"STUDIES ON SPECIES OF ASTERODIASPIS (COCCOIDEA: COCCIDAE) ON OAK IN BRITAIN".

Thesis submitted for the degree of Doctor of Philosophy of the University of London.

by

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ABSTRACT

The main interest of this work is the unusual occurence together on oak (Quercus spp) of three closely related species, of Asterodiaspis. The sympatric species are variolosum, quercicola and minus.

The validity of the species as good species was established on the basis of morphological studies on the first instar nymphs, the adult females and the second instar nymphs. The last-named were also described for the first time.

The relationships of the three species were also investigated through biological studies - population studies in the field, the reproductive performance of the adult females, and the behaviour of the first instar nymphs under experimental conditions.

From the results of the above studies it is concluded that A.variolosum, A.quercicola and A.minus are good morphological species showing a more or less consistent spectrum of similarities and differences; A.variolosum occupies the upper end, A.minus the lower, and A.quercicola is in an intermediate position.

The apparent sympathy of the three distinct species is not quite complete, and the balance between the species in their habitat is maintained by unequal pressures of biological factors, e.g. squirrels.

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PAGES

PAGES

GENERAL INTRODUCTION AND TAXONOMY

There are a number of references in British records to the occurence of Asterodiaspis (Signoret) on oak in various parts of Britain, for example, Douglas (1885,1886), Newstead (1885,1900, 1925), but all these workers considered that they were dealing with one species which they recorded under the names of Asterodiaspis quercicola or Asterolecanium variolosum which were regarded as synonyms. The generic names Asterodiaspis (Signoret)(1876) and Asterolecanium (Targioni - Tozzetti 1869) were similarly considered to be synonymous.

The work of Russell (1941) helped to lay the foundation of the present classification of the Asterolecaniidae. Her conception and composition of the genus Asterolecanium was accepted by Ferris (1955), but Borchsenius (1950) used it as a starting point for his classification of the Asterolecaniidae. Russell's work did much to clarify the status of the species described from Europe (including Britain) and from other parts of the world. Dr. Boratynski (1961) found that three closely related species of Asterodiaspis - minus (Lindinger), quercicola (Bouché) variolosum (Ratzeburg) occur on oak trees in Britain in mixed populations, and that the three species may occur together not only on the same oak tree, but even on a single twig.

On the basis of his morphological studies and general biological observations Boratynski (l.c.) concluded that, "until more information to the contrary is available and for

convenience, they are best treated as distinct morphological species" (p.5); thus he posed an interesting problem - that of closely related sympatric species, a rare biological occurence.

SCOPE OF THE WORK

The present study is aimed at extending the work of Dr. Boratynski (1961) by:

i) further comparative morphological studies on the first instar nymphs and the adults of the three species, and to describe the so far undescribed intermediate stages (second instar nymphs),

ii) to supplement the morphological studies by investigation of possible biological differences. These studies included

a) breeding experiments of isolated specimens of each species

b) detailed studies on the biology of each species, including life cycles, reproductive capacity, mortality, behaviour.

c) studies on the distribution of the species in the field and on individual hosts, and the composition of the populations on the latter.

iii) to discuss and explain the relationships of the species to one another in the light of (i) and (ii) above.

TAXONOMIC POSITION

The Family ASTEROLECANIIDAE (Position within the Coccoidea)

The scale insects (Coccoidea) have been known in many parts of the world for a long time because of the economic usefulness of some of them to man, for example, shellac used in varnishes, and the "scarlet grain" once widely used in Europe and Asia as a dye for silk and linen. According to Ferris (1957) they had no scientific name until the time of Linnaeus, though the name Coccus for the type of genus derives from pre-Linnaen literature. These insects were considered to be grains of plant origin or even galls, but not insects.

Breynius's work "Historia Naturalis Cocci Radicum Tinctorii" in 1731 was one of the earliest systematic papers on the biology of one of the scale insects, the Polish cochineal (Porphyrophora polonica L.) in which its insect nature was demonstrated; these revelational findings were at first disbelieved.

In 1758 Linnaeus (Systema Naturae) named the genus Coccus with 17 species. In the 19th century Targioni - Tozzetti in "Studii sulle Cocciniglie" (1867) and particularly Signoret in his work "Essai sur les Cochinilles" (1868 - 1877) laid the foundation of the classification of the coccids. While Targioni - Tozzetti listed 28 genera Signoret listed 331 species which he

distributed in 61 genera. Signoret proposed a system of classification which divided the Coccoidea into four sections - Diaspites, Lecanites, Coccites, Brachyscelites; the Lecanites included the Asterolecaniidae of today. This classification influenced workers like Douglas (1881-1894), Newstead (1889-1922), Green (1886-1924) in England, Comstock (1881-1916) and Cockerell (1891-1946) in the U.S.A. and Maskell (1879-1898) in New Zealand.

In 1903 M.E. Fernald produced "A Catalogue of the Scale Insects of the World" in which she listed the family COCCIDAE dividing it into 8 sub-families (Monophlebinae, Margarodinae, Ortheziinae, Dactylopinae, Tachardiinae, Conchaspinae, Coccinae, Diaspinae) with 1541 species in all. The sub-family Dactylopinae contained the genus Asterolecanium with 30 species including A.quercicola and A.variolosum.

In 1942 Balachowsky ("Essai sur la Classification des Cochenilles") accepted the coccids as a super-family Coccoidea which he divided into 3 phyla, thereby recognising broad affinities between certain families.

Ferris (1957a) recognised that Balachowsky's classification was more in accord with the findings of modern times, but believed that, "until the males have been studied thoroughly for all these groups any such arrangement as that proposed by Balachowsky cannot be but a temporary suggestion". Later Ferris (1957b) proposed his own general classification which, although in general agreement with that of Balachowsky, differed

from it on several important points. First of all Ferris substituted "ramus" for Balachowsky's "phylum" to avoid the confusion due to the use of the latter term in general biological nomenclature. He accepted the two rami, Diaspidi and Margarodi as clearly separated from the other Coccoidea, but considered the third one Lecanoidea unacceptable; it was too reminiscent of the sub-family Dactylopinae of the Fernald Catalogue (1903) where it acted as a "catch-all" for anything not known fully and Ferris divided it into 3 rami; he also added another ramus Besonii containing forms described since the publication of Balachowsky's classification.

During the 15 years between the dates of publication of Balachowsky's and Ferris's classifications, a considerable progress in coccid studies was made, and Ferris's classification appears to be more satisfactory.

The Asterolecaniinae of today were early recognised as a separate group (Asterolecanites - Targioni - Tozzetti, 1868, Signoret 1868; Lecanodiaspidae - Maskell 1879-97; Asterolecaniinae - Cockerell, 1896) and, with a few exceptions, were considered to be most closely related to the Lecaniinae (Coccidae). The exceptions were: Comstock (1881) described them together with Diaspidinae, Green (1896) included them into the Coccinae (Dactylopidae today) but later (1909) recognised as a distinct group Asterolecaniinae, and Fernald (1903) who considered them as belonging to the tribe Dactylopini of the sub-family

Dactylopinae.

Relationship of Asterolecaniidae to other families

Russell (1941) stated that within the Coccoidea the family Asterolecaniidae was more closely related to the Coccidae and the Dactylopidae than to others - "This affinity is envinced by the presence, in some representatives of Asterolecaniinae of loculate pores associated with the spiracles, by the presence of spiracular setae and modified anal plates, and by the outline of the posterior margin of the body, which may be cleft or strongly lobed. All these characters are found in the families Coccidae and Dactylopiidae".

Balachowsky (1942) said that the Asterolecaniidae were most related to the Lecaniidae (=Coccidae) and to the Eriococcidae the latter family being closely related to Dactylopiidae. Ferris (1957) put the Asterolecaniidae and the Coccidae (=Lecaniidae) together in his ramus Cocci, and created a separate ramus Eriococci which contairs both the Eriococcidae and the Dactylopiidae.

The important conclusion however is that all the three authors discussed above agree on the close relationship of Asterolecaniidae and Coccidae.

Characteristics of Asterolecaniidae

Balachowsky (1942) said that the family Asterolecaniidae was characterized by the presence of 8-shaped pores in the females at all stages.

Ferris (1955) gave a definition of the family Asterolecaniidae, with the most important points as follows:

"Germinate 8-shaped pores always present in at least the larva. Tubular ducts formed of a tube which has its inner end somewhat enlarged and reflexed into a cup or having its extremity bent and slightly prolonged. Legs lacking in the adult female of all known species except for vestiges in the form of small tubercles. Antennae for the most part mere tubercles including one, or at the most two, segments; body destitute of any but very small, slender setae except rarely with a single seta marking the point at which a series of pores extending from a spiracle attains the margin of the body. Anal ring variously developed, at its best development sclerotic and showing a few pores, at the most with 8 setae, sometimes undeveloped."

In addition, the following negative characters were given: "Coccoidae without abdominal spiracles; without brachial plates; without cerarii, dorsal ostioles, or ventral circuli; without an operculum formed of two plates overlying the anal opening; the terminal segments of the abdomen never fused into a pygidium."

Composition of the Asterolecaniidae

Russell (1941) recognised Asterolecaniinae as one sub-family of Asterolecaniidae which included 12 genera.

She divided the large genus Asterolecanium into 12 groups based primarily on the morphology of adult females and sometimes, coincidentally on geographical and ecological bases.

Balachowsky (1942) recognised two sub-families in Asterolecaniidae:

1) Asterolecaniinae with the genera Asterolecanium Targ., Lecaniodiaspis Targ., Pollinia Targ., etc.

2) Cerococcinae with the genus Cerococcus Comst.

Ferris (1955) mentioned that only about 10 genera were known under Asterolecaniidae, of which six - Mycetococcus, Mycococcus, Cerococcus, Pollinia, Lecanodiaspis and Asterolecanium, were listed by him as occuring in North America.

Borchsenius (1960) produced a classification in which in agreement with Balachowsky the family Asterolecaniidae was divided into 2 sub-families: Cerococcinae and Asterolecaniinae.

The main interest of Borchsenius's classification is that the large genus Asterolecanium in the classification by Russell (1941) has been broken down and some of Russell's groups in this genus mainly correspond to some newly erected genera; for example the group III in the classification of Russell (l.c.) corresponds to the genus Asterodiaspis in the classification of Borchsenius.

Since Asterolecanium as defined by Russell is such a large genus, the groups deliniated by her seem distinct enough to merit generic status as proposed by Borchsenius.

~~Borchsenius agrees with Balachowsky (1942) by recognising 2 sub-families (Cerococcinae and Asterolecaniinae) in the family Asterolecaniidae.~~

Definition of the sub-family Asterolecaniinae

Russell (1941) defined the sub-family as being characterised by the presence, in the adult female, of comparatively sessile 8-shaped pores and asymmetrical tubular ducts. There are, in some members of the sub-family, loculate pores associated with the spiracles, spiracular setae present; the posterior margin of the body may be cleft or strongly lobed.

The second sub-family - the Cerococcinae - differs by having a sclerotized anal plate (Cerococcini) or if this is absent the tubular ducts are also absent (Pollinіini)(Borchsenius 1960).

Asterolecanium and related genera (authority, type Species and synonymy)

The following generic names have been used by various authors but were considered by Russell (1941) as synonyms:

1) Asterolecanium Targioni - Tozzetti (1869,1892); Signoret (1870), Cockerell (1896, 1899), Russell (1941), Ferris (1957), Borchsenius (1960).
2) Planchonia Signoret (1870), Maskell (1881,1887,1895), Borchsenius (1960).
3) Asterodiaspis Signoret (1876), Comstock (1880,1881), Borchsenius (1960).
4) Bambusaspis Cockerell (1902), Sanders (1906), Borchsenius (1960).

The genus Asterolecanium was established by Targioni - Tozzetti in 1869 with Coccus aureus, Bois (=synonym Lecanium

epidendri Bonche) as the type species. It was restricted by Borchsenius (1960) to include only species of Russell's group X of this genus.

In 1876 Signoret proposed the generic name Planchonia with Coccus fimbriatus Foscolombe as the type species. Planchonia had however for long been considered by many authors to be a synonym of Asterolecanium. (It has been resurrected by Borchsenius (1960) for the species of group IV of Russell's broad classification of the genus Asterolecanium.

Later in the same year Signoret erected the generic name Asterodiaspis for Lecanium quercicola Bouché. Again this genus was resurrected by Borchsenius for reception of Russell's group III of species in her conception of Asterolecanium. It is to this group that the three species which are the subject of the present study belong.

In 1902 Cockerell suggested the sub-generic name Bambusaspis to define a new section of Asterolecanium and in 1906 Sanders designated Chermes miliaris Bois. as its type species. In Borchsenius's conception this is a valid genus, recreated for species included in group I by Russell.

Adult females, of which the genus Asterodiaspis to which the 3 species I have studied belong are characterized by the body usually being somewhat circular with hardly any tendency for lobing at the posterior margin, there are three or fewer pairs of setae on the apex of the abdomen and the anal opening is ventral, fairly close to the margin of the body. The anal ring has two setae or none. Multilocular pores are present in the posterior part

of the body.

Marginal 8-shaped pores in a single row, rarely partly double reaching more or less to the posterior setae.

Quinquelocular pores are present in groups and bands near the spiracles. Usually single row (sometimes double) accompanies the marginal 8-shaped pores. The row of quinquelocular pores may be interrupted anteriorly and posteriorly, or may be complete. In the first nymph the anterior margin of the body is provided with two pairs of setae, while there are three or fewer pairs on the apex of the abdomen.

All species of this genus are known to occur on Fagaceae and the group is represented in all six major zoo-geographical regions but Russell (1941) suggested that, originally, they were probably restricted to the Palearctic region.

Histories

A.variolosum (Ratzeburg,1870) was described as Coccus variolosus on oak from Kumersdorf, near Potsdam, Germany, in 1870 by Ratzeburg. Various authors thereafter recorded it as Asterolecanium variolosum Ratz. e.g. Fernald (1903), and some of them considered A.quercicola and A.minus as its synonyms, (Newstead, 1903; Green 1928; Lindinger, 1928; Borchsenius, 1937). Russell (1941) redescribed it as at present known, separating it from the other species. Parr (1940) investigated the biology of "A.variolosum" in Connecticut an area (the eastern seaboard of the U.S.A.) in which, according to Russell, the other two species are present

as well. Thus Parr's conception of A.variolosum may contain also the other two species. Further work was done by Borchsenius (1960) who placed this and all the other species in Russell's group III of the genus Asterolecanium in the re-erected genus Asterodiaspis.

The adult females and the first instar nymphs of A.variolosum as well as those of A.quercicola and A.minus were described in detail by Boratynski in 1961 under the generic name of Asterolecanium.

In the present work the assignment proposed by Borchsenius (1960) is adopted.

A.quercicola (Bouché, 1851) was described as Lecanium quercicola by Bouché in 1851 and in 1870 Signoret redescribed it and transferred it to Asterolecanium, and later erected for it a new genus Asterodiaspis. It was recorded as a distinct species by a number of authors e.g. Douglas (1885), Green (1895), Fernald (1903), Newstead (1900), Leonardi (1920), but some other authors considered it to be a synonym of A.variolosum (Cockerell 1899, Newstead,1903, Saunders, 1909, Lindinger, 1912). Russell (1941), established the identity and the validity of this species which was later described and recorded as such by Borchsenius (1949,1950) from U.S.S.R. and by Bodenheimer (1953) from Turkey. Borchsenius (1960) transferred it to be genus Asterodiaspis, under which name it is retained in the present work.

A.minus (Lindinger, 1912)

Asterolecanium variolosum minor was applied without description by Leonardi (1909) to specimens on Quercus sp. from Italy, and in

1912 Lindinger placed A.variolosum minor Leonardi (1909) as a synonym of A.variolosum thereby, according to Russell (1941), "validating the name of which he became the author".

Russell(1941) however showed that A.minus Lindinger was a different and valid species and not a synonym of A.variolosum.

Asterolecanium minus was mentioned by Bodenheimer from Turkey (1953), but his illustration of it indicates that the specimen actually illustrated was not A.minus but probably A.variolosum or A.quercicola for one half of the ventral side appears to show at least 24 multilocular derm pores, a number much higher than is ever found in A.minus.

In 1960 Borchsenius described it and placed it in the genus Asterodiaspis.

MORPHOLOGY

The developmental stages include:

i) egg

ii) first instar nymph

iii) second instar nymph

iv) adult female

The adult females and the first instar nymphs of the three species have been described in some detail and illustrated by Boratynski in 1961. His findings were generally confirmed and supplemented by additional detailed studies of some other characters. Second instar nymphs are described for the first time.

Materials and Methods:

1) The material for studies was collected mainly from Quercus robur L. on the grounds of Imperial College Field Station at Silwood Park, nr. Ascot, Berks., and also included specimens bred experimentally in the greenhouse. The latter were particularly useful for identification of the second instar nymphs of each species by reference to their readily identifiable mothers. The first instar nymphs of each species were taken from within the bodies of identified mothers, and from breeding experiments of isolated females (cf p.47)

The descriptions of the adult females and the first instar nymphs are based on detailed examination and measurement of 30 specimens of each species selected at random from much larger numbers of specimens used in biological studies.

The identified material of the second instar nymphs was more

difficult to obtain and it was necessary to rely mainly on material from experimental breeding. In a few cases the pharate adult females were used. A.variolosum produced a sufficiency of progeny during breeding experiments so 30 specimens of its second instar nymphs were available for examination. A.quercicola and A.minus produced fewer progeny and only 14 and 2 specimens respectively of their second instar nymphs were available.

2) Preparation of the insects for identification:

After removal from the twigs the insects were placed in 10% KOH in a solid watch glass with a cover on top. In this container they were warmed over a bench lamp until the colours changed from brown and reddish to whitish. After cooling, the insects were transferred into glacial acetic acid in a watch glass with one or two drops of acid fuchsin stain and the watch glass was covered.

Then the excess stain was removed in clean acetic acid and the insects passed through successive baths of absolute alcohol and finally carbol xylol in which they were left for about a quarter of an hour. The insects were then mounted in Canada balsam and the slides were gently dried in an oven at 42°C.

The illustrations of the adults represent young adult females soon after the second moult and those of the first instar nymphs represent the newly hatched insects. The choice of second instar nymphs was limited and the illustrations represent about half grown specimens.

All the drawings were made with camera lucida and accurately represent the specimens actually drawn.

The corresponding instars of A.variolosum, A.quercicola and A.minus are very similar and the separate descriptions of these instars for each species would involve a considerable amount of repetition. Thus, in the following descriptions of the developmental stages all three species are discussed together and treated comparatively.

The Adult Female (Figs, 1, 2, 3.)

For these morphological studies young adult females of each species were used, collected between August and September. The measurements and counts of the characters taken into consideration are summarised in App. 1. Boratynski (1961) in his morphological studies on the same species used fully grown females shortly before oviposition, and his measurements of some characters such as size of the body are much higher.

Body broadly ovoid to nearly circular, wholly membraneous. Posterior end often produced into a 'tail' which is most prominent in A.minus. The sizes measured on 30 specimens of young adult females of each species were (µ):

	A.variolosum	A.quercicola	A.minus
Length	743 - 1507	657 - 1411	543 - 714
Average	974*/1388.27	920*/1264/	634*/909.5/
Width	661 - 1363	536 - 1086	429 - 740
Average	869*/1294.07	753*/1116/	527*/843.9/

Comparing these figures with those for the fully grown

*[ ] Data by Dr. Boratyński

KEY TO FIGS. 1, 2, 3.

A - general body

B - antennae

C - anterior spiracle

D - posterior spiracle

E - anal ring

F - apical setae

G - multilocular derm pores

H - marginal 8-shaped pores

I - quinquelocular pores

J - ventral setae

K - ventral sub-lateral 8-shaped pores

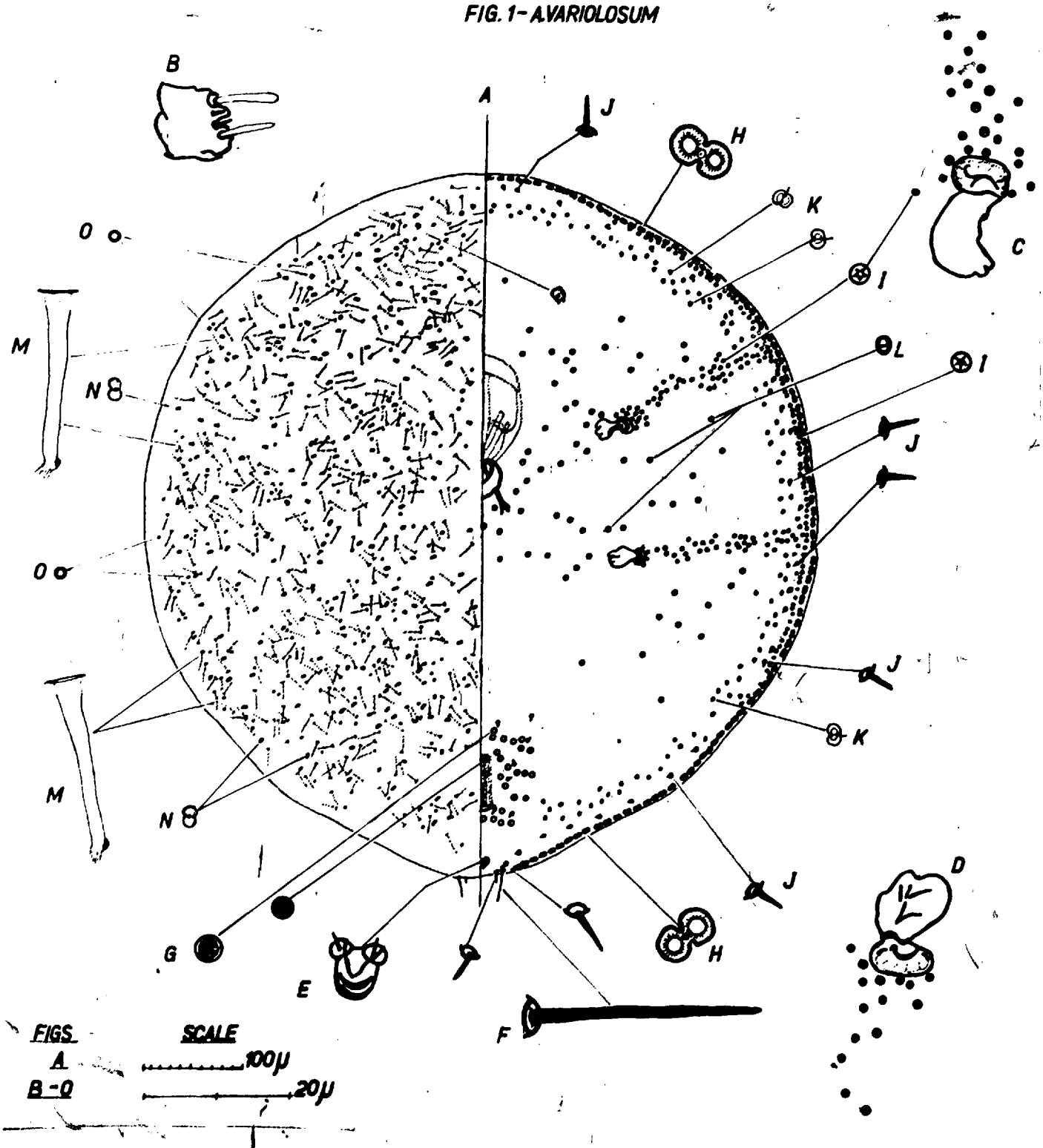
L - ventral "dark-rimmed" pores

M - dorsal tubular ducts

N - dorsal 8-shaped pores

O - dorsal disc pores

FIG. 1- A.VARIOLOSUM



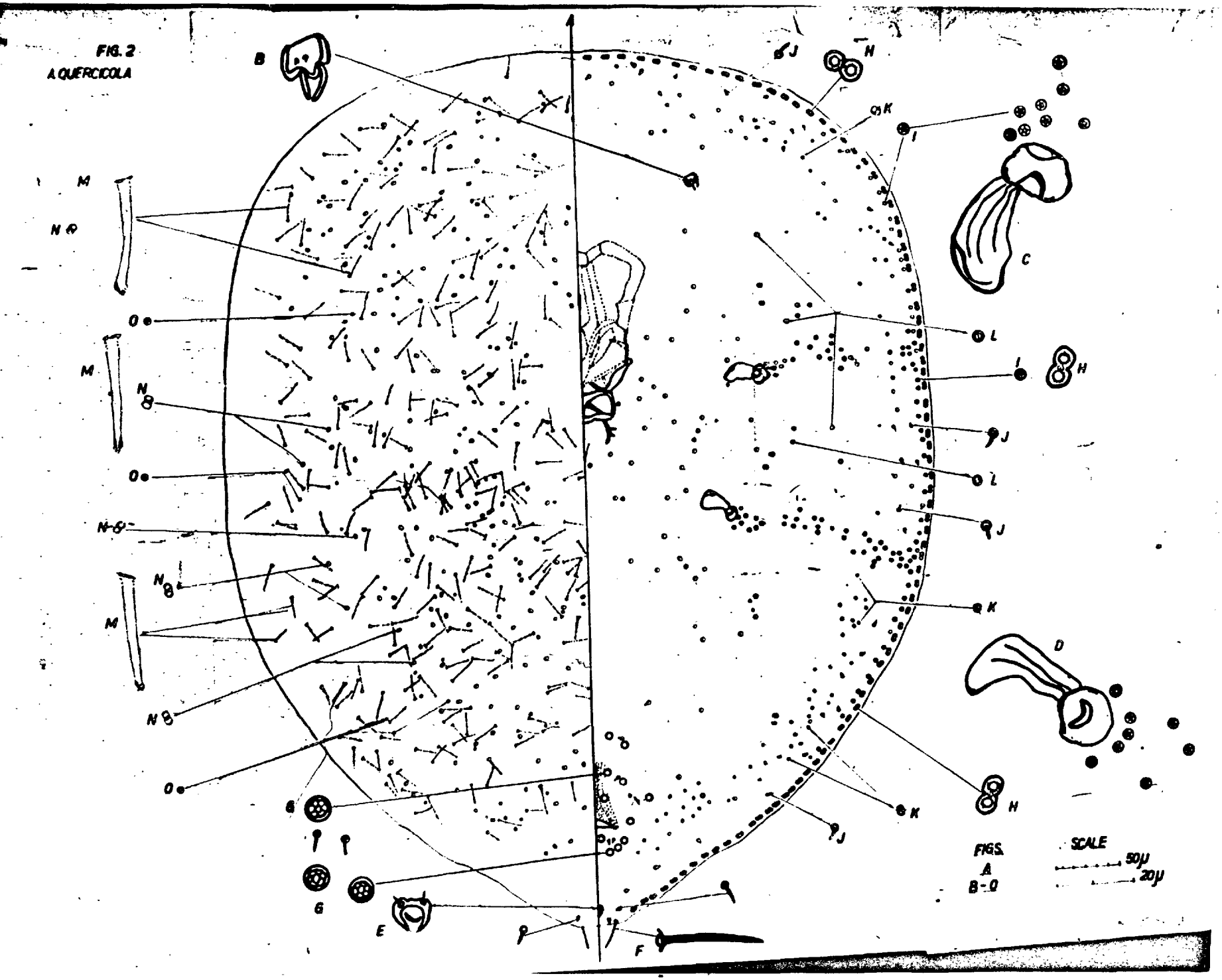
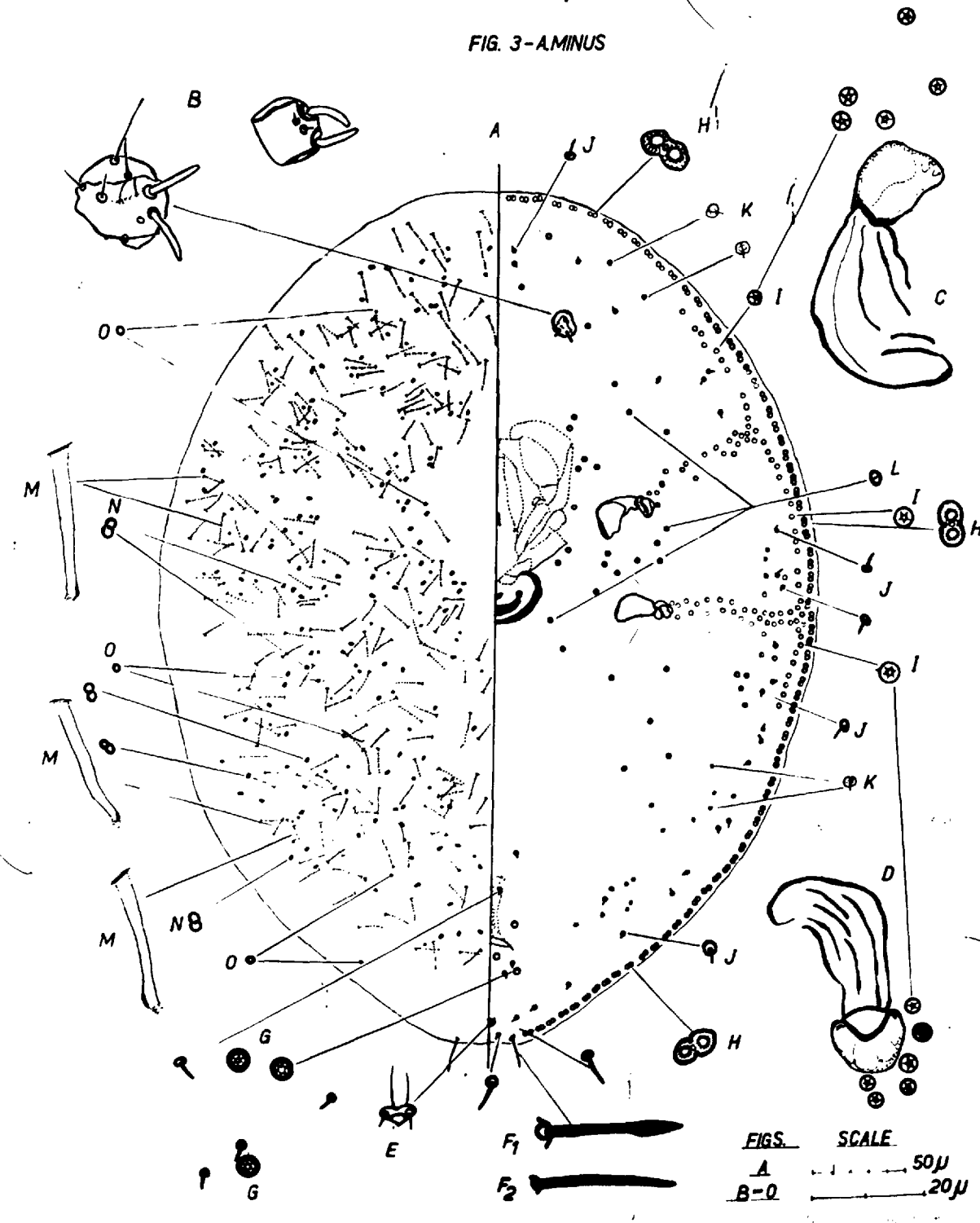


FIG. 2
A QUERCICOLA
B
J
H
K
I
C
M
N
O
L
D
G
E
F
FIGS.
A
B-O
SCALE
50μ
20μ

FIG. 3-A.MINUS

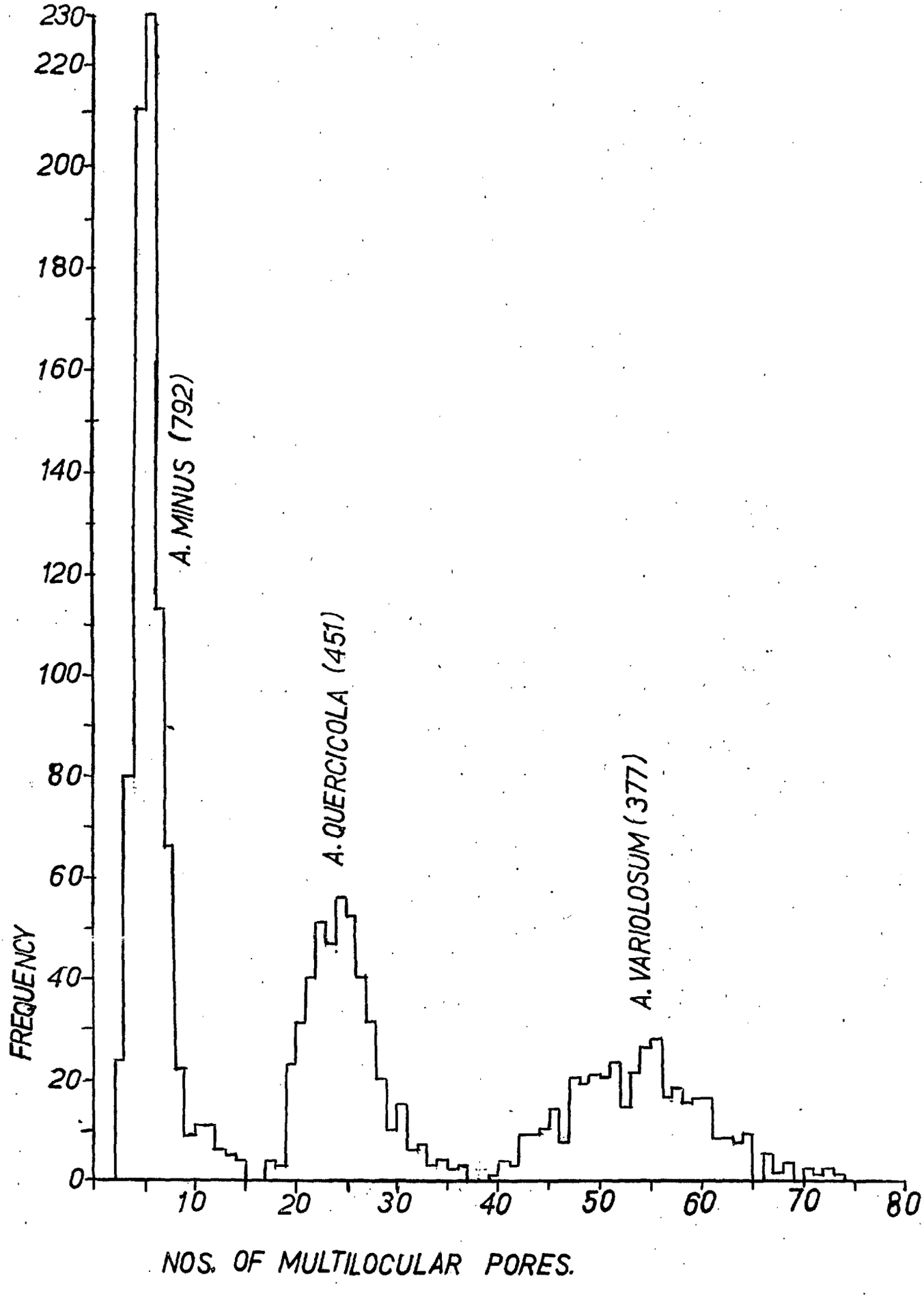


adult females it appears that the size of the body increases by about one third (A.minus, A.quercicola) to one half (A.variolosum), during the growing period. The posterior end bears a pair of apical setae (F) situated ventrally a short distance from the margin of the body. These measure (μ) 23.3 - 31 (26.8), 24.7 - 31.7(28.9), 30 - 41 (34.3) in A.minus, A.quercicola and A.variolosum respectively. A.minus has two types of apical setae, a long lancet-shaped type (Fi) and a simple, slightly shorter type of which the former is much the commoner, occuring about 8 to 9 times as often as the other type.

Associated with each apical seta in all three species are two short setae, one interapical and one anteroventral.

Perivulval multilocular derm pores (G) form the principal distinguishing character between the three species; the number is 3-15 (6.35) (usually 3-9) in A.minus, 18-37 (24.06), (usually 21-28), in A.quercicola and 40-73 (56.5) (usually 44-64) in A.variolosum. The frequency histogram (Fig 4) shows the distribution of the numbers of multilocular pores in the three species. The pores, if sufficiently numerous, are often arranged in more or less definite transverse rows; there are 1-3 rows in A.minus, 3-5 in A.quercicola and 5-7 in A.variolosum. The pores have an average diameter of 4μ in A.minus, 5.6μ in A.quercicola and 6μ in A.variolosum. In addition the numbers of loculi per pore appear to be specific, being 4-5(4.12) in A.minus, 6-8(6.5) in A.quercicola and 10 (very rarely 11) (10.04) in A.variolosum.

FIG. 4 ADULT INSECTS - FREQUENCY DISTRIBUTION OF MULTILOCULAR PORES.



Ventral setae (J) about 4 long, present among the multilocular pores (G); 2 pairs posterior to vulva, with two or more pairs in the anterior row of pores. Other ventral setae of about the same size are present in the sub-marginal area, and forming a continuous row round the body.

The antennae (B) are small, roughly conical tubercles, each with a pair of stout curved setae and two trichoid sensillae. The beak is globular and apparently one-segmented. Anal opening situated ventrally near the posterior margin of the body; anal ring (E) irregular bearing two short setae anterolaterally. Anterior (C) and posterior (D) spiracles about equal though the sizes differ in different species: (μ)

	A.variolosum	A.quercicola	A.minus
Anterior	36 - 47 (43.2)	32 - 47 (43.0)	33 - 45 (39.5)
Posterior	37 - 50 (43.7)	32 - 47 (41.8)	32 - 43 (38.1)

Each spiracle has a stout bar and a wide irregular opening distally. The proximal end is broad and less sclerotized than the distal end.

Spiracular bands of quinquelocular pores (I) extend from each spiracle to the margin of the body. A more or less discrete group of these pores, some of which may be larger and have as many as 7 loculi can often be made out close to the spiracular opening; the band of pores widens out somewhat near the body margin. Numbers of quinquelocular pores in spiracular bands:

	A.variolosum	A.quercicola	A.minus
Anterior	54 - 97 (71)	32 - 66 (43)	18 - 34 (25)
Posterior	53 - 101 (73)	35 - 58 (43)	19 - 41 (27.4)

Frequency histograms of the numbers of pores in both the anterior (Fig 5a) and the posterior (Fig 5b) spiracular bands show three groups in each, corresponding to the three species but there is some overlapping of the ranges of individual variation of the three species; this overlapping is wider in the posterior band although the numbers of pores in both bands are about the same.

At the margin the quinquelocular pores are arranged in a single row usually interrupted anteriorly and ending at some distance beyond the posterior spiracular band; usually 1-2 quinquelocular pores are associated with each marginal 8-shaped pore.

The 8-shaped pores characteristic of the family are present in a marginal row (H) and also scattered on the dorsum (N) and on the ventral side especially near the margin (K). The marginal 8-shaped pores are the largest measuring 7-10 μ long in all three species; the pores of A.variolosum and A.quercicola are, on average, larger (8.3 - 8.9μ) and those of A.minus the smallest (6.8 - 7.3μ). In all three species the posterior pores are somewhat smaller than the anterior ones. The marginal 8-shaped pores are arranged in a single row right round the margin except between the apical setae, withthe long axes of the pores parallel to the margin of the body.

FIG.5(A) ADULT INSECTS - SPIRACULAR QUINQUELOCULAR PORES. FREQUENCY DISTRIBUTIONS.

