circlet of stiff hairs around the anus that serves to hold the honeydew droplet while it is being imbibed by the ant. Wilson also notes the fact that as ants do not usually attack and eat their homopteran associates this is evidence in itself that behavioural evolution has occured which accomodates them to the mutualism. The mode of soliciting honeydew is essentially the same as that used to initiate regurgitation within the colony, but as Wilson says, the fact that it is directed at such alien arthropods seems to indicate the existence of a second major behavioural adaptation on the part of the ants. It has also been established that workers of at least some species carry their homopteran guests to the appropriate part of the foodplant, and at the correct stage of the trophobionts development. Wilson also notes that it is only members of the three phylogenetically most advanced ant subfamilies, the Myrmicinae, Dolichoderinae and the Formicinae, that attend Homopterans.

All the above points mentioned by Wilson equally apply to the ant/lycaenid association. Where the homopterans have developed mechanisms to hold the honeydew droplet while it is being imbibed by the ants, the lycaenid larvae have developed glands to produce large quantities of secretion. The ants also do not usually attack and eat their lycaenid associates and their mode of soliciting honeydew is also essentially the same as that used to initiate regurgitation within the colony. The ant workers also carry the lycaenid larvae to the appropriate parts of the foodplant at the correct stage of the trophobionts development. In addition these lycaenid larvae are also only associated with members of the three phylogenetically most advanced ant subfamilies, mainly the Formicidae and the Myrmicinae and to a lesser extent the Dolichoderinae.

Wilson (1971) says with trophobiosis as the origin of the association between species, the other forms of symbiosis which are more subtle and involve a closer co-adaptation of species concerned, could have evolved.

It should be pointed out that most of the adaptations shown by the lycaenids are also widespread in other myrmecophilous insects. The pheromone trail following of *A. dentatis* larvae can be found in several other insect orders and families, including Thysanura, Diplopoda, Staphylinidae, Histeridae, Phoridae and Limulodidae. The honey-gland of the lycaenids probably has its equivalent in the appeasement gland of some staphylinid beetles (see p. 111). Even the production of the volatile secretion that mimics the brood pheromone of the host ant has

evolved elsewhere. Hölldobler (1967) discovered that a substance identified by worker ants with their own brood can be separated from the bodies of the staphylinid beetle *Atemeles* (see p. 18).

The possible alarm pheromone mimic produced by the tubercles of *A. dentatus* is also an adaptation of other myrmecophiles. Blum (1969) reported that an inquilinous Japanese species of the staphylinid genus *Zyras* produced a scent that resembled citronellal, one of the alarm pheromones of its ant host *Lasius spathepis*. The *Zyras* substance induced a strong alarm response in the worker ants (see p. 18).

Even the transport of the newly hatched *P. lycegones* larvae to their foodplant by the host ant is not unusual. The eggs of the aphid, *Aphis maidiradius*, are kept by colonies of their ant host *Lasius neoniger* in their nest throughout the winter, and the following spring the newly hatched nymphs are transported to the nearby foodplants by the workers (Forbes, 1906).

The soliciting of regurgitations by certain lycaenid larvae from their ant hosts is also common practice among other myrmecophilous insects. The capacity to induce regurgitation in ants is possessed by the lomechusine staphylinid beetles *Atemeles*, *Lomechusa* and *Xenodusa*, by other beetles belonging to *Amphotis* and *Claviger*, by several species of the mite genus *Antennophorus* and even by adult mosquitoes (*Harpagomyia*) and phorid flies (*Metopina*) (Wilson, 1971).

From this it appears that all insects having a myrmecophilous existence have independently evolved a similar set of adaptations to that mode of life. Most of these adaptations appear to be involved in the insect insinuating itself into the communication system of the ants. It would appear, therefore, that the majority of the adaptations shown by the Lycaenidae to a myrmecophilous existence are general ones shared by all myrmecophiles.

Besides the above adaptations shared by all myrmecophiles, the Lycaenidae have also evolved a soft, but tough, cuticle of unusually thick dimensions and a lack of beating reflex, as an adaptation to the mandible construction and aggressive behaviour of the ants (see p. 36). I think all this makes the ant/lycaenid association one of the most remarkable examples of co-adaptation to be found in the animal kingdom.

Having now established the importance of chemical communication in some ant/lycaenid associations the actual chemical components of the

pheromones should be identified. This could be achieved by running the volatile secretions through a gas chromatograph-mass spectrometer combination thus obtaining the mass spectra of each component. The mass spectra so obtained could be compared with the spectra of known chemical substances. Having identified the components and calculated the quantities of each, behavioural experiments could be carried out with the pure chemicals to determine which are most important in releasing different behaviour patterns.

