Aspects of the biology and taxonomy of British myrmecophilous root aphids.

by

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ABSTRACT.

This thesis concerns the biology and taxonomy of root feeding aphids associated with British ants. A root aphid for the purposes of this thesis is defined as an aphid which, during at least part of its life cycle feeds either (a) beneath the normal soil surface or (b) beneath a tent of soil that has been placed over it by ants.

The taxonomy of the genera Paranoecia and Anoecia has been revised and some synonomies proposed. Chromosome numbers have been discovered for Anoecia spp. and are used to clarify the taxonomy. The biology of Anoecia species has been studied and new facts about their life cycles have been discovered. A key is given to the British, European, African and North American species of Anoeciinae and this is included in a key to British myrmecophilous root aphids.

Suction trap catches (1968-1976) from about twenty British traps have been used as a record of seasonal flight patterns for root aphids. All the Anoecia species caught in 1975 and 1976 were identified on the basis of new taxonomic work. Catches which had formerly all been identified as Anoecia corni were found to be A. corni, A. vagans and A. furcata. The information derived from the catches was used to plot relative abundance and distribution maps for the three species.

The relationship of British root aphids with ants is discussed and a new classification is proposed. Data on host plant relations and ten kilometre square distribution maps are given.

It is suggested that subterranean aphids possess adaptations to their mode of life and that six subfamilies of aphids show convergent evolution with respect to these adaptations.

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GENERAL INTRODUCTION.

The subject of this thesis is British myrmecophilous root aphids and is therefore defined by three parameters, (a) Geographical, (b) Ecological and (c) Behavioural.

(a) The geographical limit is mainland Britain, excluding Ireland.
(b) For the purposes of this thesis a root aphid is defined as an aphid which, during at least part of its life cycle feeds either beneath the soil surface or beneath a tent of soil that has been placed over it by ants.
(c) Only those British root aphids which have a relationship with ants are considered.

The thesis is devided into seven sections. In section 1 a key to British myrmecophilous root aphids is given, which it is hoped, will be of use to ecologists studying the group. In section 2 the taxonomy of the genera Anoecia and Paranoecia has been revised and new details of the biology of Anoecia are given. Section 3 is a list of host plants derived from field work, museum collections and the literature. Section 4 deals with relationships between root aphids and ants and a new classification is introduced. In section 5 the adaptations of root aphids to subterranean life are discussed and it is suggested that convergent evolution has occurred. In section 6 trap catches are used to deduce flight patterns in British root aphids, and relative densities of distribution in Anoecia. Section 7 gives distribution maps for 18 species.

In the biometric appendix a linear discriminant function analysis is used to separate two forms of Anoecia corni.

To avoid repetition of units all measurements are given in millimetres.

LITERATURE REVIEW.

A trophobiotic relationship with ants is largely confined to the Homoptera although there are two records from the Heteroptera, one from the Coreidae (Maschwitz and Klinger, 1974) and one from the Scutelleridae (Green, 1900). Within the Homoptera records have been found for the following families:- Aphididae (Way, 1963) ; Coccidae (Way 1963); Pseudococcidae (Mckenzie 1970); Membracidae(Hardwicke, 1829; Harting 1873; Belt 1874; Baer 1903; Mann 1915; Haviland 1925; Andrews 1929,1930); Psyllidae (Wheeler, 1910; Hollis pers. comm.); Cercopidae (Wheeler, 1910; Mann 1915); Stictococcidae (Way, 1954; Evans and Leston 1971); Jassidae (Delpino, 1875; Penzig 1904; Lamborn, 1914; Evans 1931); Fulgoridae (Perris, 1873; Lesne, 1905 a&b; Krishna Ayyar, 1935) and Delphacidae(Wolcott, 1948).

A great majority of the members of the three phylogenetically most advanced subfamilies of ants, the Myrmicinae, Dolichoderinae and the Formicinae attend Homopterans, to some extent(Wilson, 1971) and there is a record of a ponerine ant, *Odontomachus haematodus* which attends an aphid, *Toxoptera aurantii* and a Stictococcid, *Stictococcus sjostedti* (Evans and Leston, 1971).

Wheeler (1910), Nixon (1951), Way (1963), and Wilson (1971) list ways in which myrmecophilous aphids differ from non-myrmecophilous aphids. The effects of ant attendance on both behaviour and morphology have been studied by El-Ziady and Kennedy (1956), Banks and Nixon (1958) and Kunkel (1973).

Huber(1810) gives the first detailed and accurate description of ants attending aphids. Wheeler, in his comprehensive work on ants includes a chapter on the relations of ants to other insects and describes the relationship between ants and species of *Trama*, *Forda*, *Geoica*, *Tetraneura*, *Pemphigus* and *Paracletus*. He corrects the,(at that time) long perpetuated error that aphids excrete honeydew through their siphunculi. Forbes (1908) gives details of the economic importance of the Corn Root Aphis, *Aphis maidiradicis* and suggests that *Lasius niger* may be instrumental in transporting the aphid.

Mordvilko and Lichtenstein (1884) report that *Lasius niger*, *L. flavus* and *L. umbratus* clip the wings of aphids to prevent them from escaping or to make imbibing honeydew easier.

Jones (1929) gives an account of the relationship between American ants and aphids in general. Nixon (1951) reviews the literature concerned with the association of ants with aphids and coccids up to 1951. Way(1963) reviews the literature on mutualism between ants and honeydew producing Homoptera from 1951 to 1963. Aphid excretion has been studied by Andrews (1930), Broadbent (1951) and Kunkel (1972, 1973) and Andrews (1930) and Kunkel (1972) also examine ant-aphid relationships.

There is no comprehensive work specifically devoted to British root feeding aphids. Réamur (1738) first found aphids in ant's nests; but Von Heyden(1837) was the first to establish genera for these insects namely, Paracletus, Forda and Trama. Buckton (1883) discusses the problem of overwintering in root aphids,and root-feeding aphids are also mentioned in the following early monographs on aphids:- Kaltenbach (1843), Koch (1856), Van der Goot (1915) and Theobald (1929). Cutright (1925) deals with the subterranean aphids of Ohio, which are listed, and a key is given. The life cycles of various root aphids are discussed, the fact that eggs may be kept over winter in ants' nests is noted and methods of control of root aphids are examined. Crawley (1916) recorded Forda formicaria alates from Britain for the first time. Theobald (1913), Forel (1922) and Donisthorpe (1921, 1924 a&b, 1925, 1926 and 1927) recorded root aphids collected from the nests' of ants.

Tullgren (1909, 1925) worked on the systematics, morphology and biology of Swedish species. Mordvilko (1907-1935) worked on Eastern European aphids and put forward theories about the evolution of anholocycly in many genera. He also dealt with their morphology, biology, geographical distribution and phylogeny. Particularly important works are:- 'On the evolution of Aphids' (1934) and the review 'The aphids with an incomplete life cycle and their origin' (1935). More recently the following authors have included root aphids in their works:- Börner (1914-1957), Dahl (1912), Hille Ris Lambers(1950-1969), Martelli (1950), Schmidt (1952 a&b), Schouteden (1902 a&b) and Schuhmacher (1921, 1923).