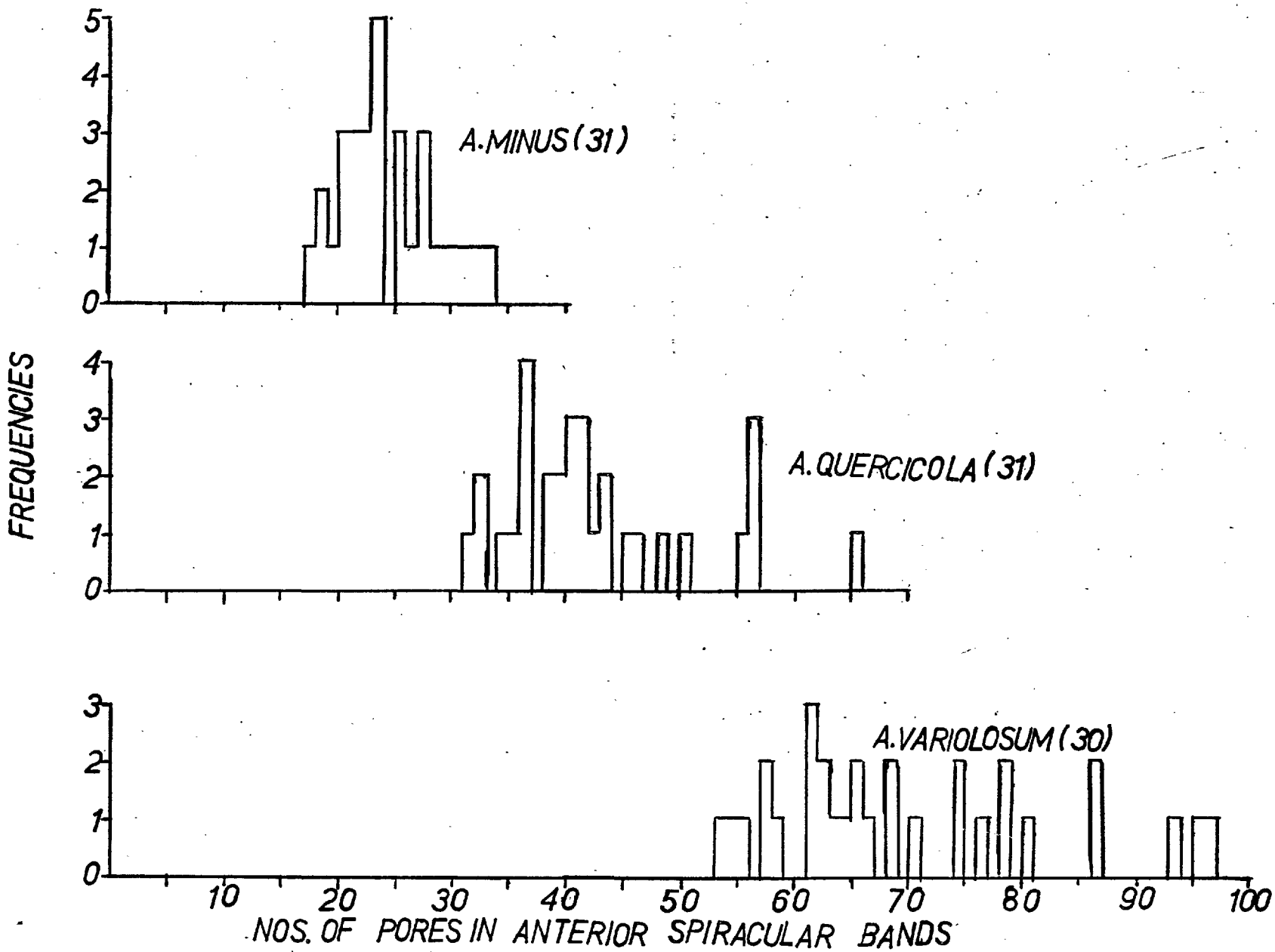
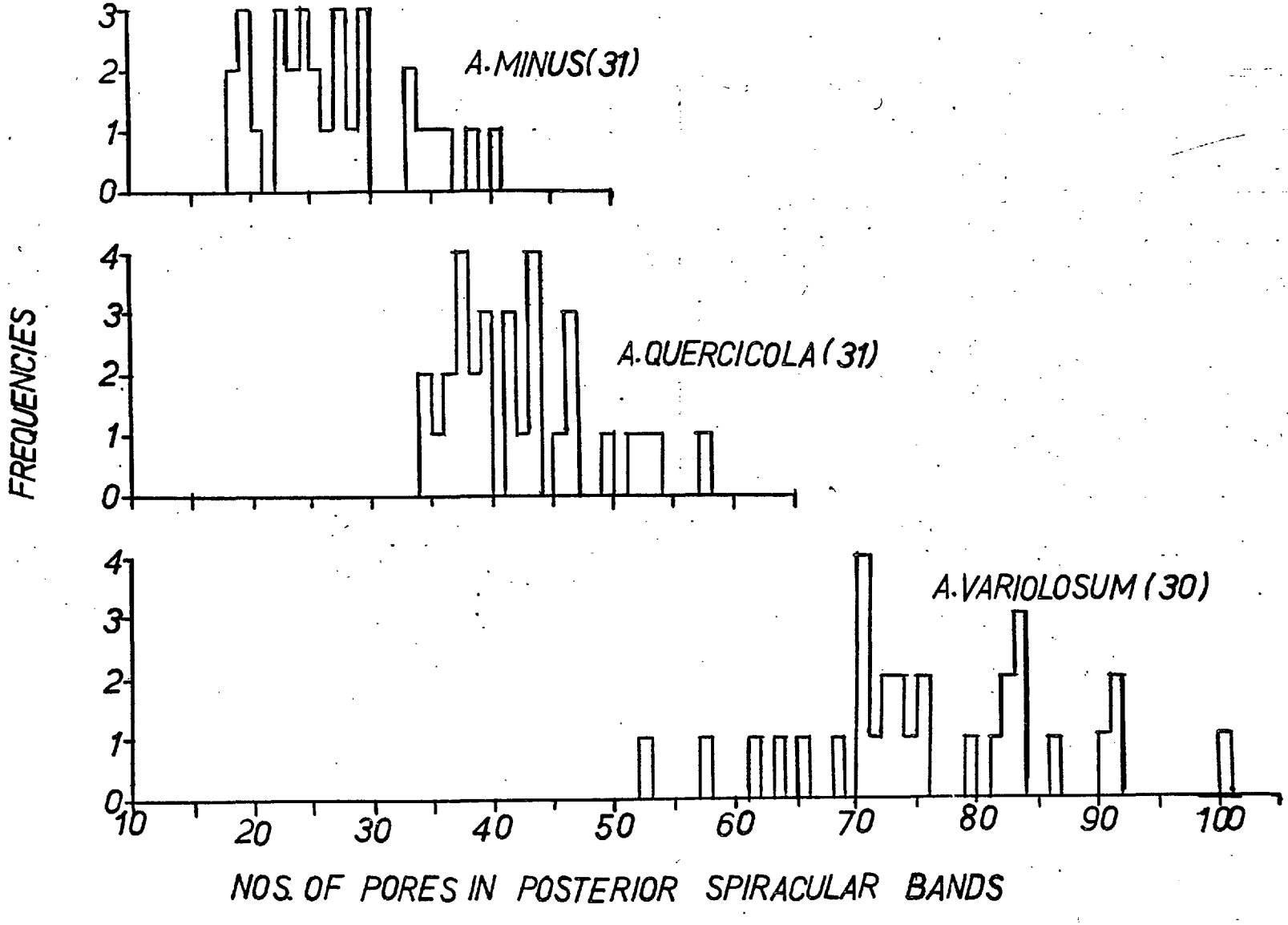


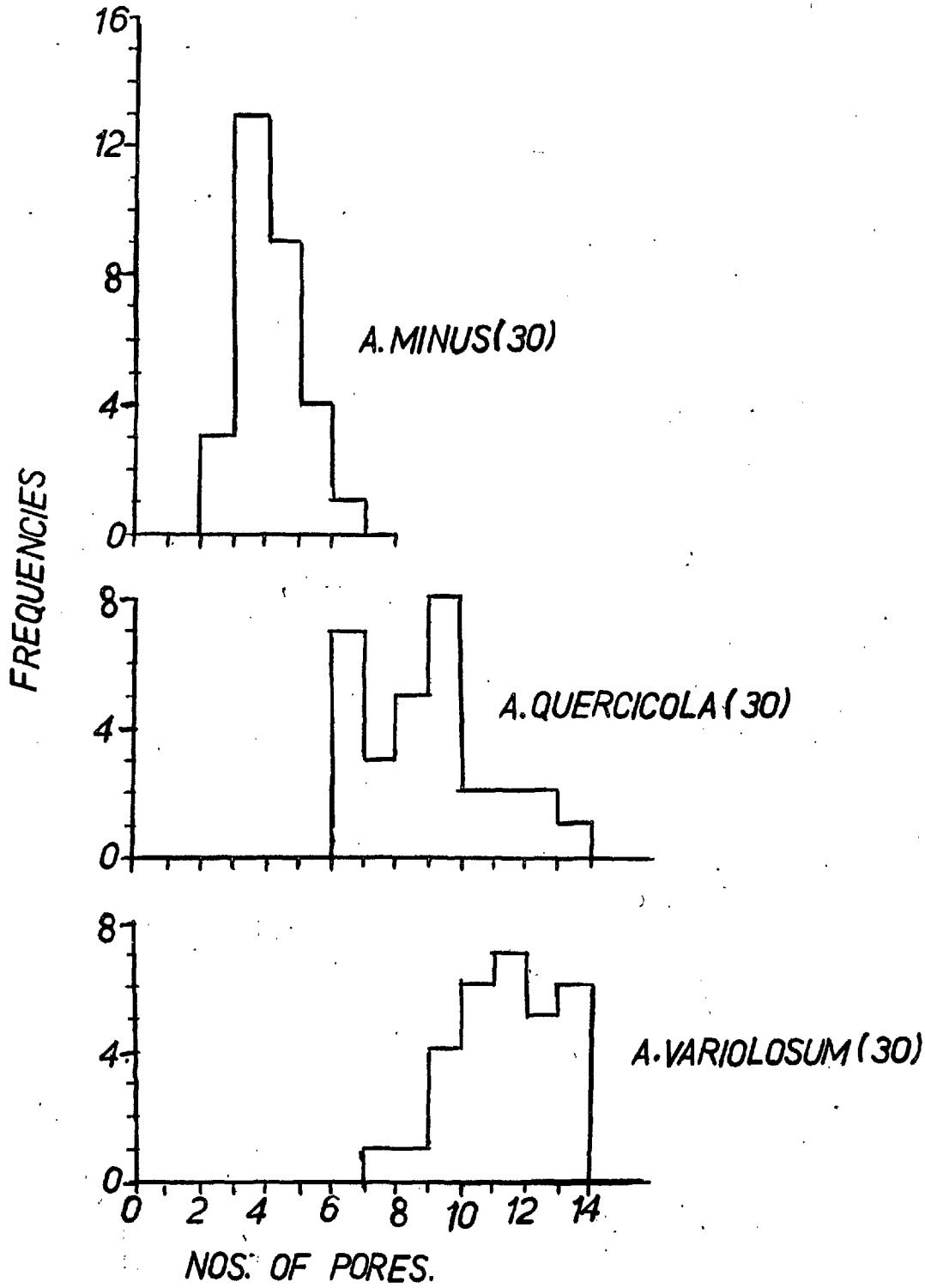
FIG 5(B) ADULT INSECTS - SPIRACULAR QUINQUELOCULAR PORES. FREQUENCY DISTRIBUTIONS.



Sub-marginal ventral 8-shaped pores are ill-defined, about 3 - 3.7 long and arranged in an irregular band all round the body except the posterior 'tail'; this band consists of 1 - 3 irregular rows. Dorsal 8-shaped pores well-defined, about the size of the sub-marginal ventral 8-shaped pores, scattered more or less evenly over the dorsum, intermingled with the asymmetrical tubular ducts (M); the latter are 16.7 - 22.7 μ long (20.0 μ) in A.minus, 23.3 - 30,7 μ long (26.8 μ) in A.quercicola and 20-30 (24.2 μ) in A.variolosum; the inner narrower end of the tubular duct has a characteristic somewhat sclerotized bulge.

Simple, minute disc (circular) pores (O) about diameter are quite profusely scattered amongst the tubular duct on the dorsum, "Dark-rimmed" bilocular ducts pores (L) of about 1 diameter with deeply invaginated short duct occur on the ventum; especially numerous around the beak and between the spiracles; they form an irregular medio-lateral band extending over the cephalic area (between the beak and the antennae), across the spiracular bands and the anterior part of the abdomen. An assessment of the comparative numbers of these "dark-rimmed" pores in the three species was made by counting the numbers present on the roughly quadilateral area bounded by the beak, the spiracular bands of quinquelocular pores and the body margin. In A.minus the numbers varied from 3-7 (3.5), in A.quercicola 7-14 (9.4) and in A.variolosum 8-14 (11.9). The frequency histogram (Fig 7c) represents these counts graphically and shows

FIG. 5(C) ADULT INSECTS - COUNTS OF "DARK-RIMMED" PORES.
FREQUENCY HISTOGRAMS.



that A.minus is fairly well separated from the other two species in which individual variation of numbers of these pores almost coincide, although the averages somewhat differ.

These studies based on larger numbers than before (Boratynski, 1961) of specimens of the three species confirmed the validity of the number of multilocular pores as the most obvious and reliable character differentiating the species.

The species differ (at least statistically) also in the number of quinquelocular pores in the anterior and the posterior spiracular bands, the frequency distribution of which within each species is approximately normal but there is considerable overlap between the species.

The number of loculi in the multilocular pores is also a specific character (A.minus, 4-5 (4.12), A.quercicola, 6-8 (6.5) and A.variolosum 10-11 (10.04).

The number of "dark-rimmed" pores clearly separates A.minus (3.7) which also shows an approximately normal distribution A.quercicola (7-14) and A.variolosum (8-14) differ little with regard to this character.

Generally however all measurable and numerical characters of the three species show progressively higher values, those of A.minus being the lowest, A.variolosum the highest, and those of A.quercicola intermediate.

The Second Instar Nymphs (Figs 6.7.8)

This stage is generally similar to the adult female from

KEY TO FIGS 6, 7, 8.

A - general body

B - antenna, B trichoid sensillae

C - anterior spiracle

D - posterior spiracle

E - anal opening

F - apical seta

G - marginal 8-shaped pores

H - quinquelocular pores

I - body (ventral) setae

J - ventral 8-shaped pores

K - "dark-rimmed" pores

L - dorsal 8-shaped pores

M - disc pores

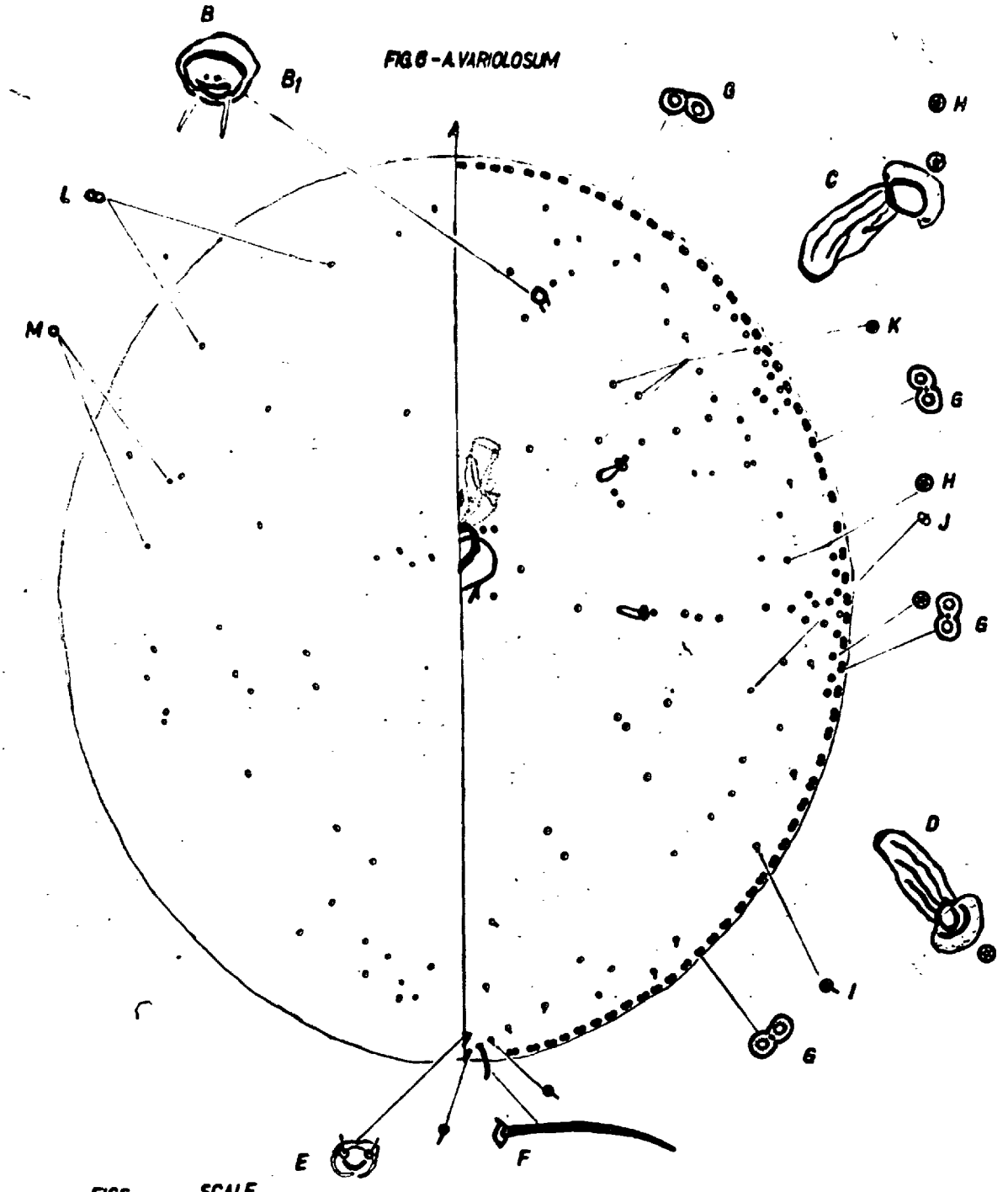
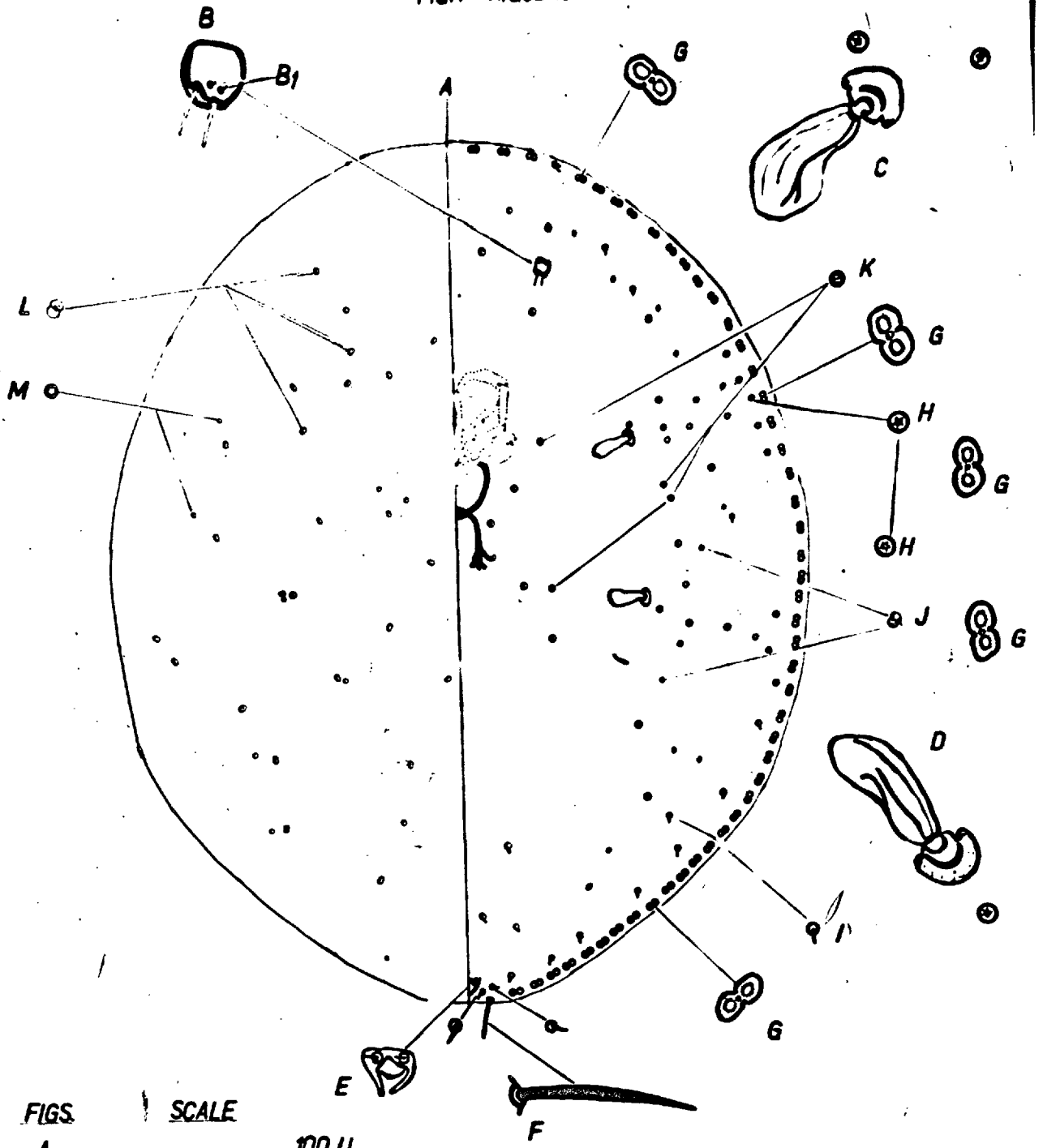


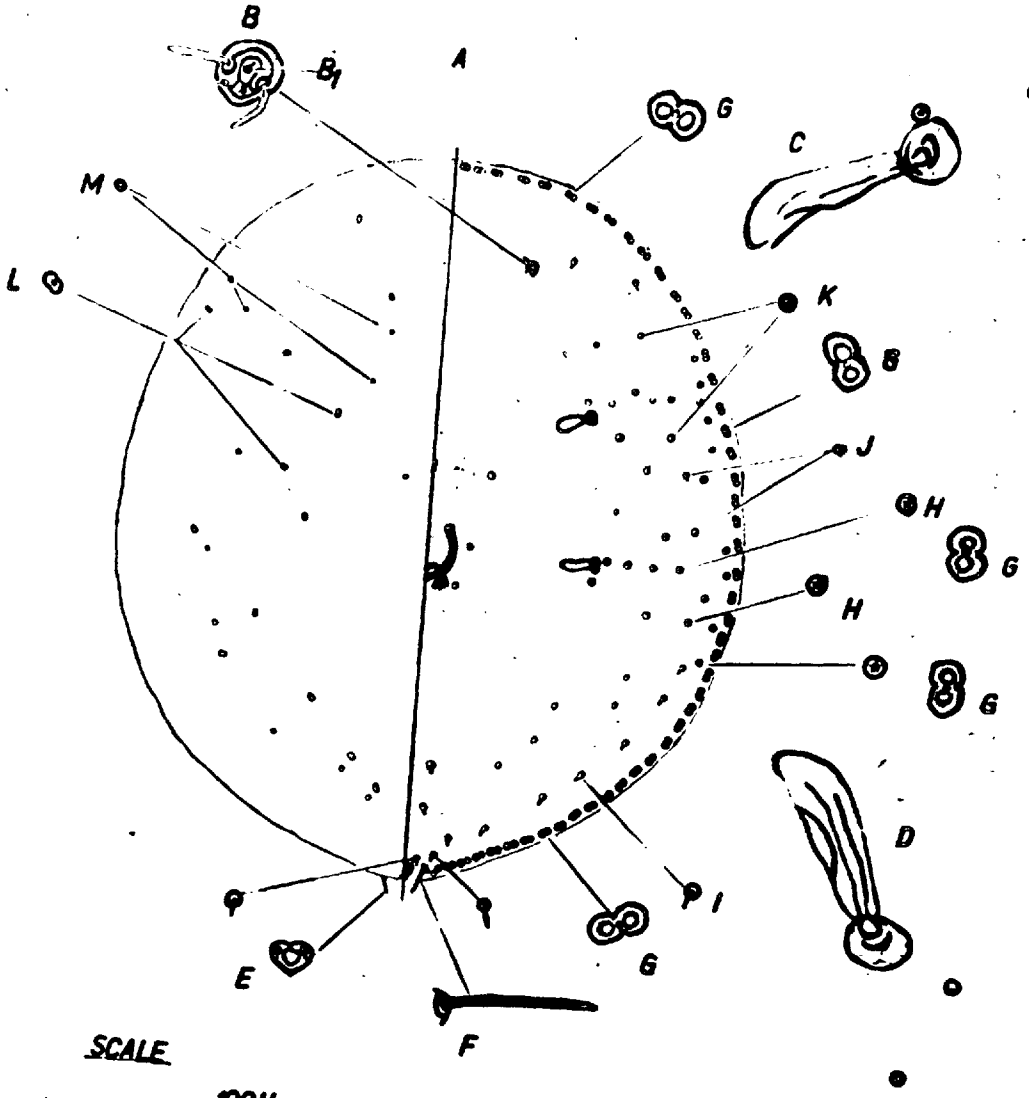
FIG. 6 - A. VARIOLOSUM

FIG. 7 - A. QUERCICOLA



FIGS.	SCALE
A	100 μ
B-M	20 μ

FIG. 8 - A. MINUS



FIGS. SCALE

A ——— 100μ

B-M ——— 20μ

which it differs however in lacking the dorsal tubular ducts and the perivulvar multilocular derm pores on the ventral side and there are much fewer of the remaining derm structures. Thus there are few characters on which the differentiation of the three species at this stage can be based. The ranges and averages of the characters measured and counted are given in Appendix P ii.

The body is broadly oval to almost circular and wholly membraneous. The margin of the body is entire with no suggestion of a posterior 'tail' as in the adult female, or lobes as in the first instar nymph.

The sizes (in μ) of the mounted available specimens are:

	A.variolosum	A.quercicola	A.minus
Length	429 - 843 (682)	380 - 751 (576)	457 , 471
Width	313 - 700 (557)	240 - 572 (313)	400 , 423

Since only two specimens of A.minus were available for measurement, no accurate idea of the range of sizes in this species is possible, but the measurements of these two specimens are given for comparison.

Because of the difficulty of obtaining specimens of this stage all readily identifiable (i.e. referred to known mothers) specimens available have been used and include individuals of different stages of growth, from the very young, to fully grown ones. Thus the lowest measurements refer to the individual just after the first moult and the highest to the fully grown

ones, the averages representing half-grown insects; the two specimens of A.minus appear to represent half-grown individuals. The figures indicate that during the growing period, the lengths of the insects nearly double, A.variolosum and A.minus becoming more circular while A.quercicola retains its oval shape.

The posterior end bears a pair of apical setae (F) situated ventrally a short distance from the margin; in A.variolosum the average length of the setae is 29 , in A.quercicola 24 and in the two specimens of A.minus they were 15 and 20 long. Associated with each apical setae are two short ones - one interapical and the other anteroventral.

The antennae (B) are short conical tubercles each with two curved, rather slender setae and two trichoid sensillae (B_1) The beak (N) is very similar to that of the adult female. Anal opening (E) is situated ventrally close to the posterior margin of the body; anal ring irregular, weakly sclerotized bearing two short setae anterolaterally.

Vulva absent.

The spiracles (C,D) have a slender bar of practically uniform width, sometimes slightly enlarged at the base; distally, with well-sclerotized arms surrounding the spiracular opening. Both the anterior and the posterior spiracles are of about the same size, the lengths (in) being:

	A.variolosum	A.quercicola	A.minus
Anterior	23 - 31 (29)	23 - 31 (26)	23.3, 26.7
Posterior	23 - 33 (27)	23 - 27 (25)	23.3, 26

Spiracular quinquelocular pores (H) arranged in a single, usually regular row extending from the distal ends of the spiracles to the margin of the body. No grouping of these pores near the spiracular opening is evident. The numbers of the pores in the spiracular rows vary considerably in all species, except - possibly - in A.minus. The figures are given below:

	A.variolosum	A.quercicola	A.minus
Anterior	5 - 12 (7.3)	4 - 10 (6.0)	4, 5.
Posterior	4 - 10 (7.0)	4 - 10 (6.0)	5, 6.

The numbers of these pores do not seem to provide a basis for separating the species, although there is a tendency for gradual decrease of the average numbers from A.variolosum to A.minus.

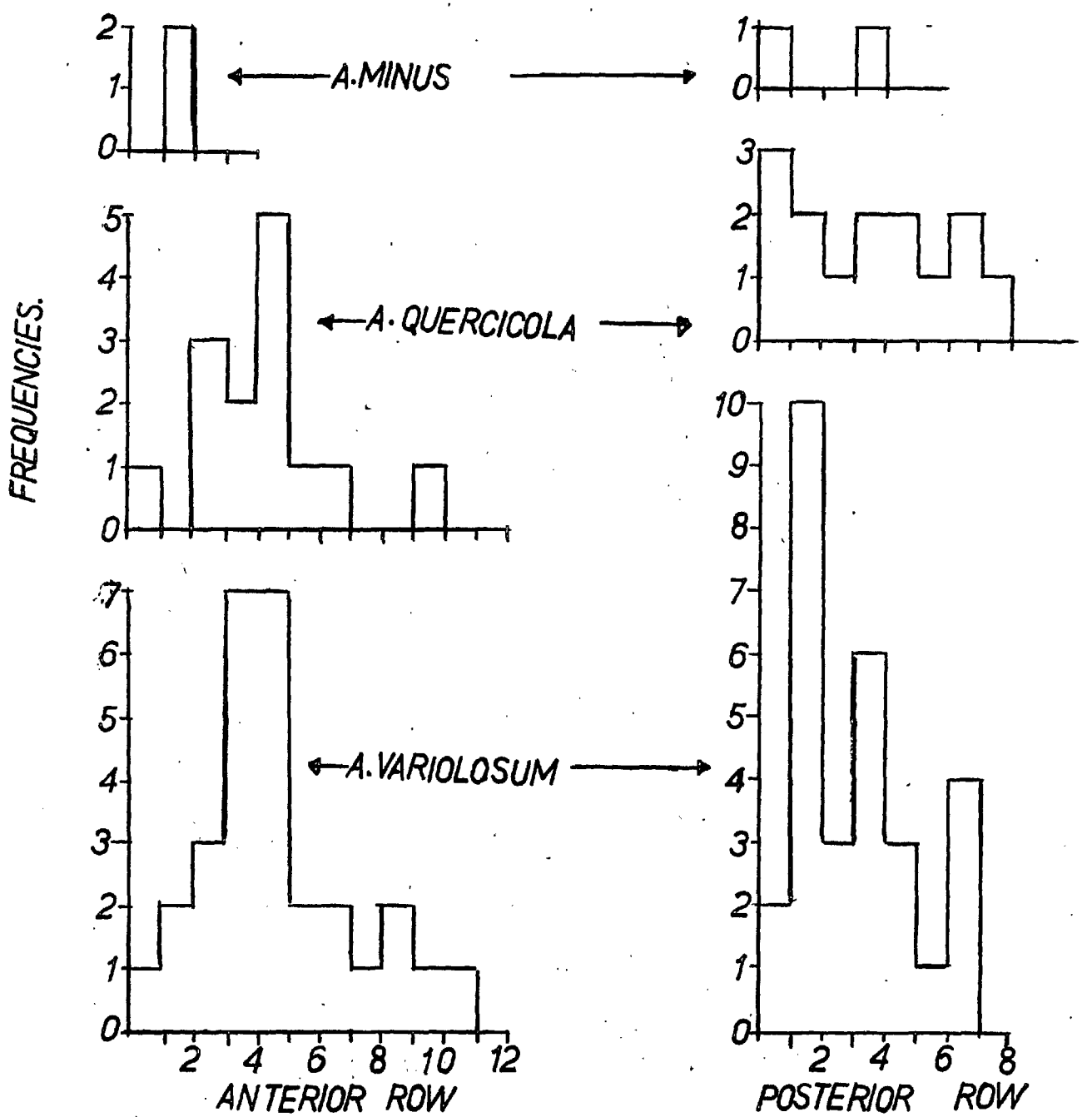
Marginal quinquelocular pores few, arranged in a separate short single row opposite each spiracle. The number of pores in these rows were:

	A.variolosum	A.quercicola	A.minus
Anterior	0 - 11 (5.0)	0 - 10 (4.29)	2, 2.
Posterior	0 - 7 (3.47)	1 - 8 (4.0)	4, 1.

and the frequency distributions are shown in Fig 9. The numbers of the quinquelocular pores in the rows do not provide any clear means for separation of the species.

The large marginal 8-shaped pores (G) are arranged in a single row extending round the entire margin of the body except between the apical setae, with the long axis of each pore in the row parallel to the margin of the body. In

FIG.9 SECOND INSTAR NYMPHS - NOS. OF MARGINAL QUINQUELOCULAR PORES. FREQUENCY HISTOGRAMS.



A.variolosum they are 6.7 - 8.7μ long (6.9), in A.quercicola 6.3 - 7.3μ(6.7μ) and about 6.7μ in A.minus. The numbers of marginal 8-shaped pores found in 30 specimens of A.variolosum, 14 of A.quercicola and 2 of A.minus were 110-127 (117.5), 80-111 (98), and 82, 86, respectively. These figures indicate that the number of marginal 8-shaped pores may be used within some limits to separate the species. By employing 7 additional specimens of A.quercicola and 48 of A.variolosum (suitable for counting 8-shaped pores but not for the other purposes) a frequency histogram of the distribution of these pores within the species was constructed as represented in Fig 10a. The histogram for A.variolosum (78 specimens) shows approximately normal distribution with the comparatively narrow range 108-128 and average of 117.9. A.quercicola (with only 21 specimens) shows a wider range of individual variation from 80-111 and the average of 98.5. The overlap between these two species is comparatively small (108-111) and the averages quite distinct.

On Fig 10b, the numbers of marginal 8-shaped pores are plotted against size perimeter of the insects (length and width) examined in detail i.e. 30 of A.variolosum and 14 of A.quercicola. As already explained the insects used were of various ages, i.e. included the young ones immediately after the first moult, as well as the half and fully-grown ones. No conclusions can be drawn concerning the relationship between the ultimate size of the insect and the number of pores by calculating correlation

FIG 10(A) SECOND INSTAR NYMPHS - FREQUENCY DISTRIBUTION OF MARGINAL 8-SHAPED PORES.

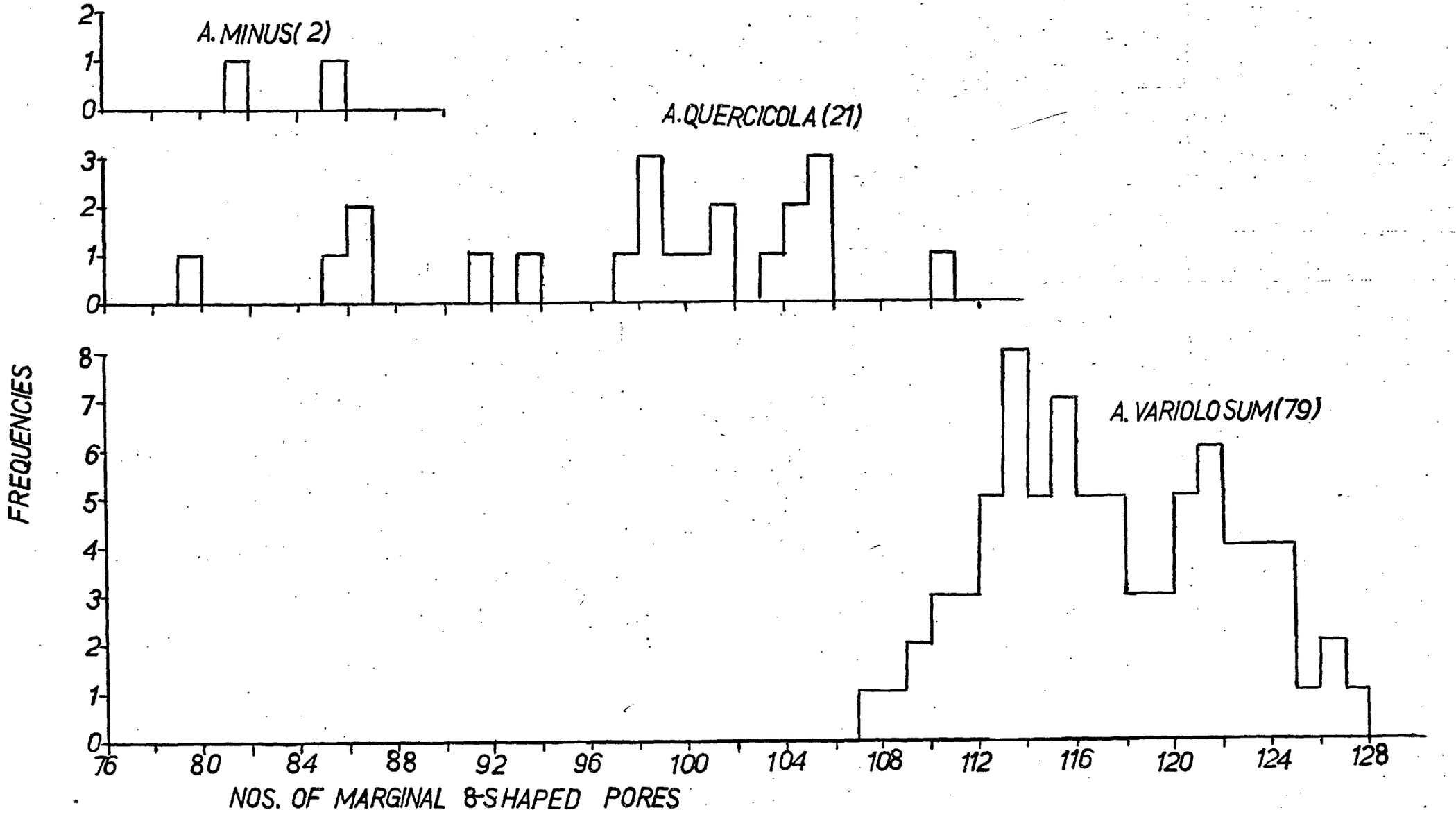
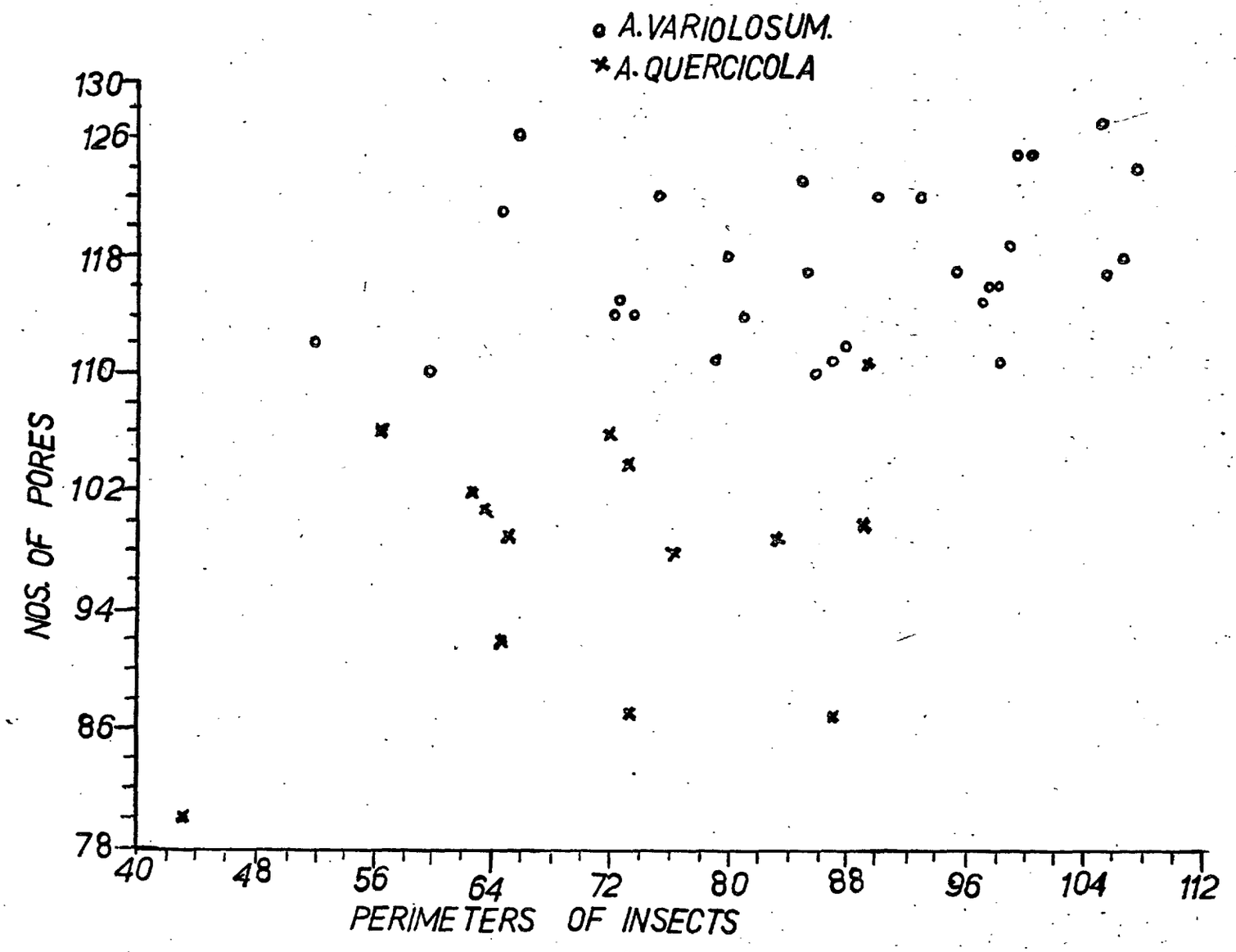


FIG.10(B) SECOND INSTAR NYMPHS - NOS. OF MARGINAL 8-SHAPED PORES COMPARED WITH SIZE.



co-efficients from theses data. In fact correlation co-efficients have been calculated and were:

A.variolosum, r = = .3253, t = 1.818, P = 0.1(-.05) cf. p. 46 also

The diagram Fig 10b shows however that in both species even the largest specimens show the full range of the number of 8-shaped pores, thus suggesting that there is no relationship between the size of the insect and the number of marginal 8-shaped pores present. This would support the view that the numbers of these pores are of specific significance.

The ventral 8-shaped pores (J) poorly defined, small, about 3-5 μ long, arranged in an irregular sub-marginal band all round the body with somewhat greater numbers around the antennae.

Ventral "dark-rimmed" pores sparsely scattered on the medio-lateral area of the cephalo-thorax and the anterior part of the abdomen. Dorsal 8-shaped pores (L) well-defined, 3-5 μ long, and the small disc pores (M) sparsely scattered over the entire dorsal side of the body. Body setae (I) sub-marginal ventral, occur along the entire margin of the body. ~~except the apical setae~~.

The study of the second instar nymphs of the three species showed that out of the altogether limited numbers of the characters present at this stage, only the number of marginal 8-shaped pores can be used for distinguishing the species. The averages for A.variolosum, and A.quercicola of which sufficient numbers of specimens were available are quite distinct

(117.9 and 98.5) and their overlap of individual variation is small (108-111). The same may be true of A.minus. The species differ also in average sizes but the overlap appears to be much wider. As in the adult females these characters as well as the others. show more or less distinctly progressively increasing values from the lowest in A.minus to the highest in A.variolosum, A.quercicola being intermediate. Unlike the adult females this stage does not show clear-cut differences between the three species.

To p.45 // A.quercicola r = .0964, t = .3371, P = 0.7 - 0.8, which indi[illegible] that there is no correlation between these two variables.

First Instar Nymphs (Figs 14, 15, 16)

The first instar nymphs of all three species were briefly described and illustrated by Boratynski (1961).

Body shape similar in all three species, elongate, narrowly oval, flat, rather rounded anteriorly, with well-developed antennae (I) and legs. Posterior end (D) with a slight median cleft giving rise to two lateral lobes. The specimens studied in detail included the newly-hatched nymphs and also half- and fully-grown ones obtained from breeding experiments. Thus in measurements of e.g. size of the body, the lower values refer to the young nymphs, the upper to the fully grown, and the averages to approximately half-grown individuals. The measurements and counts of the characters studied are summarized in Appendix III ~~Table 3~~. Dimensions in μ with averages in brackets.

	A.variolosum	A.quercicola	A.minus
Length	228 - 440 (309)	210 - 408 (262)	189 - 250 (226)
Width	140 - 302 (192)	122 - 283 (159)	120 - 157 (139)

Anteriorly there is a black eye spot (L) on both sides antero-lateral to the bases of the antennae). The presence of two pairs of setae (F) close to the anterior margin between the eye spots is characteristic for this group of species.

At the posterior end each lobe bears a long apical seta (Da) with an interapical seta and a shorter anteroventral seta.

Length of posterior apical seta in the three species (in μ) averages in brackets):

KEY TO FIGS 14, 15, 16.