Further associations could be investigated as above, particularly those involving ants and obligate carnivorous lycaenids, e.g. *Theclor dicksoni*, and those feeding on lichens, so that a better understanding could be obtained of the adaptations of the Lycaenidae to the ants.

6. SUMMARY

A study was made of the histology of the glands and organs of seven lycaenid species, *Leptomyrina henningi* (Dickson) (Theclinae), *Spindasis phanes* (Trimen), *Poecilmitis lycegenes* (Trimen), *Aloeides dentatis* (Swierstra) (Aphaeinae) and *Euchrysops dolorosa* (Trimen), *Lepidochrysops ignota* (Trimen), *Anthene definita* Butler (Lampidinae). The glands and organs were discussed in the context of what had been reported in the literature. The honey-gland and perforated cupolas appear to be derived from setae, both consisting of two cells, the tormogen cell forming the duct and the trichogen cell the secreting unit. There are two types of tubercle, the more developed one curving over the honey-gland and offering mechanical protection and in some species having a communicatory function. The function of the less well developed tubercle is unknown and appears to be undergoing reduction in some species.

The life histories of a number of species of lycaenid were studied and it appears that they fall into three distinct biological groups. The larvae of the first group are entirely phytophagous and feed on lichens (Thallophyta), are protected by long hairs, have no tubercles or honey-glands and are not dependent on ants. The larvae of the second group are mainly carnivorous feeding on Homoptera and the brood of ants, or on the regurgitations and excretions of both. They do not possess either honey-glands or tubercles, but the perforated cupolas of certain species appear to produce a volatile secretion which induces their host ants to carry them into their nests. Some species are dependent on ants.

The third group are mainly phytophagous feeding on Angiosperms (Embryophyta) and they all appear to have at one stage possessed both honey-gland and tubercles, although both or either may now be lost. Certain species have become carnivorous or partly carnivorous and a number have become dependent on ants.

Larvae from this third group with different behavioural and feeding habits were investigated to determine whether their associations with ants were mediated by chemical signals. Two associations in which the larvae are dependent on ants were chosen; these were *Aloeides dentatis* (Swierstra), dependent on *Acantholepis capensis* Mayr and *Lepidochrysops ignota* (Trimen), dependent on *Camponotus niveosetosus* Mayr. The third lycaenid species studied, *Euchrysops dolorosa* (Trimen), was not dependent

on ants, but the volatile chemicals extracted from it were compared with those of ants known to tend Lycaenidae.

The behaviour of these lycaenid larvae and that of the ants was observed in the field and in the formicarium. Extracts were made of the lycaenid larvae and the ants. Corn cob grits were soaked in the various extracts and the behaviour of the ants towards the grits was recorded.

Gas chromatographic analysis was also performed on the extracts from the lycaenid larvae and from the ants and the chromatograms produced were compared. It was found that in the two dependent lycaenid species investigated the chromatogram of the volatile secretion resembled that of the brood extract chromatogram of their host ant most closely. In addition the tubercles of *A. dentatis* appeared to produce a second volatile chemical which gave a gas chromatographic pattern very similar to the chromatogram of the alarm pheromone of its host ant *A. capensis*. The chromatogram of the non dependent *E. dolorosa* larvae was found to resemble that of the brood extracts of the two species of *Camponotus* ant with which it was compared, but not with that of the ant *Acantholepis capensis*.

From the gas chromatograms, the behavioural responses of the ants towards the extracts on the grits and the lycaenid larvae themselves, it would appear that certain lycaenid larvae produce a volatile secretion which apparently mimics the brood pheromone produced by ant larvae. The most likely origin of this secretion are the perforated cupolas as they are the only glands common to all areas under study. In addition, it appears that *A. dentatis* produces a second volatile secretion that apparently mimics the alarm pheromone of its host ant *A. capensis*.

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Appendix I

Early stages of *Aloeides dentatis* (Swierstra)

(a) Egg

Laid in pairs on the under surface of the leaves of the foodplant. The eggs take from 13-22 days to hatch. The eggs are 0.8mm in diameter and are deeply 'bun-shaped' in form. The surface is boldly patterned. The colour is at first creamy-white, becoming purplish-brown as development proceeds.