Lichtenstein (1878, 1879, 1880 a&b) found aphids on the roots of *Bromus sterilis* which resembled forms from *Pistacia* and suggested that the part of their life cycle that had been unknown until then took place on the roots of grasses. Courchet (1879) tried to rear *Aploneura lentisci* taken from *Pistacia* on grass roots but without success. He did however succeed with *Pemphigus cornicularius* (=*Baizongia pistaciae*), *P. semilunarius* (=*Forda formicaria*) and *P. follicularius*(=*Forda marginata*). Mordvilko (1921-1935) linked many of the root-feeding Fordinae with forms already described from *Pistacia*. Börner's catalogue(1952) 'Central European Aphids' unites the Northern European Fordinae with their holocyclic Mediterranean counterparts while Zwölfer(1958) gives a comprehensive account of Central European Anoeciinae, Tetraneurini, Pemphigini and Fordinae. His work deals predominantly with subterranean forms. Roberti (1938, 1939) has monographed the Pemphiginae and the Fordinae and Davatchi (1957) gives a detailed account of the biology and polymorphism of the Fordinae of *Pistacia* in central Asia, the Mediterranean basin and North Africa. Other authors who give accounts of the Fordinae of *Pistacia* are:- Rēaumur (1738), Passerini (1856) and Dèrbes (1869, 1872, 1881).

Wool and Koach (1976) have examined morphological variation in relation to environmental variation in *Geoica utricularia* in Israel and the Near East. In America the Anoeciinae have been studied by the following authors:- Gillette and Palmer (1924 and 1931), Mordvilko (1935)- *Anoecia graminis* ; Wilson(1911), Hottes and Frison (1931), Palmer (1936)- *Anoecia oenotherae*; Baker (1916), Cutright (1925), Hottes and Frison(1931), Gillette and Palmer (1931)- *Anoecia cornicola*; Gillette and Palmer (1924), Mordvilko(1935) (erroneously as a synonym of *A. cornicola*)- *Anoecia setariae*.

Stroyan (1950) discusses the taxonomic status of *Anuraphis catonii*. Stroyan (1955) deals with the taxonomy and biology of *Aphis acetosae*, *A. crepidis*, *A. lambersi*, *A. taraxacicola*, *A. thomasi*, *Trama rara*, and *Paranoecia pskovica*. Stroyan (1957, 1958, 1963) gives a key to British *Dysaphis* and discusses their biology and relations with ants. Muir (1959) studied the ant-aphid-plant relationship in West Dumbartonshire and records fourteen aphid species, including root aphids,with six species of ant. Hassan (1963) includes the morphology and taxonomy of

Anoecia corni in Egypt. Stroyan (1964^b)records *Aphis cliftonensis* *A. violae*, *Anoecia nemoralis* (=*A. furcata*), and *Neanoecia krizusi* (=*Anoecia zirnitzi*) from Britain.

Zwölfer (1958), Pontin (1960a) and Stary (1961) give details of parasites of root aphids, and Pontin (1960 b) discusses the care of aphid eggs in ants' nests.

Bolton and Collingwood (1975) provide a key to British ants and information about their distribution and biologies. Bernard (1968) also gives a key with which British ants can be identified.

MATERIALS AND METHODS.

1. Collecting Methods.

Methods employed depended on the habitat and the species of root aphid sought.

Method 1. Examination of ant mounds.

At all times of the year root aphids can be collected from mounds of Lasius flavus (F) but autumn, winter and spring are the seasons when root aphids are most numerous within ant mounds. In summer root aphids are more readily found on the roots of plants close to mounds and only rarely deep within the mound. The type of soil affects the success of examining mounds. In sandy soil which drains well mounds can easily be split open with a trowel and the soil sifted onto a small plastic tray. The aphids are usually detached from the root by this process but may be seen attached to thicker roots. In sandy soil at Silwood Park, Berkshire this method was successful for Anoecia spp., Geoica setulosa, G. eragrostidis, Tetraneura ulmi, Baizonia pistaciae, Forda formicaria, F. marginata, and Aphis etiolata. In clay soils, for example, Box Hill, Surrey, this method failed. The mounds are extremely compacted and difficult to break open and the soil clings together concealing the aphids. The only root aphid found by this method in clay soil was Forda formicaria which was feeding partly above soil level.

Method 2. Extraction in a Tullgren Funnel.

Sections of L.flavus mounds were excavated, placed intact in a large polythene bag and taken to the laboratory where they were placed in a large Tullgren funnel. The extract was collected in 95% alcohol. Several days were allowed to elapse for the sample to dry out before the extract was examined. Many L.flavus emerged from the funnel as well as root aphids and coccids. This method is particularly suitable for clay soils.

Method 3. Examination of roots growing over rocks or concrete.

Where plants, especially grasses have grown over concrete slabs, rocks or against walls it is possible to pull the vegetation back and expose the roots. Such habitats are usually attractive to ants, and root aphids are often found there. Canal banks are especially productive when edged by stone slabs. Ants move about under the mat of vegetation growing over the stone and probably derive benefit from heat retained by the stone. The following aphids have been collected by this method:- *Anoecia corni*, *A.vagans*, *A. furcata*, *Forda formicaria*, *F. marginata*, *Geoica eragrostidis*. *G. setulosa*. *Toxopterina vandergooti*, *Baizongia pistaciae*, *Aploneura lentisci*, *Smynthurodes betae*, *Pemphigus bursarius*, *Tetraneura ulmi*, *Protrama flavescens* and *Trama troglodytes*. The aphids usually remain on the roots from which they are feeding and can be removed by cutting out a section of root with a pair of scissors.

Method 4. Disused railways.

Disused railways provide a good habitat for *L. flavus* because the embankments often present a slope towards the south which provides warm conditions favoured by the ants(Waloff and Blackith, 1962). The presence of ballast means that grasses and other plants can be relatively easily removed and the roots examined. The roots are often free of soil where they have grown around the ballast. Aphids found by this method:- *Aploneura lentisci*, *Forda formicaria*, *Geoica setulosa*, *G. eragrostidis*, *Anuraphis catonii* and *Trama troglodytes*.

Method 5. Uprooting of larger plants.(with landowner's permission).

This method is most suitable for finding the Traminae, which infest relatively large plants such as *Artemisia vulgaris* and *Cirsium arvense*. Infested plants are sometimes wilted, especially in hot weather and it is usually more productive to select wilted plants. An area of soil was dug up with the roots to disturb the aphids as little as possible. The soil and plant were placed on a polythene bag and the soil carefully dislodged from the root to expose the aphids. Aphids collected by this method:- *Trama troglodytes*, *Protrama flavescens*, *Protrama ranunculi* and *Protrama radicis*.

Method 6. Examination of root collars.

A number of aphids feed on the root collars of plants and are covered with a'tent'of soil by ants which then attend the aphids beneath the soil. Many of these aphid live on Umbelliferae and can be found by examining the basal portions of these plants. Aphids found by this method:- *Anuraphis subterranea*, *Anuraphis farfarae*, *Dysaphis anthrisci*, *D. radicola*, *D. ranunculi*, *Aphis hypochoeridis* and *A.taraxacicola*.