A - general body

B - marginal 8-shaped pores

C - dorsal disc pores

D - posterior end

a) apical seta

b) interapical seta

c) antero ventral seta

E - ventral seta

F - anterior seta

G - beak

H - 8-shaped pore at base of antenna

I - antenna

J - anterior spiracular quinquelocular pore

K - posterior spiracular quinquelocular pore

FIG. 14 -- A. VARIOLOSUM

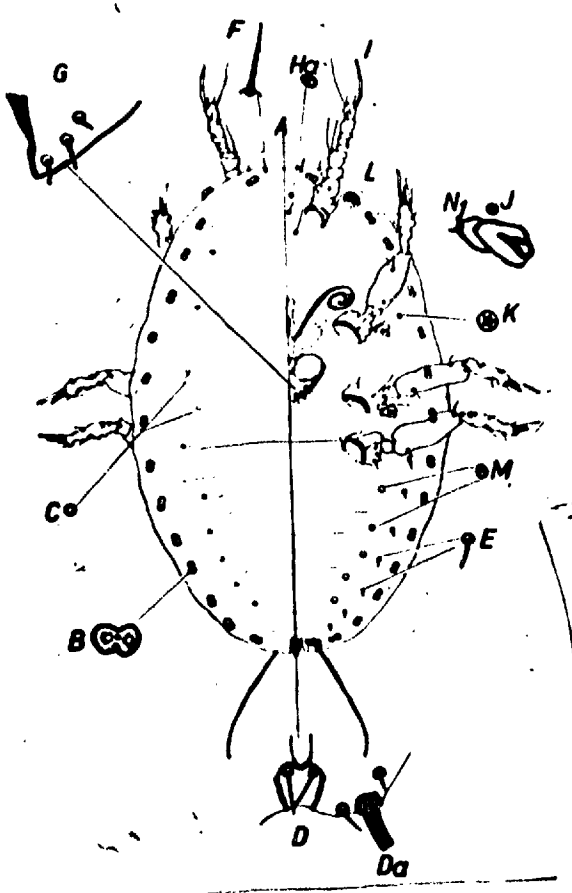


FIG. 15 - A. QUERCICOLA

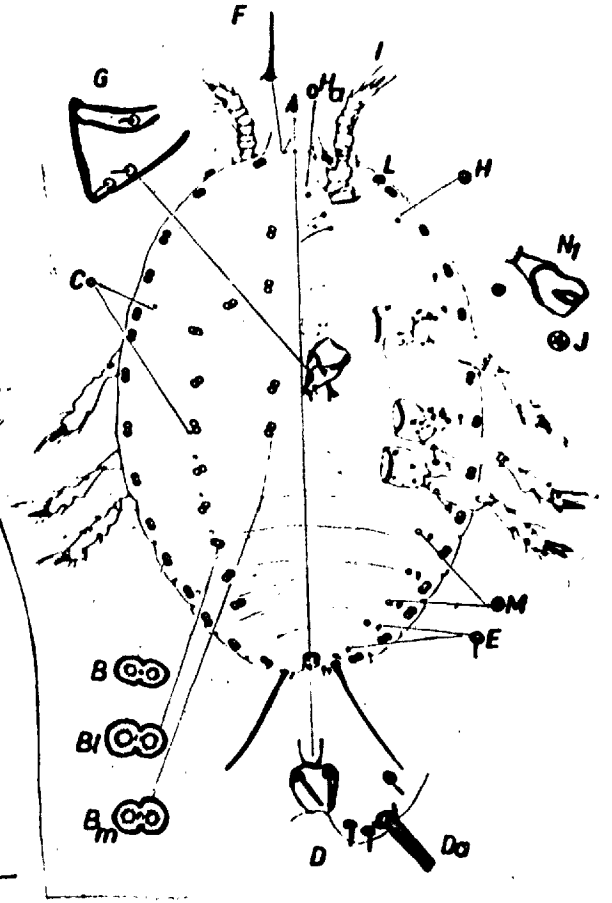
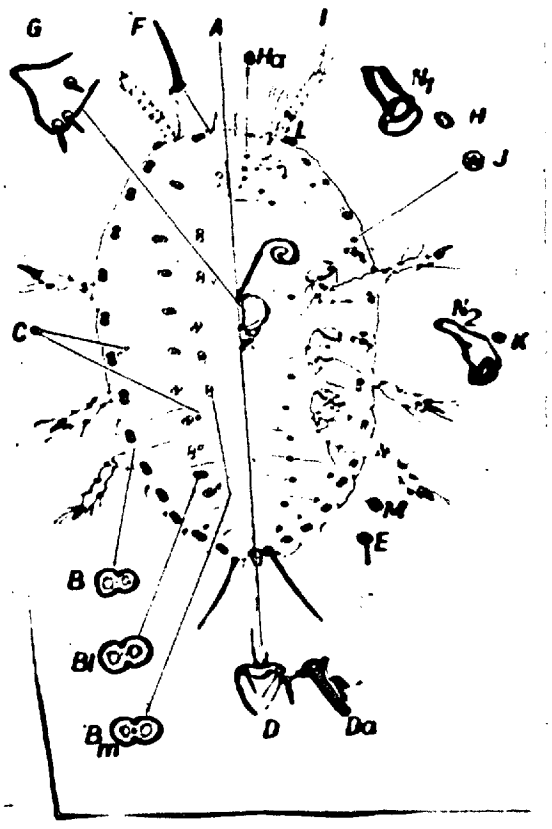


FIG. 16 - A. MINUS



FIGS	SCALE
A	50μ
B-N	20μ

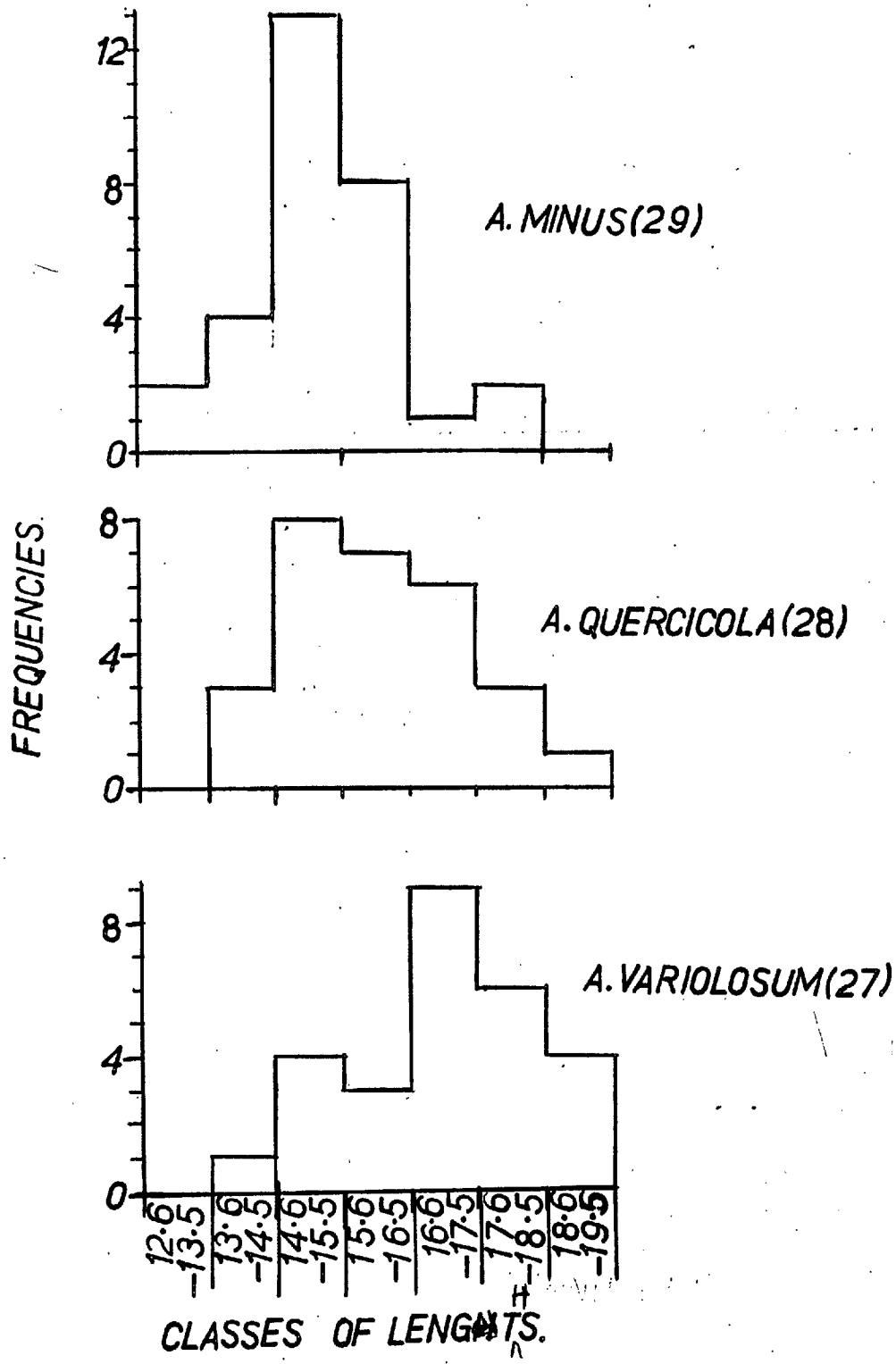
A.variolosum	A.quercicola	A.minus
47 - 64 (57)	47 - 63 (53)	43 - 60 (51)

The ranges of individual variations in the three species show almost complete overlap but on average, in A.minus the setae are shortest, in A.variolosum longest and intermediate in A.quercicola; the frequency histograms (Fig 11) of the species show somewhat different patterns of distribution in each species.

The marginal series (B) of large, 5-6 long and about 3.5 wide, 8-shaped pores are present in all species, composed of 14 pores on each side of the body; the pores are arranged in a single row with the long axes of the pores parallel to the margin of the body.

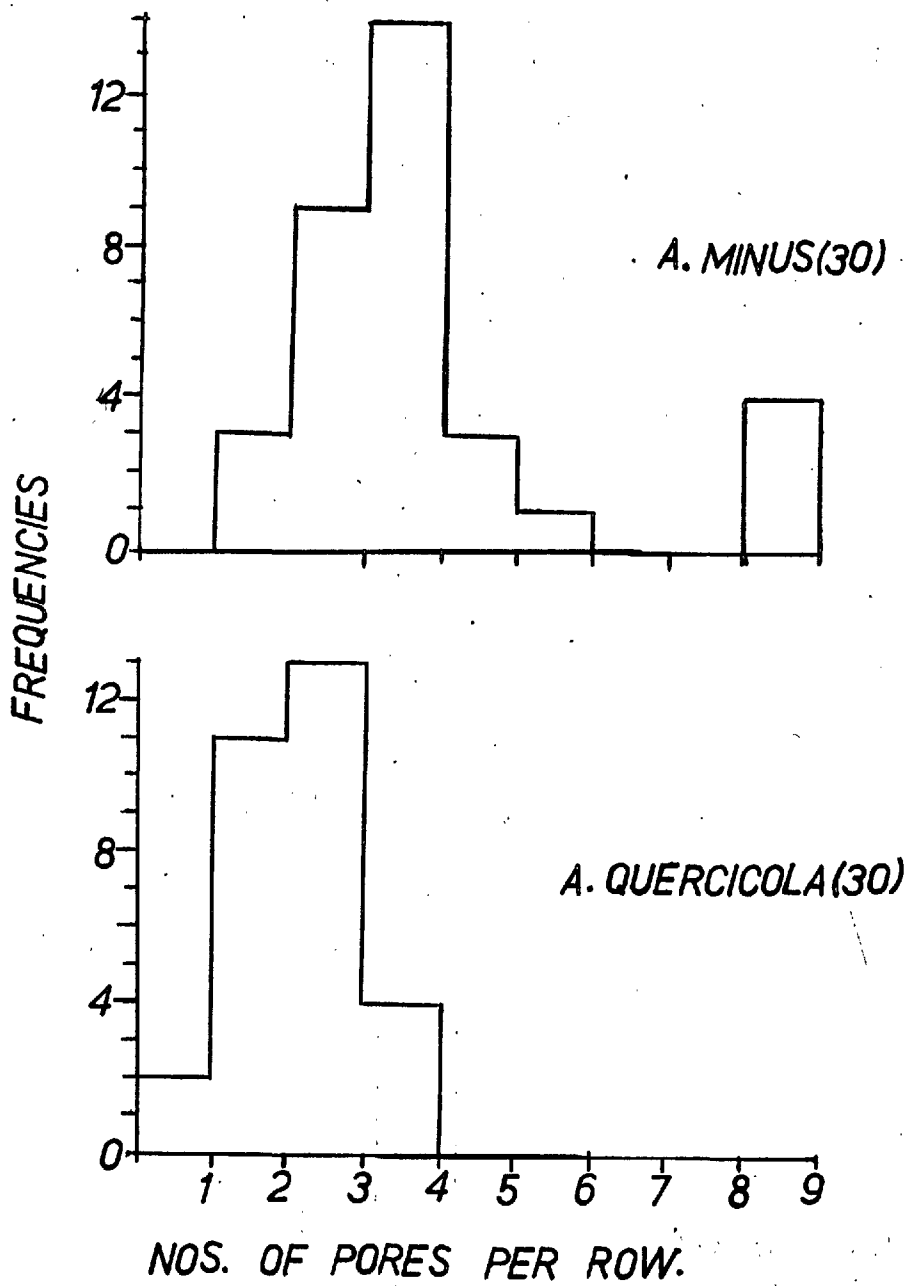
In A.quercicola and A.minus there are two additional series of similar pores, namely a sub-lateral (B_1) and a sub-median (Bm) row on each side. The sub-lateral series is the more complete each row being composed of 8-9 (av. 8.7) pores in A.quercicola and 7-10 (av. 8.5) in A.minus. The sub-median series is less complete and in A.quercicola is represented by 1-4 (av. 2.6) pores in the cephalothoracic part of the body only. In A.minus the conditions are less simple. Russell (1949) stated that in this species there are 4-5 pores per sub-median row, while Boratynski (1961)(p.10) said that "the first instar nymphs of A.minus show a considerably higher number of dorsal 8-shaped pores in the sub-median series which is normally composed of 10 pairs of pores, although in some specimens a few of the posterior

FIG. 11 FIRST INSTAR NYMPHS - SIZE DISTRIBUTION OF APICAL SETAE.



ones may be missing." Examining the 30 specimens selected for detailed studies, the author found that the range of individual variation of the number of pores in this series was 2-6 (av.3.6) pores per row. By the courtesy of Dr. Boratynski, the author was able to examine his material; on 4 out of 6 slides of this material the specimens showed 10 or 9 of these pores, while the remaining 2 slides contained the specimens with reduced numbers of pores. Examination of the author's additional material revealed the presence of the specimens with the full complement of pores as well. No specimens with intermediate numbers between the reduced (2-6 pores) and the full complement (9-10 pores) were found; moreover it appears that the individual females produce progeny all of which show either one or the other condition. Thus, several (12) available nymphs of one female (slide No.G1 12.11.62 N19) showed 9 pairs of sub-median pores and a several (22) (slide No.GIII,12.11.62 N2) nymphs of another female showed the reduced conditions of 2-6 pores in the row. It appears therefore, that with regard to this character, A.minus has dimorphic first instar nymphs. It should be pointed out that this dimorphism is not correlated with the dimorphism of the adult females discussed above with regard to the shape and length of the apical setae. The frequency distribution of the numbers of sub-median 8-shaped pores in both A.minus and A.quercicola is shown in Fig 12.

FIG. 12 FIRST INSTAR NYMPHS - 8-SHAPED PORES IN SUB-MEDIAN ROWS. FREQUENCY DISTRIBUTION.



(C)

Simple disc pores occur on the dorsum, more or less regularly accompanying the sub-lateral 8-shaped pores, and some marginal 8-shaped pores, especially in the abdominal region and occur more scattered in the cephalo-thoracic region. On the ventral side a matching row of short setae (E) occurs near the marginal 8-shaped pores and extends to mesothoracic area. Median ~~Internal~~ to the row of setae is a row of minute 8-shaped pores similar to the 'dark-rimmed' pores of the adults. This row is rather incomplete in the cephalo-thorax. Near the distal end of each spiracle there is a small quinquelocular pore (J & K).

Antennae 6-segmented, third segment sub-divided by a semi-membraneous transverse band first segment with 1 median seta, the second with 1 median and 2 lateral, fourth and fifth each with one median, sixth with 2 lateral, and 4 apical setae. Two pairs of slender setae of variable length (about 18μ) occur between the bases of the antennae and the mouthparts. The variation in the sizes of each species are not reflected in the lengths of the antennae which are as follows (in μ):

A.variolosum	A.quercicola	A.minus
60 - 78 (67)	56 - 77 (62)	53 - 77 (62)

Spiracles ( ), small, with stout bar and irregular opening; the average dimensions of the anterior spiracles are as follows (in μ):

	A.variolosum	A.quercicola	A.minus
Length	9.2	8.5	7.7
Width	4.6	3.9	3.9

The posterior spiracles are somwhat larger in all three species (cf Table 3). Beak (G), short, irregularly pentagonal with three pairs of short setae near the tip.

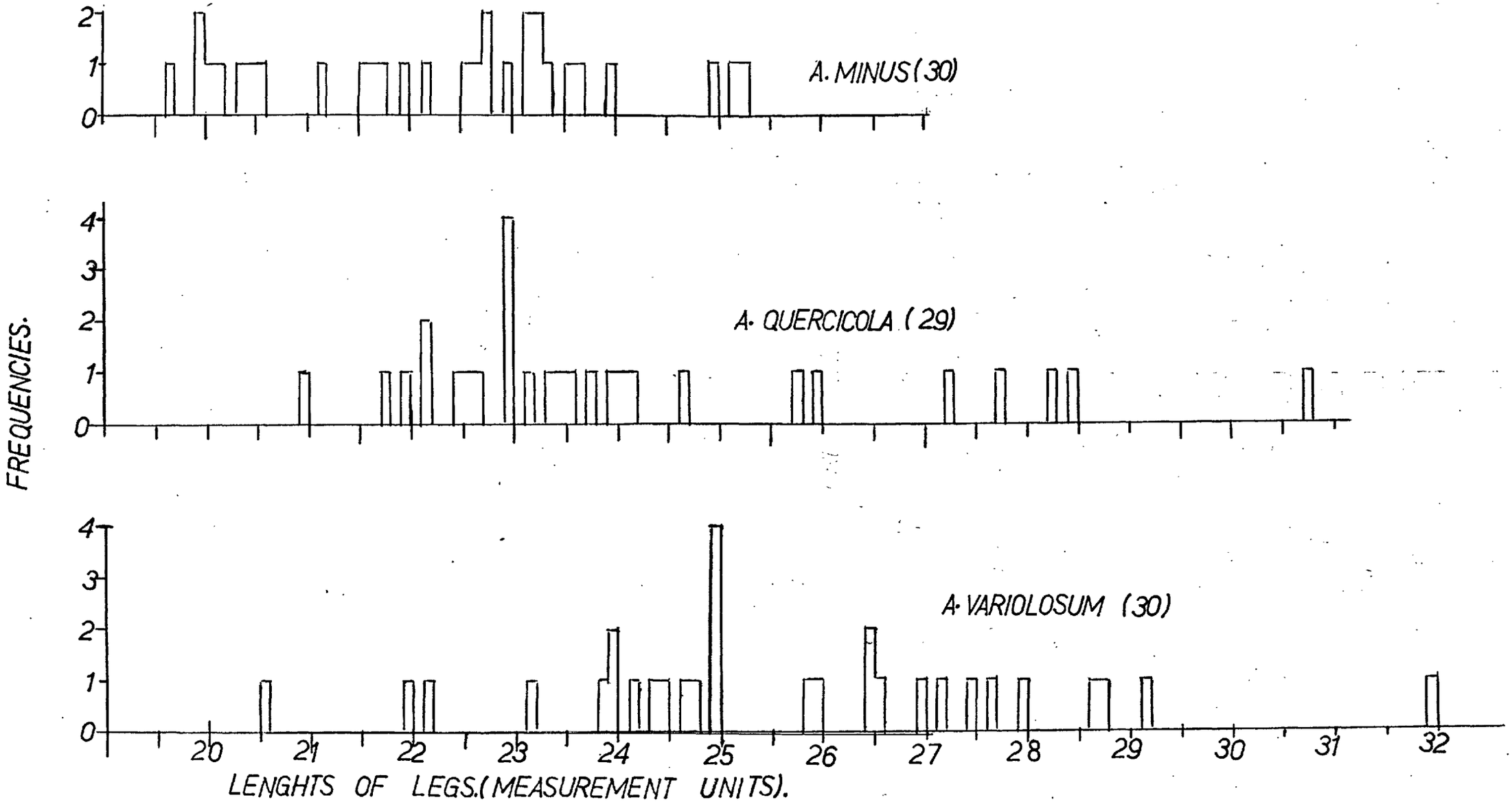
Legs well-developed in the three species, slender to stout in different specimens probably due to distortion when mounted.

Coxa of the usual conical shape, femur wide and long, tibia very short, not well separated from tarsus which is 3-4 times longer; tarsus + tibia about as long as femur; claw simple, relatively long. On average, the legs are longest in A.variolosum, shortest in A.minus and intermediate in A.quercicola. The lengths of legs, represented by the sum of the lengths of the relatively well-sclerotized femur + tibia + tarsus + claw are (in μ, averages in brackets:

	A.variolosum	A.quercicola	A.minus
prothoracic	73.0-99.7(81.8)	60.0-100.0(79.4)	66.7-83.3(74.7)
mesothoracic	73.7-98.7(84.5)	64.0-104.7(79.9)	64.0-80.3(74.6)
metathoracic	68.7-106.7(85.7)	70-102.7(80.9)	65.7-84.3(74.3)

The frequency histograms of the metathoracic legs of each species are given in Fig 13. The first instar nymphs of the three species of Asterodiaspis are very similar and differ mostly in the range of sizes, A.variolosum being the largest and A.minus the smallest. This trend is reflected also to a lesser or a greater degree in the other measureable characters such as the length of the apical setae, length of the antennae and legs, size of the spiracles. The condition of the dorsal

FIG. 13— FIRST INSTAR NYMPHS —SIZE DISTRIBUTION OF METATHORACIC LEGS. FREQUENCY HISTOGRAMS.



8-shaped pores is the main point of difference; A.variolosum with only the marginal series of these pores, is therefore readily segregated from the other two species. Both A.quercicola and A.minus have in addition, a sub-lateral and a sub-median series, with A.minus having rather more pores than A.quercicola in the sub-median series, but as the ranges of individual variation of the two species overlap, the segregation is not always easy, but in A.minus the form with the full complement of pores in this series is well defined.

The Egg:

Elongate, ovoid, with both ends broadly rounded, creamy yellowish colour with a velvety texture. Mounted specimens, have the following average dimensions (in μ):

	A.variolosum	A.quercicola	A.minus
Length	232	226	202
Width	160	140	124

These measurements are somwhat higher than the lower limits of the sizes of the first instar nymphs of each species, thus showing that these first instar nymphs are newly hatched ones.

Keys to the three stages

The keys for all three stages of the species are given below. Some characters of the adult females are sufficiently well-defined to enable one to separate the three species. With regard to the first instar nymphs, A.variolosum can be easily separated from the other two species by the absence of the dorsal 8-shaped pores and, of these two species, the condition of these dorsal 8-shaped pores separates easily, individuals of one of the two forms of A.minus.

The characters of the second instar nymphs as well as some of the other characters of both the adult females and the first instar nymphs allow only for statistical differenation between the species but not for the actual identification of the individual specimens.

Keys to Adult Females (averages in brackets)

1. Multilocular pores few, 3-15, usually 3-13 (6.35) pores; each pore about 4μ in diameter with 4-5,4.12) loculi. Spiracular bands of quinquelocular pores each with 18-41 pores (27.4 pores). Tubular ducts 16.7-22.7μ long (20.0μ). Apical setae 23-31μ long (27μ) usually either stout or lance-shaped. Body circular or nearly so; young females 543-714μ long (634μ) and 429-740μ wide (527μ);(fully grown females 780-1107μ long (909.5μ)and 670-982μ wide (843.9μ)Figures in brackets thus are of measurements made by Dr. Boratyński (1961 ; posterior tip often slightly produced into a 'tail'. Marginal 8-shaped pores

6.7-10μ long (7.3μ) and 3-4μ wide (3.2μ). "Dark-rimmed" pores in a group around the beak and inter-spiracular area, 3-7 pores (3.5) being present. Sub-marginal ventral band of 8-shaped pores each 3-3.7μ long (3.3μ) composed of 1-2 irregular rows of pores. A.minus (Lindinger).

- Multilocular pores numerous, 18-73 pores, arranged in 3-7 transverse continuous rows; each pore with 6-11 loculi. Tubular ducts 20-30μ long. Apical setae slender, pointed, 24.7-40.7 μ long. Spiracular bands of quinquelocular pores each with 32-101 pores. Body broadly oval or circular, usually larger than as above. Marginal 8-shaped pores 6.7-10.7μ long, and 3.2-3.5μ wide (3.4μ)

2. Multilocular pores 18-37, usually 20-33 pores (24.06); each pore 5.6 in diameter with 6-8 loculi (6.5). Spiracular bands of quinquelocular pores each with 32-66 pores (43.0 pores). Body oval or broadly oval, usually longer than wide; young females 657-1411μ long (920μ) and 536-1085μ wide (753.μ); (fully grown females 1107-1482μ long (1264μ) and 936-1404μ wide (1116μ)). Figures in [brackets] are of measurements made by Dr. Boratyński (1961). Sub-marginal ventral band of 8-shaped pores wider posteriorly, composed of 2-3 rows irregularly "Dark-rimmed" pores in a group around beak and inter-spiracular area, 7-14 pores (9.6 pores) A.quercicola (Bouché).

- Multilocular pores 40-73, usually 44-64 pores (56.5); each pore about 6.3μ in diameter, with 10, rarely 11, loculi (10.04

loculi). Spiracular bands of quinquelocular pores each with 53-101 (73) pores. Body circular or nearly so, sometimes wider than long; young females 743-1507μ long (974μ), and 661-1363μ wide (869μ); (fully grown adults 1092-1606μ long (1388.2μ) and 951-1528μ wide (1294.0μ)). Figures in brackets thus are of measurements made by Dr. boratynski (1961).

Sub-marginal ventral band of 8-shaped pores 1-2 irregular rows. "Dark-rimmed" pores grouped around beak and inter-spiracular area, 8-14 pores (11.9 pores),

A.variolosum (Ratzeburg).

Tentative Key to the Second Instar Nymphs (averages in brackets)

1. Marginal 8-shaped pores number 108-128μ(117.9), each pore about 7 long. Body oval or broadly so, usually somewhat longer than wide, 429-843μ long (682μ) and 313-700μ wide (557μ). Spiracular rows of quinquelocular pores number 5-12 pores (7.2 pores) and the marginal rows 0-11 pores (4.23 pores).

A.variolosum (Ratzeburg).

- Marginal 8-shaped pores number 80-111 or ~~considerably less than 111~~ about 84, each pore about 6.7μ long. Body narrowly oval or broadly so, usually somewhat longer than wide, generally smaller than as above. Spiracular rows of quinquelocular pores number 4-10 pores each and the marginal rows 0-10 pores each.

2. Marginal 8-shaped pores number 80-111 pores (98.5 pores), each pore about 6.7μ long. Body oval or broadly so, usually longer than wide, 380-751μ long (576 μ) and 240 - 572μ wide (313μ).

Spiracular rows of quinquelocular pores number 4-10 pores each (6.0) and the marginal rows 0-10 pores each (4.15 pores).

A.quercicola (Bouché) (Pl.5)

- Marginal 8-shaped pores number about 84, usually less than 111, each pore about 6.7 µ long. Body broadly oval to almost round, about 464 µ long and 411.5 µ wide. Spiracular rows of quinquelocular pores number about 5 pores each and the marginal rows about 2.25 pores each.

A.minus (Lindinger) (Pl.6)

Key to the First Instar Nymphs (averages in brackets)

1. Dorsal 8-shaped pores normally absent. Apical setae 47 - 64 µ long (57 µ), interapical about 10 µ long, anteroventral about 4 µ and anal ring setae about 6.7 µ long. Spiracles about 9.2 µ long and 4.6 µ wide. Legs 81.8-85.7 µ long (84.0 µ).

A.variolosum (Ratzeburg).

- Dorsal 8-shaped pores present in sub-lateral and sub-median series; sublateral series always complete and composed of 7-10 pairs of pores, each pore about 6.5 µ long and 4 µ wide; sub-median series complete or reduced. Spiracles, legs, apical and other setae usually shorter than as above.

2. Sub-median series of 8-shaped dorsal pores incomplete, represented by 1-4 pairs of pores in anterior part of dorsum only; each pore about 5.8 µ long, and 3 µ wide. Apical setae 47-63 µ long (53 µ), interapical 6 µ, anteroventral 3.2 µ and anal ring setae about 7.3 µ long. Spiracles about 3.5 µ long 3.9 µ wide.

A.quercicola (Bouché)

- Sub-median series of 8-shaped pores sometimes complete, and composed of 9-10 pairs of pores; often incomplete, represented by 2-5 pairs of pores in anterior part of dorsum; each pore about 4μ long and 2.7μ wide. Apical setae about 51μ long, interapical about 4 anteroventral about 3μ and anal ring setae about 6.7μ long. Spiracles about 7.7μ long and 3.9 wide. legs 74.3 - 74.7μ long (74.5μ). A.minus (Lindinger).

BIONOMICS

Studies on the biology of Asterodiaspis minus (Ldgr.) A. quericola (Bouché), and A. variolosum (Ratzeburg) were carried out at the Imperial College Field Station, at Silwood Parks, Berks.

Silwood Park (Map Appendix iv) has been described already in a series of papers on biology and ecology of other insects (Richards and Waloff, 1954, 1961), Waloff and Blackith (1962) and of other animals (Brown, 1954).

It is situated about one mile on the London side of Ascot, 51° 24'N and 0° 39'W at an altitude of 200 feet. The climate of this part of England is the nearest approach to a continental type, i.e. having relatively hot dry summers and cold winters. The grounds of the field station lie mostly on beds of Eocene age, namely Bracklesham beds (gravel and sand with some clay) on the east, and Bagshot sands (sands with some gravel) on the rest of the area.

A greater part of the grounds is covered by acid grasslands dominated by Festuca rubra L. and Agrostis tenuis Sibth. with local stands of Holcus mollis L. Two patches of woodland occur - a south-eastern one mainly of beech (Fagus) and some oak (Quercus robur L.), but containing also a number of exotics (Rhododendron, Abies, Quercus cerris L. etc.), and a northwesterly patch, mainly of elm (Ulmus) and oak (Quercus robur L., Q. petraea (Mattuschka) Liebl.)

The south-eastern woodland is the denser of the two patches and comprises South Lodge Wood to the west, the Heath and Cannon Woods in the middle, and the Garden Wood extending from south to north; the northern

extension of the Garden Wood veers somewhat westwards to reach the Main House area on the east of the Garrison Ridge. The north-western woodland covers Gunner's Hill, the Marsh and Elm Slope.

Between the two areas of woodland lie the Drive Hill, the Drive Field, Drive Lawns, Silwood Bottom and Hill Bottom, which are comparatively open, but dotted about with scattered, isolated trees.

Three species of oak are present on the grounds of Silwood Park, namely: Quercus cerris L., Q. robur L. and Q. petreae (Mattuschka) Liebl. but the studied species of Asterodiaspis occur only on the latter two species. Q. robur is the commonest of the three species, occuring all over the grounds and growing in open spaces as single trees, in small groups of two to three trees, and also in association with groups of other trees (beech, pine, birch, etc.) Q. petreae is represented by a very few trees growing in the Marsh area near Gunner's Bridge. Some trees, however, are difficult to determine and appear to be hybrids of Q. robur and Q. petreae.

METHODS:

Borat[illegible]ski (1961) already found that all three species of Asterodiaspis occur together in mixed populations on individual trees, specimens of all three species often close together on a single twig of the host. The three species are very similar in external appearance and can be reliably separated only by individual examination of mounted specimens under high power microscope. This is also true with regard to the early recognition of the successive developmental stages. Consequently it was not feasible to make direct field observations and to follow the

development and behaviour of the particular species, or of the individuals within each species.

(a) Thus the field studies were carried out along the following lines:

1) Observations on the conditions and external appearance of the insects generally, and on marked individuals which were later identified.

2) Samples of infested branches were taken at suitable intervals, preserved immediately in 70% alcohol and later, in the laboratory, the insects were removed, mounted and identified. At the time of rapid development the samples were taken one to three times a week, but less frequently during the other comparatively quiescent periods (winter, etc.).

(b) In addition, a series of breeding experiments of isolated females has been carried out.

Oak seedlings 3 to 4 years old and about 2 feet high were obtained in the field and transplanted during the winter, individually, into earthernware pots. Early in April each plant was carefully examined and given a nicotine wash to make sure that it was not infested by Asterodiaspis spp. or any other insects.

After two weeks, when the residual action of the nicotine wash had ceased, the plants were transferred into the cold greenhouse. In order to prevent the mutual contamination by crawlers later, the plants were placed in positions sheltered from the wind and draught, and at least one foot apart between the crowns.

In June-July, when gravid ovipositing females were present in the

field, slivers, each with only one gravid female on it, were taken from the infested twigs; one such sliver was tied onto a twig of each potted plant and regular observations were afterwards made to see when the crawlers emerged and where they settled. The position of each crawler was marked with white waterproof paint. At a later date, when the emergence of crawlers had ceased and no new settlers were seen, each mother insect was removed, mounted and identified.

The subsequent changes in the numbers and appearance of the young insects were noted. At intervals, samples of progeny were taken and treated in the same way as the samples taken in the field. Eventually all surviving mature daughter females were also mounted and examined.

Progeny of the individual females

The breeding experiments were primarily undertaken in order to discover if the females of each species produced progeny of their own kind, and to investigate the morphological relationship between the mother and the adult progeny, as exemplified by the number of multilocular pores, the most obvious and important character separating the species.

The experiments were carried out in 1961 and 1962. In 1961 38 potted oak seedlings, each with a single female insect on it, were used; of these 8 were successful, i.e mature progeny of the insect were recovered on the plant, and one was partially successful, i.e. some crawlers emerged and settled, but did not develop and died before reaching maturity.

The 1962 experiments were generally more successful because the habits of the insects were better understood; out of 30 experiments set, 19 were successful and 9 partially successful. (Table I summarizes these experiments)

TABLE 1

SPECIES	SUCCESSFUL			PARTIALLY SUCCESSFUL			Grand Total
	1961	1962	Total	1961	1962	Total	
A. variolosum	5	15	20	1	-	1	21
A. quercicola	3	3	6	-	1	1	7
A. minus	-	1	1	-	8	8	9
Total	8	19	27	1	9	10	37

Although it was originally intended to have the same numbers (at least 10) of each of the three species, the identification based on external appearance of the female at the time of transfer proved to be unreliable. Eventually 21 experiments were carried out on A-variolosum and only 7 and 9 on A-quercicola and A-minus respectively.

Of the three species A-minus was most difficult to breed; a small number of nymphs settled but only in one of nine experiments there was a single adult progeny obtained. On the other hand the breeding of A-variolosum was successful, and in most experiments comparatively large numbers of settlers and of the adult progeny were obtained. With A-quercicola the results were intermediate. In most experiments a proportion of the original settlers failed to develop; shortly after the apparent settling they dried up, dropped off the plant and were lost. Generally this proportion was comparatively small, though variable, in A-variolosum and did not seem to be related to the original number of settlers on the particular twig. In A-quercicola the proportion that failed to develop was also variable but rather greater. In A-minus, however, under the conditions of the experiments, the total disappearance of settlers appeared to be the rule. An explanation of these differences in breeding success will be attempted later, when the habits of the insects are discussed.

RESULTS:

The details of the experiments are shown in Tables 2 and 2a and also represented graphically in Fig. 18.

TABLE 2

Year&Species	Expt.	PROGENY: No. of set-tlors	Nymphs mounted L1+L2	Adults	No. of multilocular pores: Mother	Progeny: Mean	Progeny: Range	Individuals
A.variolo-sum	C	3	1+2	-	51			48,51(2),53,54,56(2),57,58(2),59,60,61,63,65 (40+,50+)
	PQ5	19	2+	17	?	56	48-65	47(2),48,52,53,54,55(2),56,57 (38+,41+,46+,47+), 62
	PQ9	18	-+1	15	43	53	47-62	53,56
1961	PQ10	5	1+-	2	27++	55	53-56	47(2),53,54(2),55(3),57(3)58,60(2),62,63(2),67 (36+,39+(2)
	PM3	39	-+3	25	43+	57	47-67	46,47,51,52,55(3),56,58(2),59,60,(48+)
	PM4	19	-+3	13	57	55	46-60	
1962	P2	25	1+8	13	45+	60	52-69	52,55,57,60,62(2)63,65,69, (48+,49+,50+(2)
	P3	20	-+8	8	59	60	57-65	57,59(2),60,61(2),62,65
	P4	12	-+1	6	58	62	62	62(2), (48+(2),56+,59+)
	P5	20	-+6	10	62	57	48-64	48,51,54,55,62,64(2), (41+,42+,50+)
	P6	23	1+7	11	50+	60	53-64	53,55,59,61(3),62,64. (34++,40+,51+)
	P7	38	3+9	18	53+	59	51-64	51,55,57,58(2),59(3),60(3),61,62,64, (25++,38+,45+,50+)
	P11	20	-+4	13	54	62	53-68	53,57,61,62,63(3),64,66,68(2), (46+,50+)
	P16	37	3+5	23	48	61	54-69	54(2),55,56,58(2),60(3),61(2),62(3),64,65(2),66,67,69 (54+,55+,56+)
	P17	19	-+2	5	58	62	55-65	55,63,64,65(2)
	P19	16	1+3	8	42	60	56-61	56,59,60(3),61(2) (55+)
	P21	25	-+6	4	47+	58	55-61	55,61, (40+,56+)
	P22	19	-+5	6	56	56	51-63	51,55,60,63 (23++,49+)
	P28	22	-+7	7	61	57	54-64	54,55,57,58,64, (47+,49+)
	P29	43	1+10	25	52	58	46-68	46,47,53(2),54,55(2),57(2),60(2),61(3),62,65,68 (26++)
	P31	10	-+2	2	43+			(45+,51+)
A. Quercicola								
1961	PQ6	9	-+1	7	29+	33	28-36	28,32(3)35(2),36
	PV4	55	-+8	44	26,31	26	21-33	21(3),22,23(5),24(3),25,26(8),27(3),28(3),29(4),30(4),31(3),33
	PV6	4	---	1	24,24			38
1962	P,	16	-+2	3	30	31	29-32	29,32, (15+)
	P9	17	-+4	3	25+	28	24-31	24,30,31
	P25	9	-+1	5	28	32	30-34	30(2),32,33,34
	P26	3	---	--	20			
A. Minus	P8	6	-+2		8			
1962	P10	13		1	8			11
	P13	7			6			
	P14	10			7			
	P15	6			6			
	P18	2			7			
	P27	6			6			
	P30	6			7			

FIG 18 PROGENY OF INDIVIDUAL FEMALES.
FREQUENCY DISTRIBUTION OF MULTILOCULAR PORES.

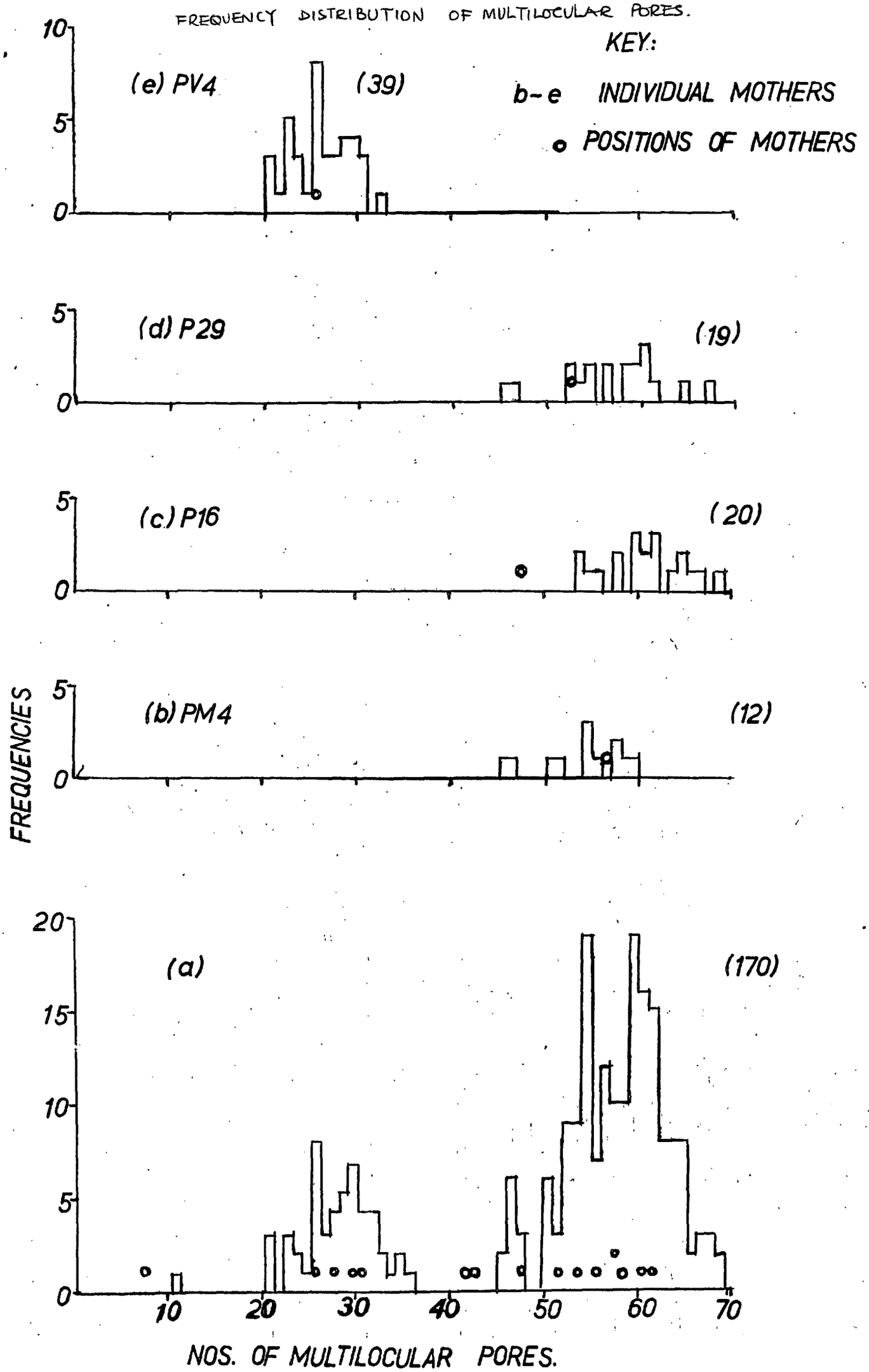


TABLE 2a

	EXP	PROGENY No. of settlers	No. of Nymphs mountd. L1	No. of Nymphs mountd. L2	Adults	No. of Multilocular pores. Mother	PROGENY Mean	PROGENY Range
A.variolosum 1961&61	21	452	14	92	231	(54) 42-62	58	46-69
A.quercicola 1961&62	7	113	-	16	63	(26) 20-31	30	21-36
A.minus	8	55	-	2	1	(7) 6-8	11	-
Total	36	620	14	110	295			

Nos. in brackets = averages.

In table 2 the following data are recorded for each experiment:

- the original number of settlers
- the number of mymphs removed and mounted for morphological studies
- the number of adult progeny obtained
- the number of multilocular pores of the mother and of the progeny, including the calculated means and ranges for the latter. The figures marked with + are incomplete because owing to damage, distortion or fungal infection of the mounted specimens, the exact number of pores was impossible to establish. These incomplete figures were not used in calculations or construction of the histogram.

In all successful experiments the parents produced offspring of their own kinds only; this has been confirmed by identification of the mounted first instar larvae (where available) and of the adult females. The conditions of the numbers of multilocular pores in all the mothers and their adult progeny are summarized in Table 2a and in the frequency histogram Fig. 18(a). In the histogram the positions of the mothers are marked by white dots (or circles). The histogram shows very clearly three distinct groups almost identical with those based on the specimens of the three species collected in the field (cf. p. 27 morphology). The range of individual variation (Table 2a) for A.variolosum is 42-62 as compared with 40-74 for the field population and for A.quercicola these figures are 20-31 and 18-37 respectively. These two species, for which sufficient numbers of adult progeny were obtained, show approximately normal frequency distribution. The only female of A.minae bred, with its 11 multilocular pores falls well within the known range (3-15 pores) of this species. In individual experiments, where the number of adult progeny was

large enough to be considered as sufficiently representing the true condition, the range of individual variation in the numbers of multilocular pores was very wide, extending over most of the range established for the species.

In A.variolosum this is well illustrated in experiments PQ5, PQ9, PM3, PM4 and P29 in Table 2, the results of the experiments PM4 and P29 are also represented in histograms, Figs. 1b and 1d respectively. The number of pores of the parents in these five experiments varied from 43 (PQ9) to 62 (P5), but the progeny of each of these females showed very similar and wide ranges of individual variation, from about 47 to over 60 pores. In experiments P_7 and P_{11} the females with rather high numbers of pores (over 53) produced progeny also with generally higher numbers of pores; these results, however, appear to be accidental, because in experiments P_{16} and P_{19} the mothers with few (48) or very few (42) pores produced a number (23 and 8 respectively) of progeny all of which had the numbers of pores much higher than the parents, and comparable with the ranges exhibited by the progeny in experiments P_7 and P_{11}. It appears therefore that the actual number of pores of the mother has no direct influence on this character in the progeny.

The experiments PQ9 and P5 are particularly instructive on this point. In experiment PQ9 in 1961 the female with 43 pores produced 15 adult progeny whose range of the numbers of pores was 47-62 (average 53) pores. One daughter, which happened to have 62 pores, was used in experiment P5 in 1962, and in spite of a very high number of pores, produced progeny (10 granddaughters) whose range of individual numbers of pores was 48-64 (average 57) i.e. very similar to that of her own generation. These two experiments would indicate that the wide range of individual

variation in the numbers of pores is characteristic even within this single family-line of this species.

Similar results were obtained for A.quercicola, although the smaller number of experiments carried out with this species and, with one exception (PV4), too small numbers of progeny obtained, make these results less conclusive; but they, certainly, do not contradict the conclusions drawn from the observations on A.variolosum. In experiment PV4, which is also represented graphically in the histogram Fig. 1(e), and in which the second female was introduced accidentally, the two females with 26 and 31 pores, respectively, produced together 44 adult progeny whose range of the numbers of pores was comparatively wide, 21-33 pores, and the average was 26 pores, i.e. less than the average for the two mothers. In most experiments the position of the mother is well within the range of the progeny, but in experiment P_{25} the female with 28 pores produced 5 daughters, all of which had higher number of pores; this, no doubt, is again due to the small number of progeny obtained.

In the only successful experiment with A.mirus (P_{10}) the female with 8 pores, which is about average number for this species, produced a single adult progeny with 11 pores; the latter is nearer the upper limit (15 pores) of the range of individual variation for A.minus.