(b) Larvae

All the instars are rather similar in appearance. The head is dark brown with light coloured setae. The broad neck-shield and small rounded anal shield are dark brown to black in colour. The body is grey with longitudinal streaks or series of broken markings of a reddish-brown or vinous colour. The tubercle casings on the eighth segment are black and bear the characteristic protective spines. The retractile tubercles are white and are clearly visible, even to the naked eye. The honey-gland on the seventh segment is absent in this species.

1st instar. On emergence it is 1.75mm in length, growing to 3.25mm in 14-21 days. The larva eats only the surface of the leaf, leaving patches of furrows.

2nd instar. It grows to 6mm in 20-28 days and also feeds only on the surface of the leaf.

3rd instar. It grows to 7.5mm in 22-28 days and starts feeding on the edges of the leaves.

4th instar. It grows to 10-10.5mm in 22-30 days and feeds on the edges of the leaves.

5th instar. It grows to approximately 13.5mm. Duration of the instar variable and can be over 200 days if diapause takes place during the winter months.

6th instar. It grows to 18-14mm in length. During the summer months the duration of the instar is from 40-44 days, but is much longer during winter if diapause takes place.

(c) Pupa

The pupae are 12.5-13.5mm in length and are golden-brown in colour. They are fairly thick in proportion to their length, rounded anteriorly, and terminate obtusely. The pupal stage lasts from 16-22 days.

Appendix II

RETENTION TIMES AND AREAS UNDER PEAKS AS GIVEN BY THE AUTOLAB MINIGRATOR WITH RELATIVE RETENTION TIMES AND PERCENTAGE OF EACH CHEMICAL

1. *Acantholepis capensis* Mayr

A. Head extract

Retention Time	Relative Retention Time	Area	%
954'	0.558		
1140	0.668	23576	4.8
1208	0.707	11807	2.4
1275	0.748	24145	4.9
1520	0.892	99432	20.2
1640	0.960	22006	4.5
1708	1.000	10719	2.2
1810	1.060	84576	17.2
1900	1.113	49967	10.2
1997	1.170	60789	12.4
2055	1.203	30788	6.3
2110	1.241	16030	3.2
2245	1.315	57537	11.7
		491372	100.0

' = Present in 2 of the 7 chromatograms

B. Abdominal extract

Retention Time	Relative Retention Time	Area
523	0.307	191694
723	0.424	127566
823	0.482	505875
930	0.545	249559
969	0.567	36978
1123	0.660	76957
1183	0.694	535557
1277	0.748	23721
1357	0.795	192322
1385	0.813	112425
1437	0.843	227848
1456	0.855	173124
1511	0.887	340035
1584	0.930	360992
1627	0.955	408679
1656	0.972	302957
1707	1.000	216566
1745	1.022	284195
1795	1.052	495003
1827	1.070	626378
1885	1.105	284263
1946	1.140	123111
1990	1.168	1781115
2051	1.204	288180
2111	1.243	173442
2161	1.268	1290944
2237	1.310	14538
2336	1.370	40204
2553	1.500	1622537

C. Brood extract

Retention Time	Relative Retention Time	area	%
652	0.386	147773	7.4
946	0.560	148312	7.5
1130	0.670	25889	1.3
1200	0.710	23653	1.2
1267	0.750	134405	7.0
1446	0.856	104235	5.2
1508	0.893	138182	7.0
1616	0.958	66223	3.3
1690	1.000	156038	7.8
1732	1.025	134215	6.7
1792	1.060	155958	7.8
1873	1.108	156022	7.8
1985	1.175	242025	12.1
2046	1.210	87147	4.4
2105	1.248	268265	13.5
		1988342	100.0

2. *Aloeides dentatis* (Swierstra)

A. Thoracic extract

Retention Time	Relative Retention Time	Area	%
649	0.381	226098	10.1
948	0.555	376345	17.0
1129	0.665	31281	1.4
1200	0.705	99491	4.5
1268	0.743	86312	3.9
1516	0.888	108303	4.9
1706	1.000	110548	5.0
1801	1.058	137501	6.2
1896	1.100	268060	12.0
1991	1.168	[illegible]	10.0
2046	1.200	[illegible]	12.2
2110	1.243	[illegible]	5.8
2162	1.268	[illegible]	7.0
		2219653	100.0