Method 7. Examination of Dogwood.

In spring and autumn dogwood was examined for fundatrices, fundatrigeniae, sexuparae and sexuales of *Anoecia*. In winter the twigs were examined for eggs stuck to the bark but none were found. Laboratory experiments showed that *A.corni* lays its eggs in the soil.

In spring buds, opening leaves and flowers were examined to find the developing fundatrices. A few fundatrices were found enclosed in unfurling leaves but most were within the opening flowers. They feed on the flower pedicels and are very well concealed within the flower heads. As fundatrigeniae are produced and numbers become greater some aphids move out from the flower heads to lower and sometimes upper surfaces of leaves. In autumn the sexuparae were found almost exclusively on the underside of leaves, feeding from one of the major veins. *Aphis corniella* was also found feeding on the same plants but could easily be distinguished by its lack of a pronounced pterostigma. As the sexuperae are produced they spread out along the leaf veins, feeding around the sexuparae. Although single sexuparae were found,most were grouped in numbers from two to about ten on the undersides of leaves.

Most of the sexuparae collected were from *Cornus sanguinea* growing on chalk downland with a lesser, though still substantial number from *Cornus stolonifera* growing in wet habitats. In spring the situation was reversed and most fundatrices were collected from *Cornus stolonifera*.

Various *Cornus* species were examined in Kew Gardens to determine the primary host range of *A.corni*.

CULTURE METHODS.

Cultures were kept to obtain specimens for taxonomic purposes and in order to see which ant species would attend root aphids.

METHOD I. Glass tanks.

Three sizes of glass tank were employed, each of the same basic design (Fig. I). The tanks were rectangular with a small space at the front leading to a narrow extension projecting down vertically in front of the bench on which the tanks were resting. Ant's nests were placed in the main body of the tank and plants were sited at the front with their roots growing down between the two surfaces of glass. These tanks were successful in rearing *Trama rara*, *Protrama flavescens*, *Forda formicaria*, *F. marginata*, *Geoica eragrostidis* and *Tetraneura ulmi*. The top was open but ants were prevented from leaving the tanks by a smear of silicone oil around the sides. Silicone oil acts as a repellant to ants and was found to be more effective than fluon.

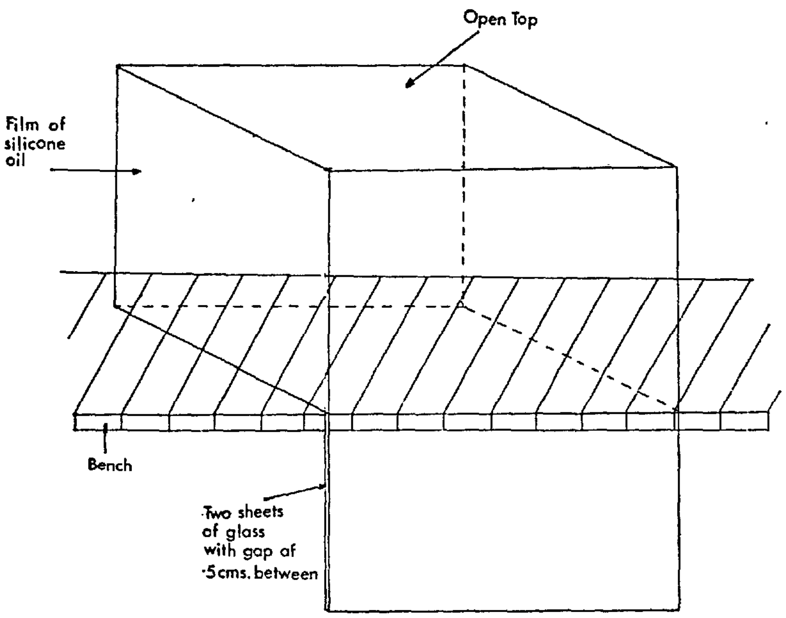
METHOD 2. Plastic boxes.

Small plastic boxes(Fig.2B) with sliding lids were lined with either perlite, soil or blotting paper. In the case of larger plants, excised roots were placed upon the soil for aphids to feed on and ants introduced into the box. Where grasses were being used most of the grass blades were cut off and the roots were washed before being laid upon, either perlite* soil or blotting paper. If possible aphids were not detached from the roots on which they were found.

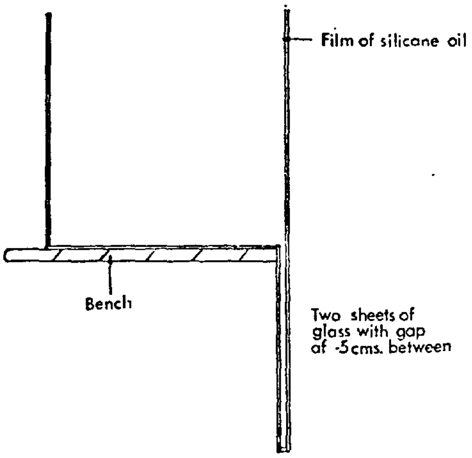
METHOD 3. Plant pot covers.

Two conical plastic plant pot covers were used.(Fig. 2A). Each was inverted and the smaller used as a plant pot with the culture plant growing within it, so that the root projected through a hole in the bottom. This plastic container was fitted with the aid of a collar into a larger one of the same shape so that an enclosed space was created between the two into which the plant roots projected Aphids were then introduced onto the exposed root and ants placed in the enclosed space. Finally the larger container was sheathed in black paper which could be removed to allow observation.

*Perlite is washed sand supplied by British Gypsum Ltd.