These experiments show that each species breeds true, i.e. each produces the progeny of its own kind; they also demonstrated that, within each species the actual number of multilocular pores of the mother does not influence this character in the progeny, i.e. the female with any number of pores appears to be capable of producing progeny whose numbers of pores may cover the whole range characteristic for the species to which it belongs. Each of the three species appears to be a separate, genetically determined entity.

PARTHENOGENESIS

At no time during the whole period of studies were any stages of the male found either in the field or in experimental breedings. Should males be present they would be expected to emerge, as in other Coccoidiza (Bliss et.al, 1935, Hoy, 1961) at the time of the appearance of the young adult females.

The absence of males in the breeding experiments in which the small plants used could be, and indeed were, most meticulously examined - particularly at the critical period (i.e. just before the young adult females appeared), with the position of every settler marked and accounted for - seems to offer sufficiently convincing grounds for assuming that all three species are parthenogenetic.

Among 142 described species of Asterodiaspis and related genera (Russell, 1941) only in 32 have males been recorded. Among 20 species referred to the genus Asterodiaspis only three (A.illicicola, A.perplexum and A.variabile) are known to be bisexual.

This may be due to inadequate knowledge of the group, but may also indicate that in this group bisexuality is the exception rather than the rule.

Reporting on his anatomical studies on "Asterolecanium variolosum" "Connecticut" Parr (1940) found that the sperm sac of the female was never observed to contain any spermatozoa, no matter what time of the year the material was cut for microscopic examination. He never found any males at any time and concluded that the insect was parthenogenetic.

LIFE CYCLE AND HABITS

Studies on the life cycles and habits of the three species of Asterodiaspis were made in the field in 1961 and 1962 and were supplemented by observations on the specimens bred in the greenhouse.

As already explained, the life cycle studies were based on samples taken at suitable intervals. At the initial periods of moulting, these samples were taken daily, and at 2-3 day intervals during the other periods of development. From the compositions of the successive samples, the periods of occurence of the stages of each species in the field were obtained, and from the dates of the first occurence of successive stages in the samples, the approximate individual duration of each stage was computed. The pharate forms (Hinton, 1946) of the second instar nymphs and of the adult females (i.e. completely formed individuals still enclosed within the skin of the preceeding instars) helped in establishing the number and the sequence of the instars. These pharate forms were particularly useful in determining the period of occurence and the duration of the second instar nymphs of each species, which at that stage exhibit no definite salient characters at all for the separation of these three species.

The direct observations on the habits were based mainly on the isolated material of each species used in breeding experiments, which assured the identity of the species. Some observations possible in the circumstances, were also made in the field on selected and marked specimens but in these cases the identity of the species studied could be established only after the observations were completed and the insects had been killed and mounted.

LIFE CYCLE

All three species have only one generation in the year and their life cycles are very similar. The whole development from the egg through the first and second instar nymphs to the adult female takes place within three summer months, June - August; the adult females hibernate, resume growth in the following spring and lay eggs in June.

As shown in Table 3, in A.variolosum and A.quercicola oviposition starts about 16th June and in about 14 and 10 days, respectively, the first crawlers begin to appear. In A.minus oviposition starts later (22nd June) but the crawlers already begin to appear within 3 to 4 days and this process continues for 6 to 7 days or more.

In all three species the beginning of oviposition of individual females varies, and in the field the eggs are to be found under the tests of females for 3 - 4 weeks till 10th July.

In all species the free life of the first instar nymphs (crawlers) is short and the settlers are to be found almost simultaneously with the appearance of the crawlers. They can be found in the field throughout July. By the first week of August all surviving individuals have moulted into the second instar nymphs; the latest date of observation of the settled first instar nymphs for A.variolosum and A.quercicola were 4th and 7th August, and a few days later (10th August) for A.minus.

The first appearance of second instar nymphs was observed on 21st and 22nd July in A.variolosum and A.quercicola, but not till 25th July in A.minus. By 31st August all surviving second instar nymphs of A.variolosum and A.quercicola have moulted into adult females, but in A.minus some second instar nymphs were still present on 9th September.

RESULTS AND OBSERVATIONS — TABLE 3

LIFE CYCLES (FIELD)

1961

	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
A.minus												
*Egg						22	10					
1st Larva						26		10				
2nd Larva							25		9			
Adult								16				
A.quercicola												
Egg						16	11					
1st Larva						26		7	Aug ↓			
2nd Larva							21		31			
Adult								10				
A.variolosum												
Egg						16	11					
1st Larva						30		4	Aug ↓			
2nd Larva							22		31			
Adult								10 Aug				

The adult females of A.quercicola and A.variolosum appeared on 10th August but those of A.minus were not observed before 16th August (Table 3).

Taking into consideration the dates of first occurence it appears that individual durations of various stages somewhat differ in the three species (Table 4). A.variolosum has a rather long period of incubation (14 days), and the lives of the first and second instar nymphs are 22 and 19 days respectively. In A.quercicola the incubation period is shorter (10 days); the life of the first instar nymph is 25 days and that of the second instar nymph 20 days. In A.minus the incubation period is very short (4 days), but the durations of the first and second instar nymphs are longer - 29 and 22 days, respectively. In all species the life of the first instar nymph is consistently longer than that of the second instar nymph. It is interesting to note that, compared with A.variolosum, the progressively shorter period of incubation in A.quercicola and A.minus is accompanied by progressively longer duration of life of the two nymphal instars. But the the complete development from the ~~appearance~~ time of the deposition of the eggs to the appearance of the adult females takes the same length of time, which from the recorded dates, surprisingly, was exactly 55 days in all three species. If, however, the incubation time is deducted, the figures for the three species are 41, 45 and 51 days respectively. As the incubation period in these three species becomes gradually shorter, the time of development of the first and second instar nymphs increases.

Thus the life cycles of the three species are very similar and follow the same pattern but they differ by degrees in the duration of oviposition period, the length of the incubation time and the length of life of the nymphal stages. A.variolosum has the longest incubation period

TABLE 4

	A. VARIOLOSUM		Q. QUERCICOLA		A. MINUS	
STAGES	Dates	Duration	Dates	Duration	Dates	Duration
EGG	16.6		16.6		22.6	
INCUBATION		14 days		10 days		4 days
1st Larva	30.6		26.6		26.6	
Duration		22 days		25 days		29 days
2nd Larva	22.7		21.7		25.7	
Duration		19 days		20 days		22 days
ADULT FEMALE	10.8		10.8		16.8	
TOTAL DURATION		55 days		55 days		55 days
POST EMBRYONAL DEVELOPMENT		41 days		45 days		51 days

and afterwards develops rapidly; A.minus has the shortest incubation period and the slowest rate of post-embryonal development, and A.quercicola is intermediate between the two. Although the first instar nymphs (crawlers) of the three species appear at about the same time, the second instar nymphs and adults of A.variolosum are the first to appear, followed by those of A.quercicola, and finally by A.minus.

Comprehensive life cycle studies in the semi-artificial conditions of experimental breeding in the greenhouse were possible only in the case of A.variolosum in which females successfully produced sufficient numbers of settlers and therefore provided an opportunity for reasonably frequent sampling.

Because the females had been previously kept in the laboratory (about 19°C) oviposition was accelerated by about two weeks and the first appearance of adult females by about the same length of time. The total developmental period was 53 days as compared with 55 days in the fields.

No similar studies of life cycles of A.quercicola and A.minus were possible because the few settlers produced were left on the plants so as to obtain as many adult progeny as possible.

H A B I T S

Early in May the fully grown adult females, each within a pit-like depression of the bark of the twig, are clearly visible through their transparent tests. The test is convex, glassy, hard and comparatively thick, with a yellowish or greenish tinge, and with a well-developed marginal fringe of short waxy threads extending all the way round; the posterior end of the test is drawn out into a "tail" with a small transverse oval

opening dorsally at the apex. The test closely envelopes the reddish brown and more or less circular, lens-shaped body of the insect. Dissection of the females at this time reveals the presence of large numbers of already formed eggs; later in the month the eggs, packed to capacity within the body of the female are clearly visible through the skin and the test. There is no salient external character by which the three species may be definitely separated. All show great variation in colour, size, shape and convexity of the test which seem to depend largely on the actual position on the twig. Generally, however, A.variolosum is larger but flatter and A.minus smaller and rather more convex; the tests of A.variolosum and A.quercicola appear to be quite smooth and that of the young mature female of A.minus shows a kind of tortoiseshell sculpturing; the marginal fringe is especially dense in A.variolosum, and the "tail" is most conspicuous in A.minus.

Oviposition

The eggs are laid under the test behind the female which, as oviposition progresses, gradually contracts and shrivels; by the time the process is completed the body of the female is reduced to a narrow dark-brown crescent under the anterior part of the test, the rest of the space being occupied by the deposited eggs. In all three species the eggs are oval, of about the same size, pale pinkish colour and velvety texture.

In A.variolosum and A.quercicola the individual females lay their eggs within about 4 days, and all eggs are deposited before the crawlers hatch, 14 and 10 days later. In A.minus, the process lasts longer, 6-7 days, but this species is ovoviviparous; the eggs are deposited in a more advanced stage and hatch immediately after they are laid. This can be seen on

mounts and also by examination of the contents under the test at various stages of oviposition. At an advanced stage of oviposition, A.variolosum and A.quercicola were found with full complements of eggs and no crawlers under the test; later when the hatching had begun there was a tangled mass of eggs, partially and fully emerged crawlers and of the eggshells. In A.minus, after oviposition had started, at no time were eggs present under the test, except one or two just deposited; usually only some crawlers and eggshells were to be found under the test. Often a few eggs remain within the body of the mother; they appear to be able to hatch but seem to be unable to emerge and on occasions fully formed first instar nymphs are found within the body of the female.

The observation with regards to oviposition in the three species is interesting because Parr (1940) reported that in Connecticut A.variolosum was also ovoviviparous. As already mentioned Parr's work was done before Russell established the identity of the three species. According to Russell (1941) all three species occur in Connecticut - thus it is not certain to which Parr's observations refer. Pritchard and Beer (1950) mentioned that both A.minus and A.quercicola in California were ovoviviparous and parthenogenetic.

Hatching

The eggs hatch by splitting along the margin round the anterior end and laterally about two-thirds of the way towards the posterior end. This has been observed in A.variolosum and A.quercicola; examination of the shed eggshells of A.minus showed that it has the same mode of hatching. Partially emerged crawlers with the eggshells still attached to the rear of

their bodies, or to the legs were seen thrashing about with their legs and antennae in an effort to free themselves. The abandoned eggshells are translucent, creamy white.

Emergence of Crawlers

The hatched crawler remains quiescent under the test for some time, probably up to 2-3 days, after which it moves towards the small oval opening at the posterior end of the mother's test and pushes its way out. Frequently, however, a number of crawlers fail to emerge and can be later found dead under the test. Sometimes this appears to be due to one crawler blocking the exit hole and so trapping later ones within the test. The crawlers usually emerge with the ventral side directed towards the surface of the twig on which the mother has settled, but occasionally they come out in the reversed position, climb over the test of the mother and then descend to the surface of the twig. The emerged crawlers did not appear to need to rest, for they immediately began to wander away from the parent, along an apparently irregular path with frequent turnings and crossings of the track previously made, but generally leading towards the terminal twigs. While moving, their antennae as well as the two long posterior setae, were seen to wave about continuously, frequently touching the surface of the bark crawled upon. The behaviour of the crawlers under experimental conditions in the laboratory will be discussed later.

Isolated crawlers bred and kept in tubes in the laboratory have been seen to be still moving after 26 hours, but in the field settling appears to take place earlier.

Settling

Eventually the nymphs settle, usually in the axil of a leaf or

bud, or under bud scales, but sometimes also on the more exposed parts of the twig. No crawlers were ever observed on leaves, though a few have been seen on the bases of leaf petioles where some actually settled. Once settled the nymphs are unable to resume further migration; recently settled nymphs were gently prodded with a feather but could not be induced to move.

In the field the nymphs appear to settle more or less evenly on one, two, three and four years old terminal sections of the twigs. But observations on the progeny of the isolated insects bred in the greenhouse showed that the three species differ in their preferences for settling sites; this was also confirmed by the detailed analysis of the distribution of the three species in the field which will be discussed later.

Table 5 shows the numbers of the crawlers which settled on twig sections one (A), two (B), three (C) and four (D) years old as observed on the potted plants in the greenhouse.

The crawlers of A.variolosum settle primarily on terminal one year-old growth on which 67% (226 out of 338) settled, with considerably fewer on second and third year growths (52 each), and only a few (8) on the four year-old twig sections. In A.minus the situation was rather reversed, and well over three-quarters (66 out of 83) of the insects settled on three and four year-old sections of the twigs, with only a few (7 and 10) on the one and two year-old growths. In the field, however, A.minus appeared to be more evenly distributed on all the four sections of the twigs.

In the experiments with A.quercicola only 58 settled nymphs were obtained; of these about three-fifths (37) were found on the older twig sections (three and four years old) and the remaining two-fifths on the younger twig sections. In the field, however, A.quercicola appeared to

TABLE 5 POSITIONS OF SETTLERS ON POTTED PLANTS

PLANT NO.	SPECIES	Twig Sections A	B	C	D	TOTAL
P2	v	20	3	-	-	23
P3	v	20	-	-	-	20
P4	v	5	2	2	-	9
P5	v	12	5	2	-	19
P6	v	15	4	2	2	23
P7	v	34	1	2	1	38
P11	v	17	1	1	1	20
P16	v	22	10	7	-	39
P17	v	6	5	7	1	20
P19	v	12	-	1	3	16
P21	v	10	6	9	-	25
P22	v	9	4	8	-	21
P28	v	14	5	4	-	23
P29	v	30	6	7	-	43
		226	52	52	8	338
%		(67)	(15.4)	(154)	(2.2)	
P1	q	-	-	16		16
P9	q	8	2	1	6	17
P25	q	2	3	1	6	12
P26	q	-	-	3		3
P31	q	4	2	4		10
		14	7	37		58
%		(24.2)	(12.1)	(63.7)		
P8	m	3	2	2		7
P10	m	-	-	-	13	13
P12	m	-	-	-	3	3
P13	m	-	-	1	6	7
P14	m	3	2	5	-	10
P15	m	-	1	-	5	6
P18	m	-	2	5		7
P23	m	-	-	7		7
P24	m	1	1	2	8	12
P27	m	-	-	5		5
P30	m	-	2	-	4	6
		7	10	66		83
%		(8.4)	(12.1)	(79.5)		

v = A. variolosum.
q = A. quercicola.
m = A. minus.

prefer the terminal one and two years old twigs with fewer specimens being present on the three and four year-old sections. The different results in the experiments were probably due to the small numbers of settlers obtained and perhaps, the young seedling used as hosts; a number of crawlers might have been lost because they actually failed to settle.

Thus the three species differ as to the twig sections on which they settle, A.variolosum occurring almost exclusively on the younger (1-2 year-old) sections of the twigs and A.quercicola, although preferring the youngest twigs, has a wider distribution over the older sections as well. A.minus is evenly distributed over all sections of twigs, and is not easily bred on seedlings. The factors responsible for these differences have not been investigated and are not understood, but the chemistry of the twig sections of the host may well be important, e.g. thickness and the anatomy of the bark.

The chemistry of the tissues of the host plant has some effect on the populations of the coccids. Steyn (1951) found that the chemistry of the host affected the development of California Red Scale (Aonidiella aurantii); for example a low nitrogen content was found to lead to earlier reproduction and the production of more generations per season.

Thompson (1942) discovered that magnesium defficiency in citrus affected the populations of Purple Scale (Lepidosaphes bechii). Where there was magnesium defficiency and the citrus leaves were 'bronzed', there was a corresponding increase in the numbers of scales counted per one hundred leaves.

It was observed in the field that where a twig is more or less horizontal, different numbers of insects settle on the upper and lower

TABLE 6

		Upper surface	Lower surface	Total
DHII	1	-	5	5
	2	2	3	5
	3	1	5	6
	4	5	8	13
	5	2	4	6
	6	1	8	9
	7	3	10	13
	8	-	9	9
	9	2	7	9
	10	4	12	16
	11	3	9	12
	12	-	3	3
	13	2	12	14
		25	95	120
	%	(21)	(79)	
DHIA	1	11	37	48
	2	2	8	10
	3	2	3	5
		15	48	53
	%	(24)	(76)	
DHIB	1	1	10	11
	2	4	9	13
	3	-	14	14
	4	4	11	15
		9	44	53
	%	(17)	(83)	
		(49)	(187)	(236)
	%	(21)	(79)	

surfaces. The Table 6 shows the results of counts on 20 horizontal twigs taken from 3 trees and shows that, in general, considerably more insects (about 80%) settle on the lower surfaces of the twigs. On the more or less vertical twigs, such as the twigs of seedlings and some of the old trees, the insects appear to settle rather evenly all around the twig. After the ambulatory stage, the larva settles down on the bark of the twig through which the mouthparts are inserted for feeding, and soon a depression begins to show in the bark. As the settler grows, its elongated body assumes a more rounded outline and its body surfaces grow more convex, both dorsally and ventrally.

Moulting, 1st - 2nd instar

This appears to take place by splitting of the skin along the margin, but the actual process was never observed and the dorsal skin never recovered, although the pharate forms have been seen. The ventral derm, however, often remains almost complete under the second instar nymph fixed in position by the new mouthparts. The shed skin is very thin and delicate.

Second instar nymphs

There is no apparent sudden change after the moult, and the insect continues to grow more and more circular in outline and in convexity. The new test is still thin and transparent; the body shows a dark longitudinal median band extending from the posterior end to about half way down the thoracic region; a series of transverse grooves on the abdomen suggest abdominal segmentation.

2nd Moulting; 2nd instar - adult

This was observed to be effected by splitting of the skin along the entire margin, separating the dorsal and the ventral derms.

The dorsal derm and the test of the nymph are shed, and drop off, while the nymphal ventral derm remains under the adult, attached to it around the mouthparts. This ventral cast skin of the second instar nymphs, as well as that of the first instar nymph, is very thin and delicate; it crumbles and is usually lost when the adult female is removed for mounting.

The adult female

Soon after the second moult the body of the adult female becomes almost round in outline, and the test produced is thicker and harder, though still transparent; traces of the marginal fringe now begin to appear. There is no apparent change during the overwintering period till the next spring. In April the growth is resumed, at which time the colour of the body becomes brighter and more intense, and the test more shiny; the insect increases in size and convexity, and the fringe of short waxy threads is quite conspicuous. The full size of the insect and the final completion of the test are attained in May when the gravid female is ready for oviposition.

BEHAVIOUR EXPERIMENTS

Since the crawlers are the only mobile stage in the life cycle of these insects, an understanding of their behaviour might help to explain the patterns of distribution of the adult insects.

It had been decided to study their reactions to the main environmental factors such as gravity and light.

LIGHT UNDER FIELD CONDITIONS:

While studying the reactions of crawlers to light, it was necessary in some experiments, to control the direction or the intensity of light. However, it was always desirable that the quality of light used should, as much as possible, approximate to the more diffused conditions found in the field.

The rays of light reaching an insect in the field are interrupted by leaves and branches, thus causing the light to diffuse. In such conditions an insect does not usually react to a point source of light or a beam, but rather to a general direction of light and various patterns of light and shade.

Fraenkel and Gunn (1960 p.53) have observed that "in nature the light often takes the form of a patchwork with sharp shadow edges instead of the ideal smooth gradients so far discussed" (with regards to experiments).

Diffuse light has therefore been used in the light experiments, and in the experiments with petri dishes, the reactions of crawlers to different patterns of light and shade have been investigated.

LIGHT EXPERIMENTS - 1st SERIES

A pyrex dish, 30 cm. diameter and 15 cm. depth, was taken and the bottom covered with tracing paper on the outside. The dish was half filled with water and placed on a tripod 25 cm. high. The light source was an electric bulb clamped to a retort stand 15 cm. above the level of the water which absorbed the radiant heat from the bulb. The paper at the bottom of the dish diffused the light which fell on to the bench. A diagram of the apparatus is given in Fig. 19.

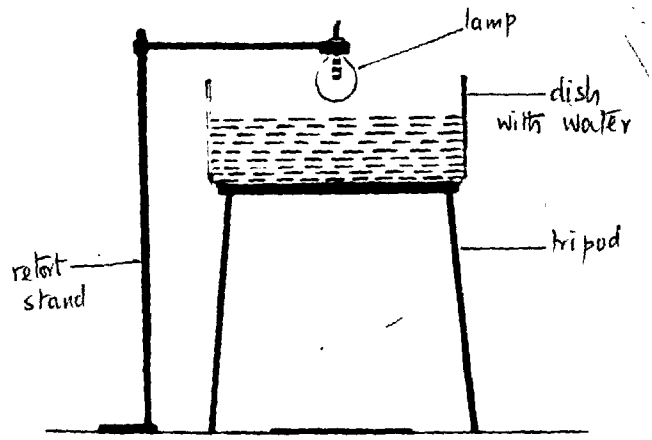
During the experiments the room was in total darkness except for the experimental light source. Two light intensities (provided by a 25 W. and a 150 W. "Osram" lamps) and two positions of a paper platform - vertical and horizontal - on which the crawler was released, were used. Room temperature during each observation was recorded.

Each observation consisted of carefully lifting a crawler from a tube containing a marked adult female, with a tipped quill feather on to a piece of white paper; the path of the crawler on the paper was marked by following the moving insect with the sharp tip of a soft pencil, for a period of 5 minutes. Distances travelled in 15-second intervals were marked off.

Between successive observations, one factor at a time was altered, either position or light intensity. Experience showed that most crawlers were "fatigued", i.e. stopped moving after four successive observations. Allowing about 2 minutes between observations for transfering the insect from one sheet of paper to another and for changing one of the factors, each crawler was used for about 30 minutes. In some exceptional cases crawlers were still noticeably active after six observations.

FIG. 19

apparatus for producing diffuse light.



SECOND SERIES:

(a) This series was designed to test the reactions of the crawlers to light coming from one direction .

The apparatus consisted of a white wooden box about 30 cm. x 30 cm. x 30 cm. with a circular hole (diameter about 12 cm.) cut in one of its sides. This hole was covered with a plate of frosted glass to diffuse light entering the box from a 100W electirc bulb clamped in a retort stand. Placed between the bulb and the frosted glass was a jar of cold water to absorb the heat radiated from the bulb. (Fig. 20)

For each observation a sheet of white paper was placed horizontally inside the box and a crawler was transferred on to the paper. The distance travelled in 5 minutes was marked at 15 second intervals. The temperature inside the box was recorded.

(b) Phototaxis: The edge of a petri dish was covered with a strip of black paper except for a "window" about 3 cms. wide. For each observation which lasted 15 minutes, the crawler was placed in the centre of the petri dish which was then covered with a sheet of black paper. Light therefore reached the inside of the petri dish only through the "window". The starting position and the positions at 5-minute intervals were marked on an appropriate sheet of paper. (Fig. 21)

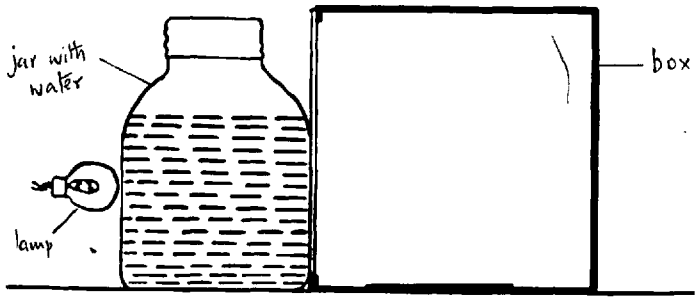
THIRD SERIES

LIGHT AND GRAVITY - TUBES

As it was observed in light experiments in which the insects crawled on a vertical plane that most of the insects crawled upwards with low and high intensity lights, it was necessary to establish whether these

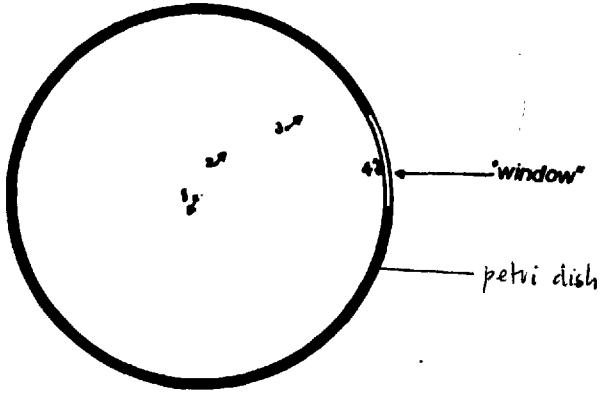
FIG. 20

apparatus for lateral illumination.



LIGHT GRADIENT

FIG. 21



1, 2, 3, 4 = successive positions of crawlers.

reactions were solely due to the stimulus of light or whether gravity was also involved.

A small tube was partially darkened by wrapping a piece of black paper round one half of it and exposing the uncovered half to light (Fig.22).

Several crawlers were placed inside the tube, one at a time, to note their reactions.

There were three possible positions of the tube:

1) darkened half of tube uppermost

2) illuminated half of tube uppermost

3) tube in a horizontal position

FOURTH SERIES:

In this series different sections of the petri dishes were painted with black and white and the reactions of the crawlers to different patterns of light and shade were tested. The experiments were carried out in a C.T. room at 21°C and 80% R.H., the petri dishes being placed in a box similar to that used in series 2 (Fig. 23). Sheets of paper with the patterns of the petri dishes were used to record the paths and positions of the crawlers at given intervals of time.

To test for Skotaxis

a) The edge of a petri dish (8 cm. diameter) was divided into 8 equal sections, alternate sections being painted black and white. One crawler at a time was placed in the centre of the petri dish and its path was traced on a sheet of paper with the pattern of the petri dish. The positions, at the start, and 5-minute intervals for 15 minutes were marked (Fig. 24).

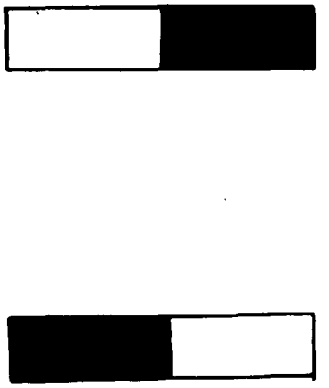


FIG 22

partially-darkened tubes.

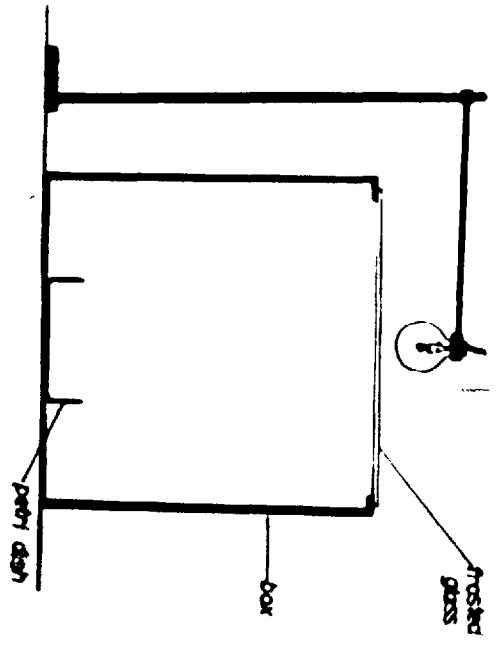


FIG 23

Illumination of petri dishes

FIG 24

SKOTOTAXIS.

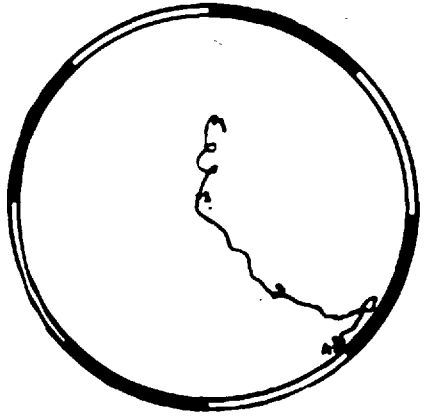
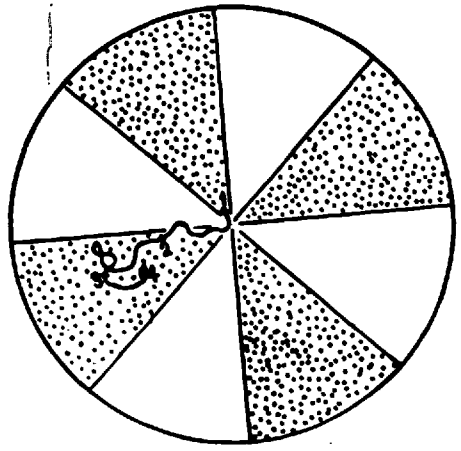


FIG 25

REFLECTED LIGHT



1, 2, 3, 4 = successive positions of crawlers and their paths.

b) The floor of the petri dish was divided into 8 equal sectors alternately painted black and white. One crawler at a time was placed in the centre of the petri dish and its path was traced on a sheet of paper with the design of the petri dish. Each observation was carried out for 15 minutes and the positions of the crawler after 5-minute intervals were marked (Fig. 25).

RESULTS AND OBSERVATIONS

The first two series of experiments involved the measurement of distance travelled by the crawler in a given period of time, from which the linear velocity could be calculated. The variation of linear velocity with light intensity (photokinesis) and the frequency of turning under varying light intensities (klinokinesis) as well as positive or negative reaction to light source (phototaxis) were assessed.

FIRST SERIES

(i) VERTICAL - LIGHT INTENSITY AND GRAVITY

In Appendix V (m), (q), (v), the following have been calculated for each species: under two light intensities: linear velocity in cms. per minute, mean angle of path to the vertical, direction of path (left or right), reaction to light (phototaxis), and summarised in Table 7.

The linear velocities under the 25 Watt lamp are 1.18, 1.40 and 1.50 cm./min. for A.minus, A.quercicola and A.variolosum respectively. The corresponding linear velocities under the 150 Watt lamp are 1.30, 1.45 and 1.55 cms./min. A.minus is seen to be the slowest and A.variolosum the fastest under both light intensities, and A.quercicola is just intermediate.

TABLE 7

LIGHT & GRAVITY - VERTICAL

AT 25W	linear velocity cm/min	mean angle to vertical	direction L=left R=right	reaction to light	changes of direction
A.minus (14)	1.18 0.63 -1.78	42.1 1-90	8L 4R	6+ 8-	4.70 1-10
Aquercicola (14)	1.40 0.75 -1.98	48.8 9-90	9L 4R	11+ 3-	4.40 0-14
Avariolosum (33)	1.50 0.95 -2.03	40.5 1-90	17L 14R	27+ 6-	3.20 0-12

Nos. in brackets = nos. of observations

TABLE 7 continued

LIGHT & GRAVITY - VERTICAL

AT 150 W	linear velocity cm/min	mean angle to vertical	direction L=left R=right	reaction to light	changes of direction
A.minus (15)	1.30 0.80 -1.88	46.6 9-90	9L 5R	8+ 7-	2.30 0-8
Aquercicola (17)	1.45 0.55 -2.08	44.9 1.5-79	8L 9R	15+ 2-	2.60 0-6
Avariolosum (35)	1.55 0.93 -2.88	31.1 2-90	15L 19R	30+ 5-	2.43 0-10

All three species have a higher linear velocity at the higher light intensity.

The numbers of changes of direction which are 4.70, 4.40 and 3.20 under 25 Watt lamp for A.minus, A.quercicola and A.variolosum respectively, show that A.minus is turning most frequently and A.variolosum the least. The corresponding figures 2.30, 2.60 and 2.43 at 150 Watt show that all three species are turning less frquently at the higher light intensity.

The reaction to light source (marked + and -) are 6+,8-; 11+,3-; and 27+,6- at 25 Watts for A.minus, A.quercicola and A.variolosum respectively, and at 150 Watts, they are 8+,7-; 15+,6-; and 30+,5-. A.minus appears to be indifferent to light source and attraction towards light is equal ~~equal~~ to movement away from light, but A.quercicola and A.variolosum show very positive attraction towards the light source. There is no significant difference in the attraction of all three species under the two light intensities.

Examination of the directions of the paths to left or right does not reveal any consistent pattern either between the species or between the two light intensities. (Figs. 26a, 26b, 26c)

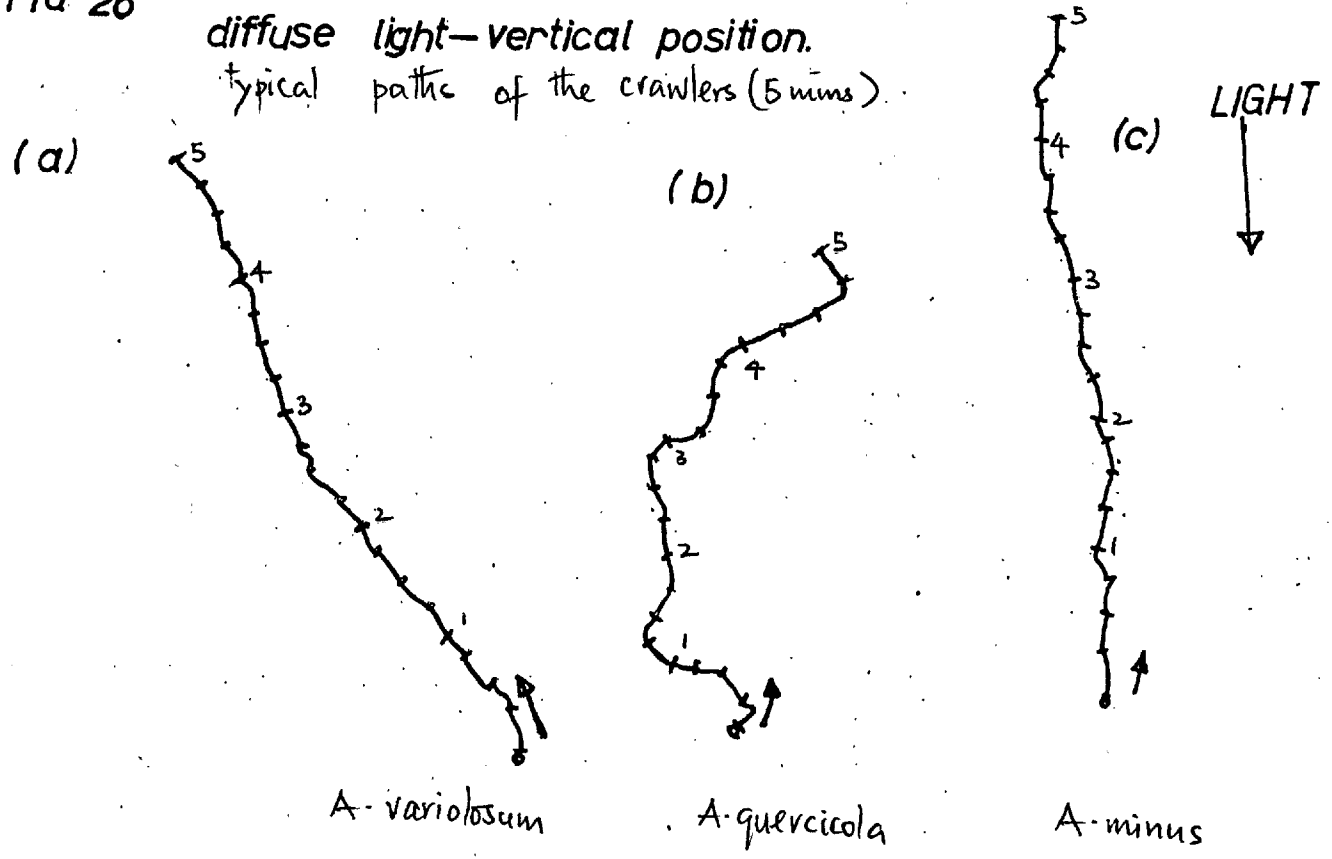
(ii) HORIZONTAL - LIGHT INTENSITY (Appendix VI)

Table 8 shows the results obtained for the horizontal position in which the operative factor was light intensity. The linear velocities and the numbers of changes of direction under 25 Watts and 150 Watts are shown for the three species.

The linear velocities under 25 Watts are 0.90, 1.18 and 1.23 cm./min. for A.minus, A.quercicola and A.variolosum respectively. A.minus is thus the slowest and A.variolosum the fastest with A.quercicola

FIG 26

diffuse light—vertical position.
typical paths of the crawlers (5 mins).



LIGHT INTENSITY - HORIZONTAL Table 8

	linear velocity	changes of direction		linear velocity	changes of direction
AT 25 Watts	cm/min	1=90°	AT 150 Watts	cm/min	1=90°
A.minus *(13)	(0.90) 0.45-1.50	(7.0) 0-14	*(16)	(1.08) 0.68-1.68	(6.9) 3-14
A.quercicola *(14)	(1.18) 0.55-1.63	(5.9) 0-15	*(16)	(1.15) 0.43-1.68	(5.7) 1-14
A.variolosum *(32)	(1.23) 0.63-2.10	(6.8) 0-19	*(32)	(1.25) 0.73-2.13	(6.2) 1-15

*( ) nos. of observations.
( ) averages.

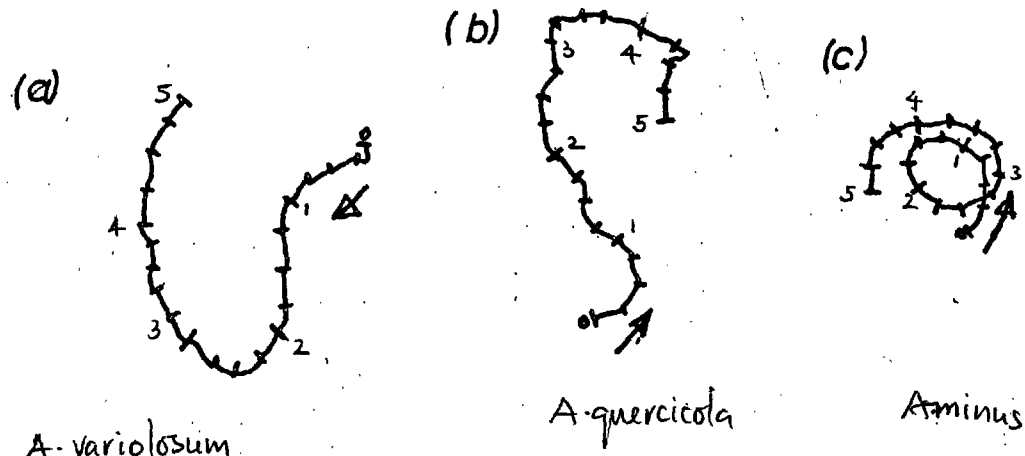
being intermediate between the two. With the exception of A.quercicola, the linear velocities 1.08,1.15 and 1.25 cm/min for A.minus, A.quercicola and A.variolosum respectively, are higher at the higher light intensity.

The number of changes of direction are not as consistent as the linear velocities. Under the lower light intensity the number of changes of direction are 7.0, 5.9 and 6.8 for A.minus, A.quercicola and A.variolosum respectively, and under 150 Watts, the corresponding figures are 6,9, 5.7 and 6.2 respectively. In all three species there is a very slight reduction in the rate of turning under the higher light intensity. (Figs. 27a, 27b, 27c.

The effects of changing the intensity or the direction of light and of changing the position of thenymph in relation to gravity were also assessed.

It is possible that a nymph may not immediately begin to react to a new set of factors after a change of a factor,i.e. its reactions under the previous set of factors may persist into the new condition. Thus a nymph observed under a set of factors after one or more changes of factors might be expected to react differently from when it is freshly observed under the same conditions.

FIG. 27 diffuse light — horizontal position.
typical paths of crawlers for 5 mins.



A. variolosum

A. quercicola

A. minus

The observations on (1) fresh nymphs (2) nymphs after one factor change and (3) nymphs after two changes of factors are shown in Appendix VIIIa VIIIb and VIIIc respectively, and summarized in Appendix VIII.

From Table 7 it is seen that the average linear velocity for fresh nymphs of A.variolosum under the 150 Watt lamp on the vertical plane was 150 cm/min, and 1.27 cm/min. in the horizontal position (Section A). The corresponding results after on change (Section B) were 1.58 cm/mih. and 1.35 cm/min. The number of changes of direction on the vertical and the horizontal planes were 2.0 and 5.7, 2.4 and 6.9, 1.7 and 10 in sections A, B and C respectively.

In the three sections the linear velocity was consistently higher on the vertical plane than on the horizontal, and there were fewer changes of direction, i.e. less turning, on the vertical plane. Both these observations agree with the overall differentiation between the vertical plane and the horizontal plane observed in the nymphs of the three species.

The results for A.quercicola and A.minus are comparable with those for A.variolosum although A.quercicola was rather less consistent than the other two species.

It may also be expected that fatigue may modify the reactions of a nymph with successive observations on the same nymph., However the linear velocities as

have been observed did not decrease from section A to Section C but rather increased somewhat. On the other hand, the numbers of changes of direction tended to increase from section A to section C in both the vertical and the horizontal planes.

LATERAL ILLUMINATION Second Series

The results are presented in Appendix VIII for individual experiments and summarized in Table 9. They show the linear velocities, the numbers of turns, the angle of the paths, and positive or negative movement towards the light (marked +,-)

As there were only 5 experiments with A.quercicola the results for this species are not used in discussing this series of experiments. Only A.variolosum and A. minus are compared. The linear velocities for the two species are respectively 1.45, and 1.20 cm/min though A.variolosum shows a wider range (0.65-2.00) than A.minus (0.88-1.50). A.variolosum is faster than A.minus.

The numbers of turns are 4.6 for A.minus and 2.8 for A.variolosum so the former is turning more often.

A.minus appears to exhibit a ~~more~~ less positive phototaxis (17+, 6-) than A.variolosum (11+, 3-) in this experiment.

The paths of the crawlers did not lead them directly towards the source of light; the direction of each path was at an angle to the straight line

LATERAL LIGHT (HORIZONTAL) - SUMMARY OF RESULTS

TABLE 9

SPECIES		linear velocity cm/min	No. of turns 1=90°	angle of path to light source	attraction to light
A.variolosum	(23) av.	1.45	2.8	66°	17+
	range	.65-2.00	0-10	10°-180°	6-
A.quercicola	(5) av.	1.08	3.6	24°	5+
	range	.68-1.48	2-6	4°-85°	
A.minus	(14) av.	1.20	4.6	59°	11+
	range	.88-1.50	0-11	24°-180°	3-

representing the direction of the light. The average angle for A.minus was 59°, and for A.variolosum 66°. In some cases there was movement away from the light but in these individuals the negative direction was preceeded by circular motion.

The illustrations (A.quercicola is included for comparison) Figs 28a - c show paths leading to light and figs d - f show paths with negative direction.

LIGHT & GRAVITY - TUBES Third Series

In the twovertical positions of the tube the insects were seen to crawl away from the darkened half into the illuminated half. The path often meandered but it led the insect very definitely away from the darkened half.

In the horizontal position of the tube, the insects often wandered about the middle close to the edge of the black paper and then away towards the light. (Fig 29)

PETRI DISHES

SKOTOTAXIS

(a) It was observed that crawlers of all three species behaved similarly. There was much movement about so that the path was re-crossed again and again but the resultant position was that the crawlers were almost wholly restricted to a section of the petri dish opposite theedge of a black section (Fig 24)

(b) Most of the movement was in the black sectors

FIG. 28 horizontal lateral light
typical paths of crawlers for 5 mins.