B. Tubercles and surrounding area

Retention Time	Relative Retention Time	Area	%
645'	0.383		
945'	0.5[illegible]5		
1145	0.6[illegible]	86235	0.9
1210	0.709	96121	1.0
1275	0.750	188012	2.0
1462	0.859	384260	4.0
1525	0.895	373854	3.9
1590	0.933	264414	2.8
1640	0.962	325534	3.4
1705	1.000	360261	3.8
1750	1.025	710659	7.4
1812	1.062	1364735	14.4
1901	1.113	833065	8.7
2004	1.17[illegible]	933291	9.7
2049	1.200	1158289	12.1
2110	1.243	1352600	14.1
2240	1.312	1134578	11.8
		9565908	100.0

' = Present in only 2 of the 10 chromatograms

Appendix III

Early Stages of *Lepidochrysops ignota* (Trimen)

(a) Egg

Laid singly on the buds and flowers of the foodplant. The eggs are pale greenish-white in colour. They are 0.6mm in diameter by 0.3mm in height. The micropyle is slightly concave, from which radiate a network of raised ribs. The eggs take from 4-6 days to hatch.

(b) Larvae

1st instar. On eclosion it is 0.9mm in length, growing to about 1.7mm in 4 days. The head is brown and the body whitish, covered with translucent setae. The prothoracic and suranal plates are greyish-brown. Both honey-gland and tubercles are absent. The caterpillars usually feed by boring in to the calyx of the flowers and feed on the young seeds (achenes).

2nd instar. It grows to 2.5mm in 4 days. The head is brown and the body is yellowish-white. The honey-gland is present but the tubercles are absent. The caterpillar feeds in a manner similar to the first instar. There are 4 achenes in each calyx and they appear to be able to supply sufficient food both to the first and second instars. Neither instar leaves the protection of the calyx.

3rd instar. It grows to about 3.5mm in length. The head is brown and the body yellowish-white. The honey-gland is present and functional but the tubercles are absent. Soon after the second moult the larva will leave the calyx, where it has spent its first two instars, and venture on to the surface of the plant. If not immediately discovered by the host ant, the larva will actually wander off its foodplant. The larva is eventually discovered by the host ant and carried into the ants' nest, where it will spend the remainder of its life cycle. The larvae feed on ant pupae and occasionally larvae. The duration of the instar was not recorded as all the larvae had died or had been used for experiments before the moult into the final instar.

4th instar. Not recorded.

(c) Pupa

The pupa was not recorded.

Appendix IV

RETENTION TIMES AND AREAS UNDER PEAKS AS GIVEN BY THE AUTOLAB MINIGRATOR WITH RELATIVE RETENTION TIMES AND THE PERCENTAGE OF EACH CHEMICAL

1. *Camponotus niveosetosus* Mayr

A. Head extract

Retention Time	Relative Retention Time	Area	%
697	0.416	32035	2.8
830	0.496	64169	5.6
921	0.550	55083	4.8
991	0.592	50152	4.3
1122	0.670	99287	8.6
1194	0.712	54321	4.7
1466	0.875	29768	2.6
1500	0.895	47328	4.1
1520	0.908	275924	23.9
1675	1.000	445350	38.6
		1153417	100.0

B. Abdominal extract

Retention Time	Relative Retention Time	Area
445	0.269	7657316
557	0.338	118478
607	0.374	237002
687	0.417	157517
795	0.481	71780
913	0.553	188379
1115	0.675	204368
1313	0.796	444060
1462	0.880	812827
1509	0.913	188101
1651	1.000	252907
1774	1.074	569015
1812	1.098	594159
1927	1.165	2718728
1965	1.189	3135222

C. Brood extract

Retention Time	Relative Retention Time	Area	%
1186	0.706	18746	1.6
1498	0.891	86668	7.5
1526	0.908	77989	6.7
1690	1.000	193571	16.8
1796	1.069	550471	47.8
1832	1.090	226420	19.6
		1153865	100.0

2. *Lepidochrysops ignota* (Trimen)

A. Thoracic area

Retention Time	Relative Retention Time	Area	%
814	0.494	15470	1.5
1108	0.672	18840	1.7
1176	0.714	13404	1.2
1456	0.882	45618	4.1
1508	0.914	69211	6.2
1650	1.000	247991	22.3
1774	1.075	516810	46.7
1814	1.098	180930	16.3
		1108274	100.0

B. Honey-gland and surrounding area

Retention Time	Relative Retention Time	Area	%
814	0.492	13200	1.4
1110	0.673	14670	1.6
1176	0.713	12800	1.4
1458	0.881	48818	5.3
1507	0.913	81559	8.9
1654	1.000	157704	17.2
1776	1.072	587939	64.2
		916690	100.0

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