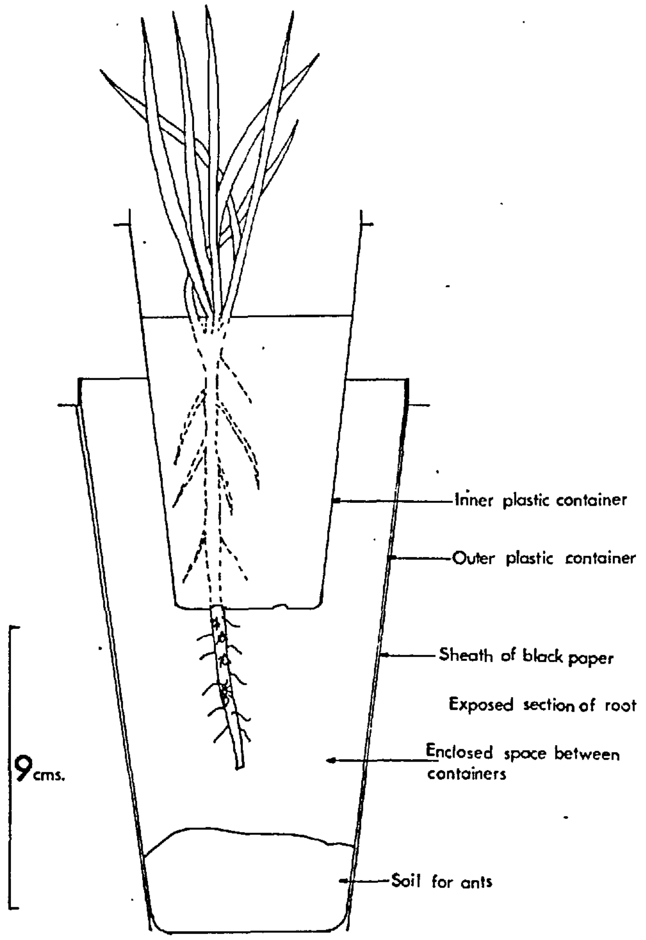


Glass tank used to house ants and root aphids

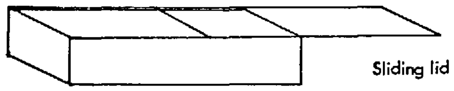


Cross-section of glass tank

FIG 1



Apparatus used for rearing root aphids



Plastic specimen box used to rear aphids

FIG 2

CHROMOSOME SQUASHES.

Blackman's technique for obtaining chromosome squashes (Blackman and Takada, 1975) was used. Embryos were dissected from freshly collected specimens in slightly hypotonic (0.75%) solution of potassium chloride, fixed in 3:1 methanol/acetic acid and squashed in 45% proprionic acid. After freezing off the coverslip, the preparation was stained in Giemsa's solution(10% in phosphate buffer at pH 6.8) and mounted in Depex.

KEY TO BRITISH MYRMECOPHILOUS ROOT APHIDS.

INTRODUCTION.

The key is intended to assist the identification of British root feeding aphids found either with ants in attendance or actually within ant's nests. The key, except for the section on the Anoeciinae, applies only to apterous virginoparae which is the morph most commonly found.

The section dealing with the Anoeciinae includes European, African and American species as well as British but is constructed so that it can be used as an integral part of the key for the identification of British root aphids. The section on Anoeciinae is an original contribution to the taxonomy of the group which can be used on its own for the identification of all morphs. The abbreviation SE is used for Standard Error.

1. Terminal process of antenna longer than the base of the last antennal segment. Figs. 68-71. Aphidinae. (31)
   Terminal process of antennae shorter than or the same length as the base of the last antennal segment. (2)
2. Second segment of hind tarsus much longer than fore and mid tarsi, unusually elongated. (Fig. 42). Traminae. - (7)
   Second segment of hind tarsus normal in length. (3) ?
3. Rosetted wax pore plates present on the head, thorax and abdomen (Figs. 66,67) Eriosomatinae. (Tetraneura ulmi)
   Without rosetted wax pore plates. Not pink or purple in colour. (4)
4. Siphunculi present. (6)
   Siphunculi absent. (5)
5. Virginoparae with large wax plates on abdomen and thorax but not on head. Pemphiginae. (Pemphigus bursarius)
   Virginoparae without wax plates or if wax plates present then found on the head as well as the thorax and abdomen. Fordinae. (13)
6. Marginal tubercles present on prothorax and on abdominal segments 1-7 or 1-4 and 7. (Figs. 3-37) Feeding on grass roots or roots of Carex spp. Anoeciinae. (20)

Marginal tubercles absent. Not feeding on grass roots or Carex spp. Lachninae. (56)

TRAMINAE.(Key adapted from Eastop 1953).

7\. Alatae with 25-50 rhinaria on 3rd antennal segment and with 6th antennal segment as long as 5th or longer. Apterae always with siphunculi which are placed on only slightly elevated cones. Processus terminalis at least a quarter (usually more) of the base of the 6th antennal segment in length and bearing six or more normal antennal hairs in addition to the short terminal setae. Dorsal abdominal pigmentation only very rarely absent. On Ranunculus, Cynareae and Anthemideae.(Fig 39) Protrama (9)

Alatae with 0-5 rhinaria on 3rd antennal segment. Apterae and alatae with 5th antennal segment longer than 6th. Siphunculi absent or present; when present they are placed on distinctly elevated cones. Live only on Ligulatiflorae(British speces at least). Processus terminalis one quarter or less of the base of the 6th antennal segment in length and without any, or rarely with one, normal hair in addition to the short terminal setae. On many Compositae. (8)

8\. Siphunculi present.(Fig. 38) Neotrama (II)

Siphunculi absent. (Figs. 40-42) Trama (I2)

9\. Hind tarsus/tibia ratio = 0.5-0.7. Hind tibia/4th antennal segment ratio = 6.7-8.2. Dorsal rostral hairs 6-10, usually 6-9. On Anthemideae and Ranunculus spp. (10)

Hind tarsus/tibia ratio = 0.72-0.9. Hind tibia/4th antennal segment ratio = 5.1-6.4. Dorsal rostral hairs 8-12. On Cynareae. Protrama radicis.

I0\. Hind tibia/ 3rd antennal segment ratio= 0.5-0.63. Dorsal rostral hairs 6-10, usually 9. On Ranunculus spp. Protrama ranunculi.

Hind tibia/3rd antennal segment ratio = 2.2-2.6. Hind tarsus/ tibia ratio = 0.6-0.7. Dorsal rostral hairs 6-8, usually 7. On Anthemideae. (Fig. 39) Protrama flavescens.

11. 3rd antennal segment / 5th antennal segment ratio= 0.9- 1.35.(usually 1.0-1.25); 3rd antennal segment/ 4th antennal segment ratio = 1.8- 2.35 (usually 2.0-2.2). Found inland, often in cultivated ground.
(Fig. 38) Neotrama caudata s.str.

3rd antennal segment/ 5th antennal segment ratio = 1.4- 1.8 (usually 1.5- 1.7); 3rd antennal segment / 4th antennal segment ratio = 2.2- 2.8 (usually 2.4-2.7); On plants growing behind sand dunes and on cliffs by the sea. Neotrama caudata maritima Eastop.

12. Hind tarsus/ hind tibia ratio = 0.84-0.92, eyes of many facets. On Taraxacum (only?).
(Fig. 40) Trama rara.

Hind tarsus/hind tibia ratio =0.65-0.82, eyes of only three facets if of more then alatiform and hind tarsus/ tibia ratio is less than 0.8. On many Compositae including Taraxacum. (Fig. 41) Trama troglodytes.

FORDINAE

13. Wax glands present. (14)
Wax glands absent. (15)

14. Body rounded almost spherical, only a small amount of wax filaments. Facets of wax glands are large (Fig.46D). The prothorax is reduced in width compared with the meso- and metathorax, not much wider than the head. Attended by ants, usually Lasius flavus.
(Figs. 45,46) Baizongia pistaciae.

Body spindle-shaped, usually wax covered. Facets of wax glands are small (Fig.44B). The prothorax is not reduced in width compared with meso-and metathorax. Very rarely ant attended. (Figs. 43,44) Aploneura lentisci.