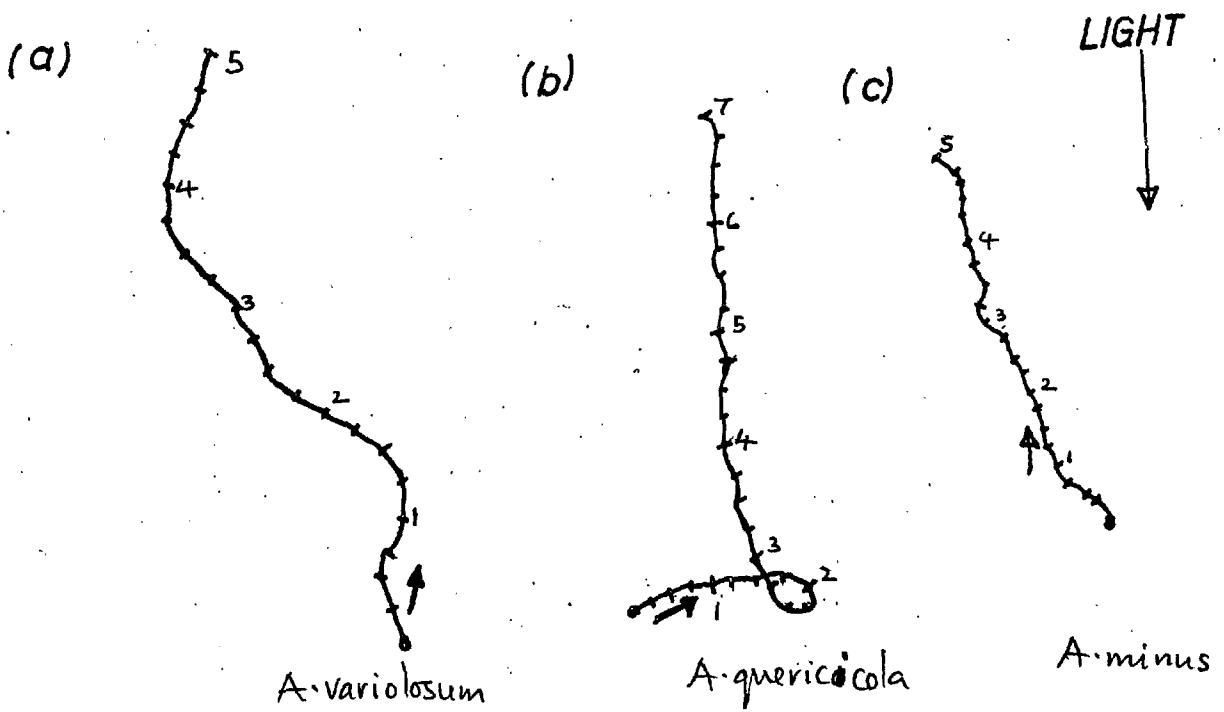


FIG. 28

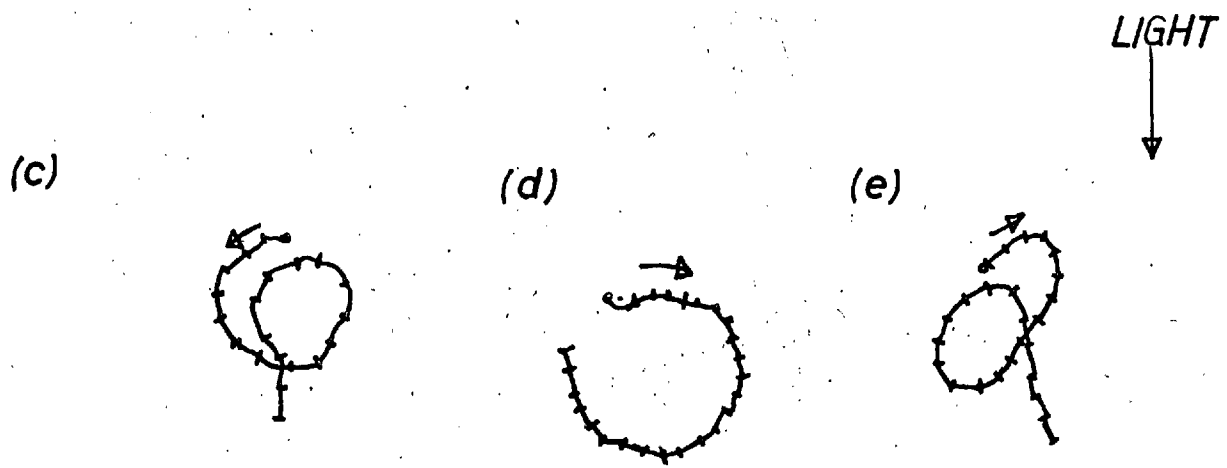
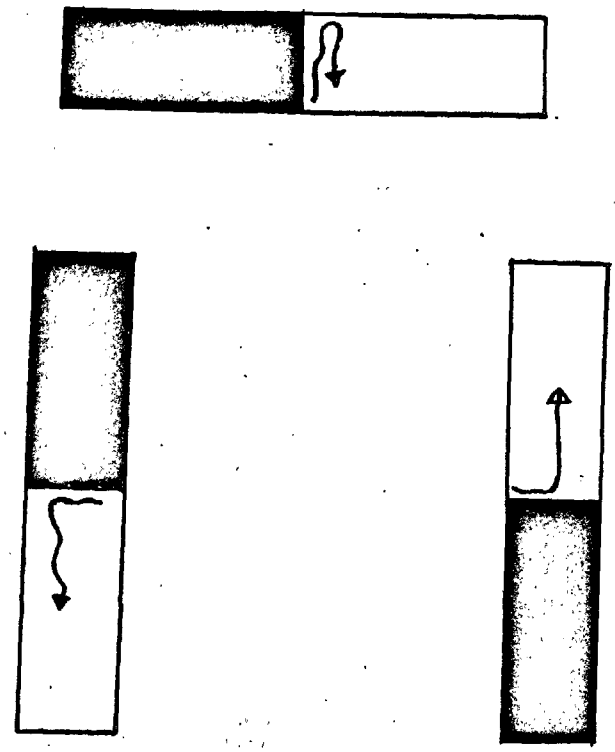


FIG. 29

PARTIALLY DARKENED TUBES



~→ = paths of crawlers.

of the petri dish in all three species. The path looped a lot but ended to straighten out or to loop less near the border between black and white sectors. (Fig 25)

(c) PHOTOTAXIS

The successive positions from the starting point in the centre of the petri dish indicated movement towards the "window" in all three species. The path towards the "window" was mostly along ~~its~~ the edge of the beam of light from the "window". Some crawlers began to climb upwards on reaching the edge of the petri dish.

In some experiments the "window" was accidentally turned away from the illuminated part of the box containing the petri dish. Thus the inside of the petri dish was completely dark. The positions of crawlers marked in these experiments indicated totally random movement, positive phototaxis. The experiments with a partially darkened tube however showed that light is by far the stronger of the two stimuli. Parr (1950) reported that crawlers were tested in the laboratory and were found to be positively phototropic (=phototactic) and negatively geotropic (geotactic), but that the latter reaction was much weaker than the former reaction.

LIGHT COMPASS REACTIONS:

In the light experiments with the nymph walking on a vertical plane, the direction of the path, towards or away from the source of light was seldom direct, but

was inclined at an agle to the direction of the rays of light. This kind of orientation is known as a light compass reaction and it is also very evident in the results of the experiments with lateral illumination on a horizontal plane. The average angle of approach on the vertical plane were 31.1° and 46.6° for A.variolosum and A.minus. With the lateral light on a horizontal plane the respective angles of approach were 66° and 59°. In those few (4) individuals in which the path was directly away from the light (approach angle= 180°) the final path was prefaced by circular movement, so these individuals may be regarded as being exceptional.

A comparison of theselight compass reaction results on a horizontal plane (Table 8) with the results of those on a vertical plane (Table 7) shows some consistent differences. On the horizontal plane A.variolosum and A.minus have angles of approach to light of 66° and 59° respectively, but 40.5° and 42.1° respectively under 24 Watts and 31.1° and 46.6° under 150 Watt lamp in the vertical plane. Their linear velocities on the vertical plane (Table 7) were 1.55 cm/min and 1.30 cm/min (150 Watt lamp) respectively, compared with 1.45 cm/min and 1.20 cm/min in the horizontal plane with lateral illumination (Table 9)

Although light compass reactions were exhibited in both sets of experiments, negative geotaxis appears to be an additional, reaction of lesser importance.

BEHAVIOUR EXPERIMENTS - DISCUSSION AND CONCLUSIONS

Light: In all three species the linear velocity at the higher light intensity is greater than at the lower light intensity when both the horizontal and the vertical positions are considered, i.e. all three species exhibit positive photokinesis. Aminus is, on the average, the slowest and A.variolosum the fastest, A.quercicola is intermediate.

In the horizontal position, in which the light rays are not directed along the plane of the paper on which the nymph is crawling, there is no significant increase in the frequency of turning with the higher light intensity, i.e. there is no positive relationship between light intensity and klinokinesis evident. But in the vertical position in which the light rays are directed along the plane of the surface on which the nymph is crawling, there is a positive attraction towards the light (positive phototaxis) which results in the path of the nymph being straighter with fewer turnings, i.e. klinokinesis is secondary to phototaxis. In the vertical position also the nymphs turns less frequently at the higher light intensity than at the lower one. Therefore as photokinesis increases klinokinesis decreases.

The attraction to the source of light (phototaxis) is not equal in the three species of Asterodiaspis. At the lower light in the vertical position both

A.quercicola and A.variolosum show an excess of positive reaction to light over negative (11+, 3- and 27+, 6- respectively), while the individuals of A.minus exhibit about equal reactions towards and away from light (6+,8-). At the higher light intensity the positive attraction towards light displayed by A.quercicola and A.variolosum increases (15+,2- and 3)+, 5- respectively) while A.minus is still practically neutral (8+, 7-). A.quercicola and A.variolosum are therefore strongly positively phototactic while A.minus is at best weakly so.

In the petri dishes the nymphs of all three species of Asterodiaspis appear to be similar in their reactions. Although the nymphs reacted in such a way that they were mainly confined to the dark areas, light appeared still to be the positive stimulus inducing this reaction. The attraction to light is well illustrated in the experiments with a "window" in the side of the petri dish. When this "window" was accidentally directed away from the light, the successive positions of the nymphs suggested hapharzard movement, but when the "window" was turned towards the light, the nymphs moved towards the "window" but along its edge.

The results of light experiments with the nymphs on a vertical plane may well involve negative geotaxis as well ~~as reaction on the vertical plane~~, leading to a more direct and a more rapid approach to the source of light.

A consideration of the reactions displayed by the nymphs in the behaviour experiments makes it possible to attempt an explanation of the patterns of the populations of the insects observed in the field and also the patterns of settling of the nymphs on potted plants during breeding experiments.

The periphery of the crown of a tree receives more light than the inside of the crown which is therefore relatively darker. Positively phototactic nymphs would tend to migrate outwards towards the terminal twigs of branches on the outside of the crown.

Population studies have shown that most of the insects are to be found on terminal twig sections one to four years old. It is possible that other factors such as negative geotaxis, chemical and physical factors associated with the twig also influence the pattern of settling of the nymphs. For example, the youngest shoots with their thin bark and relatively low lignification are more suitable as sites for feeding than elder twigs and may well contain stiumuli (chemical and physical) which both attract and induce the nymphs to settle mainly on them.

The generally comparatively weaker phototactic responses exhibited by the nymphs of A.minus in

comparison with those of A.quercicola and A.variolosum may partly, if not wholly, account why the latter two species are more concentrated towards the tips of twigs whilse A.minus tends to have a more even distribution on all sections of twigs one to four years old.

Light compass reactions combined with the edge effect seen in skototaxis may explain why about four times as many insects settle on the lower surfaces of the twigs as are found on the upper surface. Also as the lower surface of the twig is less exposed to the direct rays of sunlight it has a more moist microclimate in which the nymphs can more easily avoid the danger of desiccation.

EFFECT ON THE HOST

The three species of Asterodiaspis on oak cause the formation of galls in the form of pit-like depressions in the bark. The only other recorded instance of gall-forming British Coccoidea is that of Acanthococcus devoniensis Green which causes considerable distortion of the twigs of Heath (Erica) and heather (Calluna).

Within 24 hours of the settling of the first instar nymph of any of the three species of Asterodiaspis a shallow depression appears in the bark of the twig under the body of the settler. The ease with which pits are formed depends on the texture of the bark; pits appear more readily on the soft bark

of young green twigs than on the bark of older twigs.

As the insect develops, its profile changes from flat to a double convex and the pit deepens to accommodate the ventral convexity. At the same time the rim of the pit is raised to form the crater-like gall.

Severe damage and killing of oak trees by these insects have been reported by Signoret (fide Newstead 1903) who stated that certain oaks in Bois de Boulogne near Paris had been practically destroyed by them. Maskell (1895), reported that some twigs of oak from Nelson, in New Zealand were almost completely covered by the scale while Froggart (1900) reported that oak twigs from Sydney, Australia attacked by these insects were in a dying condition with withered leaves.

Parr (1940) investigated the effects "Asterolecanium variolosum"on the oak host tress in Connecticut, U.S.A., and found that young trees between 6 feet and 10 feet tall were more readily killed than older trees, the killing of the trees apparently resulting from the galls girdling the wood. He also found that Quercus montana was more heavily infested than Q-robur. This is probably partly due to the higher reproductive capacity of the insects on Q.montana reported by Parr.

Parr also reported that these insects were introduced into U.S.A. on Q-robur, and the catalogues of timber trees of U.S.A. show that Q.montana is native to that country, It is conceivable that Asterodiaspis found in Q.montana a ~~soft~~ susceptible and "soft" host to which its attack has proved very injurious and sometimes, fatal. With long association between the host tree and the insect pest, such as that between Q-robur and Asterodiaspis spp. a state of equilibrium may have been reached; the host developed a tolerance towards the insect whose population is maintained at a sub-lethal level by a combination of this and some other factors.

Parr (1940) has studied the anatomy of the twig in relation to pit-formation and he found that the cells immediately below the tips of the stylets of the insect were collapsed and dead. The layer of dead cells gradually thickens and expands radially as well. The collenchyma cells in the periphery of the pit area proliferate actively, causing the rim of the pit to swell.

In certain cases nymphs have been observed to colonize and develop within abandoned pits, suggesting that thetissue of the pit is capable of regeneration if the damage to it is not too severe. Where the twig is growing vigorously and the pit is not too deep, it may fill out and leave only a very shallow depression.

The regeneration after damage may be effective after two or three seasons depending on the severity of the initial injury and the subsequent rate of growth of the twig.

Twigs with a very high number of pits on them are distorted and stunted in growth (Fig 29A). The pits formed by the three species are similar.

FIG 29A

POPULATION STUDIES

Population studies have been undertaken in order to determine the nature of, and the possible differences in the patterns of distribution of the three species of Asterodiaspis (minus, quercicola, variolosum) in the areas studied and on the individual hosts.

There are few purely biological papers (often supporting the applied work) in which some aspects of population ecology of Coccoidea are discussed. Spiller (1952) in his studies on Aonidiella aurantii Mask found that it has truncated lognormal distribution on the leaves of citrus. Habib & Khalifa (1957) and Avidov (1960) discussed the distribution and population trends of Chrysomphalus ficus Ashmead on Ficus nitida and citrus respectively and Habib (1957) studied the mortality and population density of Eulecanium cornii Bché on various host plants. Cabido Garcia (1949) studied the influence of temperature on the distribution of Chrysomphalus dictyospermi Morgan in Portugal. Possibilities of forecasting changes in populations of Chrysomphalus ficus Ashmead and of Lepidosaphes bechii Newman were discussed by Griffiths and Thompson (1949) and Pratt (1956) and of Pseudoaonidia duplex Ckll by Cressman et al.(1935). Smirnov and Polejaeff (1934a.b.) studied the relationship between population density and sterility of the females of Lepidosaphes ulmi L. Chiu and Cheng (1957) studied the population density in the field of Pseudococcus comstocki Ckll. in Formosa, Kossarzewskaya (1956) of Leucaspis

(Ckll.)
japonica in Abchasia (USSR) and Hoy (1961) studied the ecology of Eriococcus orariensis Hoy on Leptospermum scoparium Forst. in New Zealand.

A large amount of information on individual and population ecology of Coccoidea however has been connected with the modern applied work, especially on chemical and biological control. The importance of ecological studies in chemical control work is obvious and well understood (Griffiths, 1951). In problems of biological control the interraction of various factors involved may be very complex indeed (Clausen, 1958) and can be satisfactorily understood and solved only through ecological studies (Smith and De Bach, 1942, Clausen, 1958). The data thus obtained have been frequently used to illustrate various points in general text-books of ecology (Allee et al 1949, Andrewartha and Birch, 1954, 1963, ~~McFadyen~~ Macfadyen, 1963).

Particularly many data on population ecology of Coccoidea can be found in:

1) The literature on citrus pests, among which Coccoidea are responsible for some of the most serious entomological problems (Bodenheimer, 1951, Ebeling, 1950, Boyce, 1950, Jepson and Carmen, 1960). For example, ecological information is contained in papers on chemical control (Cressman, Broadbent, Munger, 1953 1954, Griffiths and Thompson, 1949, Griffiths and Fisher, 1950, McGregor, 1942, Hough et al. 1945), biological control (De Bach, 1949, De Bach and Bartlett, 1951, Muma, 1955, Smith and Mathis, 1946, Steyn, 1951, Thompson, 1942, etc.).

2) A series of important ecological works on the mealybugs on cacao e.g. Strickland, 1952; Cornwell, 1953, 1955, 1957; Entwistle, 1958; Hanna et al 1955.

3) Papers concerned with the association of Coccoidea with ants e.g. Bess (1958), Carter (1961), Way (1954), (recently revised by Way ~~revised~~(1963)).

It is true that the data in such works are frequently recorded in a raw undigested form, e.g. Carpenters (MS) life tables of Pseudoaonidia duplex Ckll in Allee et al p.279 based on the data of Bliss et al (1935) and Cressman et al (1935).

SAMPLING

In population studies accurate assessment of changes in the populations is essential and requires a proper method of sampling designed to fit the purpose of the work and the habit of the insect involved (Morris, 1960).

In the case of insects which are permanently sedentary (Diaspididae, some Coccidae), random collection of infested parts of the host plant is a comparatively simple operation, thus Smirnov and Polejaeff (1934,a.b.) used random bark samples $2cm^2$ in studies of population density and sterility of females of Lepidosaphes ulmi L Avidov (1960), Habib and Khalifa (1957), Osborne and Mathis (1946), Schweig and Grunberg (1935), Thompson (1942) etc. counted the scales of various Diaspididae on random samples of leaves, and McGregor (1942) used standardized twigs, collected at random, in his study on Black Scale (Saissetia oleae

Bern
~~Bem~~). In studies of Coccoidea which are active throughout life (Pseudococcidae, Margarodidae), the method of sampling is less simple; Strickland (1952) and, later, Cornwell (1955, 1957), and Entwistle (1958) in their studies of the mealybugs on cacao, counted all insects on individual whole trees selected at random and cut down; in addition Hanna, Judenko and Heatherington (1955) counted also the colonies of mealybugs per tree and the number of insects in the colony. Hough et al (1945) adopted a method of sampling Pseudococcus comstocki Ckll based on man/hour collection, and Dutt (1925) counted the number of specimens of Monophlebus octocaudatus Green (Margarodidae) caught on sticky bands round the trunks of his experimental trees. Hoy (1961) studied the populations of Eriococcus orariensis Hoy on a series of artificially infested seedlings of Leptospermum scoparium Forst by dissecting, at intervals, the whole individual seedlings and counting all the specimens present on them.

It appears that no population studies have been undertaken on Asterolecaniidae though Habib (1943) studied the influence of humidity on the mortality rate and the distribution of Asterolecanium pustulans Ckll. in Egypt, and Parr (1940) discussed briefly the reproductive capacity and the density of population of Asterolecanium 'variolosum' Ratz. on English and chestnut oaks in Connecticut, USA.

The early observations and general survey of Asterolecanium variolosum Ratz., A.quercicola Bche., and A.minus Ldgr. at

Silwood Park showed that:

a) the insects occur on the terminal twigs, chiefly on twigs of 1-4 years old, with only very few individuals on the older sections of branches.

b) although all three species were present together on individual host trees all over the ground, the absolute as well as relative numbers of the specimens of each species somewhat varied from host tree to host tree and from area to area.

For the purpose of more detailed and methodical studies a number of oak trees from different areas of the grounds were selected. Of necessity most of the selected trees comprised the more common Q.robur and included the following: (see Map 1) in Appendix IV).

a) solitary trees (Hut II, Store, House I and ~~D I + II~~ DH II)

b) trees growing in small groups of two- in open areas (DHIA, DHIB).

c) oak trees growing in association with other trees and mostly in heavily wooded areas (GI, GII, GIII, StopI, StopII, [illegible], House II, House III)

d) seedlings from the area of the Cannon Wood and the Garden Ridge

e) A young Q.petreae from the Marsh on the edge of Gunnes's Hill.

The populations of these trees were assessed by means of regular sampling.

METHOD & TIME OF SAMPLING

Initially some difficulty was encountered in defining the "standard sample" which would be practicable, sufficiently unbiased, comparable with others and represent as closely as possible, the true conditions in the field.

As the insects occur mainly on the twigs 1-4 years old, it was obvious that the sampling should be based on the terminal sections of branches comprising only twigs 1-4 years old. The infestation, however, was found to be very uneven, and not heavy, thus the numbers from individual branches would be very low, often nil. It was decided therefore to adopt as a "standard sample" a "handful", ie. 5-6 such terminal parts of branches taken at random from various sectors and heights of the host's crown. Such a sample represented an overall length of about 500cm of twigs with an average diameter of 0.4cm. A few examples are given in Table (10) showing the lengths, average diameters and the areas of twigs in the four categories of age. (A,B,C & D) and the total length and area per sample of each host tree. The figures vary to a considerable degree in both the area (327-716 cm^2) and in relative and absolute lengths of twigs of different ages, and in the total length of twigs in the sample (319-607 cm). These differences appear to be due to different rates of growth in different years, of the same branch, and also due to generally different rates of growth of the whole branch; frequently some of the younger twigs (1-2 years old) were missing, and for this

TABLE 10 - Size of samples

	A			B			C			D			Total	
	L	(cm) av q	(cm2) area	L	(cm) av q	(cm2) area	L	(cm) av q	(cm2) area	L	(cm) av q	(cm2) area	L	(cm) av q	(cm2) area
GI	233.0	.262	191.8	91.4	.305	87.6	36.0	.415	46.9	24.7	.607	47.1	375.1	.397	467.7
GIII	301.5	.302	286.1	104.7	.392	128.9	77.1	.529	128.1	7.1	.637	14.2	490.4	.465	716.3
STOP I	252.4	.235	186.3	137.7	.318	137.9	67.7	.358	76.1	67.2	.512	108.1	525.0	.356	587.0
STOP II	227.8	.235	186.7	189.1	.310	184.2	86.2	.465	125.9	83.1	.519	135.5	586.2	.389	716.1
HOUSE I	195.8	.286	175.9	157.8	.295	146.2	109.2	.375	128.6	144.9	.507	230.9	607.7	.369	704.4
DJ IA	146.8	.299	137.9	119.4	.343	128.6	70.7	.367	79.7	195.1	.503	308.2	532.0	.378	631.7
DH II	120.8	.294	111.5	91.5	.324	93.1	59.7	.361	67.8	160.4	.495	249.4	432.5	.369	501.3
MARSH I	126.3	.211	83.7	82.7	.264	68.8	99.8	.339	106.3	38.7	.383	47.1	347.5	.300	327.4
MARSH II	109.3	.186	63.9	107.7	.241	81.5	76.5	.253	60.8	26.3	.353	29.2	319.8	.258	259.2

A, B, C, D = twig sections.
L = length.

foraging squirrels were found to be responsible. The severity of this foraging was noticeably higher in the wooded areas of Cannon Wood and South Lodge Wood than elsewhere. The woods around The House were also substantially affected.

The semples were taken between February and May when the rapid fall in numbers of the developmental stages during the summer and of the females during the winter had eased up and when the numbers of the adult females had established a profile of the potential parents of the next season's insects.

HANDLING THE SAMPLES:

After the leaves had been removed from them, the twigs in each sample were broken up into sections according to age, and thus segregated into four categories - A, B, C & D, representing sections one, two, three and four years old respectively.

On these sections of the twigs the following counts were made:

a) empty pits

b) live insects

(i) healthy (H)

(ii) parasitized (Pte)

c) dead insects

(i) with no parasites (+)

(ii) parasitized (Pte)

The insects present were removed, mounted, and as far as possible, identified as to the species (Idf). The results are

shown for each host tree in Appendix IX. (in columns marked as shown above in brackets). The sum of (a), (b) and (c) above represents the potential population. In Table II (J) the summaries of sampling are given together with averages per samples for each tree (extreme right hand column) and the grand total of the counted and identified insects.

The live insects counted at any one time from all the twig sections belong to the same season and the heathy ones are the potential parents of the next season's population.

Since the pits, especially deep ones on slowly growing twigs, persist for more than one season, the pits on twig sections more than one year old belonged to more than one season's population. This same consideration applies to the dead insects which may remain on the twigs for several seasons.

For the purpose of defining the composition of the population on individual hosts and the distribution of the species on the grounds, all identifiable insects were used; the assessment of mortality and survival however was based on the counts on the one year-old twig sections for only on these twigs was there a complete certainty that all the insects and the pits belonged to a single (current) generation.

TABLE IIJ SAMPLING : SUMMARY

Host		A					B					C					D					Total					Av./sample			
		Pp	Dead		Alive		Pp	Dead		Alive		Pp	Dead		Alive		Pp	Dead		Alive		Pp	Dead		Alive		Pp	All idf.	Alive H	sp
			+	Pte	Pte	H		+	Pte	Pte	H		+	Pte	Pte	H		+	Pte	Pte	H		+	Pte	Pte	H				sp
G I	6	159	24 - -	- - -	- - -	20 4 1	1162	17 6 -	- - -	2 - -	53 1 -	443	3 - -	- - -	- - -	27 - -	660	- - -	- - -	- - -	7 - -	2424	44 6 -	- -- -	2 - -	107 5 1	404	25.5 1.8 0.1	17.8 0.8 0.16	m q v
G II	3	45	- - -	- - -	- - -	1 5 1	18	- 1 1	- - -	- - -	- - -	8	- - -	- - -	- - -	1 - -	4	- - -	- - -	- - -	- - -	75	- 1 1	- - -	- - -	1 6 1	25	0.3 2.3 0.7	0.3 2.0 0.3	m q v
G III	5	1285	11 - -	4 - -	3 1 1	60 4 -	3787	21 - 1	7 - -	3 - -	36 1 -	2512	6 - -	1 - -	- - -	44 - -	2321	43 - -	3 - -	4 - -	33 - -	11322	81 - 1	15 - -	10 1 1	173 5 -	2264	56.0 1.2 0.4	34.6 1.0 0.0	m q v
STOP I	2	133	- 1 3	- - -	- - 1	6 6 -	55	1 - -	- - -	- - -	- 1 -	16	- 2 -	- - -	- - -	- 1 -	-	- - -	- - -	- - -	- - -	204	1 3 3	- - -	- - 1	6 8 -	102	3.5 5.5 2.0	3.0 4.0 0.0	m q v
STOP II	3	69	1 - -	- - -	- - -	3 3 1	420	- - 1	- - -	- - -	9 - -	304	5 - -	1 - -	- - -	1 - -	287	3 - -	- - -	1 - -	1 - -	1080	9 - 1	1 - -	1 - -	14 3 1	360	8.3 1.0 0.7	4.7 1.0 0.3	m q v
HOUSE I	15	312	2 1 2	- 1 1	- - 1	18 2 5	656	10 1 2	- - -	- - -	24 1 -	362	2 - -	- - -	- - -	10 - 1	293	4 - -	- - -	- - -	4 - 1	1580	18 2 4	- 1 1	- - 1	56 3 7	105	4.9 0.4 0.9	3.7 4.2 0.47	m q v
HOUSE II	3	18	2 - -	- - -	- - -	- - -	25	- 1 -	- - -	- - -	- - -	13	- - -	- - -	- - -	1 - -	6	- - -	- - -	- - -	- - -	62	2 1 -	- - -	- - -	1 - -	21	1.0 0.7 0.0	0.0 0.3 0.0	m q v
HOUSE III	3	354	4 2 5	1 1 1	- 1 -	3 6 -	260	1 - -	1 - -	- - 1	3 - -	76	2 1 -	1 1 -	- - -	- 1 -	99	2 - -	- - -	- - -	2 1 -	789	9 3 5	2 2 1	- 1 1	8 8 -	263	6.3 4.7 2.3	2.7 2.7 0.0	m q v
DH IA	11	431	1 5 3	- 1 1	- - -	1 15 20	216	- 1 2	- 2 -	- 1 -	- 1 3	113	1 5 -	- 1 -	- - -	1 3 -	42	- - -	- - -	- - -	- - -	803	2 11 5	- 4 1	- 1 -	2 19 23	80	0.36 3.2 2.6	0.18 1.7 2.1	m q v
DH IB	2	104	- - -	- - -	- - -	- 2 5	59	- 1 -	- - -	- - -	- - -	30	- - -	- - -	- - -	- 1 -	5	- - -	- - -	- - -	- - -	198	- 1 -	- - -	- - -	- 3 5	99	0.0 2.0 2.5	0.0 1.5 2.5	m q v
DH II	9	782	- 3 -	- - -	- 1 -	- 54 13	587	- 6 2	- - -	- 1 -	- 7 -	211	- 3 -	- - -	- - -	- 7 -	173	- 2 -	- - -	- - -	- 2 -	1753	- 14 2	- - -	- 2 -	- 70 13	194	0.0 9.6 1.7	0.0 7.8 1.4	m q v
STORE	3	140	1 - 2	- - -	- - -	- - -	185	- 5 -	- - -	- - -	- - -	144	- - -	- - -	- - -	1 1 -	134	- - -	- - -	- - -	- - -	603	1 5 2	- - -	- - -	1 1 -	201	0.7 2.0 1.0	0.3 0.3 0.0	m q v
HUT II	6	129	- 1 3	- - 1	- - -	- 7 2	94	- 1 3	- - -	- - -	- - -	57	- 1 1	- - -	- - -	- - -	70	- - -	- - -	- - -	2 - -	350	2 43 7	- - 1	- - -	2 7 2	58	0.7 1.8 1.7	0.3 1.1 0.3	m q v
MARSH	2	54	- 1 6	- - -	- - -	- - -	30	- - 2	- - -	- - -	- - -	24	- - -	- - 1	- - -	- - -	16	- - -	- - -	- - -	- - -	124	- 1 8	- - 1	- - -	- - -	62	0.0 0.5 4.5	0.0 0.0 0.0	m q v
SEED-LINGS			- - -	- - -	- - -	- 3 5		- - -	- - -	- - -	- 2 -		- - -	- - -	- - -	- - -		- - -	- - -	- - -	- 1 -		- - -	- - -	- - -	- 6 5				m q v
Grand Total	73	4015	46 14 24	5 3 4	3 3 3	112 111 53	7554	50 23 14	8 2 0	5 2 1	125 14 3	4313	19 12 1	2 2 1	- - -	84 16 1	4110	52 2 -	3 - -	5 - -	49 4 1	21367	167 51 39	18 7 5	13 5 4	370 145 58				m q v
Total			166				188					105					109					568								m
Identified			131 84				41 18					30 3					6 1					208 106								q v

DISTRIBUTION AND ABUNDANCE OF THE SPECIES ON THE GROUNDS OF THE IMPERIAL COLLEGE FIELD STATION

Early observations and general survey have shown that the three species may be found together on one host tree, but that they occur in different relative and absolute numbers on different hosts.

a) Distribution of the species on the grounds

Detailed analyses of the samples from the selected trees showed that the occurence of greater or lesser numbers of any one of the three species is independent of the geographical location on the grounds, but dependent on the position of the host tree in relation to other trees.

In this respect the host trees studied fall into two distinct groups (Table [illegible])

Group I (Table IIa) comprises theoak trees growing in association with other trees in wooded areas; they are characterized usually by a marked preponderance of A.minus, with comparatively very few specimens of the other two species. To this group belong trees marked GI, GII, GIII, Stop I, Stop II, House I, House II and House III. Here A.minus represents from 31.8% to 97.2 % of the entire population of identifiable insects, and from 42.9% to 98.9% of the alive and healthy insects, but where the larger numbers of specimens were available the latter proportion was between 77.7% and 98.9%. On some of these trees A.variolosum is absent altogether.

TABLE 11 showing nos (all identified & Live healthy) of each species on different hosts - composition of populations on individual hosts

(a)

HOSTS / SPECIES	GI				GIII				STOP I				STOP II				HOUSE I				HOUSE II				HOUSE III				GII			
	All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)	
	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%
A.minus	153	92.7	107	94.7	279	97.2	175	98.9	7	31.8	6	42.9	25	83.3	14	77.7	74	79.5	56	84.8	2	50.0	-	-	19	47.5	8	50.0	1	10.0	1	12.5
A. quercicola	11	6.7	5	4.4	6	2.1	2	1.1	11	50.0	8	57.1	3	10.0	3	16.7	6	6.5	3	4.5	2	50.0	1	100	14	35.0	8	50.0	7	70.0	6	75.0
A. variolosum	1	0.6	1	0.9	2	0.7	-	-	4	18.2	-	-	2	6.7	1	5.6	13	14.0	7	10.7	-	-	-	-	7	17.5	-	-	2	20.0	1	12.5
TOTAL	165		113		287		177		22		14		30		18		93		66		4		1		40		16		10		8	

(b)

HOSTS / SPECIES	DHIA				DHIB				DHII				HUT II				STORE			
	All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)		All Idf		Live(H)	
	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%
A.minus	4	5.9	2	4.6	-	-	-	-	-	-	-	-	2	9.0	-	-	2	20.0	1	50.0
A. quercicola	35	51.5	19	43.2	4	44.5	3	37.5	86	85.2	70	84.3	10	45.5	7	77.7	6	60.0	1	50.0
A. variolosum	29	42.6	23	52 2	5	55.5	5	62.5	15	14.8	13	15.7	10	45.5	2	22.3	2	20.0	-	-
TOTAL	68		44		9		8		101		83		22		9		10		2	

Idf = identified.
H = healthy

Group II (Table 11b) comprises the trees growing in the open singly or in pairs, and on these A.minus is either absent or occurs only in small proportions (0% - 20%), A.quercicola or A.variolosum being predominant; of the latter two species generally A.quercicola appears to be more numerous (DH IA, DH II) but the two species may occur in equal numbers (Hut II), or A.variolosum may be slightly more numerous (DH IB). Fig 30 (a & b) illustrates graphically the specific compositions of the populations on trees from which the numbers of specimens obtained were sufficient to be considered as representing the true conditions obtaining; the numbers represented are of all identified specimens of each species.

The trees G II and March (Group I) and Store (Group II) do not conform to the patterns of their respective groups, but this may be due to the low infestation of these trees, small numbers of samples obtained and few identifiable specimens available.

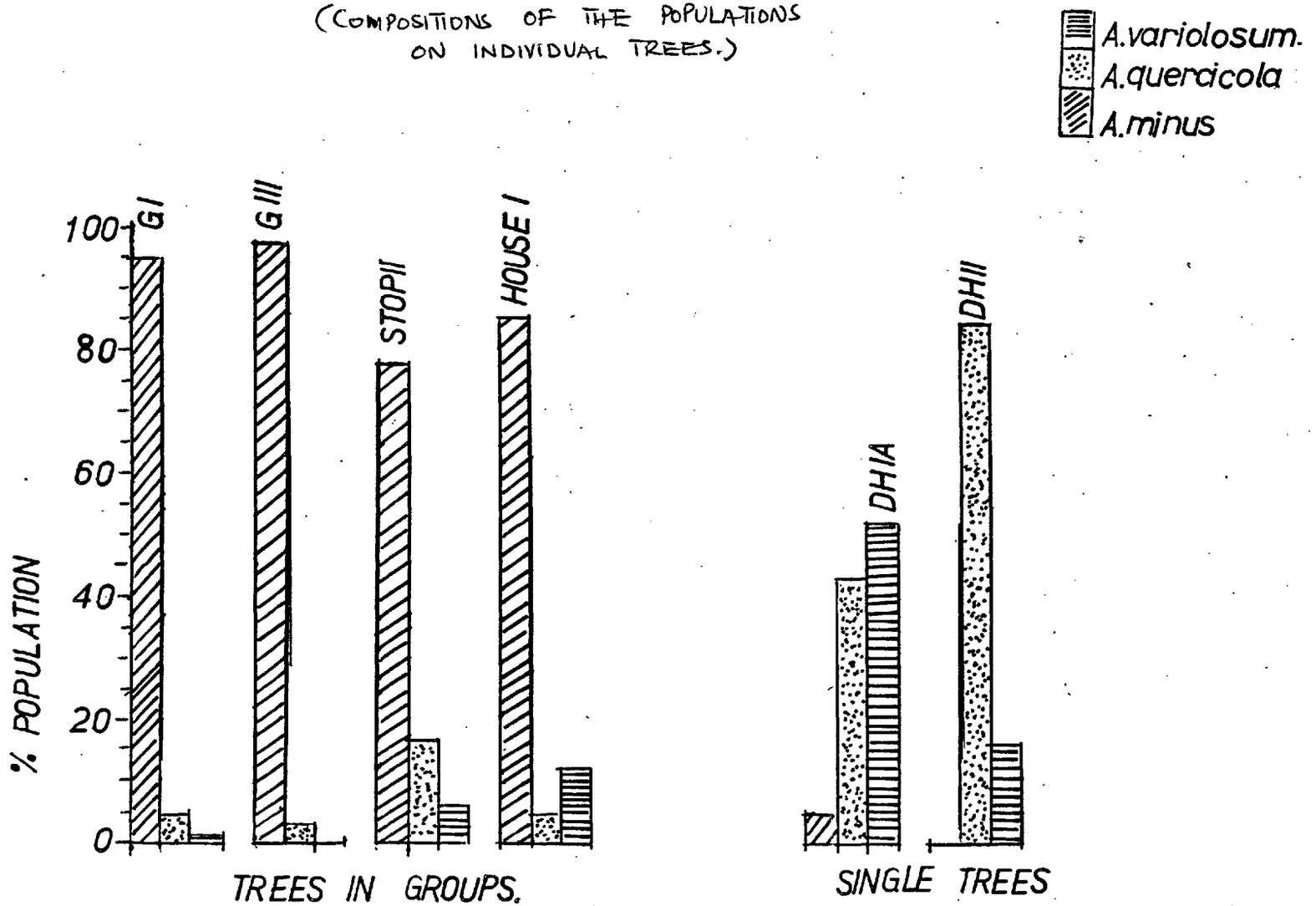
The seedlings which occur under trees growing in the open showed very low infestation by A.variolosum and A.quercicola but no A.minus, although this latter is predominant there. This would indicate that seedlings are somehow unsuitable for this species, a fact reflected in the difficulty encountered in breeding it on seedlings in the greenhouse.

Abundance of the insects on the grounds

The assessment of the degree of infestation by all the three species taken together on the individual host trees has

FIG 30 DISTRIBUTION OF THE SPECIES ON THE GROUNDS.

(COMPOSITIONS OF THE POPULATIONS ON INDIVIDUAL TREES.)



been based on the average numbers per sample of: the potential population, all the identified specimens, and of the alive, and healthy individuals (Table 12 and Figs 31a, 31b). All these figures give consistent results and indicate that there is no definite relationship between the numbers of insects occuring on the host tree and the geographical location of the host on the grounds.

Potential population: (cf Table 12) Oak trees associated with other trees (Group I, is with A.minus predominant) show marked variation in the degree of infestation, from very low 25(G II) to very high, 2264(G III), i.e. about 100 fold, and the tree Stop I (102) is only 1/20 that of G III. These named trees are of about the same age and stand in close proximity in the same area (South Lodge Wood - Cannon Wood, see Map Appendix IV). Less wide but still considerable variation is exhibited by trees of this group from another area, eg. House II (21) and House III (263).

The single isolated oak trees (Group II - A.minus absent or very few) show narrower ranges of variation in the numbers of potential population, from 58 (Hut II) to 201(Store), i.e. about four-fold.

On average however, the potential population per sample of Group I is higher (443) than in Group II (126.4). But in both groups there are trees of about the same potential population e.g. Stop I in Group I and DH IB in Group II.

TABLE 12- Averages per sample

(a)

HOSTS	Potential population	All identified m	q	v	Total	Alive healthy m	q	v	Total	Potential population	All identified	Alive Healthy
GI	404	25.5	1.8	0.1	27.4	17.8	0.8	0.16	18.76			
GII	25	0.3	2.3	0.7	3.3	0.3	2.0	0.3	2.6			
GIII	2264	56.0	1.2	0.4	57.6	34.6	1.0	0.0	35.6	443	16.3	10.5
STOP I	102	3.5	5.5	2.0	11.0	3.0	4.0	0.0	7.0			
STOP II	360	8.3	1.0	0.7	10.0	4.7	1.0	0.3	6.0			
HOUSE I	105	4.9	0.4	0.9	6.2	3.7	4.2	0.47	8.37			
HOUSE II	21	1.0	0.7	0.0	1.7	0.0	0.3	0.0	0.3			
HOUSE III	263	6.3	4.7	2.3	13.3	2.7	2.7	0.0	5.4			

(b)

DH IA	80	0.36	3.2	2.6	6.16	0.18	1.7	2.1	2.98			
DH IB	99	0.0	2.0	2.5	4.5	0.0	1.5	2.5	4.0	126.4	5.97	3.9
DH II	194	0.0	9.6	1.7	11.3	0.0	7.8	1.4	9.2			
STORE	201	0.7	2.0	1.0	3.7	0.3	0.3	0.0	0.6			
HUT II	58	0.7	1.8	1.7	4.2	0.3	1.1	0.3	1.7			

m = A. minus.
q = A. quercicola.
v = A. variolosum.

