Proc. Indian Acad. Sci. (Anim. Sci.), Vol. 93, No. 4, June 1984, pp. 275–282.

A preliminary review of some interesting aspects of bio-ethology of the chalcids (Hymenoptera: Chalcidoidea) associated with plant galls

T C NARENDRAN
Department of Zoology, University of Calicut, Calicut 673 635, India

Abstract. The interactions and inter-relationships between plant galls and the chalcids with them are often extremely intricate and it is not easy always to assess correctly a given species as a gall former or an inquiline or a parasite of another inhabitant of a gall. The chalcids show complex inter-relationships with other inhabitants of a gall in many instances. The existence of both phytophagy and entomophagy in the same species or in the same individual is an interesting phenomenon met with in some species of chalcids associated with plant galls. The host-finding and host-acceptance behaviour of some of the gall-chalcids are other interesting aspects discussed.

Keywords. Phytophagy; entomophagy; host-finding; plant galls; chalcids.

1. Introduction

The superfamily Chalcidoidea constitutes one of the most economically important groups of Hymenoptera. It comprises several thousands of species contained in more than 2100 genera. The chalcids vary widely in size from 0·25 mm to more than 15 mm in length. They have diverse host relationships and marvellous dietary specialisations. While the majority of chalcids are entomophagous in habit, some are undoubtedly phytophagous. A few of the chalcids are interestingly phytophagous as well as entomophagous too. Many chalcids are associated either directly or indirectly with plant galls. However the exact nature of inter-relationship between a given species of chalcids and the plant galls associated with it, is often very difficult to study since many of these chalcids have very intricate and complex host relationships.

2. Review

Among the 16 families of Chalcidoidea, 11 are associated either directly or indirectly with plant galls (Narendran 1983). Among these 11 families (table 1), Agaonidae which comprises 42 genera (Noyes 1978), is perhaps the only family which is completely associated with plant galls. The agaonids are commonly known as "fig wasps". According to Wiebes (1979, 1982a, b) the ecology of fig wasps is for greater part the ecology of fig flowers and there is only one biogeography for both. No fig wasp can propagate outside figs and no fig can thrive without the specific fig wasps (Wiebes 1979, 1982a, b). Thus the fig and the fig wasp are believed to have evolved together. Related figs have related pollinators and both groups probably descended from a common ancestor fig and its pollinator wasp. However the existence of two species of agaonids in the receptacles of the same species of *Ficus* as reported by some authors (Joseph

Table 1. The number of genera of chalcids associated with plant galls.

Family	Total number of genera	Genera associated with plant galls	Percentage
Agaonidae	42	42	100
Torymidae	104	33	31·73
Eurytomidae	77	14	18·18
Pteromalidae	560	50	8·93
Eulophidae	325	22	6·77
Eupelmidae	71	7	9·90
Encyrtidae	513	10	1·95
Aphelinidae	48	2	4·17
Mymaridae	95	2?	2.11?
Trichogrammatidae	70	3?	4·29?
Chalcididae	115	1	0·87
Leucospidae	4	0	0
Elasmidae	8	0	0
Eucharitidae	55	0	0
Tetracampidae	13	0	0
Signiphoridae	6	0	0
Total	2106	186	8·83

1953, 1954; Wiebes 1964), makes the acceptance of the theory with some reservation (Wiebes 1964).