15. Anal plate displaced dorsally (Fig.56F). Primary rhinarium with ciliated margins. Rounded body shape, whitish cream colour, usually attended by Lasius flavus
(Figs 53-61) Geoica (18)
Anal plate not displaced dorsally. (16)

16. Second antennal segment not elongate. (17)
Second antennal segment unusually elongate(Fig.62B)
Smynthurodes betae.

I7. Antennae of adult 5-segmented. Greenish or whitish colour. (Figs. 47-52) *Forda*. (I9)

Antennae of adult 6-segmented. Whitish colouration. Almost always found with *Tetramorium caespitum*(L) occasionally with *Lasius flavus*.(F). *Paracletus cimiciformis*

I8. Proximal primary rhinarium of adult apterae oval in shape. Anal plate bearing I2-I6 long (0.08) hairs in two parallel rows. First instars are grey-green in colour and this colour which also applies to the embryos can often be seen through the abdomen of the adult. (Figs 57-61) *Geoica setulosa*.

Proximal primary rhinarium of adult apterae roundish. Anal plate bearing many short irregularly arranged hairs (about 60). First instars are whitish in colour and no dark colouration is visible in the abdomen of the adult.(Figs 53-56) *Geoica eragrostidis*.

I9. Distal primary rhinarium very large so that it occupies about 2/3 of the circumference of the last antennal segment. Antennae long (I.I SE. ± 0.03). Lack thorn-like cuticular sculpturing. (Fig.47). *Forda formicaria*.

Distal primary rhinarium small, occupies about half the diameter of the last antennal segment (Fig.50Ci). Antennae short (0.5-0.64; mean 0.56 SE. ±0.02). Antennal length/body length 0.I9-0.29;(mean 0.24 ,SE± 0.0078). Thorn-like sculpturing of the cuticle especially well developed on head and thorax (Plate 44). Feeding on fine roots of Graminae. *Forda marginata*.

Key to the Anoeciinae of Europe, Africa and North America.

20. Processus terminalis of last antennal segment less than one tenth of the length of the entire segment. A large aphid, length 2.0-2.5;mean 2.26 SE.± 0.065. Holocyclic on roots of *Carex* (Figs. 3-4) . European. *Paranoecia pskovica*.

Processus terminalis approximately one quarter of the last antennal segment. Holocyclic, either migrating between Cornaceae and grass roots or anholocyclic on grass roots or holocyclic on grass roots. (21)

2I. Abdominal tergites 1-4 and 7 each with a pair of lateral abdominal tubercles , tergites 5 and 6 without lateral abdominal tubercles. (22)

Abdominal tergites 1-7 each bearing one pair of lateral abdominal tubercles. (27)

22. Virginoparae on grass roots or alate sexuparae on dogwood or on grass roots. (23)

Sexuales or Fundatrigeniae on dogwood. (30)

23. Apterae with either unsclerotized dorsal abdominal surface or with sclerotized discoidal plate, never with banding.
Alatae with oval secondary rhinaria.(Fig.16B) (24)

Apterae with 3 or 4 dorsal abdominal cross bands.
Alatae with round secondary rhinaria. (26)

24. Alatae and apterae with discoidal plate, apterae with single rows of spatulate hairs on the dorsal abdominal surface and compound eyes of more than 25 facets. Alatae with at least a few dorsal abdominal spatulate hairs. Holarctic. (25)

Apterae without sclerotized discoidal plate and usually with small compound eyes of less than 15 facets. Alatae sometimes with incompletely sclerotized discoidal plate and without spatulate hairs. Nearctic.

(Fig.35) <u>A. setariae</u>.

25. Apterae:- Abdominal segments 2-7 of apterous verginoparae always with single rows of spatulate hairs. Sometimes spatulate hairs are also found on the thorax, head, antennae and legs with irregular acute hairs. All intermediates between these forms can be found. Most of the British population is monoecious and anholocyclic on grass roots. Body length of apterae = 1.96 SE. ±0.042

Alatae:- Dorsal surface of abdominal segments 3-6 with single rows of very small spatulate hairs (one row per segment). Abdominal segments 1 and 2 each with a scerotized band bearing a mixture of spatulate and acute hairs. Chromosome number 2n=12, 2n=13. Palaearctic.

(Figs.21-27) <u>A. furcata</u>.

Apterae:- Head, thorax and abdomen covered with irregular densely distributed acute hairs. Monoecious and holocyclic on grass roots.

Alatae:- Unknown.

European. (Figs. 5,6) A. krizusi.

26\. Alatae without abdominal discoidal plate but with sclerotized crossbands on abdominal segments 4,5,6 and 7. Secondary rhinaria are very small(diameter= 0.012-0.015, mean 0.124 SE. ±0.0008). Antennal segment III bears 0-3 secondary rhinaria.

(Fig. 37) A. oenotherae.

Alatae with dorsal abdominal discoidal plate though it may be reduced in size with unsclerotized cuticle at the margins of the abdomen. Secondary rhinaria are larger (diameter= 0.012-0.029, mean,0.021 SE. ± 0.0019) Antennal segment III bears 4-9,(mean 6, SE.± 0.34.) secondary rhinaria. Nearctic and Neotropical.

(Fig. 34) A. cornicola.

27\. Compound eyes small, usually less than I0 facets, or lacking altogether. Ratio of second antennal segment to third antennal segment = 0.35-0.5 Holocyclic and monoecious on grass roots. Alatae unknown.

European. (Figs.7-9) A. zirnitsi.

Eyes large, no fewer than 25 facets and usually more than 40. Ratio of second antennal segment to third antennal segment = 0.2-0.3. (28)

28\. Alatae with very large marginal tubercle on Ist. abdominal tergite(diameter = 0.06-0.13, mean, 0.085, SE. ± 0.0096. European. A. disculigera.

Alatae with smaller marginal tubercle on Ist abdominal tergite 0.04- 0.055, mean,0.045,SE.±.002. (29)

29\. Apterae:- Each abdominal tergite with only a single row of very short hairs (0.0I2-0.0I5,mean,0.0I3,SE. ±0.0007). Spatulate hairs may be found anteriorally as far as the head and antennae. There are usually 8 or fewer accessory hairs on the last rostral segment in two parellel rows. None of the hairs is displaced from the row.

Alatae:- Fundatrigeniae without sclerotized dorsal abdominal discoidal plate, green in colour. Virginoparae and sexuparae with narrow transverse sclerotized patches on abdominal segments I and 2, each with a single row of short (0.026) spatulate hairs, often mixed with longer acute hairs(0.061). Short spatulate hairs occur, one row per segment, on dorsal abdominal segments 3-6.(Figs.30-32) Holocyclic,migrating from Cornaceae to roots of Gramineae. Palaearctic and Etheopian. Chromosome number 2n=12. (Figs. 28-32) A. vagans.