FIG 31(a) ABUNDANCE OF THE SPECIES ON THE GROUNDS.
(ALL IDENTIFIED INSECTS)

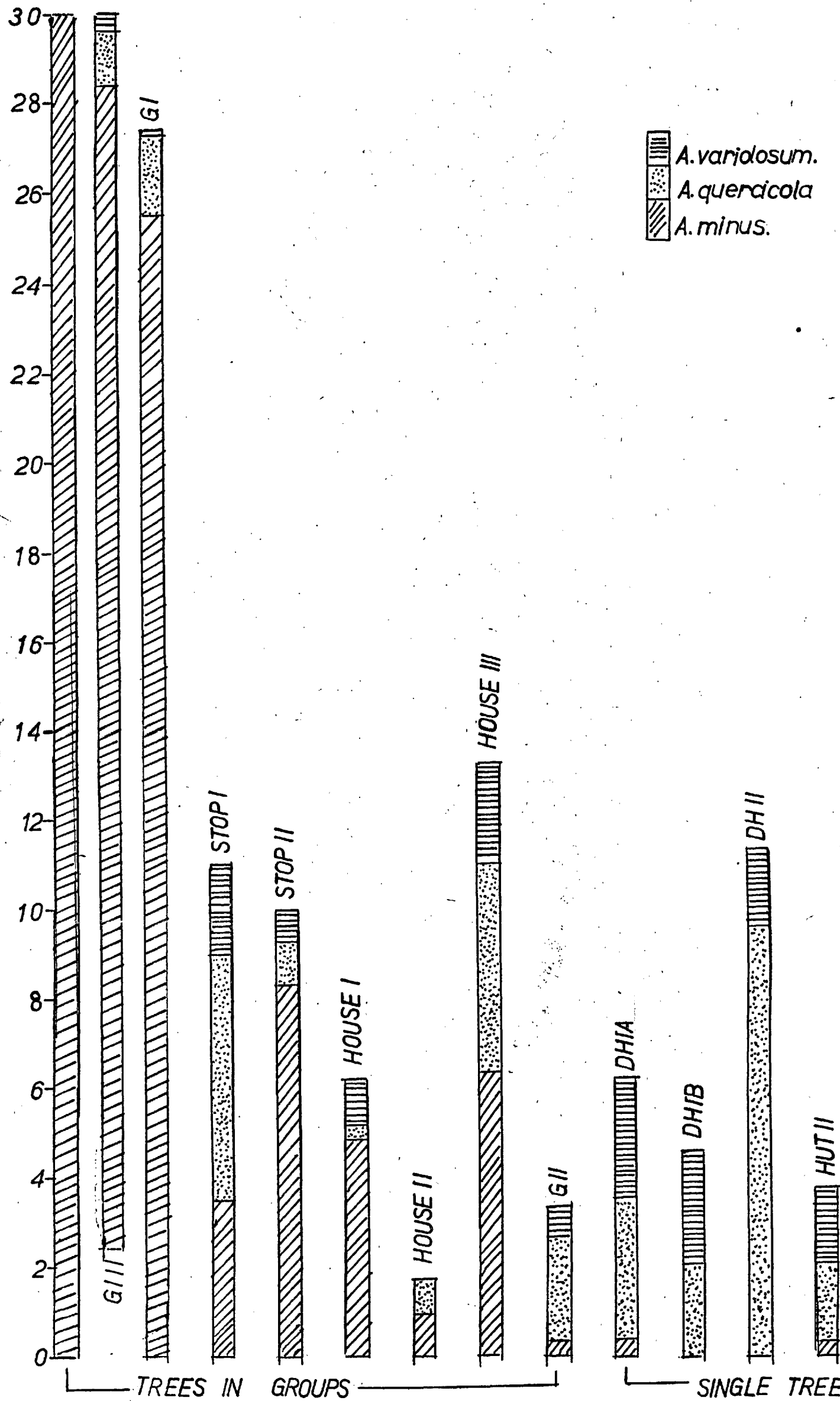
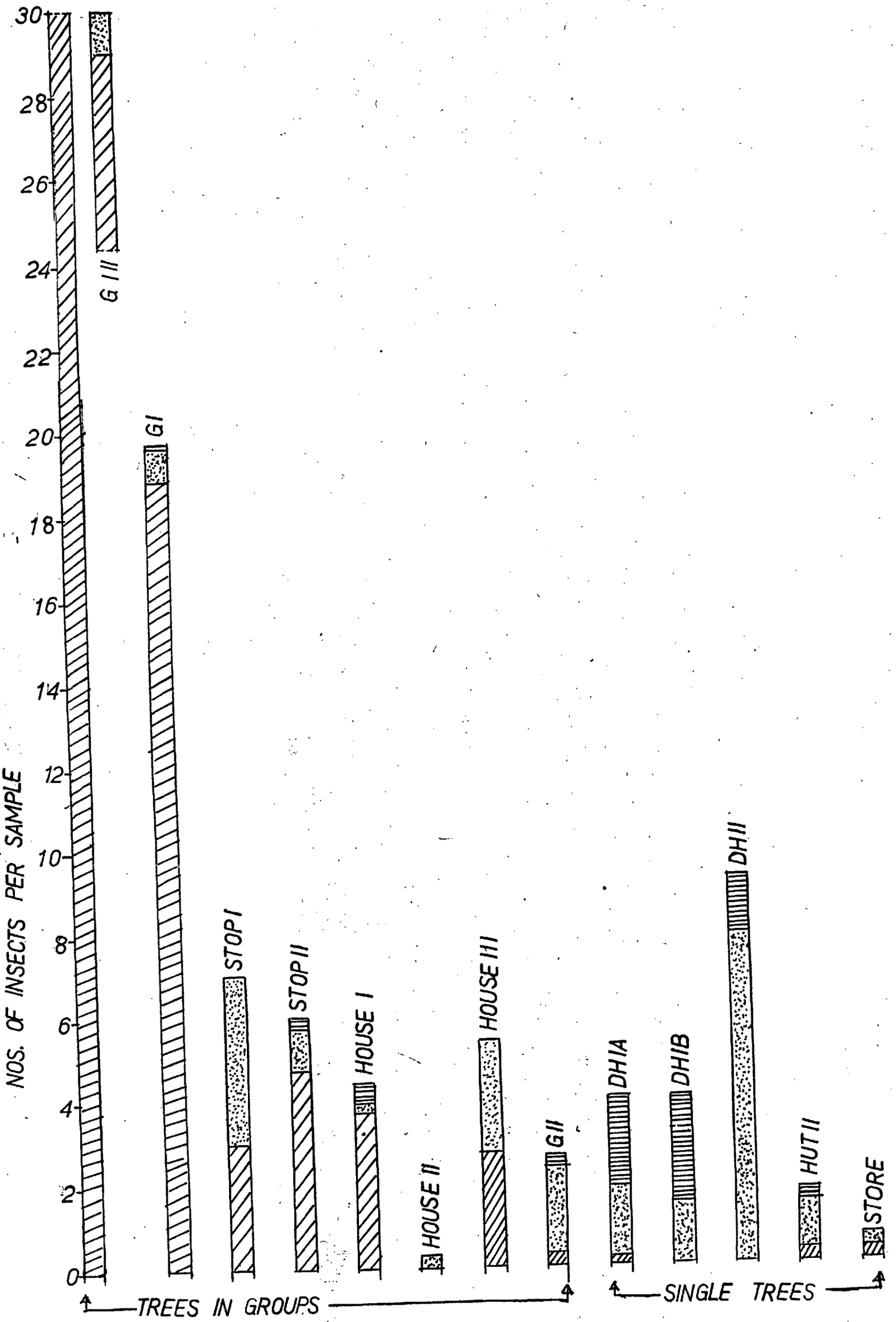


FIG 31(B) ABUNDANCE OF THE SPECIES ON THE GROUNDS (ALIVE, HEALTHY)



All identified insects: similar results are shown by the numbers of identified insects per sample (Table 12, Fig 31a). In Group I these numbers vary from 3.3 (G II) to 57.6 (G III) i.e. about 17-fold, and in Group II from 3.7 (Store) to 11.3 (DH II) i.e. about a three-fold difference. The numbers per average sample for the groups are 16.3 for the former group and 5.97 for the latter. However, Stop I and House I of Group I and DH II DH IA of Group II, for example, have almost identical numbers of insects per average sample.

Living healthy insects: The numbers of living healthy insects per sample (Table 12, Fig 31b) representing the individuals of only one (current) generation and potentially determing the next generation, are perhaps most significant in assessing the degree of infestation, These numbers also show similar trends as above. In Group I they vary from 0.3 (House II) to 35.6 (G III), i.e. almost 120-fold, while in Group II only from 0.6 (Store) to 9.2 (DH I) i.e. about 15 times, with the averages of 10.03 and 3.9 for Groups I and II respectively. But here again House III of Group I has very similar numbers of individuals per sample (5.4) as DH IB (4.0) in Group II.

To give more precise meaning to the degree of infestation as expressed in average numbers per sample, it was decided to obtain a measure of the densities of the insects on various hosts. For this purpose special samples of infected twigs were taken from a number of host trees (Table 13) and all the insects

Table 13 special samples for density assessment.

HOST	A cm² Area	A Insects	A Area/Insect	B cm² Area	B Insects	B Area/Insect	C cm² Area	C Insects	C Area/Insect	D cm² Area	D Insects	D Area/Insect	TOTAL cm² Area	TOTAL Insects	TOTAL Area/Insect	Group Average Area per Insect
GI	191.8	154	1.25	87.6	89	.99	46.9	118	.40	47.1	38	1.24	467.7	399	1.17	4.25
GII	286.1	552	.52	128.9	331	.39	128.1	185	.69	14.2	49	.29	716.3	1017	.71	
Stop I	186.3	46	4.05	137.9	15	9.20	76.1	7	10.87	108.1	15	7.2	587.0	83	7.07	
Stop II	186.7	238	.79	184.2	95	1.94	125.9	36	3.50	135.5	31	4.37	716.1	400	1.79	
House I	175.9	15	11.72	146.2	12	12.18	128.6	8	16.75	230.9	35	6.6	704.4	70	10.5	
DHIA	137.9	30	4.60	128.6	19	6.77	79.7	2	39.85	308.2	3	102.73	631.7	54	11.7	6.65
DHII	111.5	123	.91	93.1	94	.99	67.8	27	2.51	249.4	70	3.56	501.3	314	1.60	

A, B, C, D = twig sections.

found on them were counted without being identified as to the component species, and the samples were analysed to provide the following information:

a) total surface area of the twigs in the sample

b) the numbers of all the insects counted

c) the average area of twig per insect; this method of assessing the density of the insect population has been preferred to the usual one involving the numbers of insects per unit area of twig surface, because, with the generally low infestation on the twigs, the latter method would give rather low and unrealistic fractions of insects.

The figures for the hosts belonging to Group I (as recognised above) vary from 0.71 (G III) to 10.5 (House I) and two hosts from Group II have figures of 1.60 (DH II) and 11.7 (DH IA). Here again the trees in Group I have a wide variation but on average have a higher density, i.e. lower area per insect (4.25) than Group II (6.65), although individual trees from the two groups may in fact have similar densities eg. Stop II (1.79) in Group I and DH I (1.60) in Group II.

All these counts indicate that the infestation of the individual trees is very variable: the trees growing in association with other trees (Group I) have a wider variation in the numbers of the insects on individual hosts, but on average they have a relatively high degree of infestation.

The trees growing singly in the open show relatively uniform, and, on average, lower degree of infestation.

The cause of the higher average infestation on the trees growing in groups has not been investigated but a tentative explanation may be advanced. The trees standing in groups may mutually act as windbreaks to each other, thus, in part, reducing the possibility of the crawlers being blown off by the wind andlost, a risk which appears to be greater in the case of the isolated trees. Among the grouped hosts, even a blown-off crawler may have the chance to land on a neighbouring oak. Parr (1940) has observed that some crawlers are blown off by the wind.

Distribution of the species on the host trees

It was at first intended to investigate the distribution of the populations of Asterodiaspis spp on the host oak trees in relation to the points of the compass and to the height of the branches above the ground. Accordingly the directions and the heights at which a number of smaples from various hosts were taken were noted, and a prelimnary analysis of these samples showed that the infestation as assessed by the potential population numbers was generally low and that the distribution was irregular and patchy, giving in consistent figures with regard to direction and height on individual trees, as well as on different host trees. For example, samples 29, 51 and 82 from House I (Table II B, Appendix IX D) which were taken from

the same direction and similar altitudes (7' - 9'), had potential populations of 320,117 and 62 respectively. Although on this host the potential population on the northern side appears to be higher (av. = 139.4) than on the other sides (Av. = 97.7), this is apparently accidental and not confirmed by the counts on the other trees, e.g. DH II (Table G, Appendix IX G) on which the western side shows the highest average potential population (236), while with other sides (150.4). The numbers of identifiable insects or healthy living ones were too low to give reliable results. For this reason this aspect of the studies was discontinued.

Analysis of the compositions of the populations on different sections of the twigs showed differences in the proportions of the three species. The numbers of all identified specimens of each of the three species found on the one, two, three and four years old respectively, sections of the twigs are tabulated in Table 14a and graphically represented in Fig 32a A.minus is to be found in numbers on all sections of the twigs (e.g. G III) and although on some hosts it is found in greater numbers on one year-old sections (Stop I, House III), generally large numbers of specimens are to be found on the three and four years old sections (House I, House III, G III, Stop II). In many cases the two years old twig sections are the most heavily infested (Stop II, G I, House I). On the isolated trees A.minus was found on one and three years old twigs (Store, DH IA).

ALL IDENTIFIED INSECTS

HOSTS	A			B			C			D			Total			Grand Total
	m	q	v	m	q	v	m	q	v	m	q	v	m	q	v	
GI	44	4	1	72	7	-	30	-	-	7	-	-	153	11	1	165
GII	1	5	1	-	1	1	-	1	-	-	-	-	1	7	2	10
GIII	78	5	1	67	1	1	51	-	-	83	-	-	279	6	1	286
STOP I	6	7	4	1	1	-	-	3	-	-	-	-	7	11	4	22
STOP II	4	3	1	9	-	1	7	-	-	5	-	-	25	3	2	30
HOUSE I	20	4	9	34	2	2	12	-	1	8	-	1	74	6	13	93
HOUSE II	2	-	-	-	1	-	-	1	-	-	-	-	2	2	-	4
HOUSEIII	8	10	6	5	-	1	2	3	-	4	1	-	19	14	7	40
DH IA	2	21	24	-	5	5	2	9	-	-	-	-	4	35	29	68
DH IB	-	2	5	-	1	-	-	1	-	-	-	-	-	4	5	9
DH II	-	58	13	-	14	2	-	10	-	-	4	-	-	86	15	101
STORE	1	-	2	-	5	-	1	1	-	-	-	-	2	6	2	10
HUT II	-	8	6	-	1	3	-	1	1	2	-	-	2	10	10	22
MARSH	-	1	6	-	-	2	-	-	1	-	-	-	-	1	9	10
SEEDLINGS	-	3	5	-	2	-	-	-	-	-	1	-	-	6	5	11

ALIVE HEALTHY INSECTS

HOSTS	A			B			C			D			Total			Grand Total
	m	q	v	m	q	v	m	q	v	m	q	v		q	v	
GI	20	4	1	53	1	-	27	-	-	7	-	-	107	5	1	113
GII	1	5	1	-	-	-	-	1	-	-	-	-	1	6	1	8
GIII	60	4	-	36	1	-	44	-	-	33	-	-	173	5	-	178
STOP I	6	6	-	-	1	-	-	1	-	-	-	-	6	8	-	14
STOP II	3	3	1	9	-	-	1	-	-	1	-	-	14	3	1	18
HOUSE I	18	2	5	24	1	-	10	-	1	4	-		56	3	7	66
HOUSE II	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	1
HOUSEIII	3	6	-	3	-	-	-	1	-	2	1	-	8	8	-	16
DH IA	1	15	20	-	1	3	1	3	-	-	-	-	2	19	23	44
DH IB	-	2	5	-	-	-	-	1	-	-	-	-	-	3	5	8
DH II	-	54	13	-	7	-	-	7	-	-	2	-	-	70	13	83
STORE	-	-	-	-	-	-	1	1	-	-	-	-	1	1	-	2
HUT II	-	7	2	-	-	-	-	-	-	2	-	-	2	7	2	11
MARSH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SEEDLINGS	-	3	5	-	2	-	-	-	-	-	1	-	-	6	5	11

A, B, C, D = Twig sections.

m = A. minus.

q = A. quercicola.

v = A. variolosum.

FIG. 32(A) ADULT INSECTS - DISTRIBUTION ON INDIVIDUAL TREES. (ALL IDENTIFIED)

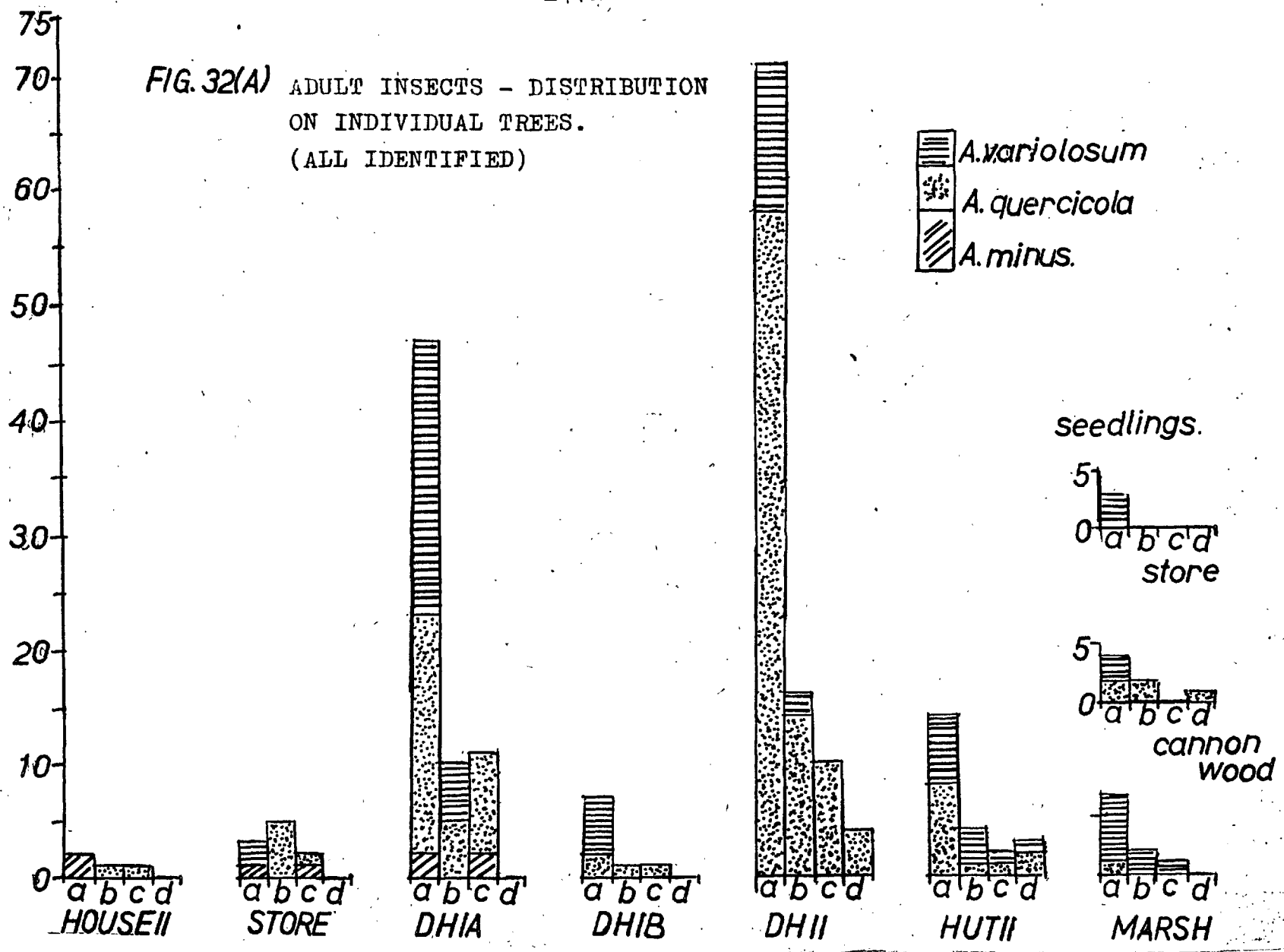
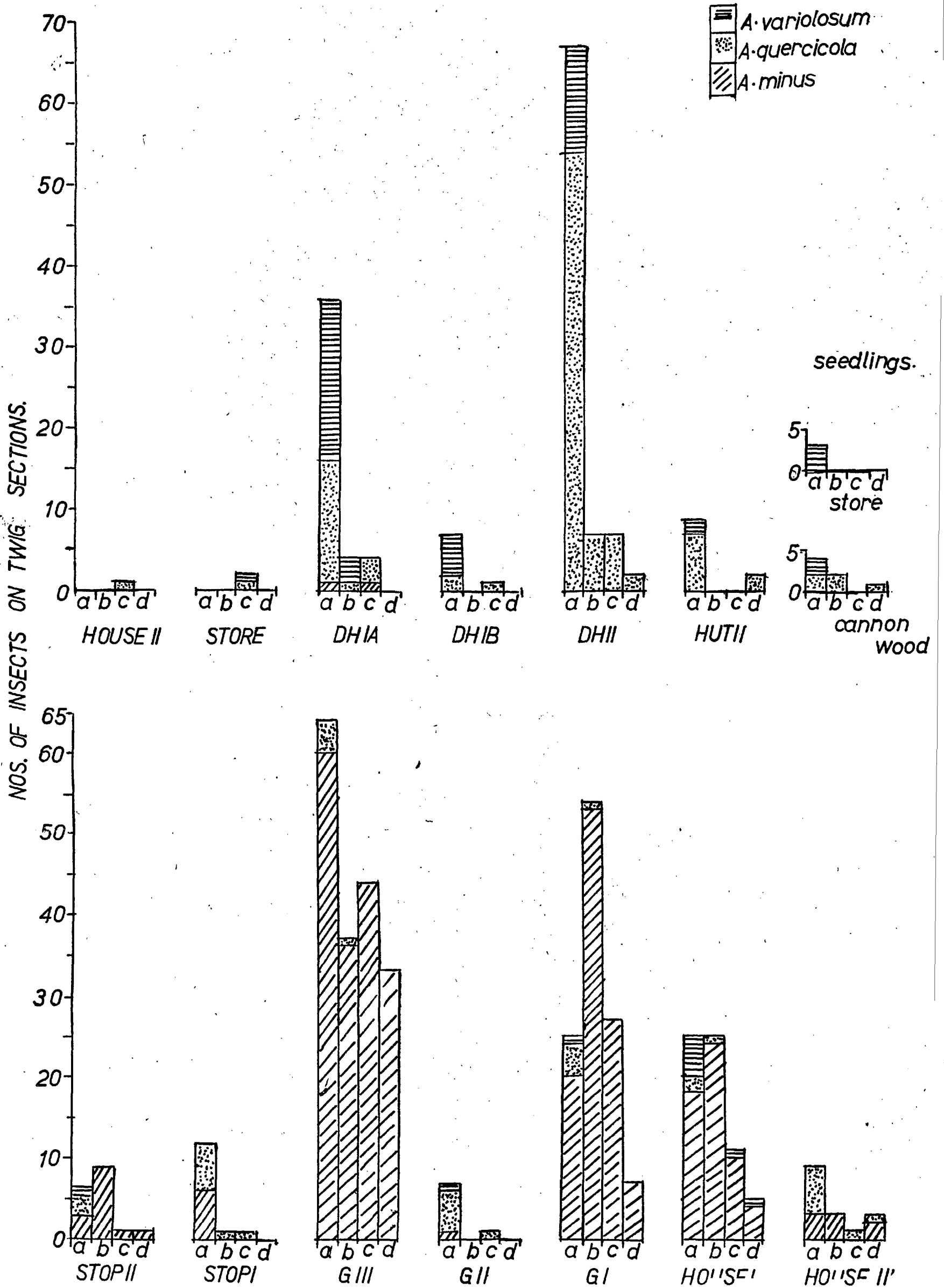


FIG. 32(b) ADULT INSECTS - DISTRIBUTION ON INDIVIDUAL TREES.
(ALIVE, HEALTHY)



In the case of Aquercicola the preference appears to be for the youngest twigs, particularly the one year-old (DH IA, DH II), with gradually decreasing numbers of individuals on the two, three and four years old sections (DH II), but with still appreciable numbers on the three or even four years old sections (DH IA, House III, Hut II, Stop I).

A.variolosum however appears to be restricted almost entirely to the one, or two years old twigs (DH IA, DH II) with very few (Hut II, House I), but frequently none (DH IA, DH II, House III) on the three and four years old sections.

The same, but perhaps more emphasized pattern of distribution of the species is shown when only the living healthy insects are taken into account (Table 14b, Fig 32b). All living insects belong to one generation and more accurately represent the true natural pattern of distribution of the species.

The pattern of distribution of the species on different sections of the twigs is clearly shown when the total numbers of all identified specimens recovered fron the sections of the twigs are considered for each species separately as given in Table 15 and represented graphically in Fig 33. Both the actual numbers (Fig 33a) and the percentages (Fig 33b) show that A.minus occurs in numbers on all four sections of the twigs with the highest number on sections two years old, on which 33.1% are present, with slightly less (29.2%) on one year-old sections, but still 18.5% and 19.2% on the three and four years old sections

TABLE 15a

showing the total numbers of each species identified from the four sections of the twigs

SPECIES	A	B	C	D	Total
A minus	166	188	105	109	568
A quercicola	131	41	30	6	208
A variolosum	84	18	3	1	106

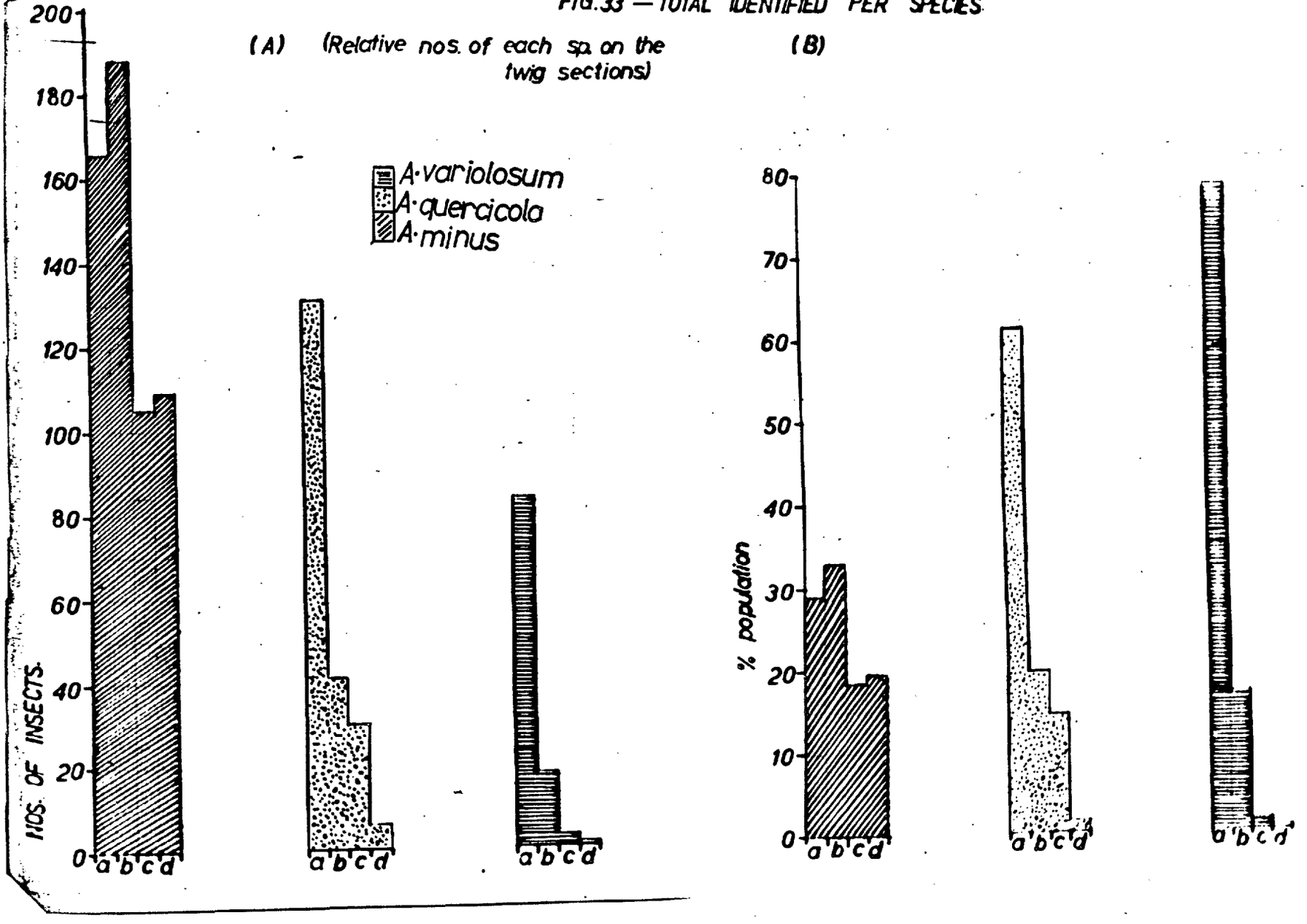
TABLE 15b

expressed as percentages for each species

SPECIES	A	B	C	D	Total
A minus	29.2	33.1	18.5	19.2	100%
A quercicola	63.0	19.7	14.4	2.9	100%
A variolosum	79.3	17.0	2.8	0.9	100%

A, B, C, D = Twig sections.

FIG. 33 — TOTAL IDENTIFIED PER SPECIES



respectively.

In A.variolosum 79.3% of the specimens were found on one year-old sections, with very rapid decrease of the numbers of individuals on the two, three and four years old sections which carried 17.0%, 2.8% and 0.9% respectively.

The numbers of living healthy insects which definitely belong to a single generation and certainly better represent the true natural trend of distribution of these species emphasize the different patterns obtained when all identified specimens were used, as shown in Table 16 and graphically represented in Fig 34 which show that the percentage of surviving individuals of A.quercicola and particularly A.variolosum on the year-old sections is very high indeed, 76.5% and 91.5% respectively.

These results indicate that the three species differ in their preferences for settling sites, and although occuring together, they occupy slightly different positions on the twigs; A.variolosum strongly favours the youngest sections, but occuring in numbers on the other sections as well. A.minus appears to prefer the two year-old sections but large numbers of it are found on the other sections too. Thus A.variolosum and A.quercicola are characterized by concentration on the youngest sections while A.minus is rather widely dispersed over all four sections.

The observations on the patterns of distribution of the

TABLE 16a

showing all live and healthy insects from the four sections of the twigs

SPECIES	A	B	C	D	Total
A minus	112	125	84	49	370
A quercicola	111	14	16	4	145
A variolosum	53	3	1	1	58

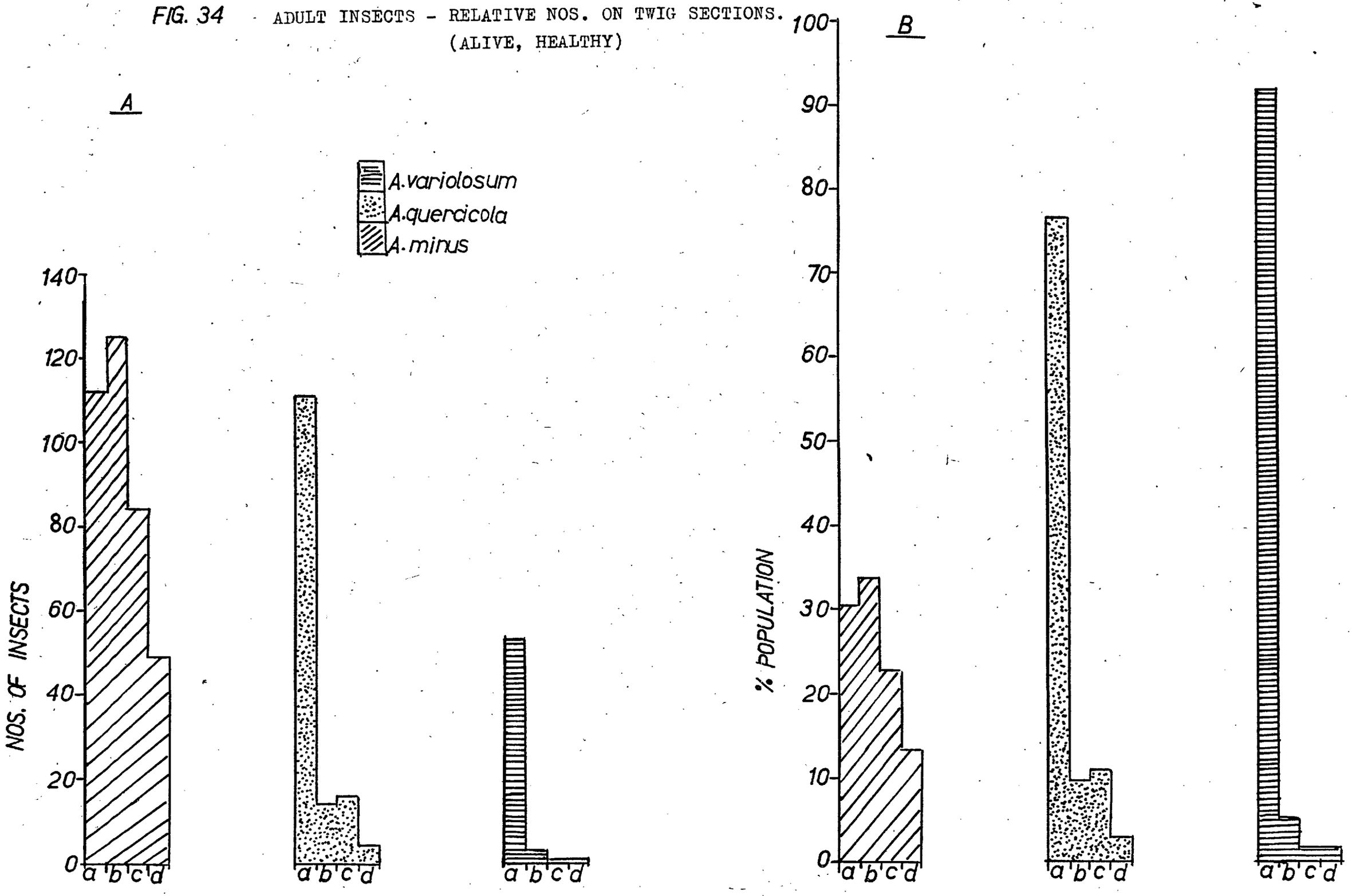
TABLE 16b

figures expressed as percentages for each species

SPECIES	A	B	C	D	Total
A minus	30.2	33.8	22.7	13.3	100%
A quercicola	76.5	9.7	11.0	2.8	100%
A variolosum	91.5	5.1	1.7	1.7	100%

A, B, C, D = Twig sections.

FIG. 34 ADULT INSECTS - RELATIVE NOS. ON TWIG SECTIONS. (ALIVE, HEALTHY)



adult insects on individual hosts, are generally in line with the observed patterns of settling of the first instar nymphs of the three species during breeding experiments. The nymphs of A.variolosum occupied, almost exclusively, the terminal two sections of the twigs while the nymphs of A.minus settled on older sections usually close to the mothers. In the experiments the settling of the nymphs of A.quercicola did not clearly conform with the pattern of distribution of the adults in the fields, probably because the semi-artificial conditions of the experiments and the comparatively small numbers of nymphs obtained.

REPRODUCTIVE CAPACITY has been assessed by:

1) counting the deposited eggs (fecundity) and 2) by counting the first instar nymphs produced by individual females (fertility).

1) In A.variolosum and A.quercicola the counting of eggs was made on specimens collected in the field in an advanced stage of oviposition i.e. showing through the transparent test the shrivelled crescent-shaped body of the female at the anterior margin of the test and with the deposited eggs occupying practically the whole space under the test. The test was removed and the eggs were counted. In A.minus which is ovoviviparous and never has a full complement of eggs, the considerably shrivelled body of the female was indicative of the advanced stage of oviposition, and in this species the counts

included the few, if any, eggs present, and the egg shells less the already hatched nymphs found under the test. The results are tabulated in Table 17 which shows that the number of produced eggs varies from 19 to 56 in A.minus, 36 - 52 in A.quercicola and 44 to 77 in A.variolosum, with the averages of 33, 42.5 and 57 eggs respectively.

2) To assess the fecundity, isolated gravid females on pieces of twigs were kept in the laboratory in separate tubes covered with damp cotton wool to provide adequate humidity and aeration, and at the same time to prevent the nymphs from escaping Sufficient time was allowed for all the eggs to hatch after which the obtained nymphs were counted. The results are presented in Table 22b and show that except for one female of A.quercicola which produced 89 crawlers, the figures for both fecundity and fertility are very similar indicating that all deposited eggs are most probably viable and hatch in due course.

This is also supported by the observation that no eggs were found under the old tests after the emergance of nymphs unless the females were infested and the eggs damaged by fungus.

Apparently even the eggs which are not deposited but for some reason remain inside the body of the female may hatch; adult females when mounted after oviposition sometimes contain within their bodies hatched nymphs which failed to liberate themselves.

It appears legitimate, therefore, to treat the two counts

TABLE 17 - Reproductive Capacity

C = A + B

A	M	Q	V
	26	37	44
	36	44	54
	53	36	52
	29	52	77
	29	47	76
	19	39	50
	30	36-52	50
	33	42.5	53
	36		44-77
	56		57
	25		
	24		
	19-56		
	33		
B			
	58	59	95
	22	54	32
	25	24	55
	19	52	88
	18	27	33
	51	55	33
	41	40	32-95
	14	57	56
	29	89	
	36	24-89	
	19	50.8	
	24		
	18-58		
	29.5		

M	Q	V
26	37	44
36	44	54
53	36	52
29	52	77
29	47	76
19	39	50
30	59	50
33	54	53
36	24	95
56	52	32
25	27	55
24	55	88
58	40	33
22	57	33
25	89	32-95
19	24-89	56.5
18	45-5	
51	45-5	
41	47.5	
14		
29		
36		
19		
24		
14-58		
31.3		

M = A. minus.
Q = A. quercicola.
V = A. variolosum.

A = EGG COUNTS

B = LARVAL COUNTS

C = A + B = REPRODUCTIVE CAPACITY

together as shown in Table 17c. In all species the individual reproductive capacity varies considerably; 14 to 58 in A.minus 24 to 89 in A.quercicola and 32 to 95 in A.variolosum.

A.variolosum shows an average reproductive capacity of 56.5 i.e. almost twice as high as in A.minus which has 31.3 A.quercicola with its average of 47.5 progeny is intermediate.

This would suggest that A.variolosum has an overall advantage in reproduction, i.e. initial population colonizing the habitat, over the other two species and A.minus is in the most disadvantageous position in this respect.

While investigating the effects of "Asterolecanium variolosum" on oak trees in Connecticut (USA), Parr (1940) carried out some studies on the reproduction and reproductive capacity of the insect. Some of his results are noteworthy in so far as they are at variance with the observations of the present author.

Parr assessed the reproductive capacity of the insects by dissecting out the ovaries of mature adult females and counting the ova in them. He found that on chesnut oak (Quercus montana) 22 insects had an average reproductive capacity of 129.5 while 23 females on white oak (Q.robur) had an average of 67.7, but he also found that in insects on both species of oak, an average of 12 ova failed to develop into nymphs; the corrected reproductive capacities were therefore 117.5 and 55.7 on Q.montana and Q.robur respectively.

At Silwood Park where the majority of oak trees are Q.robur and where Q.montana is absent, only the reproductive capacity (56.5) of A.variolosum which is the highest of the three species investigated, is similar to Parr's lower figure (55.7) obtained on Q.robur.

It is possible that Q.montana is more suitable for the physiology of the insect than the original host. Q.robur.

With regard to the method of reproduction, Parr reported that the insect was ovoviviparous and that he never at anytime found eggs deposited under the tests of the females; on the other hand he reported finding fully-formed nymphs within the oviducts. The experience of the present writer on the material studied on oak at Silwood Park is that only A.minus is ovoviviparous while both A.quercicola and A.variolosum are oviparous; deposited eggs were certainly found in large numbers and on several occasions under the tests of the latter two species.

MORTALITY

Crawlers: The breeding experiments have shown that a large number of the first instar nymphs (crawlers) failed to settle. This is apparent from a comparison of average numbers of the crawlers normally produced by the individual females of each species and the average numbers of settled individuals obtained in experiments (Table 18).

Table 18

	A.variolosum	A.quercicola	A.minus
Reproductive capacity	56.5 (32-95) 14 females	47.5 (24-89) 15 females	31.3 (14-58) 24 females
Nos of settlers on potted plants	21 (37.2%) (3-43)	16.1 (33.8%) (4-28)	7 (22.4%) (2-13)

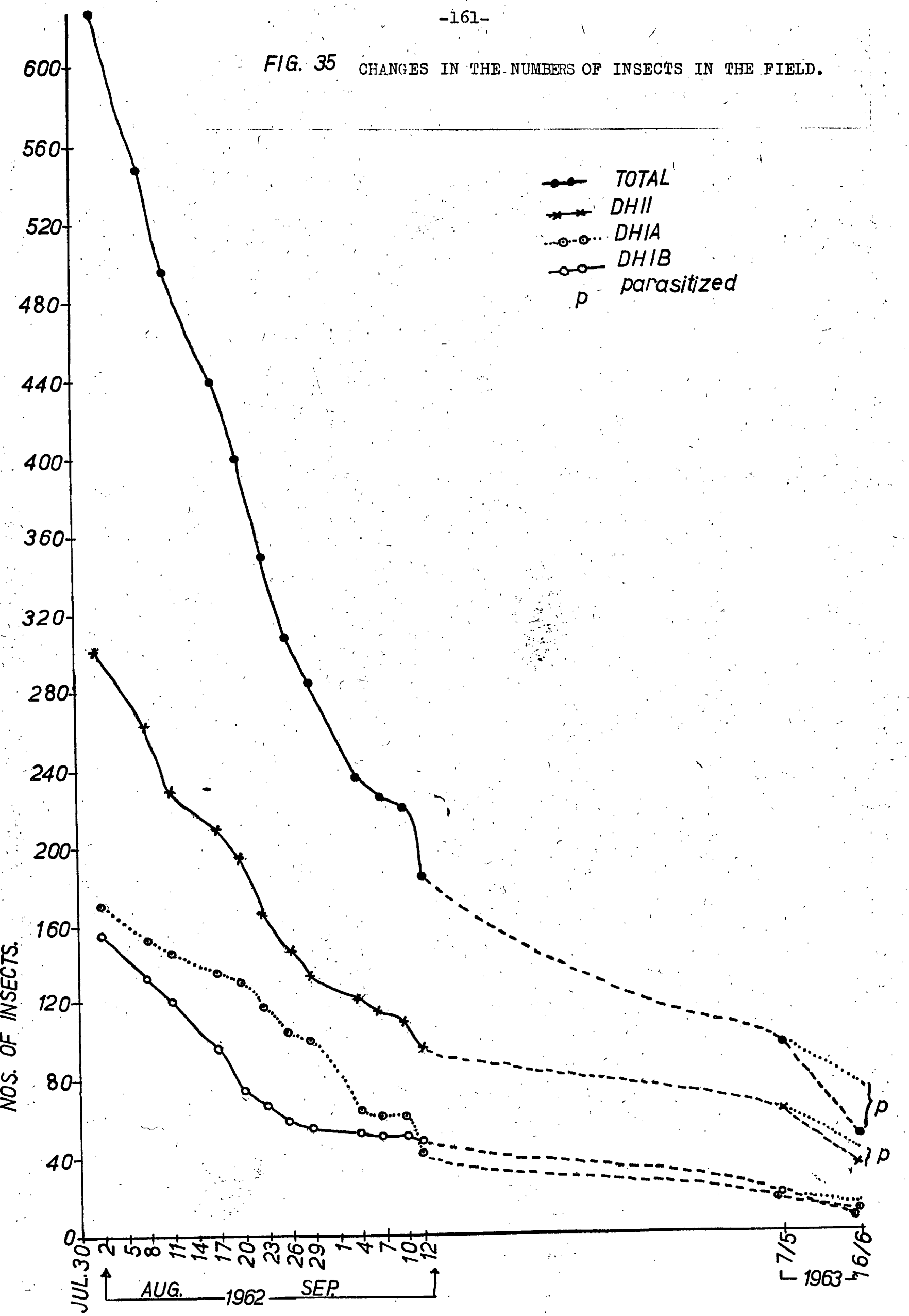
The loss appears to be quite considerable, ranging from $\frac{2}{3}$ to $\frac{3}{4}$ of the reproductive capacity of the females.

These results may have been affected by the semi-artificial conditions of the experiments, usage of seedlings, which, in the field show slight infestation, and which particularly in the case of A.minus are apparently unsuitable for the development of this species. The assessment of the loss in the field is difficult but it seems to be also very high, probably of the same magnitude as that shown in the breeding experiments. Parr (1940) in his studies on "Asterolecanium variolosum" in Connecticut, USA, also reported that in the field a high

proportion of the crawlers failed to settle, but gave no estimates of the numbers lost; he indicated, however, that many crawlers were blown off by the wind or were washed away by rain, particularly from the smooth bark of the terminal twigs. In the breeding experiments carried out in the cold greenhouse the influence of these factors (wind and rain) was practically eliminated, thus the semi-artificial conditions of the experiments may have been largely counterbalanced.

Settlers: For studies of the mortality after settling, a number of twigs were selected on three trees in the field (DH IA, DH IB, DH II). At the end of July, 1962 when all the settling of the insects was completed, the position of each settler was marked with white waterproof paint, and thereafter regular counts were made at 3 day's intervals till 12th September when all surviving insects moulted into adult females. In May of the following year (1963) another count was made, and in July the final count of the surviving and ovipositing females, was made. The results of these counts are shown in ~~Table M~~, Appendix X and represented graphically in Fig 35. It appears that during the six weeks of development over $\frac{2}{3}$ of the original number of settlers perished, with a further, though smaller, reduction in numbers of insects during the winter and spring. The proportion of surviving specimens on individual twigs varied from nil to 23.8%, and of the total potential population of 628 settlers counted and marked in

FIG. 35 CHANGES IN THE NUMBERS OF INSECTS IN THE FIELD.



July 1962 only 48, i.e. 7.64% survived to produce the next generation. If it is assumed that the 628 settlers represented only 33 to 25% of the total number of crawlers originally produced, the 48 specimens which survived to lay eggs in 1963 represent only 1.9 to 2.8% of the reproductive capacity of their parents. It should be mentioned that the three trees on which these counts were made were infested mainly by A.variolosum and A.quercicola with only a very small proportion of A.minus on one of them (DH IA).