The family Torymidae was referred in the past as Callimomidae. It forms an extensive family which include forms of diverse structures and habits including both phytophagous and parasitic forms. The family contains more than 100 genera and among these, 33 genera are associated either firmly or loosely with plant galls. The family Eurytomidae comprises many species which are parasitic upon various insects, chiefly gall formers. However quite a few eurytomids are phytophagous, developing in the seeds of various plants and in the grass stems, where some like the genus *Tetramesa* make distinctive galls (Peck 1963; Boucek 1964). The family Eurytomidae contains more than 75 genera and out of these, 14 genera contains species associated with galls of plants. The family Pteromalidae is the largest family of Chalcidoidea and it has been stated that this family is perhaps one of the most difficult groups of Hymenoptera to study taxonomically (Prinsloo 1980). The great majority of pteromalids are primary or secondary parasitoids attacking a large range of insects including some plant gall inhabitants, in their various stages of development. A few pteromalids like *Asparagobius braunsi* (which make galls on the stems of *Asparagus stricta*), *Odontofroggatia galili* Wiebes (which causes galls on *Ficus microcarpa* L.), *Hemadas nubilipennis* (Ashmead) (which causes hard wood galls on the stems of Vaccinium) etc., are true gall inducers (Gahan and Ferriere 1947; Galil and Copland 1981; Prinsloo 1980). The family Pteromalidae comprises 560 genera at present and of these, 50 genera contain species associated with plant galls. The family Eulophidae is another extensive and complex family of Chalcidoidea. It contains 325 genera of which only 22 are associated with galls of plants. Most of these eulophids associated with plant galls are parasitic on other gall formers or inquilines. However some members such as *Tetrastichus cecidophagus* W., *T. ardisiae* Ishi etc are gall inducers (Ishi 1931; Wanberg 1977). The members of the family Encyrtidae are primary or secondary endo-parasitoids of insects (mostly coccids) and also arachnids, with a preference for larval

stages of their hosts, although the eggs and very rarely the adults are also parasitised (Prinsloo 1980). Though this family comprises more than 510 genera, only 10 of them contain species associated with plant galls and even in these most of the species are very loosely associated with the galls. Eupelmidae is one of the widely distributed families of Chalcidoidea. This family comprises 71 genera of which 7 are reported to contain species associated with plant galls. While the majority of species associated with plant galls are parasitic on other gall inhabitants, a few are gall inducers also. According to Burks (1979) all the species of the eupelmid subfamily Tanostigmatinae with the exception of one, are known to be gall formers. Most members of the family Aphelinidae are not associated with plant galls. However genera like *Aphelinus* and *Protoaphelinus* contains species indirectly associated with plant galls of aphids, cecidomyiids and psyllids. The family Mymaridae includes very tiny chalcids which include some of the smallest insects known. Almost all members of this family are parasites in the eggs of other insects with the exception of a few which parasitises other stages of coccids, aleurodids, etc. There are a few reported cases (Subba Rao 1976; Smith 1970; Nikol'skaya 1952) of mymarids associating with plant galls either directly or indirectly. According to Boucek (in personal communication with the author in 1982) it is very improbable that mymarids are associated with plant galls and these reported cases may be taken with reservation. The same opinion may be also applicable to the family Trichogrammatidae since the trichogrammatids are also somewhat similar to mymarids in parasitising eggs of insects etc. The family Chalcididae comprises species which are primary or secondary parasites of larvae or pupae of a large number of species of insects mostly belonging to Lepidoptera and Diptera. There is only a single reliable record (Boucek 1982) where it is reported that a species viz. *Hockeria tamaricis* Boucek has been reared from the galls of *Amblypalpis olivierella* Ragonot (Lepidoptera) on *Tamarix*.

Most species of chalcids are entomophagous and a few are parasitic on other arthropods and a few others have reverted to phytophagy (Nikol'skaya 1952). According to Nikol'skaya (1952) "our present knowledge of chalcid biology is such that we are able to draw up a scheme illustrating the transformations from a predacious habit to various parasitism, and from entomophagy to phytophagy". Regarding the origin of phytophagy in chalcidoidea there is unanimous opinion among chalcidologists that it evolved completely independently in several families associated with parasitism of various species on gall inducers or seed-eaters. According to Gordh (1979) phytophagy probably has evolved several times in Chalcidoidea because it is seen in several distantly related taxa and many unrelated species of plants which serve as hosts. According to the same author phytophagy in chalcids is found most frequently with gall forming habits but the evolutionary significance of this observation remain unknown. A change from entomophagy to phytophagy can be observed in several species of chalcids. According to Grissel (1976) in the genus *Torymus* several species have been reported to eat the plant tissue after the host larva of the gall is consumed. Philips (1927) gave an interesting account on the eurytomid species *Eurytoma parva* Girault developing on a mixed diet. This interesting American species lays its eggs into the gall of another eurytomid *Tetramesa tritici* (Fitch) which makes galls in the stems of wheat. When the parasite *E. parva* hatches, it first attacks and devours the young larva of *Tetramesa tritici* inside its gall. When the host larva is completely consumed by the parasite, it shifts its feeding to the plant sap. It is reported that (Clausen 1940) there is considerable laceration of the gall tissue by the parasite *E.*

