* restricted to *R. acicularis* or does only this host have tissues susceptible to galling when *D. polita* oviposits? Transplanting larvae of *Diplolepis* species into meristematic tissues of other hosts may yield interesting results.

Many theories on how the habits of several closely related hymenopterans may have evolved can be further studied by examining cynipid galls. For example, have the inquiline that induce cell hypertrophy and hyperplasia lost the ability to cause galls, or are they in the process of developing the ability to initiate their own galls? Transplant experiments may provide clues. Two chalcidoid species, *Eurytoma longavena* and *Glyphomerus stigma* were found to be both entomophagous and phytophagous in their larval stages. It would be interesting to know if these species could complete their development on only one food. Has the phytophagous habit of these species which are normally considered entomophagous, developed because of the reduced biomass in monothalamous galls, or do they exhibit the same habit in other *Diplolepis* galls?

A useful contribution to our knowledge of community structure can hopefully be made by continued studies of population assemblages in insect galls. Insect gall communities are simple communities and their attributes can be determined with relative ease. Granted, my definitions and use of community attributes differ somewhat from the classical usage developed by plant ecologists such as Whittaker (1970). But nearly all aspects of community ecology such as diversity, organization, succession, climax, productivity and biomass, and nutrient cycling can be articulated by examining gall communities. Further research will supply data on these various aspects of gall community ecology and it will be of great interest to compare results and conclusions with those of other community ecologists. Zoogeographical studies of *Diplolepis* communities would be valuable. From distribution maps (Lewis, 1959) it appears that *R. acicularis* spread into North America through Beringia. They probably brought *Diplolepis* species with them and comparisons of communities from Alaska to California should provide information useful to those postulating theories of how natural communities evolved (Whittaker and Woodwell, 1972). Studying series of all known *Diplolepis* species, their galls and communities, should reveal a great deal of information about the evolution of the rose gall complex.

In the past, most workers have taken the descriptive approach to studies of plant galls. It has been my aim to consider galls in terms of ecology rather than simply gall morphology or taxonomy of inhabitants. Before botanists can effectively study developmental processes associated with insect galls, information on the ecology of associated inhabitants is required. Botanical information on galls will be found useful in studies of gall formers and associated species. By combining knowledge from various disciplines of biology, we will be in a better position to understand cynipid galls and the intricacies of these fascinating insect-plant relationships.

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