Similar assessments of the mortality were made without artifical marking, but taking advantage of the fact that as soon as the settler begins to feed, a pit appears in the bark under its body. In this way original numbers and the positions of the settlers are naturally marked. The pits persist for one more seasons depending on their size which in turn depends on the length of the feeding time before removal of the insects. On one year old sections of the twigs all pits and insects, living or dead, present, belong to only one, i.e. the last generation, and the sum of their numbers represent the potential population of that generation on the particular section of the twig. From the number of living healthy individuals the percentage of survival can be calculated. The counts for 13 host trees based on a number of samples taken between January and May for each tree are shown in Table 19 (p.168); the table shows separately the numbers of empty pits and of the alive healthy

alive parasitized, dead and dead parasitized insects found, the sum total of which gives thepotential population, and also the percentage of survival. The percentage of survival on different trees varies considerably - from nil to 15.72%. The first 8 trees on the list (GI to House III) were infested predominantly by A.minus and showed greater variation in mortality; but on average only 6.23% of the original number of settlers survived. The remaining 5 trees (Store - DH II) were infested mainly by A.variolosum and A.quercicola, and showed higher survival percentages which, on average, was 7.5% for all these 5 trees together. This figure is very close to that (7.64) calculated for the three of these trees from counts on twigs marked with white paint. (Table 18).

Again, if it is assumed that the potential population of settlers represents 25-33% of the reproductive capacity of their parents, the overall average percentage of survival for all the trees was 1.69 - 2.23%; for the trees predominantly infested by A.minus this percentage was low, 1.56 - 2.06% and for those infested by A.variolosum and A.quercicola, 1.88% - 2.47%. This would suggest that A.variolosum and A.quercicola have somewhat higher survival ratio than A.minus.

In some cases, when a nymph drops off a twig, the thin ventral skin of the previous instar remains in the pit. This subject has not been studied in detail, but it is possible that after moulting the insect somehow fails to reinsert its

stylets into the bark of the twig and so dies of starvation; not being anchored to the bark it drops off and is lost.

The known causes of mortality include parasites, predators and possibly fungi; the suspected but not investigated factors may include climatic factors (wind, rain), physical and chemical state of the parts of the host trees, "natural organic causes", mites.

Climatic factors and perhaps the physical and chemical state of the host trees as well as "natural causes" appear to be responsible for the mortality among crawlers, and the latter two factors also for the mortality among settlers during the development period.

Parasites: Three species of hymenopterous parasites (Euaphycus variolosus, Alam, Psyllaephagus cocci Alam and Aphytis variolosum Alam) have been described by Alam (1956,1957) from A.variolosum on Q.robur L from Silwood Park, but from the Asterodiaspis material specially collected for breeding parasites by the present writer only two species were obtained these were mostly Metaphycus variolosus Alam, and only one Habrolepis dalmani Westw. (Table 20)

Table 20

Parasite	Asterodiaspis Hosts		
	Minus	Quercicola	Variolosum
Metaphycus sp? variolosum Alam	38	16	3
Habrolepis dalmani Westw.	1	-	-

The parasites were kindly identified by Dr. R.D. Eady of the British Museum (Natural History) and Mr. Harold Compere of University of California, it appears that there is no discrimination between the three species by the parasite. The biology of the parasites is not known, but the adult parasites are on wing in summer just about the time when the second instar nymphs are present in the field. No parasites or their eggs were found in the immature stages and it seems that only the adult females are attacked and provide sufficient medium for the parasite to develop and reach maturity.

The parasitized females at first do not differ from the healthy ones, but later, in May when the eggs of the latter began to show through the skin and transparent test, the parasitized insects showed a dark area in the centre of the body which marked the developing single pupa of the parasite within the body of the host; sometimes the parasitized insect dies before the parasite completes its development, thus the parasite dies with the host. The parasitized females do not oviposit at all.

The percentage of parasitism among the living insects is comparatively low and the numbers obtained from samples of twigs 1 to 4 years old taken from the 13 investigated host trees are shown in Table 21. Out of the total of 584 specimens 24 were parasitized, which represents 4.11%. Parasitism in A.minus and A.quercicola were about equal, 3.92% and 3.47%

Table 21 Live insects on twigs.

HOSTS	ALIVE IDENTIFIED				ALIVE PARASITIZED				ALIVE HEALTHY				% PARASITIZED			
	m	q	v	Total	m	q	v	Total	m	q	v	Total	m	q	v	Total
GI	109	5	1	116	2	-	-	2	107	5	1	113	1.8	-	-	1.7
GII	1	6	1	8	-	-	-	-	1	6	1	8	-	-	-	-
GIII	183	6	1	190	10	1	1	12	173	5	-	178	5.5	16.7	100	6.3
Stop I	6	8	1	15	-	-	1	1	6	8	-	14	-	-	100	6.7
Stop II	15	3	1	19	1	-	-	1	14	3	1	18	6.7	-	-	5.26
House I	58	3	8	69	2	-	1	3	56	3	7	66	3.45	-	12.5	4.35
House II	-	1	-	1	-	-	-	-	-	1	-	1	-	-	-	-
House III	8	9	1	18	-	1	1	2	8	8	-	16	-	11.1	100	11.1
Store	1	1	-	2	-	-	-	-	1	1	-	2	-	-	-	-
Hut II	2	7	2	11	-	-	-	-	2	7	2	11	-	-	-	-
DHIA	2	20	23	45	-	1	-	1	2	19	23	44	-	5	-	-
DHIB	-	3	5	8	-	-	-	-	-	3	5	8	-	-	-	-
DHII	-	72	13	85	-	2	-	2	-	70	13	83	-	2.8	-	2.4
	385	144	57	186	15	5	4	24	370	139	53	562	3.9	3.47	7.02	4.10

m = A. minus
q = A. quercicola
v = A. variolosum

respectively, while in A.variolosum it was about twice as much, 7.02%.

On the one year old sections of the twigs (Table 19) the percentage of parasitism among living insects for all species together was less, 3.25%, those for A.minus being only 2.61% for A.quercicola 2.70% and for A.variolosum again the highest at 5.9%. Among the insects which for some unknown reasons died prematurely on these twigs the corresponding proportions of parsitism were higher, 7.85%, 6.25% and 13.6%, respectively, with an overall figure of 9% for three species together. The percentage of parasitism in both living and dead insects together for the whole population on one year old twigs was 4.65%; for A.minus, A.quercicola and A.variolosum separately it was 4.22%, 3.15% and 8.22%.

All these figures indicate that the proportion of parasitized individuals in A.variolosum is about twice as high as in the other two species.

Unknown Causes: A number of insects were found dead on the twigs, with no apparent cause of death. Among the samples of one year old sections of twigs there were 81 such specimens (Table 19), which represents about 2.04% of the total potential population and is just under $\frac{1}{3}$ of the number of living insects.

It is possible that proding and piercing of the skin of the scales by the parasite with its ovipositor, without actually laying eggs is the cause of their death. This problem was not

Nos. of the individual species on

Table 19 one-year-old twig sections.

HOST	Potential Population	Identified m	q	v	Total	Dead m	q	v	Total	Dead parasitized m	q	v	Total	Alive parasitized m	q	v	Total	Alive healthy m	q	v	Total	% Survival m	q	v	Total
GI	159	44	4	1	49	24	-	-	24	-	-	-	-	-	-	-	-	20	4	1	25	12.58	2.52	.63	15.72
GII	45	1	5	1	7	-	-	-	-	-	-	-	-	-	-	-	-	1	5	1	7	2.2	11.1	2.2	15.6
GIII	1285	78	5	1	84	11	-	-	11	4	-	-	4	3	1	1	5	60	4	-	64	4.67	.31	-	4.98
Stop I	133	6	7	4	17	-	1	3	4	-	-	-	-	-	-	1	1	6	6	-	12	4.5	4.5	-	9
Stop II	69	4	3	1	8	1	-	-	1	-	-	-	-	-	-	-	-	3	3	1	7	4.35	4.35	1.45	10.15
House I	312	20	4	9	33	2	2	2	6	-	-	1	1	-	-	1	1	18	2	5	25	5.9	.65	1.6	8.0
House II	18	2	-	-	2	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
House III	354	8	10	6	24	5	2	6	13	-	1	-	1	-	1	-	1	3	6	-	9	.84	1.7	-	2.54
Store	140	1	-	2	3	1	-	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hut II	129	-	8	6	14	-	1	3	4	-	-	1	1	-	-	-	-	-	7	2	9	-	5.4	11.55	6.95
DHIA	431	2	21	24	47	1	6	3	10	-	-	1	1	-	-	-	-	1	15	20	36	.23	3.48	4.65	8.35
DHIB	104	-	2	5	7	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5	7	-	1.9	4.8	6.72
DHII	782	-	58	13	71	-	3	-	3	-	-	-	-	-	1	-	1	-	54	13	67	-	6.9	1.67	8.57
	3961	166	127	73	366	47	15	19	81	4	1	3	8	3	3	3	9	112	108	48	268	2.83	2.72	1.21	6.76

$\frac{148}{2375} = 6.23\%$

$\frac{119}{1586} = 7.5\%$

m = A. minus
q = A. quercicola
v = A. variolosum

investigated by the present writer, but it is known to occur in other scale insects, notably Saissetia oleae Bern. (De Bach 1943), indicating that the efficiency of the parasite may be greater than would appear from the numbers of Asterodiaspis with obvious evidence of the presence of parasites. Some dead insects, including those with dead hymenopterous parasites inside their bodies revealed after mounting, the presence of fungal mucelia and spores inside their bodies. The fungi were identified as Trichothecium roseum and a Penicillium sp. According to a personal communication from Dr. Madelin the (Bristol University) the mycologist formerly, in the Botany Department, Imperial College, "these fungi are not normally pathogenic but may become weakly so in insects which already for some reason lack full vigour".

Predators: The observations in the field showed that large numbersof the insects, after being already firmly anchored to the twigs, suddenly disappeared, often leaving traces of the broken test and four white lines in the pit corresponding to the spiracular bands of pores in the adult and intermediate stages; this evidence points to some kind of forcible removal of the insects. Newstead (1895) reported that some birds, notably titmice were very fond of Asterodiaspis spp. (I believe firmly that this species is eagerly sought for by various species of tits), and emphasized the beneficial effect of tit-mice in controlling these scale insects in Britain. He also

suggested that serious damage to oak in New Zealand reported by Frogatt was due to the absence of the European species of Paridae there. Parr (1940) found that young trees 6 feet to 10 feet tall were more readily killed than older ones. He explained that this was due to the fact that the older trees were visited by chickadee (=titmice) which devoured large numbers of the insects. The insects on younger trees were protected from the foraging birds by the low hanging branches, the undergrowth and often, snow drifts in winter. Betts (1955, 1956) analysed the contents of the crops of 4 species of titmice (Parus major newtoni Prazak, P. caeruleus obscurus Prazak, P. ater britannicus Sharpes Dresser, and P. palustris dresseri Stejn.) throughout the year in the Forest of Dean (Gloucester) during 1948-51, and found that the Coccids constituted a large proportion of their diets and that, particularly from September to January, these Coccids were represented exclusively by Asterodiaspis from oak. In February and March the proportion of Asterodiaspis in the diet decreased rapidly and were replaced by some other species of Coccoidea (Lecanium coryli, Lepidosaphes ulmi) with no Asterodiaspis being found at all from April till the next September.

At Silwood Park, six species of tits are found. The Great Tit (Parus major), the Blue Tit (P. caeruleus) and the Longtailed Tit (Aegithalos caudatus)are reported to be common, the Coal Tit (Parus ater britannicus) is

quite common, the Marsh Tit (Parus palustis) is present in small numbers and the Willow Tit (Parus atricapillus) also breads.

They are all known to feed around the oak trees and by the end of June to July they have bred and are in flocks.

During the period from September to January titmice were found to be very active around the oak trees, often protesting loudly at the presence of the writer during his investigations. No analysis has been made of the contents of the crops of the titmice which are among the protected birds in Britain, but the period of rapid disappearance of the scales from the twigs coincides with the time of the intensive feeding by titmice on them reported by Betts (l.c.). The proportion of the insects eaten by titmice can be therefore assessed only indirectly.

Assuming that a mortality of about 70% occured during the developmental period into adult females, of the potential population of 3961 insects on one year-old sections of twigs, only 30% (1188) survived to reach the adult stage. However of this figure (100% of potentially reproducing females), only 268 insects, i.e. 22.6% were left on the twigs; parasitized dead and living insects numbered 8 and 9 respectively, i.e. 0.67% and 0.76%. In addition 81 insects (6.81%) died of unknown causes. All these losses account for a total of 366 insects (30.8%, Table 22)

TABLE 22

Initial potential population	Potential population	ADULT INSECTS ONLY alive	dead	parasitized alive	parasitized dead	disappeared
3961	1188 =100% adults	268 22.6%	81 6.8%	9 0.76%	8 0.68%	822 69.2%

The missing 822 adult insects may well have been eaten by the titmice. It is fully realized that this figure is only approximately indicative of the magnitude of the numbers of the insects devoured by titmice, but in view of Bett's findings this magnitude appears to be quite probable.

The data on reproductive capacity, survival, parasitism of the three species would appear to suggest that A. minus has the least chance of survival when in competition with the other two species; its reproductive capacity is about half that of A. variolosum, and about ⅔ that of A. quercicola; its survival rate is somewhat lower than those of the other two species. The only advantage possessed by A. minus in relation to A. variolosum and A. quercicola was shown in the lower proportion of of parasitism which was generally low for all species anyway and is hardly sufficient to explain the anomalous fact that on some trees A. minus occurs in far greater numbers than the other two species on trees of similar age.

This situation remained a puzzle for some time, until it was discovered from the analysis of samples

taken from the field that the prepondrance of A. minus was confined to host trees which were in groups or clumps and in association with other trees. It was also noted that, although grey squirrels (Sciurus carolinensis Gmelin.) were present all over the grounds of Silwood Park, they were especially active in the wooded areas where there are facilities for swinging from tree to tree.

Middleton (1931) and Shorten (1954) have reported extensive cutting of the terminal twigs of oaks by grey squirrels from different parts of Britain. These activities were most intensive in mixed woods (including e.g. oak, beech, pine, etc.) - similar to conditions found at Silwood Park - where the trees provide some food, but only a small proportion of the broken-off twigs was used either as food or for nest construction.

In May 1962, there was an unusually intensive activity on the part of the squirrels resulting in their cutting down many terminal twigs of oaks, particularly extensively in the wooded areas. On examination the cut-off twigs were seen to be mostly sections one or two years old.

No quantitative measurements of the numbers of twigs thus cut off were made but the impression was that at least $\frac{1}{4}$, (but doubtless more) of terminal growth was lost naturally with the specimens of Asterodiaspis which settled on them

TABLE 28 (a) All living healthy specimens of each species

SPECIES	A	B	C	D	TOTAL
A. minus	112	125	84	49	370
A. quercicola	111	14	16	4	145
A. varisolosum	53	3	1	1	58

(b) (a) above expressed as percentages for each species

SPECIES	A	B	C	D	TOTAL
A. minus	30.2	33.8	22.7	13.3	100%
A. quercicola	76.5	9.7	11.0	2.8	100%
A. variolosum	91.5	5.1	1.7	1.7	100%

Table 28 shows the actual numbers (a) and these expressed as percentages (b) of living healthy insects of each species (i.e. potentially reproducing females) on the four sections of the twigs. A loss of about 25% of the two terminal sections means reductions of 16.0%, 21.55% and 24.15% respectively in the number of A. minus, A. quercicola and A. variolosum. The losses are even more impressive when considered in relation to the populations on the one year old twigs which are the ones most often lost. In A loss of 25% in this category of twigs means reductions of 7.5%, 19.12% and 22.9% in the numbers of reproducing females of A. minus, A. quercicola and A. variolosum respectively. The latter figures indicate that the losses in A. variolosum may be about thrice as high as in A. minus.

A loss of this magnitude, if it persists long enough, may well redress the advantage in reproductive

capacity enjoyed by A. variolosum in favour of A.minus and seems to explain why A. minus occurs in such large numbers where the squirrels are most active.

This natural compensation may have more than an academic interest. When for example, the forester complains that squirrels damage new growth on oak trees and hamper regeneration of plants, it may well be that he should rather thank the squirrel for a service rendered. The squirrel, by helping to reduce especially the population of the more vigorous A.variolosum and A. quercicola, may in fact be preventing a greater threat to the survival of the trees than itself. As A. minus which enjoys a relative advantage in this respect is the least vigorous of the three species it may therefore probably constitute only a minor threat to the trees.

The intervention of the grey squirrel upon the populations of Asterodiaspis spp. is a very interesting phenomenon. It enables a less vigorous species to survive in a niche to the detriment of a more vigorous one.

~~Results and Conclusions~~

~~1. The extended detailed morphological studies of all stages (including the hitherto undescribed second instar nymph) of Asterodiaspis minus Lindinger, A. quercicola Bouche and A. variolosum Ratzeburg confirmed their status as good morphological species.~~

RESULTS AND CONCLUSIONS

1. The extended detailed morphological studies of all stages (including the hitherto undescribed second instar nymph of Asterodiaspis minus Lindinger, A. quercicola Bouché and A. minus variolosum Ratzeburg confirmed their status as good morphological species.

2. The differences between these species are quantitative, all three forming a simple sequential series, A. minus occupying the lower end, A. variolosum the higher, with A. quercicola being intermediate. The same relationship is reflected also in the bionomics of these species.

3. Most of the characters of all stages differentiate the three species only statistically, i.e. they show different mean values for each, with a more or less wide overlap of individual variation between the species; this is particularly true with regard to the second instar nymph. In adult females such characters include: size of body, length of apical setae, length of spiracular bar, number of quinquelocular pores in spiracular bands and along the margins, and the number of ventral "dark-rimmed" pores. The second instar nymphs of all three species are very similar and even statistical differences exhibited by characters such as size of the body, length of ~~apcial~~ apical setae, length of spiracular bars, and numbers of quinquelocular poresin spiracular and marginal rows, are very small; but the numbers of marginal 8 -shaped pores show very distinct differences in averages for each species and very narrow overlap of individual variation

between the species. In the first instar nymphs the characters which statistically differentiate the species include: size of the body, length of antennae, length of apical setae and length of legs.

4. There are, however, a few characters which well separate the species. In the adults these include the number of perivulvar multilocular pores, and the number of loculi in these pores. In the first instar nymphs the absence of the large dorsal 8-shaped pore separates A. variolosum, and the different numbers of these pores segregate A. quercicola and A. minus. Incidentally, with regard to this character, the prevaling trend is reversed, and A. minus has the highest number of these and A. variolosum none. The second instar nymphs may be separated in most cases by the numbers of marginal 8-shaped pores.

5. A. minus has two forms of adult females (differing by the condition of the apical setae), and also two distinct forms of the first instar nymphs (differing sharply in the condition of the sub-median series of dorsal 8-shaped pores); the two forms of the first instar nymphs are "nest-true", i.e. all progeny of a single female are either of one, or the other form. Apparently no correlation exists between the two forms of the adults and the two forms of the first instar nymphs.

6. The constructed keys allow for ready identification of the adult females, the first instar nymphs, and also of the second instar nymphs.

7. In external appearance all three species are very similar and cannot be reliably identified without being mounted and examined under high power microscope.

8. All three species are parthenogenetic.

9. In experimental breeding all species bred true, each female producing the progeny of its own kind. The offspring of a single female often showed the full range of individual variation characteristic for the species, and independent of the actual condition of the particular character in the ~~matter~~ mother.

10. A. variolosum and A. quercicola are oviparous and A. minus ovoviviparous.

11. The life cycles of the three species are similar, but the incubation period is longest in A. variolosum and shortest in A. minus, and the post-embryonal development is shortest in A. variolosum and longest in A. minus; A. quercicola is intermediate in both respects.

12. Observations on the settling habits of the first instar nymphs revealed that A. variolosum settles at the tips of the twigs, A. minus preferred the older sections of the twigs, A. quercicola being intermediate.

13. The behaviour experiments showed that A. variolosum is the most active, and A. minus the least, A. quercicola being intermediate: All three species exhibited definite positive photokinesis and phototaxis as well as skototaris, and less definite negative geotaxis; klinokinesis is also exhibited and appears to be secondary to phototaxis.

In all these reactions A. variolosum was the most vigorous and A. minus the least; A. quercicola was intermediate

14. All three species occur mainly on 1-4 years old sections of the twigs and produce identical galls on the bark of the twigs in form of depressions with raised edges. Heavy infestation results in severe distortion and retardation of growth of the twig.

15. In the areas studied, the infestation on the host trees is very variable but generally low and no serious damage to the oak trees has been observed; this may be explained by probable partial resistance of the host, together with the other natural controlling factors operating there.

16. All three species may occur together in mixed populations, but A. minus is predominant on oak trees growing in association with other trees; it is absent or occurs only in small numbers on host trees which grow singly in the open. On the latter hosts either A.quercicola or A. variolosum may be predominant.

17. On the average the oak trees growing among other trees (in wooded areas) are more heavily infested. It is probable that the trees standing in groups may mutually act as windbreaks to each other, thus in part reducing the possibility of the crawlers being blown off by the wind and lost.

18. A variolosum occurs predominantly on one year-old sections of twigs, with very few specimens on the older

(2-4 years old) sections; A. quercicola also prefers the one year-old sections but a fair number of individuals are found also on the 2-3 years old sections. A minus occurs in greatest numbers on the two year-old sections and is more evenly distributed over the one, and the three to four years old sections. Thus each species occupies a more or less well-defined "sub-niche" on the twig.

19. The reproductive capacity of A. minus is the lowest, that of A. variolosum being twice as high, and that of A. quercicola intermediate.

20. A number of crawlers fail to settle and are lost, probably being blown off by the wind, washed away by rain, or failed to pierce the bark with their mouth-stylets. Estimated proportions of lost crawlers are about 62.8% in A. variolosum, 66.2% in A. quercicola and 77.6% in A. minus.

21. The mortality during the developmental period is very high, being about 70% of the original settlers, and appears to be the same in all three species.

22. Parasitism due to hymenopterous parasites (Metaphycus sp? variolosum Alam, Habrolepis dalmarri Westw.) is generally very low, about 3.9% and 3.47% in A. minus and A. quercicola respectively, and about twice as high (7.02%) in A. variolosum.

23. Some 6.8% of the adult insects die of unknown causes, some of the weakened specimens probably killed by entomogenous fungi (Trichothecium roseum Pencillium sp)

24. All three species are known to be heavily preyed upon by titmice (Parus major, P. caeruleus, Aegithalos caudatus) particularly between September and January. From the collected data it appears that up to 70% of the adult insects are devoured by these birds during the winter; this activity thus represents a major factor in destroying the insects.

25. All the obtained data indicate that A. minus is the least vigorous species and that it has a considerable disadvantage in competition with the other two species, especially with A.variolosum; although the parasitism in A. variolosum is about twice (7.02% compared with 3.9%) as high as in A. minus, it does not appear high enough to counterbalance the difference in reproductive capacity and in the numbers of crawlers lost of the two species, since parasitism is, in any case, generally very low.

26. The factor responsible for the unexpected predominance of A. minus in wooded areas appears to be the abundance of the squirrels in these areas, and their habit of cutting off the terminal shoots of oaks in the spring, mainly the one year, but also two year-old sections. About $\frac{1}{4}$ or more terminal twigs are thus destroyed with the insects in them. Because of the different distributions pattern of each species this action imposes differential losses on the population of the three species. The loss incurred by A. variolosum is about three times as high as that by A. minus, thus the biological balance is reversed in favour of the latter in the wooded areas. The single trees growing in the open are rarely visited by

squirrels, and the cutting off of the twigs is negligible if any, with the result that on these trees A. variolosum and A. quercicola occur in numbers, with very few, or often, none of A. minus.

27. From the results of these morphological and bionomical studies it is concluded that A. minus, A. quercicola and A. variolosum represent a sequential series of closely related, but separate species.

THE SPECIES CONCEPT (with special reference to sympatric and morphological species).

The modern species concept regards reproductive relationship as the principal criterion for defining species, while in the Linnaean era species were defined mainly on the basis of morphological relationships. Ideally, however, it should be possible to separate species not only on the basis of differences in their morphological characters but also from the point of view of the differences in their cytology, ethology and distribution.

In connection with the modern species concept Mayr (1963) defined species as groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups, while Dobzhansky (ibid). described the species as "the largest and most inclusive.... reproductive community of sexual and cross-fertilizing individuals which share a common gene pool". These ideas are ~~seen~~ seen to be mainly concerned with the genetic make-up (genotype) of the species and are distinguished from the morphological (phenotypic), on basis of the species.

However the conflict of these two views is more apparent than real in so far as any present organism is based on its genotype, its phenotype being merely the external product of how this genotype has reacted with external factors. Mayr (l.c.) said that the existing types are the survivors among a great number of

produced forms, the survivors being clustered around a limited number of adaptive peaks, and ecological factors have given the former continuum a taxonomic structure (i.e. discontinuity). Each adaptive peak is occupied by a different kind" of organisms, and if each "kind" is sufficiently different from other kinds it will be legitimate to call such a cluster of genotypes a species. He further stated that the striking discontinuity noted between sympatric populations is the basis of the species concept in biology.

Sexually reproducing species can be compared morphologically as well as being proven on the basis of generic relationship through breeding, but asexual species are not easily referred to their genotypes and so they are defined mostly on morphological characters. In groups where facultative parthenogenesis alternates with a phase of sexual reproduction (e.g. Aphidoidea) genetic comparisons are possible but where parthenogenesis is obligatory (e.g. some Coccoidea), the only basis of describing the species is morphological.

White (1954) said that in most parthenogenetic coccids, weevils, sawflies and stick insects we can speak of "species" without impropriety, since many of the specific characters are probably older than the asexual method of reproduction, and have been handed down from the time when these forms were bisexual. Asexuality therefore appears to be secondary to sexuality and all asexual animals appear to have arisen from sexual forms.

With closely related species the separation of different species may be very difficult, e.g. sibling species.

Sibling species are morphologically similar, but are reproductively isolated. They are then recognized on biological basis such as habits, ecology, or physiology. Sibling species normally originate by geographical isolation. Parthenogenetic species are special sibling species. In complete parthenogenesis every clone is isolated from every other sister clone, as well as from the parental species

Where sibling species are sympatric their ~~is~~ mutual isolation may depend on biological characters. Ross (1957) noted that insects of different species sometimes appear to live their entire lives in identical situations. He concluded that many insects can share such habitats without competing with each other. This contradicts Gause's rule that species with identical ecological requirements cannot co-exist.

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Appendix I Adult Females - Summary of Measurements.

SPECIES	No. of specimens	Size (μ) ♀	Size (μ) ♂	Multilocular pores (μ) No.	Multilocular pores (μ) ♀	Multilocular pores (μ) Locule	Apical seta (μ)	Tubular duct (μ)	Marginal 8-shaped pores length (μ) ant.	Marginal 8-shaped pores length (μ) mod.	Marginal 8-shaped pores length (μ) postr.	Spiracles length (μ) antr.	Spiracles length (μ) postr.	Spiracular bands of quinquelocular pores antr.	Spiracular bands of quinquelocular pores postr.
A.variolosum range	30	742.7	661	46	5.3	10.0	30	20	6.7	7.3	6.7	35.7	37.3	54	53
		2507	1363	73	6.7	11.0	40.7	30	10	10	9.3	46.7	50.0	97	101
av.		974	869	56.5	6.3	10.04	34.3	24.2	8.8	8.9	8.3	43.2	43.7	70.5	73.0
A.quericicola range	31	657	536	21	4.0	6	24.7	23.3	7.3	7.3	6.7	31.7	31.7	32	35
		1411	1086	28	6.7	8	31.7	30.7	10	10.7	10	46.7	48.3	66	53
av.		920	753	24.06	5.6	7	28.9	26.8	8.9	8.9	8.8	43.0	48.3	43.3	42.9
A.minus range	31	543	429	3	3.3	4	23	16.7	6.7	6.7	6.7	33	32	18	19
		714	740	9	5.0	5	41	22.7	10	8.3	7.3	45	43	34	41
av.		634	527	6.35	4.0	4.1	27.0	20.0	7.3	6.9	6.8	39.5	38.1	24.9	27.4

Marginal rows of quinquelocular pores ant.row	inter-sp.row	postr.row	Marginal 8-shaped pores without quinquelocular pores ant.	post.	Dark-rimmed pores
17	24	12	11	25	8
52	47	38	44	40	14
31.0	34.2	27.5	29.1	31.2	11.9
14	16	9	2.0	13	7
35	36	38	34	27	14
22.1	21.0	22.5	19.5	19.2	9.6
5	9	7	11	16	3
20	21	24	36	30	7
9.4	13.1	12.0	28.4	23.1	3.53

Appendix II Second Instar Nymphs - Summary of Measurements.

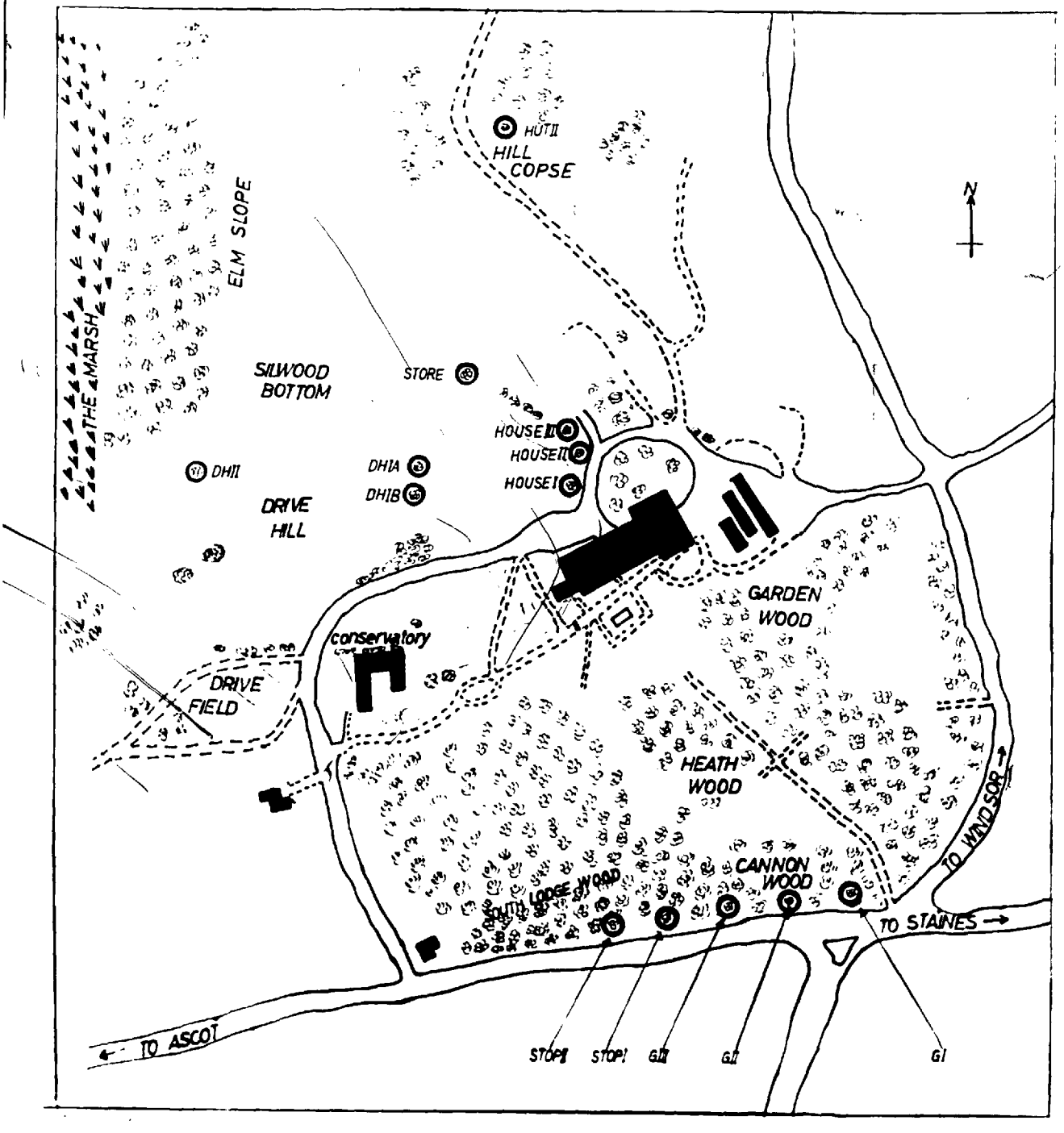
SPECIES	No. of Specimens	Size (μ) l	Size (μ) w	Length of apical seta (μ)	Marginal 8-shaped pores lengths No.	ant.	med.	postr.	Spiracle length (μ) ant.	post.	Quinquelocular pores spiracular rows ant.	post.	marginal rows ant.	post.	8-shaped pores without quinquelocular pores ant.	post.	"Dark-rimmed" pores
A. variolosum	30	429	313	23.3	110	6.7	6.7	6.7	23.3	23.3	5	4	0	0	20	18	2
		843	700	38.7	127	8.7	8.0	8.7	31.0	32.7	12	10	11	7	40	32	6
		(682)	(557)	(29.4)	(117.5)	(6.9)	(6.9)	(6.8)	(27.2)	(27.0)	(7.3)	(7.0)	(5.0)	(3.47)	(31.0)	(25.2)	(3.7)
A. quercicola	14	380	240	17.3	80	6.3	6.3	6.0	23.3	23.3	4	4	0	1	21	15	3
		751	572	28.7	111	7.3	7.0	6.7	30.7	26.7	10	10	10	8	35	24	6
		(576)	(313)	(24.0)	(98)	(6.7)	(6.7)	(6.6)	(25.8)	(25.0)	(6.0)	(6.0)	(4.29)	(4.0)	(26.4)	(19.2)	(3.8)
A.minus	2	457	400	15.0	82	6.7	6.7	6.7	23.3	23.3	4	5	2	4	24	18	1
		471	423	20.0	86	6.7	6.7	6.7	26.7	26.0	5	6	2	1	25	19	2

Appendix III First Instar Nymphs - Summary of Measurements.

SPECIES	No. of samples	(μ) size l	w	No. of 8-shaped pores Sub-lateral	Sub-lateral	Sub-median	antenna (μ)	Spiracles (μ) anterior l	w	posterior l	w	Legs (μ) pro-thoracic	meso-thoracic	meta-thoracic	apical seta (μ)
A.variolosum	30	228	140	14	-	-	60.0	6.7	3.3	7.3	3.3	73.0	73.7	68.7	46.7
		440	302				78.0	10	6.7	10	6.0	99.7	98.7	106.7	64.3
		(309)	(192)				(67.0)	(9.2)	(4.6)	(9.4)	(4.8)	(81.8)	(84.5)	(85.7)	(57.7)
A.quercicola	30	210	122	14	8	1	55.7	6.0	3.0	7.0	2.7	60.0	64.0	70.0	47.3
		408	283		9	4	76.7	11.3	5.0	10.0	6.0	100.0	104.7	102.7	63.3
		(262)	(159)		(8.7)	(2 6)	(61.9)	(8.5)	(3.9)	(8.5)	(3.9)	(79.4)	(79.9)	(80.9)	(53.3)
A.minus	30	189	120	14	7	2	53.3	6.0	3.3	6.7	3.3	66.7	64.0	65.7	43.3
		250	157		10	5	76.7	10.0	4.7	10	5.0	83.3	80.3	84.3	60.0
		(226)	(139)		(8.5)	(3.6)	(61.6)	(7.7)	(3.7)	(7.8)	(3.8)	(74.7)	(74.6)	(74.3)	(51.2)

Appendix IV

MAP 1—SILWOOD PARK.



A. variolosum - vertical

Appendix V (var)

		in/min linear velocity	Angle to vertical	direction	changes direction	l=90°			
	ii	0.42	9L	+	2				
	i	0.70	11L	-	12				
	*ii	0.76	22R	+	10				
25W	i	0.42	28L	+	6	0.72	15L	+	1
		0.78	16R	+	-	0.55	60L	+	6
		0.70	48L	+	5	0.65	5L	+	3
		0.58	53R	+	1	0.81	51R	+	-
		0.52	50R	+	-	0.65	83L	+	-
		0.52	3R	+	-	0.51	52L	+	10
		0.70	58R	-	4	0.45	28L	+	-
		0.33	32L	+	1	0.70	11L	-	12
		0.38	27L	+	1	0.60	17L	27+	3.2
		0.42	1L	+	2	0.38	14R	6-	
		0.70	55R	+	3	-0.81			
		0.69	9R	+	1				
		0.62	46R	+	8				
		0.64	16R	+	5				
		0.75	20	-	2				
		0.58	87L	-	5				
		0.64	10R	+	1				
		0.67	180, 90	-	2				
		0.72	57L	+	6				
		0.51	47R	+	5				
		0.60	26R	+	3				
		0.35	74L	+	3				
		0.55	76L R	+	2				
		0.67	72L	-	3				
		0.65	16R	+	4				
		0.60	11L	+	3				

For Appendices V, VI, VII,

i = 25 Watts

ii = 150 Watts

L = Left

R = Right

b = A-minus with broad apical setae.

n = " " narrow " " .

A variolosum - vertical l=90°

Appendix V (var) contd.

	in/min linear velocity	Angle to vertical	direction	changes direction					
150 W ii	0.61	30L	+	1		0.50	74R	-	2
	0.74	11L	+	-		0.42	9L	+	2
	0.80	41L	+	-	*	0.76	22R	+	10
	0.98	61L	+	-		0.62	15L	30+	2.43
	0.70	11L	+	-		0.37	19R	5-	
	0.50	35L	-	4		-1.15			
	0.72	56R	+	6					
	0.73	13L	+	-					
	0.44	74R	+	-					
	0.46	22R	+	2					
	0.75	2L	+	3					
	0.42	50R	+	4					
	0.44	56R	+	4					
	0.78	12R	+	2					
	0.73	30L	+	-					
	0.45	59R	+	7					
	1.15	12L	-	2					
	0.40	22R	-	4					
	0.45	25L	+	4					
	0.38	50L	+	-					
	0.64	15R	+	4					
	0.79	5L	+	4					
	0.69	55R	-	4					
	0.97	8R	+	2					
	0.65	40R	+	5					
	0.64	3R	+	2					
	0.48	53R	+	-					
	0.62	10L	+	1					
	0.45	62R	+	-					
	0.37	22R	+	-					
	0.50	0.90	+	4					
	0.68	8R	+	2					

A. quercicola - vertical Appendix V(q)

	in/min linear velocity	Angle to vertical	direction	1=90° changes of direction
ii	0.52	60°L	+	4
i	0.62	9°L	+	1
ii	0.59	56°L	+	4
i	0.56	49°L	+	5
ii	0.50	63°R	-	2
i	0.45	49°R	+	14
ii	0.58	2½°R	+	5
ii	0.62	50 L	+	3
i	0.60	86L	+	3
ii	0.71	10R	+	6
i	0.66	62R	-	7
i	0.71	69L	+	2
ii	0.69	68L	+	2
ii	0.62	49R	+	1
i	0.41	42L	+	4
i	0.71	50L	+	5
i	0.47	15R	+	4
ii	0.58	79L	+	1
ii	0.64	66L	+	4
i	0.46	180,90	-	8
ii	0.27	65L	+	2
ii	0.22	34R	-	-
i	0.30	76L	-	1
ii	0.83	26R	+	-
i	0.50	29L	+	3
ii	0.55	35R	+	1
ii	0.80	58R	+	4
i	0.79	40R	+	2
i	0.62	58L	+	4
ii	0.70	40L	+	3
ii	0.51	1½R	+	2

	in/min linear velocity	L to vertical	reaction to light direction	1=90° changes of direction
25W	0.62	9L	+	-
	0.56	49L	+	5
	0.45	49R	+	14
	0.60	86L	+	3
	0.66	62R	-	7
	0.71	69L	+	2
	0.41	42L	+	4
	0.71	50L	+	5
	0.47	15R	+	4
	0.46	180,90	-	8
	0.30	76L	-	1
	0.50	29L	=	3
	0.79	40R	+	2
	0.62	58L	+	4
	0.56	9L	11+	4.4
	0.30	4R	3-	
	-0.79			
150W	0.52	60L	+	4
	0.59	56L	+	4
	0.50	63R	-	2
	0.58	2½R	+	5
	0.62	50L	+	3
	0.71	10R	+	6
	0.69	68L	+	2
	0.62	49R	+	1
	0.58	79L	+	1
	0.64	66L	+	4
	0.27	65L	+	2
	0.22	34R	-	-
	0.83	26R	+	-
	0.55	35R	+	1
	0.80	58R	+	4
	0.70	40L	+	3
	0.51	1½R	+	2
	0.58	8L	15+	
	0.22	9R	2-	2.6
	-0.83			

A. minus - vertical

Appendix V(m)

		in/min linear velocity	Angle to vertical	direction	changes of direction		in/min linear velocity	L to vertical	direction	changes of direction
						25W				
b	ii	0.37	57°L	+	6	bi	0.43	90	-	2
n	ii	0.41	69°L	-	-	ni	0.60	9L	+	10
b	ii	0.41	49 R	+	2	ni	0.65	30L	+	8
b	i	0.43	90		2	ni	0.48	55R	-	1
n	ii	0.65	31R	+	3	ni	0.40	66L	-	4
n	i	0.60	9L	+	10	ni	0.54	10L	+	3
n	i	0.65	30L	+	8	i	0.52	90	-	9
n	i	0.48	55R	-	1	i	0.64	70R	+	4
n	ii	0.55	90		2	ni	0.30	45R	-	2
n	i	0.40	66L	-	4	i	0.27	5L	-	3
n	ii	0.66	47L	+	-	i	0.28	24R	+	3
n	i	0.54	10L	+	3	ni	0.45	70L	-	3
n	ii	0.75	9L	+	-	ni	0.71	25L	+	10
	i	0.52	90		9	i	0.25	1L	-	2
							0.47	8L	6+	4.7
	i	0.64	70R	+	4		0.25			
n	i	0.30	45R	-	2		-0.71			
						150W				
n	ii	0.32	35R	-	-	bii	0.37	57L	+	6
	ii	0.47	41L	-	8	nii	0.41	69L	-	-
	i	0.27	5L	-	3	bii	0.41	49R	+	2
	ii	0.49	25R	-	6	nii	0.65	31R	+	3
	i	0.28	24R	+	3	nii	0.55	90	-	2
n	ii	0.66	39L	+	1	nii	0.66	47L	+	-
n	i	0.45	70L	-	3	nii	0.75	9L	+	-
n	i	0.71	25L	+	10	ii	0.69	42L	+	-
n	ii	0.64	64L	+	4	nii	0.32	35R	-	-
n	ii	0.38	51R	-	3	ii	0.47	41L	-	8
	i	0.25	1L	-	2	ii	0.49	25R	-	6
	ii	0.32	50L	-	-	nii	0.66	39L	+	1
						nii	0.64	64L	+	4
						nii	0.38	51R	-	3
						ii	0.32	50L	-	-
							0.52	9L	8+	2.3
							0.32	5R	7-	
							-0.75			

b = A. minus with broad apical setae.

n = " " narrow " "

A. variolosum - horizontal

	in/min linear velocity	changes of direction		in/min. linear velocity	changes of direction
			150W		
25 W	0.35	6	ii	0.38	3
	0.52	14		0.58	6
	0.50	19		0.45	8
	0.58	5		0.48	2
	0.35	1		0.52	4
	0.38	6		0.40	3
	0.48	8		0.74	15
	0.36	6		0.35	6
	0.55	5		0.48	6
	0.56	5		0.48	1
	0.38	12		0.68	10
	0.58	9		0.35	10
	0.48	3		0.35	4
	0.51	4		0.50	8
	0.25	8		0.56	3
	0.63	2		0.43	11
	0.42	6		0.66	4
	0.50	7		0.85	10
	0.52	7		0.58	8
	0.35	5		0.51	2
	0.84	11		0.70	6
	0.49	8		0.35	4
	0.50	1		0.38	14
	0.35	8		0.65	2
	0.30	8		0.32	4
	0.56	8		0.55	5
	0.57	3		0.29	7
	0.47	5		0.55	8
	0.52	1		0.67	3
	0.65	5		0.35	7
	0.45	7		0.36	1
	0.52	16		0.50	15
	0.49	68		0.50	6.2
	0.25	0-14		0.29	1-14
	-0.84			-0.85	