Apterae:- Dorsum covered with irregularly placed acute hairs except for abdominal segments 5,6,and 7 where hairs may be in single rows and some hairs (length 0.046-0.063, mean, 0.058,SE. ±0.0025) may have spatulate apices. The last rostral segment bears 8 or more accessory hairs in two parallel rows usually with at least one hair displaced sideways from each of the main rows (Fig.17B)

Alatae:- Dorsal surface of the first and second abdominal segments bear sclerotized transverse oval patches covered in densely packed long acute hairs. The dorsal surface of abdominal segment 3 bears 2 or 3 rows of short acute hairs. Holocyclic migrating from Cornaceae to roots of Grasses or anholocyclic on roots of Grasses. (30)

30. Body length of adult apterae 2.46-2.8,mean,2.58,SE. ±0.046. Rostrum length of adults 0.76-0.94(mean,0.87, SE.±0.038),reaching to the end of the abdomen. Number of accessory hairs on last rostral segment in apterous virginoparae = 13-17 (mean,14.75, SE. ±1.03). Holocyclic, migrating from Cornaceae to Phalaris arundinacea.European. A. major.

Body length of adult apterae=1.9-2.27 (mean,2.1,SE.±0.026). Rostrum length of adults = 0.52-0.85 (mean,0.659,SE.±0.017). Rostrum of Ist instars reaching to middle of abdomen. Last rostral segment bears 8-13 (mean,11.0,SE. ±0.17) accessory hairs. Holocyclic, migrating between Cornaceae and roots of Grasses. Chromosome number 2n=6, 2n=7, and 2n=8. Holarctic. A. corni.

APHIDINAE.

31. With large frontal tubercles (Fig. 75A). Nymphs with spinose hind tibiae. Jacksonia papillata.

Without large frontal tubercles (Fig.70,for example) Nymphs without spinose hind tibiae. (32)

32. Siphunculi with transverse rows of spinules(Fig.72C) Anuraphis (40)

Siphunculi without transverse rows of spinules (33)

33. Dorsal abdomen with spinules arranged in polygons, usually enclosing a central spinule or group of spinules.(Figs. 70,72D) *Rhopalosiphum insertum*.

Dorsal abdomen not covered in spinules arranged in polygons. (34)

34. Siphunculi swollen for distal 2/3 of their length. (Fig.72B) *Rhopalomyzus poae*.

Siphunculi not swollen for distal 2/3 of their length. (Fig. 73C, for example) (35)

35. Cauda elongate finger-shaped or elongate triangular (width less than length). *Aphis*.(73A,74) (42)

Cauda very short and rounded(width greater than length). (36)

36. Abdominal spiracles reniform and lateral abdominal tubercles present. *Dysaphis*.

(For a key to *Dysaphis* see Stroyan 1957a, 1963.)

Either the abdominal spiracles are not reniform or if reniform then lateral abdominal tubercles are not present. (37)

37. Siphunculi without rim near operculum (Fig. 72A) Abdomen unsclerotized. *Acaudinum scabinosae*.

Siphunculi with distinct rim at operculum (Fig. 72A) Abdomen sclerotized. *Brachycaudus*. (38)

38. Cauda with 10-17 hairs. Last segment of rostrum 1.1-1.35 times as long as 2nd segment of hind tarsi. *Brachycaudus linariae*.

Cauda with 6-8 hairs. Last segment of rostrum 1.4-1.8 times as long as 2nd segment of hind tarsi. (39)

39. Hairs on abdominal tergum 8, 0.07-0.105; hairs on 3rd antennal segment 0.008-0.038. Marginal tubercles inconsistently present on abdominal terga 1-4 , small , markedly convex.Siphunculi usually lighter than contiguous spot on abdomen. Antennae of apterae without secondary rhinaria. On upper parts of roots of Compositae and Borginaceae as well as on stems and flower stalks. *Brachycaudus cardui*.

Hairs on abdominal tergum VIII. 0.01-0.025, hairs on 3rd. antennal segment 0.005-0.008. Marginal tubercles either absent or slightly convex. Siphunculi darker than spot or stripes on abdomen. 3rd. antennal segment of apterae sometimes with secondary rhinaria.

<u>Brachycaudus lucifugus</u>

40. Marginal and median tubercles present on abdominal terga I-7 ; head with two pairs of tubercles , one on the occiput and one on the frons. Abdominal terga without transverse green stripes. (41)

Marginal and median tubercles present on abdominal terga I-5; head with one pair of tubercles on occiput. Well marked transverse green stripes which are interrupted in the middle, usually present on all thoracic terga and Ist 6 abdominal terga. On <u>Tussilago farfara</u> and <u>Petasites</u> spp. , root collars <u>Anuraphis farfarae</u>. (Fig.68)

4I. Siphunculi with 27-39 rows of spinules. Adults 2.4-3.4. On <u>Pastinaca</u> spp., <u>Heracleum</u> spp. and several other Umbelliferae. <u>Anuraphis subterranea</u>.

Siphunculi with 14-23 rows of spinules. Cuticle of first 5 abdominal terga with plates forming a pattern of cells. Adults I.8-2.I. On <u>Pimpinella</u> spp. (Fig.69) <u>Anuraphis catonii</u>.

42. Processus terminalis 4.1-6.0 times longer than the base of the last antennal segment. (Fig.71) <u>Aphis(Toxopterina) vandergooti</u>.

Processus terminalis not more than 4 times longer than the base of the last antennal segment. (43)

43. Length of siphunculi/basal diameter of siphunculi less than 2.8. <u>On Verbascum</u>. <u>Aphis verbasci</u>.

Length of siphunculi/basal diameter of siphunculi greater than 2.9. On other plants. (44)

44. Cauda short and rounded. (Fig.74 A) (48)

Cauda finger-shaped or triangular. (Fig.74 B orC) (45)

45. Cauda triangular (Fig. 74 B) (55)

Cauda finger-shaped. (Fig.74 C) (46)

46. Cauda finger-shaped with median bulge.(Fig.73A)

Length of siphunculi/length of penultimate antennal segment greater than I.3. On <u>Parietaria</u>. <u>Aphis parietatiella</u>.

Cauda finger-shaped with parallel sides. Length of siphunculi /penultimate antennal segment greater than I.4. (47)

47. Siphunculi weakly sclerotized. *Aphis thomasi*.

Siphunculi strongly sclerotized (50)

48. Length of siphunculi/basal width of siphunculi greater than 4.5. *Aphis sambuci*.

Length of siphunculi/basal width of siphunculi less than 3.9. (49)

49. Apterae pale yellowish-white or bluish green in life; siphunculi, apices of antennae and tibiae, cauda and tibiae, cauda and tarsae slightly dusky. Without a strongly developed pattern of black sclerotic bars on the dorsum in apterae. Completely subterranean.

Aphis etiolata.

Apterae in life blackish-green with a strongly developed pattern of black sclerotic bars on the dorsum in apterae. Lives either at or below ground level under soil protection erfected by ants. *Aphis actoei*

50. Apterae yellow in life; on roots of *Hypochoeris*.

Aphis hypochoeridis.

Apterae dark in life; On roots of other plants. (51)

51. Transverse sclerotized bar on seventh abdominal tergite extends nearly the whole distance between marginal tubercles. On *Daucus*. *Aphis lambersi*.

Transverse sclerotized bar on seventh tergite not more than I/3 of the intertubercular distance. (52)

52. Ratio of processus terminalis to base of last antennal segment greater than 3.0. On *Viola*.

Aphis violae.