parva which is probably more than that would have been done by its host. Philips (1927) reported that in experimental conditions *E. parva* could develop quite normally on a vegetable diet. According to the same author the larva of *E. parva* is in a highly plastic or adaptive condition and it is in the process of changing over from parasitism to phytophagy while as yet entirely dependent upon *T. tritici* for the stimulus leading to oviposition. The dietary habits of *Eurytoma inquilina* Rim-Kors. and *Eurytoma brevitergis* Bugbee are also reported to be similar to that of *Eurytoma parva* (Rimskii-Korsakov 1914; Wanberg 1977). Puzanova-Malysheva (1930) reported that the female torymid *Syntomaspis eurytomae* Puz.-Mal. deposits its eggs into blackthorn fruits containing young almond seed-eater larvae of *Eurytoma amygdali* End. After killing the larvae of *E. amygdali* the parasite turns to feed on the seed. According to Chernoponevkina (1949) the species *Liodontomerus perplexus* Gah. usually parasitises the larvae of clover and sainfoin seed-eaters but often changes its diet to plant tissue, under certain conditions, after destroying the young seed-eater larvae. Another torymid species *Torymus aea* (Walker) (reported as *amelanchieris* (Cushman)) has been shown to develop on the host larva as well as phytophagously in surrounding plant tissue (Milliron 1949). *T. aucupariae* (Rodzianko) is believed to have similar habits (Milliron 1949) as those of *T. aea.* In contrast to the above type of dietary habits, in some other chalcids like the torymid *Syntomaspis cyanea* (Boh.) a different type of dietary habit can be seen. This torymid lays its eggs singly in young galls of *Cynips divisa* and *C. longiventris* when these hosts are about 2 mm in diameter. The *Cynips* larva, which is usually in its first instar is not stung or paralysed by the ovipositing female *S. cyanea.* The two larvae live alongside feeding the gall tissue for some time. However the torymid larva grows rapidly feeding on the tissue of the gall and when it is half grown the *Cynips* larva is apparently eaten by the torymid (Askew 1961a). Another type of behaviour is seen in the cleptoparasitic torymids. According to Joseph (1957, 1958, 1959) *Philotrypesis caricae* (L.) is a cleptoparasite of *Blastophaga psenes* (L.). The larva of *P. caricae* is phytophagous in the fig galls of *Ficus carica* and when it reaches its second instar, it destroys the *Blastophaga* larva by more active feeding. Abdurahiman and Joseph (1978) have shown that the torymids *viz Philotrypesis pilosa* Mayr and *Apocrypta backeri* Joseph are cleptoparasitic on the agaonid larvae of *Ceratosolen marchali* Mayr in the galls of *Ficus hispida* (L.). According to them when the amount of food in the *Ficus* ovary diminishes due to active feeding by the agaonid and torymid, the available and remaining food is more actively eaten by the torymid larva. When the whole of the available food in the fig ovary is exhausted by this competitive feeding, the torymid is believed to be probably killing the agaonid host.