A. quercicola - horizontal

	in/min linear velocity	changes of direction l=90°
ii	0.30	1
i	0.49	6
ii	0.38	9
ii	0.32	2
i	0.36	1
i	0.55	8
ii	0.59	14
ii	0.60	11
i	0.60	7
ii	0.60	6
i	0.65	15
i	0.61	3
ii	0.61	2
i	0.50	4
ii	0.47	8
ii	0.35	5
i	0.30	3
ii	0.54	14
i	0.55	12
ii	0.32	3
ii	0.17	2
i	0.22	2
ii	0.67	5
i	0.45	8
ii	0.28	3
ii	0.60	3
i	0.42	9
ii	0.50	3
i	0.50	3
i	0.38	2

	in/min linear velocity	changes of direction
i	0.49	6
i	0.36	1
i	0.55	8
i	0.60	7
i	0.65	15
	0.61	3
	0.50	4
	0.30	3
	0.55	12
	0.22	2
	0.45	8
	0.42	9
	0.50	3
	0.38	2
	0.47	5.9
	0.22	
	-0.65	

25W

	in/min linear velocity	changes of direction
ii	0.30	1
ii	0.38	9
	0.32	2
	0.59	14
	0.60	11
	0.60	6
	0.61	2
	0.47	8
	0.35	5
	0.54	14
	0.32	3
	0.17	2
	0.67	5
	0.28	3
	0.60	3
	0.50	3
	0.46	5.7
	-0.67	

A minus - horizontal

Appendix VI (m)

		linear velocity	changes of direction l=90°
n	ii	0.42	9
n	i	0.32	11
b	ii	0.35	3
b	i	0.32	3
n	ii	0.40	3
n	ii	0.43	9
n	ii	0.43	9
n	i	0.32	8
n	i	0.45	9
n	ii	0.51	5
n	ii	0.54	7
n	i	0.60	14
	i	0.35	12
	ii	0.42	11
n	i	0.54	6
n	ii	0.30	3
n	i	0.20	6
	ii	0.41	3
	i	0.31	1
	ii	0.40	3
n	ii	0.58	5
n	i	0.47	7
n	ii	0.47	14
n	ii	0.67	12
n	i	0.30	8
n	ii	0.27	9
n	ii	0.37	5
	i	0.18	1
	i	0.29	5
b	ii		

25W

		in/min linear velocity	changes of direction
n	i	0.30	11
b	i	0.32	3
n	i	0.32	8
n	i	0.45	9
n	i	0.60	14
	i	0.35	12
n	i	0.54	6
n	i	0.20	6
	i	0.31	1
n	i	0.47	7
n	i	0.30	8
	i	0.18	1
	i	0.29	5
		0.36	7.0
		0.18	
		-0.60	

150W

		in/min linear velocity	changes of direction
n	ii	0.42	9
b	ii	0.35	3
n	ii	0.40	3
n	ii	0.43	9
n	ii	0.43	9
n	ii	0.51	5
n	ii	0.54	7
	ii	0.42	11
n	ii	0.30	3
	ii	0.41	3
	ii	0.40	3
n	ii	0.58	5
n	ii	0.47	14
n	ii	0.67	12
n	ii	0.27	9
n	ii	0.37	5
		0.43	6.9
		0.27	
		-0.67	

LATERAL LIGHT (HORIZONTAL) Appendix VII

	VARIOLOSUM			QUERCICOLA			MINUS		
	linear velocity (cm/min)	turns	angle	linear velocity (cm/min)	turns	angle	linear velocity (cm/min)	turns	angle
1	1.32	2	+50°	.68	3	+16°	1.08	2	+58°
2	1.23	3	+65°	1.33	6	+85°	1.05	4	+35°
3	1.50	-	+73°	1.48	3	+ 5°	.98	11	+24°
4	1.75	2	-42°	.88	2	+ 4°	.88	5	-180°
5	1.23	-	+90°	1.02	4	+10°	.93	4	+31°
6	1.21	10	-53°	1.08	3.6	24°	1.50	1	+54°
				.68	2-6	4			
7	1.62	5	+50°	- 1.48		-85	1.50	4	+63°
8	1.45	-	+48°				1.50	2	+36°
9	1.57	5	-180°				1.13	8	-180°
10	1.20	4	-49°				1.23	3	+51°
11	1.57	5	+54°				1.32	5	-180°
12	1.32	4	+49°				1.08	6	+30°
13	1.02	2	+73°				1.23	-	+25°
14	2.00	2	+62°				1.40	10	+30°
15	1.88	2	+17°				1.20	4.6	59°
							.88	0	24°
16	1.62	-	+10°				1.50	-11	-180°
17	1.75	5	-180°						
18	1.78	4	+50°						
19	1.50	3	-180°						
20	1.50	4	+35°						
21	.65	-	+19°						
22	1.55	3	+49°						
23	1.20	-	+52°						
	1.45	2.8	66°						
	.65	0	10°						
	2.00	-10	-180°						

FRESH INSECTS

Appendix VIII

(Section A) — linear velocity in/min

	Hor.25 l.v.	dir.	c.o.d.	Vert.25 l.v.	dir.	c.o.d.	Hor.150 l.v.	dir.	c.o.d.	Vert.150 l.v.	dir.	c.o.d.
	(10)			(7)			(6)			(10)		
A.variolosa	1.10		6.7	1.57	5+	3.0	1.27		5.7	1.50	11+	2.0
	0.87		0	0.82	2-	0-11	0.80		2-8	0.92		2-5
	-1.57		-19	-1.87			-1.75			-2.45		
	(3)			(3)			(6)			(3)		
A.quercicola	1.27		5.7	1.35	3+	7.0	1.27		6.3	1.12	2+	2.3
	0.95			1.22			0.75			0.55	1-	0-6
	-1.52		2-12	-1.77		3-12	-1.67		1-14	-1.77		
	(5)			(4)			(5)			(5)		
A.minus	0.80		6.8	1.10	2+	4.2	1.13		5.2	1.23	3+	3.0
	0.45			0.70	2-	2-12	0.93			0.93	2-	
	-1.13		1-11	-1.78			-1.45		4-10	-1.89		0-8

(Section B)

	Hor-Vert 25			Vert - Hor 25			Hor-Vert 150			Vert-Hor 150		
	(10)			(5)			(5)			(10)		
A.variolosa	1.43	9+	3.7	1.15		8.6	1.58	3+	2.4	1.30		6.9
	0.80	1-		0.75			1.20	2-		0.73		
	-1.80		0-8	-1.30		2-17	-2.43		1-6	-2.13		2-14
	(2)			(2)			(5)			(3)		
A.quercicola	1.48	1+	4	1.30		7	1.70	5+	2.8	1.18		4.3
	1.15	1-	2-6	1.25		6-8	1.30			0.43		
	-1.78			-1.38			-2.08		0-4	-1.50		2-8
	(2)			(2)			(4)			(2)		
A.minus	0.98	1+	5.5	0.98		4.5	1.35	3+	4.3	0.98		6.5
	0.63	1-	3-8	0.78		2-7	0.95			0.88		4-9
	-1.30							1-	1-11	-1.05		

(Section C)

	25-150 Hor			25-150 Vert			150-25 Hor			150-25 Vert		
	(4)			(10)			(7)			(5)		
A.variolosa	1.35		10	1.65	8+	1.7	1.23		9.3	1.35	4+	4.4
	1.20			0.95	2-	1.05				1.13	1-	
	-1.70		1-20	-2.88		-2.10			5-14	-1.68		1-13
	(2)			(2)			(3)			(4)		
A.quercicola	1.33		12	1.20	2+	3	1.15		7.3	1.55	4+	3.0
	1.18			0.68			0.55		2-16	1.25		
	-1.48		8-16	-1.73		2-4	-1.63			-1.98		1-4
	(2)			(2)			(2)			(3)		
A.minus	1.08		12	1.25	1+	1	0.78		8	1.10	1+	5.8
	1.00			0.80			0.75			0.68		
	-1.18		4-20	-1.73	1-		-0.80		2-14	-1.50	2-	3-11

FRESH INSECTS

Appendix VIIIa

	Hor 25 (in/min)			Vert 25 (in/min)			Hor 150 (in/min)			Vert 150 (in/min)		
	l.v.	dir.	c.o.d.	l.v.	dir.	c.o.d.	l.v.	dir.	c.o.d.	l.v.	dir.	c.o.d.
.variolosum.	-0.35		4	0.60	+	2	0.48		2	0.64	+	2
	0.63		-	0.67	-	2	0.35		7	0.45	+	4
	0.38		13	0.64	+	-	0.67		4	0.40	+	4
	0.55		4	0.74	+	2	0.55		8	0.44	+	1
	0.36		6	0.33	+	-	0.32		6	0.98	+	-
	0.48		7	0.70	-	11	0.70		7	0.74	+	-
	0.35		-	0.65	+	4	0.51		5.7	0.37	+	-
	0.50		19	0.62	5+	3.0	0.32					
				0.33	2-	0-11	-0.70		2-8	0.45	+	-
	0.35		6	-0.75						0.64	+	2
	0.49		8							0.65	+	5
	0.44		6.7							0.79	+	4
	0.35									0.60	11+	2.0
	-0.63		0-19							0.37		
										-0.98		2-5
.quercicola	0.38		2	0.45	+	12	0.60		6	0.71	+	6
	0.55		12	0.47	+	3	0.38		9	0.51	+	1
	0.61		3	0.71	+	6	0.30		1	0.22	-	-
	0.51		5.7	0.54	3+	7.0	0.60		2	0.48	2+	2.3
	0.88			0.45						0.22	1-	0-6
	-0.61		2-12	-0.71		3-12	0.67		6	-0.71		
							0.54		14			
							0.51		6.3			
							0.30					
							-0.67		1-14			
.minus	0.45		7	0.48	-	-	0.43		10	0.75	+	-
	0.29		5	0.71	+	12	0.40		4	0.41	+	2
	0.18		1	0.28	+	3	0.37		4	0.41	-	-
	0.30		10	0.30	-	2	0.58		4	0.37	+	8
	0.35		11	0.44	2+	4.2	0.41		4	0.49	-	5
	0.31		6.8	0.28	2-	2-12						
	0.18		1-11	0.71			0.44		5.2	0.49	3+	3.0
	-0.45						0.37		4-10	0.37	2-	0-8
							-0.58			-0.75		

l.v. = linear velocity (in./min.)
dir. = direction (+ or -)
c.o.d. = changes of direction (1=90°).

Appendix VIIIb

	Hor-Vert 25 (in/min)			Vert-Hor 25 (in/min)			Hor-Vert 150 (in/min)			Vert-Hor 150 (in/min)		
	l.v.	dir	c.o.d.	l.v.	dir	c.o.d.	l.v.	dir	c.o.d.	l.v.	dir	c.o.d.
variolosa	0.55	+	2	0.52		17	0.50	-	2	0.29		8
	0.35	+	3	0.30		11	0.68	+	1	0.65		3
	0.72	+	4	0.50		8	0.48	+	1	0.38		14
	0.62	+	8	0.51		5	0.97	+	2	0.85		11
	0.70	+	-	0.48		2	0.50	-	6	0.66		2
	0.38	+	1	0.46		8.6	0.63	3+	2.4	0.56		3
	0.70	-	3	0.30		2-17	0.48	2-	1-6	0.35		4
				-0.52			-0.97					
	0.52	+	-							0.48		6
	0.70	+	8							0.45		12
	0.42	+	8							0.58		6
	0.57	9+	3.7							0.52		6.9
	0.32	1-	0-8							0.29		
	-0.72									-0.85		2-14
quercifolia	0.46	-	6	0.55		8	0.59	+	3	0.60		8
	0.71	+	2	0.50		6	0.52	+	4	0.50		3
	0.59	1+ 1-	4	0.52		7	0.80	+	4	0.17		2
							0.83	+	-	0.47		4.3
										0.17		2-8
							0.64	+	3	-0.60		
							0.68	5+	2.8			
							0.52		0-4			
							-0.83					
minus	0.25	-	3	0.47		7	0.38	+	4	0.35		4
	0.52	+	8	0.31		2	0.66	+	1	0.42		9
	0.37	1+ 1-	5.5	0.39		4.5	0.47	-	11	0.39		6.5
							0.65	+	1			
							0.54	3+	4.3			
							0.38	1-	1-11			
							-0.66					

	25-150 Hor (in/min)			25-150 Vert (in/min)			150-25 Hor (in/min)		150-25 Vert (in/min)		
	l.v.	dir	c.o.d.	l.v.	dir	c.o.d.	l.v.	c.o.d dir	l.v c.o.d	dir	c.o.d.
A variolo-sum.	0.50		7	0.38	+	-	0.52	8	0.52	+	-
	0.68		12	1.15	-	2	0.42	5	0.45	+	1
	0.48		1	0.42	+	2	0.58	10	0.51	+	13
	0.50		20	0.75	+	2	0.58	5	0.55	+	6
	0.54		10	0.44	+	-	0.52	14	0.67	-	2
	0.48		1-20	0.73	+	1	0.56	9	0.54	4+	4.4
	-0.68								0.45	1-	0-13
				0.72	+	4	0.84	14	-0.67		
				0.80	+	2	0.59	9.3			
				0.61	+	2	0.42	5-14			
				0.58	-	2	-0.84				
				0.66	8+	1.7					
				0.38	2-	0-2					
				-1.15							
A quercicola	0.47		8	0.69	+	4	0.65	16	0.79	+	3
	0.59		16	0.27	+	2	0.50	4	0.50	+	4
	0.53		12	0.48	2+	3	0.22	2	0.56	+	4
							0.46	7.3	0.62	+	1
							0.22	2-16	0.62	4+	3.0
							-0.65		0.50		1-4
									0.79		
A minus	0.47		0.20	0.32	-	1	0.32	2	0.60	+	11
	0.40		4	0.69	+	1	0.30	14	0.45	-	3
	0.43		12	0.50	1+ 1-	1	0.31	8	0.27	-	3
									0.44	1+	5.8
									0.27	2-	3-11
									-0.60		

COUNTS IN SAMPLES FROM INDIVIDUAL HOST TREES. SAMPLING. APPENDIX IXA

G I. Quercus robur L., Cannon Wood - mixed stand.

No	Date	Dir	Ht	A						B						C						D						Total						sp
				Pp	Idf	Dead		Alive		Mort	Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		sp
						+	Pte	Pte	H				+	Pte	Pte	H			+	Pte	Pte	H			+	Pte	Pte	H			+	Pte	Pte	H	sp
58	28/4 60	S	10'	105	25	21	-	-	4	94.3	305	34	15	-	-	19	93	12	2	-	-	10	-	-	-	-	-	-	503	71	38	-	-	33	m
					2	-	-	-	2			6	6	-	-	-		-	-	-	-	-		-	-	-	-	-		8	6	-	-	2	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
61	28/4 60	S	6'	1	-	-	-	-	-	0.0	67	15	-	-	1	14	8	1	-	-	-	1	-	-	-	-	-	-	76	16	-	-	1	15	m
					1	-	-	-	1			1	-	-	-	1		-	-	-	-	-		-	-	-	-	-		2	-	-	-	2	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
66	13/5 60	S	6'	9	-	-	-	-	-	100.0	47	4	-	-	1	3	29	-	-	-	-	-	-	-	-	-	-	-	85	4	-	-	1	3	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
78	21/2 61	S	8' to 11'	39	17	2	-	-	15	56.4	708	16	1	-	-	15	300	17	1	-	-	16	649	7	-	-	-	7	1696	57	4	-	-	53	m
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	q
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	v
87	31/5 61	S	8' to 11'	3	1	1	-	-	-	100.0	3	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	6	2	1	-	-	1	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
75	17/1 61	E	8' to 11'	2	1	-	-	-	1	50.0	32	2	1	-	-	1	13	-	-	-	-	-	11	-	-	-	-	-	58	3	1	-	-	2	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
Total				159	44	24	-	-	20	84.9	1162	72	17	-	2	53	443	30	3	-	-	27	660	7	-	-	-	7	2424	153	44	-	2	107	m
					4	-	-	-	4			7	6	-	-	1		-	-	-	-	-		-	-	-	-	-		11	6	-	-	5	q
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	v

Dir. = Direction
Ht = Height
Pp = Potential population
Idf = Identified
Pte = Parasitized
H = Healthy
Mort = Mortality

m = A. mimus
q = A. quercicola
v = A. variolosum.

G II. Quercus robur L., Cannon Wood - mixed stand. SAMPLING.

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
62	28/4 60	S	11'	37	-	-	-	-	-	94.6	18	-	-	-	-	-	5	-	-	-	-	1	4	-	-	-	-	-	64	-	-	-	-	2	m
					1	-	-	-	1			1	1	-	-	-		-	-	-	-			-	-	-	-			3	1	-	-	1	q
					1	-	-	-	1			1	-	-	-	-		-	-	-	-	-		-	-	-	-			2	1	-	-	1	v
86	31/5 61	S	10' to 11'	4	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	4	m
					4	-	-	-	4			-	-	-	-	-		-	-	-	-			-	-	-	-			4	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-			-	-	-	-			-	-	-	-	v
67	13/5 60	E	11'	4	1	-	-	-	1	75.0	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	7	1	-	-	1	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-			-	-	-	-			-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-			-	-	-	-			-	-	-	-	v
Total				45	1	-	-	-	1	84.5	18	-	-	-	-	-	8	-	-	-	-	1	4	-	-	-	-	-	75	1	-	-	-	1	m
					5	-	-	-	5			1	1	-	-	-		1	-	-	-			-	-	-	-			7	1	-	-	6	q
					1	-	-	-	1			1	-	-	-	-		-	-	-	-			-	-	-	-			2	1	-	-	1	v

SAMPLING.

G III. Quercus robur L., Cannon Wood - mixed stand.

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
68	13/5 60	E	11'	518	24	3	1	1	19	95.9	585	18	2	1	-	15	533	29	4	1	-	24	596	58	30	2	3	23	2682	129	39	5	4	81	m
					3	-	-	1	2			1	-	-	-	1		-	-	-	-	-		-	-	-	-	-		4	-	-	-	1	3	q
					1	-	-	1	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	-	v
69	13/5 60	S	11'	565	14	5	3	2	4	99.2	1103	35	17	6	1	11	-	-	-	-	-	-	-	-	-	-	-	-	1668	49	22	9	3	15	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-	v
74	13/1 61	S	9' - 11'	34	4	2	-	-	2	91.2	487	4	-	-	-	4	453	4	-	-	-	4	760	5	5	-	-	-	1789	17	7	-	-	10	m
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-	v
76	16/2 61	S	9' - 11'	129	23	-	-	-	23	81.4	1444	10	2	-	2	6	1076	14	-	-	-	14	1065	13	3	-	-	10	3799	60	5	-	2	53	m
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			1	1	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	-	v
88	31/5 61	W	11'	39	13	1	-	-	12	69.3	168	-	-	-	-	-	450	4	2	-	-	2	900	7	5	1	1	-	1384	24	8	1	1	14	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-	v
Total				1285	78	11	4	3	60	95.2	3787	67	21	7	3	36	2512	51	6	1	-	44	2321	83	43	3	4	33	11322	279	81	15	10	173	m
					5	-	-	1	4			1	-	-	-	1		-	-	-	-	-		-	-	-	-	-		6	-	-	-	5	q
					1	-	-	1	-			1	1	-	-	-		-	-	-	-	-		-	-	-	-	-		2	1	-	-	-	-	v

Stop I Quercus robur - mixed stand - (S. Lodge Wood) SAMPLING APPENDIX IX C

No	Date	Dir	Ht	A							B							C							D							Total							sp
				Pp	Idf	Dead		Alive		Mort	Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			sp
						+	Pte	Pte	H				+	Pte	Pte	H				+	Pte	Pte	H			+	Pte	Pte	H				+	Pte	Pte	H		sp
63	28/4 60	S	10'	97	6 7 3	- 1 2	- - -	- - 1	6 6 -	87.64	26	1 1 -	1 - -	- - -	- - -	- 1 -		- - -	- - -	- - -	- - -	- - -	- - -		- - -	- - -	- - -	- - -	- - -	- - -		123	7 8 3	1 1 2	- - -	- - 1	6 7 -		m q v
64	28/4 60	S	11 to 12'	36	- 1	- 1	- - -	- - -	- - -	- -	29	- - -	- - -	- - -	- - -	- - -		16	3 - -	2 - -	- - -	- - -	1 - -		- - -	- - -	- - -	- - -	- - -	- - -		81	3 1	2 1	- - -	- - -	1 - -		m q v
Total				133	6 7 4	- 1 3	- - -	- - 1	6 6 -	90.98	55	1 1 -	1 - -	- - -	- - -	- 1 -		16	3 - -	2 - -	- - -	- - -	1 - -		- - -	- - -	- - -	- - -	- - -	- - -		204	7 11 4	1 3 3	- - -	- - 1	6 8 -		m q v

Stop II Quercus robur - mixed stand - (S. Lodge Wood) SAMPLING

No	Date	Dir	Ht	A							B							C							D							Total							sp
				Pp	Idf	Dead		Alive		Mort	Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			Pp	Idf	Dead		Alive			sp
						+	Pte	Pte	H				+	Pte	Pte	H				+	Pte	Pte	H			+	Pte	Pte	H				+	Pte	Pte	H		sp
16	28/1 60	O	10'	19	1 - -	- - -	- - -	- - -	1 - -	94.74	116	5 - -	- - -	- - -	- - -	5 - -		148	1 - -	1 - -	- - -	- - -	- - -		117	4 - -	2 - -	- - -	1 - -	1 - -		400	11 - -	3 - -	- - -	1 - -	7 - -		m q v
65	28/4 60	S	11 to 12'	33	3 - -	1 - -	- - -	- - -	2 - -	93.94	292	4 - -	- - -	- - -	- - -	4 - -		128	6 - -	4 - -	1 - -	- - -	1 - -		159	1 - -	1 - -	- - -	- - -	- - -		612	14 - 1	6 - 1	1 - -	- - -	7 - -		m q v
77	16/2 61	W	10 to 12'	17	- 3 1	- - -	- - -	- - -	3 1	76.5	12	- - -	- - -	- - -	- - -	- - -		28	- - -	- - -	- - -	- - -	- - -		11	- - -	- - -	- - -	- - -	- - -		68	- 3 1	- - -	- - -	- - -	3 1		m q v
Total				69	4 3 1	1 - -	- - -	- - -	3 3 1	89.85	420	9 - 1	- - 1	- - -	- - -	9 - -		304	7 - -	5 - -	1 - -	- - -	1 - -		287	5 - -	3 - -	- - -	1 - -	1 - -		1080	25 3 2	9 - 1	1 - -	1 - -	14 3 1		m q v

SAMPLING

House I Quercus robur L., North side of the main building - solitary oak in close vicinity of a group of other trees.

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
8	28/1 60	O	5' to 6'	26	-	-	-	-	-	100.0	90	1	-	-	-	1	70	-	-	-	-	-	41	-	-	-	-	-	227	1	-	-	-	1	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
17	10/2 60	O	5' to 7'	60	3	-	-	-	3	95.0	82	4	1	-	-	3	46	-	-	-	-	-	67	-	-	-	-	-	255	7	1	-	-	6	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
18	10/2 60	O	5' to 7'	5	-	-	-	-	-	100.0	14	-	-	-	-	-	10	1	-	-	-	1	5	-	-	-	-	-	34	1	-	-	-	1	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
42	14/3 60	E	7' to 8'	7	1	-	-	-	1	85.7	30	-	-	-	-	-	10	-	-	-	-	-	10	-	-	-	-	-	57	1	-	-	-	1	m
					-	-	-	-	-		2	-	1	-	-	1		-	-	-	-	-		-	-	-	-	-		2	1	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
57	28/4 60	E	6'	5	-	-	-	-	-	100.0	7	-	-	-	-	-	17	-	-	-	-	-	16	-	-	-	-	-	45	-	-	-	-	-	m
					1	-	-	1	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	1	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
53	30/3 60	E	11'	17	-	-	-	-	-	94.1	16	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	33	1	-	-	-	1	m
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
40	14/3 60	S	6' to 7'	29	3	-	-	-	3	89.6	28	4	-	-	-	4	14	-	-	-	-	-	15	1	1	-	-	-	86	8	1	-	-	7	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
50	30/3 60	S	6' to 7'	2	1	-	-	-	1	50.0	26	1	-	-	-	1	12	1	-	-	-	1	19	3	2	-	-	1	59	6	2	-	-	4	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
52	30/3 60	S	10'	9	2	-	-	-	2	77.8	12	-	-	-	-	-	12	-	-	-	-	-	12	1	1	-	-	-	45	3	1	-	-	2	m
					-	-	-	-	-			-	-	-	-	-		-	1	-	-	-	1		-	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
41	14/3 60	W	6' to 8'	38	1	-	-	-	1	89.5	120	4	2	-	-	2	22	-	-	-	-	-	6	-	-	-	-	-	186	5	2	-	-	3	m
					6	2	1	-	3			1	1	-	-	-		-	-	-	-	-		-	-	-	-	-		7	3	1	-	3	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
83	28/3 61	W	11'	6	3	-	-	-	3	33.3	17	-	-	-	-	-	10	4	1	-	-	3	15	-	-	-	-	-	48	7	1	-	-	6	m
					1	-	-	-	1			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
29	26/2 60	N	7' to 9'	96	1	1	-	-	-	97.9	151	13	4	-	-	9	73	1	1	-	-	-	-	-	-	-	-	-	320	15	6	1	-	9	m
					4	1	1	-	2			1	1	-	-	-		-	-	-	-	-		-	-	-	-	-		4	1	1	-	2	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	v
51	30/3 60	N	7' to 8'	7	1	-	-	-	1	85.7	43	4	3	-	-	1	11	-	-	-	-	-	46	-	-	-	-	-	117	5	3	-	-	2	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
82	28/3 61	N	8'	5	4	1	-	-	3	40.0	3	1	-	-	-	1	32	5	-	-	-	5	22	2	-	-	-	2	62	12	1	-	-	11	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		1	-	-	-	-		1	-	-	-	1	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
84	28/3 61	N	12'	-	-	-	-	-	-	-	17	1	-	-	-	1	23	-	-	-	-	-	19	1	-	-	-	1	59	2	-	-	-	2	m
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
Total				312	20	2	-	-	18	92.0	656	34	10	-	-	24	362	12	2	-	-	10	293	8	4	-	-	4	1580	74	18	-	-	56	m
					4	1	1	-	2			2	1	-	-	1		-	-	-	-	-		1	-	-	-	1		6	2	1	-	3	q
					9	2	1	1	5			2	2	-	-	-		1	-	-	-	1		-	1	-	-	-		13	4	1	1	7	v

House II Quercus robur - mixed stand

SAMPLING

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
19	10/2 60	0	5 to 7'	14	2	2	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	6	-	-	-	-	-	23	2	2	-	-	-	m
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
30	26/2 60	E	4 to 6'	3	-	-	-	-	-	-	24	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	33	-	-	-	-	-	m
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
49	30/3 60	E	10	1	-	-	-	-	-	-	-	1	1	-	-	-	5	1	-	-	-	1	-	-	-	-	-	-	6	2	1	-	-	1	m
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
Total				18	2	2	-	-	-	-	25	-	-	-	-	-	13	-	-	-	-	-	6	-	-	-	-	-	62	2	2	-	-	-	m
					-	-	-	-	-	-		1	1	-	-	-		-	-	-	-	1		-	-	-	-	-		2	1	-	-	1	q
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v

SAMPLING

House III Quercus robur L. - mixed stand - North side of main building

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
20	10/2 60	0	5 to 7'	176	2	2	-	-	-		94	-	-	-	-	-	27	1	1	-	-	-	63	4	2	-	-	2	360	7	5	-	-	2	m
					2	1	-	-	1	99.4		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		2	1	-	-	1	q
					2	2	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		2	2	-	-	-	v
21	10/2 60	0	5 to 7'	14	-	-	-	-	-	100	12	1	1	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-	54	1	1	-	-	-	m
					1	1	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
31	26/2 60	S	5 to 7'	164	6	2	-	-	3		154	4	-	1	-	3	49	1	1	-	-	-	8	-	-	-	-	-	375	11	3	2	-	6	m
					7	-	1	1	5	95.1		-	-	-	-	-		3	1	1	-	1		1	-	-	-	1		11	1	2	1	7	q
					4	3	-	-	-			1	-	-	1	-		-	-	-	-	-		-	-	-	-	-		5	3	1	1	-	v
Total				354	8	4	-	-	3		260	5	1	1	-	3	76	2	2	-	-	-	99	4	2	-	-	2	789	19	9	2	-	8	m
					10	2	1	-	6	97.46		-	-	-	-	-		3	1	1	-	1		1	-	-	-	1		14	3	2	1	8	q
					6	5	-	-	-			1	-	-	1	-		-	-	-	-	-		-	-	-	-	-		7	5	1	1	-	v

DH IA. Quercus robur L., Drive Hill - isolated group of two oak trees (DH IA and DH IB).

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
9	28/1 60	O	5' to 6'	104	1 2 7	1 1 -	- - -	- - -	- 1 7	92.3	34	- - -	- - -	- - -	- - -	- - -	24	- 2 -	- 1 -	- 1 -	- - -	- - -	7	- - -	- - -	- - -	- - -	- - -	169	1 4 4	1 2 -	- 1 -	- - -	- 1 7	m q v
24	10/2 60	O	5' to 6'	58	- 1 -	- - -	- 1 -	- - -	- - -	100.0	32	- - -	- - -	- - -	- - -	- - -	18	- 1 -	- 1 -	- - -	- - -	- - -	9	- - -	- - -	- - -	- - -	- - -	117	- 2 -	- 1 -	- 1 -	- - -	- - -	m q v
25	10/2 60	O	5' to 6'	56	- 9 4	2 1 1	- 1 -	- - -	7 2	83.9	19	2 -	- - -	1 1 -	1 -	- - -	7	6 -	3 -	- - -	- - -	3 -	-	- - -	- - -	- - -	- - -	- - -	82	17 4	5 1	1 1	1 -	10 2	m q v
26	10/2 60	O	5' to 6'	137	1 - 2	- 1 -	- - -	- - -	1 - 1	98.5	65	- - 2	- 1 -	- - -	- - -	- 1	32	2 - -	1 - -	- - -	- - -	1 - -	-	- - -	- - -	- - -	- - -	- - -	234	3 - 4	1 - 2	- - -	- - -	2 - 2	m q v
39	14/3 60	N	5' to 9'	20	- 3 2	- - -	- - -	- - -	3 2	75.0	8	- - 2	- 1 -	- - -	- - -	- 1	5	- - -	- - -	- - -	- - -	- - -	2	- - -	- - -	- - -	- - -	- - -	36	- 3 4	- - 1	- - -	- - -	3 3	m q v
46	30/3 60	N	12'	1	- - 1	- - -	- - -	- - -	- 1	0.0	15	- - -	- - -	- - -	- - -	- - -	5	- - -	- - -	- - -	- - -	- - -	21	- - -	- - -	- - -	- - -	- - -	42	- - 1	- - -	- - -	- - -	- 1	m q v
38	14/3 60	E	5' to 8'	19	- 2 4	1 1	- - -	- - -	1 3	78.9	16	2 1	1 1	1 -	- -	1	2	- - -	- - -	- - -	- - -	- - -	-	- - -	- - -	- - -	- - -	- - -	37	4 5	2 1	1 -	- -	1 4	m q v
80	28/3 61	E	5'	18	- - -	- - -	- - -	- - -	- - -	100.0	8	- - -	- - -	- - -	- - -	- - -	9	- - -	- - -	- - -	- - -	- - -	3	- - -	- - -	- - -	- - -	- - -	38	- - -	- - -	- - -	- - -	- - -	m q v
85	28/3 61	E	5'	5	- - 3	- - -	- - -	- - -	- 3	40.0	16	- - -	- - -	- - -	- - -	- - -	10	- - -	- - -	- - -	- - -	- - -	-	- - -	- - -	- - -	- - -	- - -	31	- - -	- - -	- - -	- - -	- - -	m q v
81	28/3 61	W	5'	13	- 4 1	1 - -	- - -	- - -	- 1	69.2	3	- 1 -	- - -	- - -	- - -	1 -	1	- - -	- - -	- - -	- - -	- - -	-	- - -	- - -	- - -	- - -	- - -	17	- 5 1	1 - -	- - -	- - -	4 1	m q v
Total				431	2 21 24	1 5 3	- 1 1	- - -	1 15 20	91.6	216	- 5 5	- 1 2	- 2 1	- 1 -	- 1 3	113	2 9 -	1 5 -	- 1 -	- - -	1 3 -	42	- - -	- - -	- - -	- - -	- - -	803	4 35 29	2 11 5	- 4 4	- 1 -	2 19 23	m q v

DH IB

10	28/1 60	O	5' to 6'	65	- 2	- -	- -	- -	- 2	96.92	26	- -	- -	- -	- -	- -	20	- -	- -	- -	- -	- -	1	- -	- -	- -	- -	- -	112	- 2	- -	- -	- -	- 2	m q v
27	10/2 60	O	5' to 6'	39	- 2 3	- -	- -	- -	- 2 3	87.18	33	- 1 -	- 1 -	- -	- -	- -	10	- 1 -	- -	- -	- 1	- -	4	- -	- -	- -	- -	- -	86	- 4 3	- 1 -	- -	- -	- 3 3	m q v
TOTAL				104	- 2 5	- 7	- -	- -	- 2 5	93.28	59	- 1 -	- 1 -	- -	- -	- -	30	- 1 -	- -	- -	- 1	- -	5	- -	- -	- -	- -	- -	198	- 4 5	- 1 -	- -	- -	- 3 5	m q v

DH II. Quercus robur L., Drive Hill - solitary tree in the open area.

No	Date	Dir	Ht	A							B						C						D						Total						sp
				Pp	Idf	Dead		Alive		Wort	Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		Pp	Idf	Dead		Alive		sp
						+	Pte	Pte	H				+	Pte	Pte	H			+	Pte	Pte	H			+	Pte	Pte	H			+	Pte	Pte	H	sp
11	28/1 60	O	5' to 6'	125	4 1	1 -	- -	- -	3 1	96.8	78	- -	- -	- -	- -	- -	39	- -	- -	- -	- -	- -	21	- -	- -	- -	- -	- -	263	4 1	1 -	- -	- -	3 1	m q v
12	28/1 60	O	5' to 6'	108	- -	- -	- -	- -	- -	-	89	2 -	2 -	- -	- -	- -	15	1 -	1 -	- -	- -	- -	47	- -	- -	- -	- -	- -	259	3 -	3 -	- -	- -	- -	m q v
37	14/3 60	W	8' to 9'	197	23 2	1 -	- -	1 -	21 2	88.3	121	3 -	2 -	- -	- -	1 -	24	2 -	1 -	- -	- -	1 -	6	1 -	- -	- -	- -	1 -	341	29 2	4 -	- -	1 -	24 2	m q v
47	30/3 60	W	7'	67	3 2	- -	- -	- -	3 2	92.5	46	1 -	- -	- -	- -	1 -	13	1 -	- -	- -	- -	1 -	5	- -	- -	- -	- -	- -	131	5 2	- -	- -	- -	5 2	m q v
36	26/2 60	E	7' to 8'	66	3 -	- -	- -	- -	3 -	95.5	37	1 1	1 1	- -	- -	- -	20	- -	- -	- -	- -	- -	51	2 -	2 -	- -	- -	- -	174	6 1	3 1	- -	- -	3 -	m q v
48	30/3 60	E	11'	41	3 2	- -	- -	- -	3 2	87.8	73	3 -	- -	- -	- -	3 -	41	5 -	- -	- -	- -	5 -	10	- -	- -	- -	- -	- -	165	11 2	- -	- -	- -	11 2	m q v
79	21/2 61	E	9' to 11'	34	9 -	- -	- -	- -	9 -	73.5	25	2 -	- -	- -	- -	2 -	21	1 -	1 -	- -	- -	- -	4	1 -	- -	- -	- -	1 -	84	13 -	1 -	- -	- -	12 -	m q v
45	30/3 60	N	7'	125	4 1	1 -	- -	- -	3 1	96.8	97	2 1	1 1	- -	1 -	- -	25	- -	- -	- -	- -	- -	18	- -	- -	- -	- -	- -	265	6 2	2 1	- -	1 -	3 1	m q v
70	12/1 61	N	5' to 8'	19	9 5	- -	- -	- -	9 5	26.4	21	- -	- -	- -	- -	- -	13	- -	- -	- -	- -	- -	11	- -	- -	- -	- -	- -	64	9 5	- -	- -	- -	9 5	m q v
Total				782	58 13	3 -	- -	1 -	54 13	91.4	587	14 2	6 2	- -	1 -	7 -	211	10 -	3 -	- -	- -	7 -	173	4 -	2 -	- -	- -	2 -	1753	86 15	14 2	- -	2 -	70 13	m q v

Store Quercus robur - solitary SAMPLING APPENDIX IX H

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
22	10/2 60	O	-	29	1	1	-	-	-	-	49	-	-	-	-	-	95	1	-	-	-	1	88	-	-	-	-	-	261	2	1	-	-	1	m
			-		-	-	-	-	-	-		1	1	-	-	-		1	-	-	-	1		-	-	-	-	-		2	1	-	-	1	q
			-		-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
32	26/2 60	E	-	65	-	-	-	-	-	-	83	-	-	-	-	-	21	-	-	-	-	-	19	-	-	-	-	-	188	-	-	-	-	-	m
			-		-	-	-	-	-	-		1	1	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	q
			-		1	1	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	v
33	26/2 60	N	-	46	-	-	-	-	-	-	53	-	-	-	-	-	28	-	-	-	-	-	27	-	-	-	-	-	154	-	-	-	-	-	m
			-		-	-	-	-	-	-		3	3	-	-	-		-	-	-	-	-		-	-	-	-	-		3	3	-	-	-	q
			-		1	1	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	v
Total				140	1	1	-	-	-	-	185	-	-	-	-	-	144	1	-	-	-	1	134	-	-	-	-	-	603	2	1	-	-	1	m
					-	-	-	-	-	-		5	5	-	-	-		1	-	-	-	1		-	-	-	-	-		6	5	-	-	1	q
					2	2	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		2	2	-	-	-	v

Hut II Quercus robur - solitary (Hill Copse) SAMPLING

No	Date	Dir	Ht	A Pp	A Idf	A Dead +	A Dead Pte	A Alive Pte	A Alive H	A Mort	B Pp	B Idf	B Dead +	B Dead Pte	B Alive Pte	B Alive H	C Pp	C Idf	C Dead +	C Dead Pte	C Alive Pte	C Alive H	D Pp	D Idf	D Dead +	D Dead Pte	D Alive Pte	D Alive H	Total Pp	Total Idf	Total Dead +	Total Dead Pte	Total Alive Pte	Total Alive H	sp
23	10/2 60	O	6 to 8'	61	-	-	-	-	-	-	32	-	-	-	-	-	18	-	-	-	-	-	9	-	-	-	-	-	120	-	-	-	-	-	m
					2	-	-	-	2	93.5		1	1	-	-	-		-	-	-	-	-		1	-	-	-	-		4	1	-	-	2	q
					2	-	-	-	2			3	3	-	-	-		-	-	-	-	-		-	-	-	-	-		5	3	-	-	2	v
34	26/2 60	S	6 to 7'	9	-	-	-	-	-	-	13	-	-	-	-	-	6	-	-	-	-	-	13	-	-	-	-	-	41	-	-	-	-	-	m
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	q
					-	-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
35	26/2 60	N	46'	50	-	-	-	-	-	-	20	-	-	-	-	-	13	-	-	-	-	-	5	-	-	-	-	-	88	-	-	-	-	-	m
					1	1	-	-	-	100		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		1	1	-	-	-	q
					4	3	1	-	-			-	-	-	-	-		1	1	-	-	-		-	-	-	-	-		5	4	1	-	-	v
72	13/1 61	W	6 to 8'	3	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	24	-	-	-	-	-	40	-	-	-	-	-	m
					2	-	-	-	2	33		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		2	-	-	-	2	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
71	13/1 61	N	6 to 8'	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	m
					3	-	-	-	3	50		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		3	-	-	-	3	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
73	13/1 61	E	6 to 8'	-	-	-	-	-	-	-	29	-	-	-	-	-	7	-	-	-	-	-	19	2	-	-	-	2	55	2	-	-	-	2	m
					-	-	-	-	-	-		-	-	-	-	-		1	1	-	-	-		-	-	-	-	-		1	1	-	-	-	q
					-	-	-	-	-			-	-	-	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	v
Total				129	-	-	-	-	-	-	94	-	-	-	-	-	57	-	-	-	-	-	70	2	-	-	-	2	350	2	-	-	-	2	m
					8	1	-	-	7	93.03		1	1	-	-	-		1	1	-	-	-		1	-	-	-	-		11	3	-	-	7	q
					6	3	1	-	2			3	3	-	-	-		1	1	-	-	-		-	-	-	-	-		10	7	1	-	2	v

Appendix X

1962

		30.7.	31.7.	1.8.	2.8.	9.8.	13.8.	19.8.	22.8.	25.8.	28.8.	31.8.	4.9.	7.9.	10.9.	12.9.	7.5.63	Para-sitized	Ovi-posited	% Survival	Oviposited Identified m	q	v
DHII	1	19				14	13	11	7	7	7	5	5	5	5	5	5	-	2	10.5	-	2	-
	2	12				9	8	7	6	6	6	5	5	4	4	4	2	1	0	0	-	-	-
	3	26				23	22	17	17	17	10	7	6	6	6	6	6	-	3	11.5	-	2	1
	4		28			28	28	28	24	24	24	15	13	13	8	7	4	-	3	10.7	-	2	1
	5		15			15	15	11	9	8	8	7	6	6	6	6	2	-	1	6.7	-	1	-
	6		20			19	17	16	15	14	12	12	9	9	9	9	5	2	2	10.0	-	-	2
	7			31		27	27	25	25	25	25	14	13	13	12	10	8	3	6	19.3	-	1	4
	8			21		17	15	14	13	12	12	10	9	9	9	9	6	-	5	23.8	-	2	1
	9			25		21	21	13	13	12	11	9	9	9	9	7	6	2	2	8.0	-	1	-
	10			24		22	22	20	19	19	17	17	16	16	16	16	8	1	4	16.7	-	4	-
	11			23		23	22	22	22	17	17	13	13	12	12	9	6	-	3	13.0	-	2	1
	12			18		12	10	4	4	3	3	3	3	3	3	2	2	-	0	0	-	-	-
	13			39		22	29	21	21	21	17	14	14	9	9	5	3	-	1	2.6	-	-	1
				301		262	249	209	195	185	169	131	121	114	108	95	63	9	32	10.6	-	17	11
DHIA	1				81	77	76	72	72	67	63	61	48	48	48	34	10	2	4	5.0	-	-	1
	2				54	44	43	36	32	27	21	19	10	10	10	5	5	1	2	3.7	-	-	-
	3				36	32	27	27	27	24	19	19	5	3	3	2	2	-	1	2.8	-	-	-
					171	153	146	135	131	118	103	99	63	61	61	41	17	3	7	4.1	-	-	1
DHIB	1				38	24	21	16	15	15	13	11	10	9	9	8	4	1	1	2.6	-	-	1
	2				56	51	48	36	23	16	15	13	12	12	12	12	9	-	6	10.7	-	2	4
	3				30	30	25	23	20	20	17	16	16	16	16	16	6	1	2	6.7	-	-	2
	4				32	28	28	22	17	17	15	15	15	14	14	13	0	1	0	0	-	-	-
					156	133	122	97	75	68	60	55	53	51	51	49	19	3	9	5.8	-	2	7
					628	548	517	441	401	371	332	285	237	226	220	185	99	15	48	7.64	-	19	19
				%	100	87.3	82.4	70.2	63.9	59.1	52.9	45.4	37.8	36.0	35.0	29.5	15.8	2.39	7.64				