Ratio of processus terminalis to base of last antennal segment less than 2.5. On other plants. (53)

53. Tibial hairs on the outside of the third quarter of the hind tibia equal to the tibial diameter. On *Plantago*.

Aphis plantaginis.

Tibial hairs on the outside of the third quarter of the hind tibia not more than one half of the tibial diameter. (54)

54. On Taraxacum. Aphis taraxacicola.

On Crepis. Aphis crepidis.

55. Length of last rostral segment/Length of 3rd. antennal segment greater than 0.55. Width of last rostral segment at base/Length of last rostral segment greater than 0.55. On Plantaginaceae. Aphis longirostris.

Length of last rostral segment/ Length of 3rd. antennal segment greater than 0.5. Width of last rostral segment/ Length of last rostral segment less than 0.55. On Helianthemum roots Aphis cliftonensis.

LACHNINAE.

56. Extremely elongate rostrum; longer than the length of the body. On bark of oak trees but may be found in nests of Lasius fuliginosis or L.brunneus. Stomaphis quercus.

Rostrum of normal length; not longer than the length of the body. On roses, at the base and on upper parts of the roots where it is covered with a tent of soil by ants. Maculolachnus submacula.

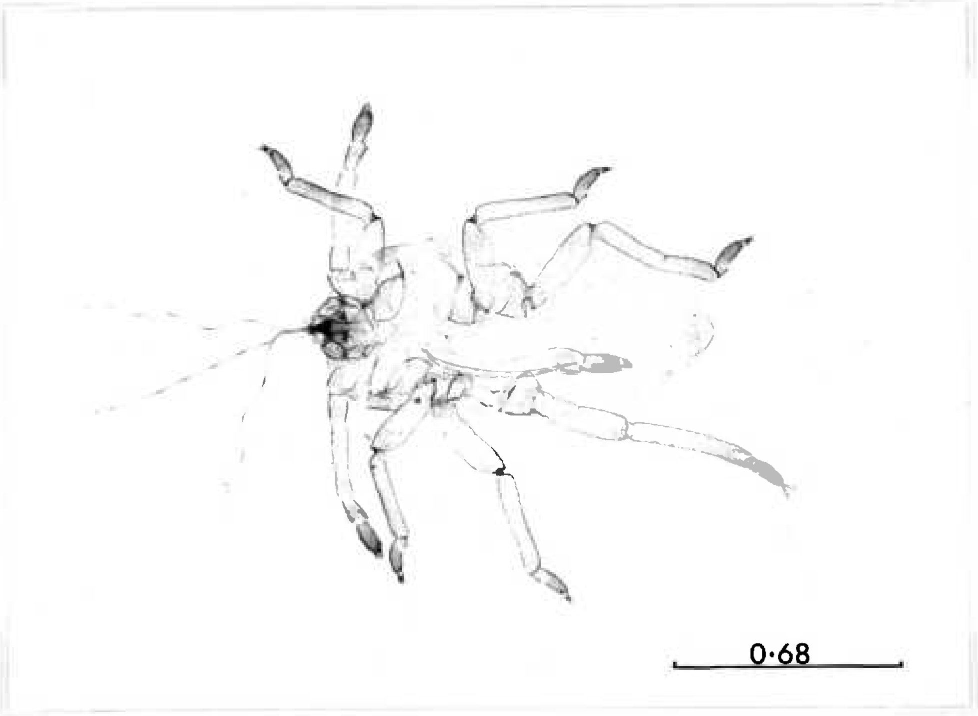


Plate 1. *Paranoecia pskovica.* Fundatrix 1st. instar.

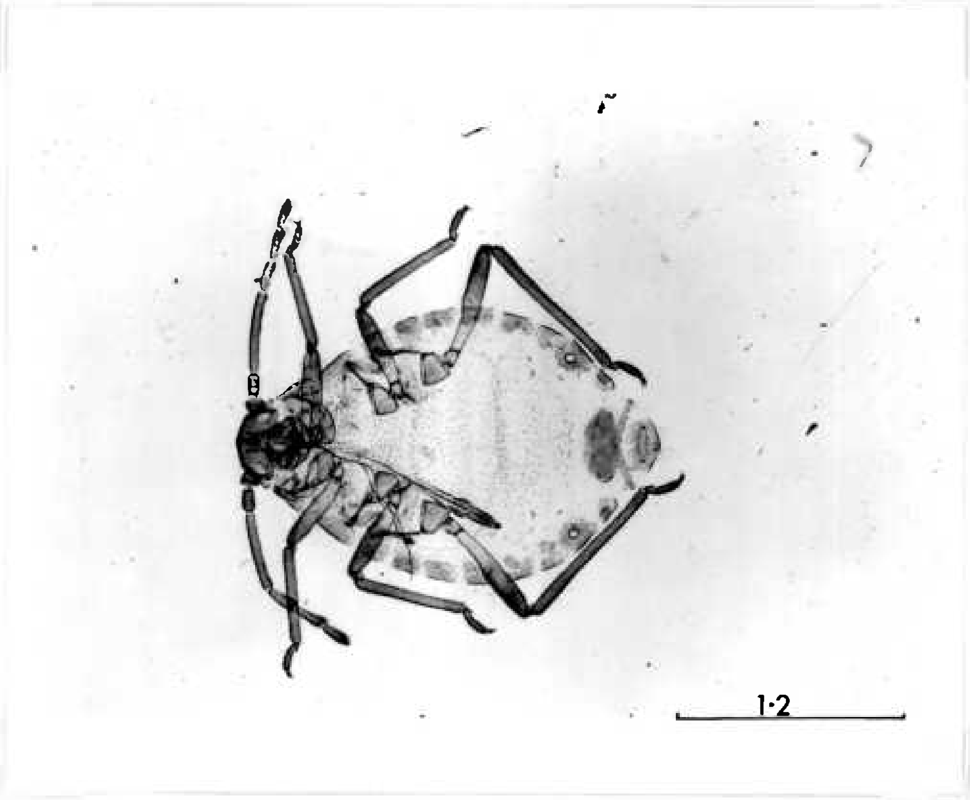


Plate 2. *Paranoecia pskovica*. Apterous virginopara.