Among the various plant galls, Oak (*Quercus*) galls caused by Cynipid wasps perhaps form hosts to the greatest number of species. Rearing of the inhabitants of Cynipid oak galls has been of popular interest among entomologists particularly in the begining of 20th century (Askew 1961b). However, mainly because of the difficulty involved in correctly identifying many of the inhabitants of these galls (particularly Chalcidoidea) many entomologists could not pursue their investigations further on the biology of oak gall inhabitants. Recently Blair (1944, 1946) and Askew (1961–1965) did commendable work on the biology of Oak gall inhabitants. Blair (1944) stated that the larva of *Eurytoma rosae* Nees is a predator rather than a parasite since each *Eurytoma* larva usually consumes more than one host larva in the rose gall of *Diplolepis rosae* (L.). According to Askew (1961b) similar habit has also been noticed in a few

other chalcidoid species of oak galls and it is thought best to avoid unnecessary complications by not using the term predator. The inter-relations between the inhabitants of Oak galls are often very complex and Askew gave an excellent account on them including diagrams illustrating the inter-relationships of the inhabitants of a large number of oak galls (figure 1).

The host-finding habits of chalcids, particularly chalcids associated with plant galls is an interesting and worthy field of investigation since no detailed work on this aspect has been done. According to Noyes (1982) the main reason for entomologist's distaste for chalcids is that most species they are likely to encounter are less than 2 mm in length and in turn this has led to the belief that chalcids are extremely difficult to study. Askew (1961c) observed that when a female *Mesopolobus* (Pteromalidae) walks over the leaves of oak bearing Cynipid galls, she seems to be unaware of the presence of the galls until she passes within about 4 mm of a gall and then suddenly she deviates from her original course and walks directly to the gall. According to the same author the female *Mesopolobus* is attracted to the gall by the visual sense when it is within the short 4 mm range of its gall. Askew (1961c) concluded from his experiments that olfactory sense plays little or no part in attracting the female *Mesopolobus* to host galls though the galls are probably distinguished from other objects by antennal chemoreception. Varley (1941) has shown that *Eurytoma curta* Walker which attacks the trypetid fly *Urophora jaceana* Hering living in the flower heads of black knapweed (*Centaurea nigra* L.), recognises the flower heads as objects of special significance, probably by visual sense as well as by olfactory sense. Several workers (Ullyet 1936; Edwards 1954, 1955; Schneider 1939, 1940; Laing 1937; Narendran 1975) have reported that the chalcids in their search, were not in a position to notice their hosts from great distances and in general had to fly randomly till they reached within a particular distance from the host.

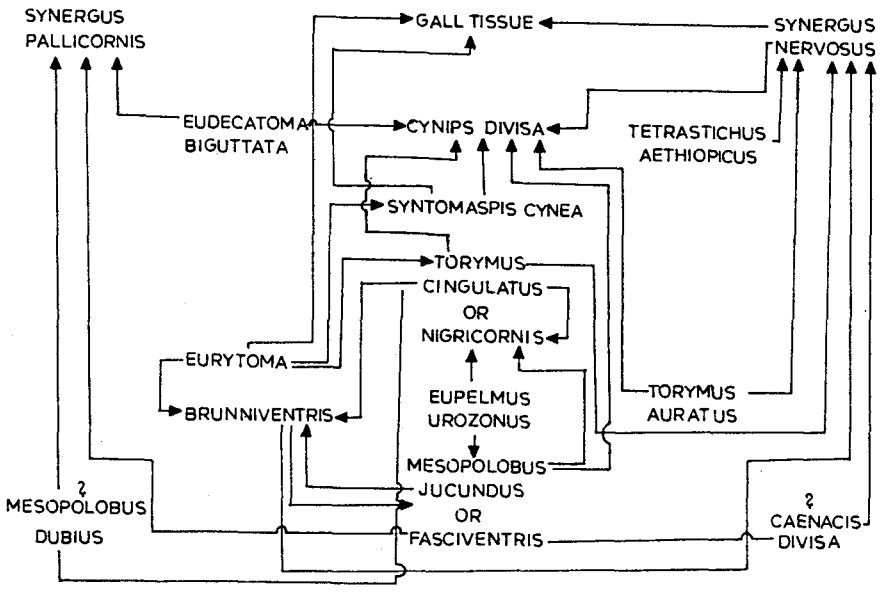

Figure 1. The inter-relationships of the inhabitants of a *Cynips divisa* gall (after Askew 1961, partly modified).

When once they reached this particular observation field by chance encounter, then the olfactory as well as optical senses helped them to find their hosts. When a chalcid locates its gall, the suitability of the gall is tested probably by the antenna and ovipositor. The implication of antenna and ovipositor as agents helping host detection has a long history of random observations but there is insufficient critical experimental work to establish their precise function (Fisher 1971). This is especially so in the case of chalcids associated with plant galls. It is reported (Askew 1961c) that when a female *Mesopolobus* encountered its gall or an object resembling its gall, she repeatedly examined the surface by drumming with her antennae. It has been shown that galls are distinguished from other objects by the female *Mesopolobus* by antennal chemoreceptors. After the primary selection of the gall by the female *Mesopolobus* using her antennae, she inserted her ovipositor into the gall and if a larva of the host was present, she stung it with her ovipositor. According to Askew (1961c) the sense organs of the ovipositor must have helped the female *Mesopolobus* to detect her host larva inside the gall. Askew (1961c) also stated that "A gall's form, time of growth and position on the tree determine its liability to be attacked by a given species of *Mesopolobus*". Joseph (1958) observed that olfactory sense perceived by the antennae of *Philotrypesis caricae* was responsible for the preliminary selection of a suitable spot for oviposition across the fig into a fig ovary in which *Blastophaga psenes* had already oviposited. According to the same author, the chemoreceptor sensillae of the ovipositor of *P. caricae* probably helped it to detect the secretion of the agaonid *B. psenes* inside the *Ficus* ovary. In other chalcids which are not associated with plant galls, there are several reports showing that the primary selection of the host is made by the antennae and the final suitability or acceptance of the host is tested by the ovipositor.

3. Conclusion

From the above review the following conclusions can be postulated: Among the 16 families of Chalcidoidea, about 11 are associated with plant galls. Phytophagy in Chalcidoidea evolved completely independently in several families. The chalcids fly randomly in the beginning in their search for galls and during this random search if they come within a particular distance from the gall (this distance varies from species to species), they find their particular gall either by visual sense or by olfactory sense or by both visual and olfactory senses. The primary selection of the gall is made by the antennae and the final acceptance or suitability of the host is tested by ovipositor.

Acknowledgements

The author is very grateful to Dr R R Askew of University of Manchester for permission to quote from his papers and reproduce a figure from one of his papers. He is also grateful to Dr J T Wiebes of Rijksuniversiteit, Leiden and to Dr Karl V Krombein of Smithsonian Institution for similar courtesies.

References

Abdurahiman U C and Joseph K J 1978 Cleptoparasitism of the fig wasps (Torymidae: Chalcidoidea) in *Ficus hispida* L.; *Entomon* **3** 181–186

Askew R R 1961a On the Palaertic species of *Syntomaspis* Forster (Hym. Chalcidoidea, Torymidae); *Entomol. Mon. Mag.* **6** 184–191

Askew R R 1961b On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain; *Trans. Soc. Br. Entomol.* **14** 237–268

Askew R R 1961c A study of the biology of species of the genus *Mesopolobus* Westwood (Hymenoptera: Pteromalidae) associated with Cynipid galls on oak; *Trans. R. Entomol. Soc. Lond.* **113** 155–173

Askew, R R 1965 The biology of the British species of the genus *Torymus* Dalman (Hymenoptera: Torymidae) associated with galls of Cynipidae (Hymenoptera) on oak, with special reference to alternation of forms; *Trans. Soc. Br. Entomol.* **16** 217–232

Bhagat R C 1982 Aphid galls and their parasitoids from Kashmir, India; *Entomon* **7** 103–105

Blair K G 1944 A note on the economy of the rose bedeguar gall, *Rhodites rosae* L.; *Proc. S. Lond. Entomol. Nat. Hist. Soc.* 1943–1944 55–59

Blair K G 1946 On the economy of the oak marble gall (*Cynips kollari*, Hartig); *Proc. S. Lond. Entomol. Nat. Hist. Soc.* 1945–1946 79–83

Boucek Z 1964 In *Keys to the chalcidoidea of Czechoslovakia (Insecta: Hymenoptera)* (eds); O Peck, Z Boucek, A Hoffer *Mem. Entomol. Soc. Canada* **34** 1–120

Boucek Z 1982 Description of a new *Hockeria* (Hymenoptera: Chalcididae), a parasite of a lepidopterous gall-causer on *Tamarix Israel J. Ent.* **16** 49–51

Burks, B D 1979 In *Catalog of Hymenoptera in America North of Mexico, Symphyta and Apocrita* (eds) K V Krombein *et al.* (Washington D C: Smithsonian Institution Press) 1198 pp.

Chernoponevkina S M 1949 *Pests of sainfoin seeds and methods for their control* (in Russian); *Sobornik rabot Kurskoi oblastnoi sel'skokhozyaistvennoi opytnoi stantsii* 112–125

Clausen C P 1940 *Entomophagous insects* (New York: Hafner Publishing Co.) 661 pp

Edwards R L 1954 The host-finding and oviposition behaviour of *Mormoniella vitripennis* (Walker) (Hym., Pteromalidae), a parasite of muscoid flies; *Behaviour* **7** 88–112

Edwards R L 1955 How the hymenopteran parasite *Mormoniella vitripennis* (Walker) finds its host; *Br. J. Anim. Behav.* **3** 37–38

Fisher R C 1971 Aspects of physiology of endoparasitic Hymenoptera; *Biol. Rev.* **46** 243–278

Gahan A B and Ferriere Ch 1947 Notes on some gall inhabiting chalcidoidea (Hymenoptera); *Ann. Entomol. Soc. Am.* **11** 271–302

Galil J and Copland J W 1981 *Odontofoggatia galili* Wiebes in Israel, a primary fig wasp of *Ficus microcarpa* L. with unique ovipositor mechanism (Epichrysomalinae, Chalcidoidea); *Proc. Kon. Ned. Akad. Wetensch* **84** 183–195

Gordh G 1979 In *Catalog of hymenoptera in America north of Mexico, Symphyta and Apocrita,* (eds) K V Krombein *et al* (Washington, D C: Smithsonian Institution Press) 1198 pp

Grissel E E 1976 A revision of the western nearctic species of *Torymus* Dalman (Hymenoptera: Torymidae); *Univ. Calif. Pub. Entomol.* **79** 1–120

Ishii T 1931 Notes on phytophagous habits of some chalcidoids with descriptions of two new species; *Kontyu* **5** 132–138

Joseph K J 1953 Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India IV. Descriptions of three new and records of four known species of Agaonini; *Agra Univ. J. Res.* **2** 267–284

Joseph K J 1954 Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India, VI. On six species of Agaoninae; *Agra Univ. J. Res.* **2** 401–416

Joseph K J 1957 Le parasitisme de *Philotrypesis* caricae L. (Hym. Chalcidi Callimomidae) et l'influence de la vie parasitatire sur le parasite; *C.V. Acad. Sci. Paris* **244** 1269–1272

Joseph K J 1958 Rescherches sur les Chalcidiens *Blastophaga psenes* (L) et *Philotrypesis caricae* (L.) du figuier *Ficus carica* (L.); *Ann. Des. Sci. Nat. Zool.* **20** 197–260

Joseph K J 1959 The biology of *Philotrypesis caricae* (L.), parasite of *Blastophaga psenes* (L.); *Proc. XV. Int. Cong. Zool.* 662–664

Laing J 1937 Host-finding by insect parasites I. Observations on the finding of hosts by *Alysia manducator, Mormoniella vitripennis* and *Trichogramma evanescence*; *J. Anim. Ecol.* **6** 298–317

Milliron H E 1949 (Taxonomic and biological investigations in the genus *Megastigmus; Am. Midl. Nat.* **41** 257–420

Narendran T C 1975 *Studies on biology, morphology and host-parasite relationships of Brachymeria lasus (Walker) (Hymenoptera: Chalcididae)*, Ph.D thesis, Calicut University

Narendran T C 1983 On the chalcids and sawflies associated with plant galls; In *The biology of gall insects.* (eds) T N Ananthakrishnan and A Raman (New Delhi: Oxford and IBH) (in press)

Nikol'skaya M N 1952 *The chalcid fauna of USSR (Chalcidoidea)*, translated from Russian by A Birron and Z S Cole in 1963 for the National Science Foundation, Washington, D C and the Smithsonian Institution by the Israel program for scientific translations 593 pp

Noyes J S 1978 On the numbers of genera and species of Chalcidoidea (Hymenoptera) in the world; *Entomol. Gaz.* **29** 163–164

Noyes J S 1982 Collecting and preserving chalcidoid wasps (Hymenoptera: Chalcidoidea); *J. Nat. Hist.* **16** 315–334

Peck O 1963 A catalogue of the neactic Chalcidoidea (Insecta: Hymenoptera) *Can. Entomol. Suppl. Ottawa* 1092 pp

Philips W J 1927 *Eurytoma parva* (Girault) Philips and its biology as a parasite of wheat jointworm *Harmolita tritici* (Fitch); *J. Agric. Res. Washington* **34** 743–758

Prinsloo G L 1980 An illustrated guide to the families of African Chalcidoidea (Insecta: Hymenoptera); *Sci. Bull. Dep. Agric. Fish. Repub. S. Afr* 1–48

Puzanova-Malysheva E V 1930 The biology of *Eurytoma amygdali* End., a pulum pest; *Entomol. Obozrenie* **24** 166–178 (in Russian)

Rinskii-Korsakov M N 1914 Isosomes harmful to cereals (in Russian); *Trudy Byuro Entomologii* **10** 1–84

Schneider F 1939 Ein Vergleich von Urwald und Monokultur in bezug auf ihre Gefahrdung durch phytophage Insecten, auf Grund einiger Beobachtungen an der Ostkuste von Sumatra; *Schweiz. Z. Forstwes.* **90** 41–55

Schneider F 1940 Schadineseketen und ihre Bekampfung in ostindischen Gambirkulturen; *Mitt. Schweiz. Entomol. Ges.* **18** 150–161

Smith E L 1970 Biosystematics and morphology of symphyta. II. Biology of gall-making nematine sawflies in the California region; *Ann. Entomol. Soc. Wash.* **63** 36–51

Subba Rao B R 1976 *Narayana* gen. nov from Burma and some synonyms (Hymenoptera: Mymaridae); *Orient. Insects* **10** 87–91

Ullyett G E 1936 Host selection by *Microplectron fuscipennis* Zett. (Hymenoptera: Chalcididae); *Proc. R. Soc. London* **120** 253–291

Varley G C 1941 On the search for hosts and the egg distribution of some chalcid parasite of the knapweed gall-fly; *Parasitology* **33** 47–66

Wanberg J K 1977 A new *Tetrastichus* parasitising Tephritid gall-formers on *Chrysothamnus* in Idaho; *The Pan-Pacific Entomol.* **53** 237–240

Wiebes J T 1964 Host specificity of fig wasps (Hymenoptera: Chalcidoidea: Agaonidae); *Proc. XII Int. Congr. Entomol. London* 1964–1965, Systematic Section, **1** 95–96

Wiebes J T 1979 Co-evolution of figs and their insect pollinators; *Ann. Rev. Ecol. Syst.* **10** 1–12

Wiebes J T 1982a The phylogeny of the Agaonidae (Hymenoptera: Chalcidoidea); *Neth. J. Zool.* **32** 395–411

Wiebes J T 1982b Fig wasps (Hymenoptera); *Monographiae Biologicae* (The Hague: Dr W Junk Publishers) **42** 735–755