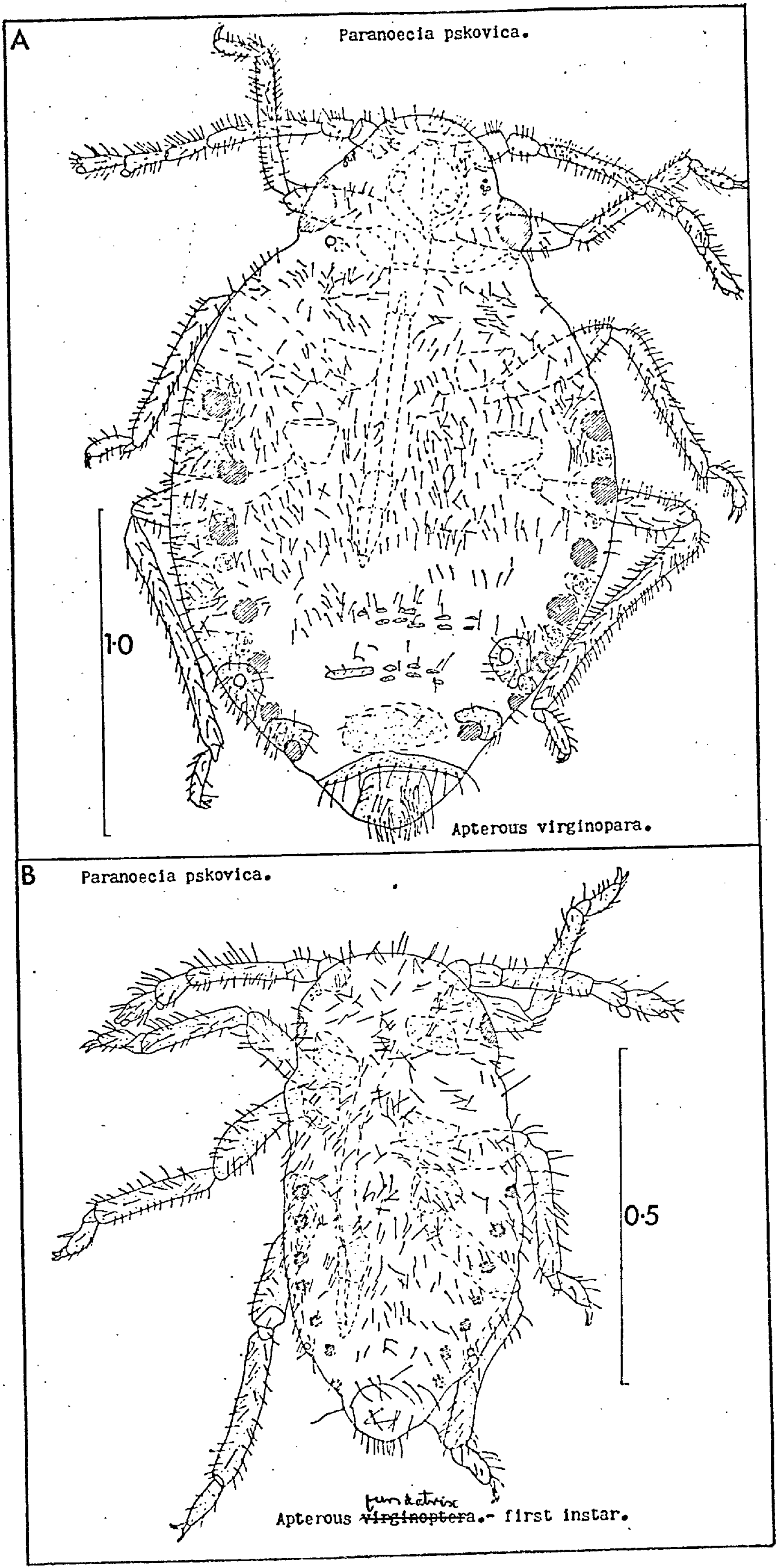
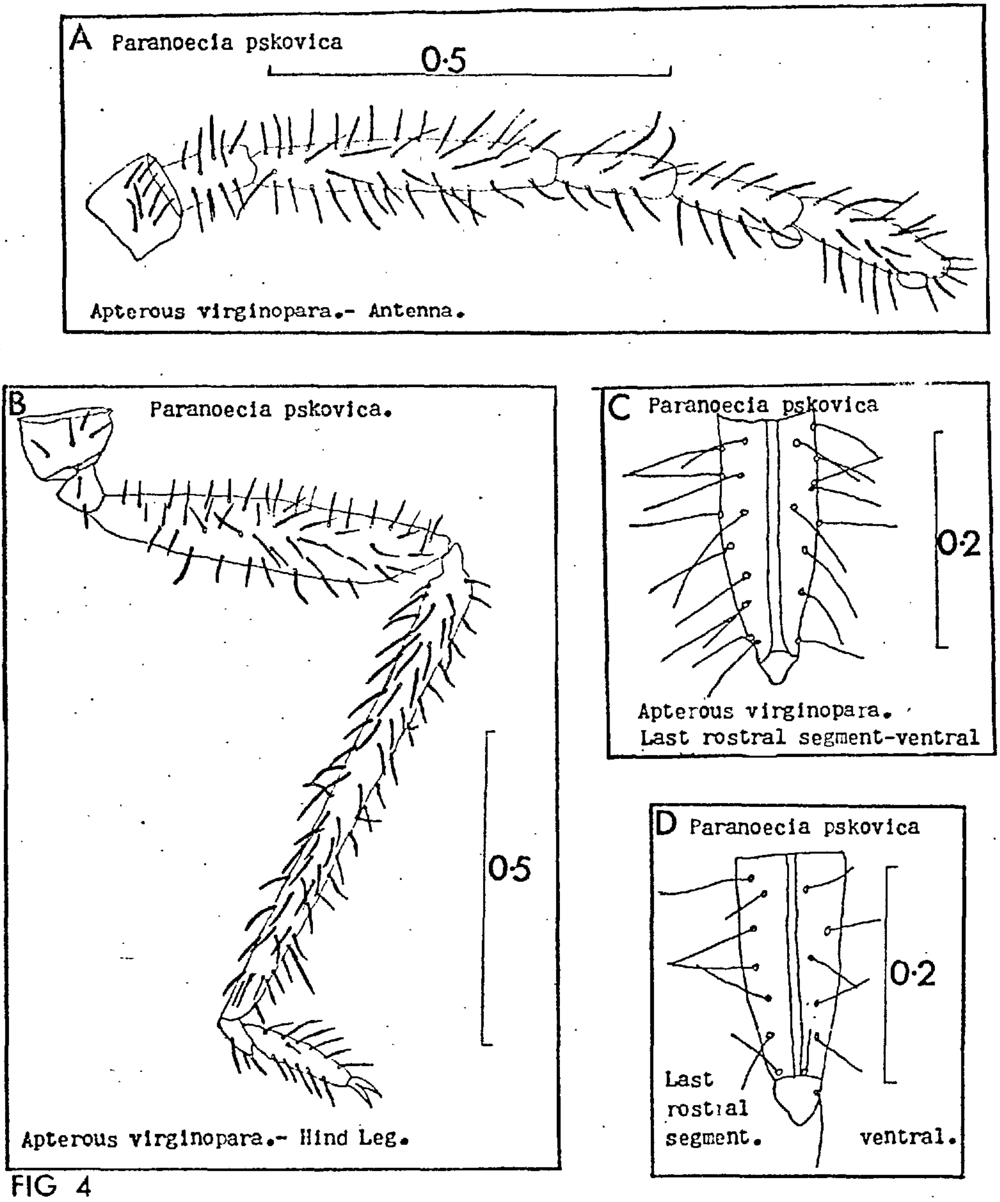

A
Paranoecia pskovica.
1·0
Apterous virginopara.
B
Paranoecia pskovica.
0·5
Apterous ~~virginoptera~~ fundatrix.- first instar.

FIG 3

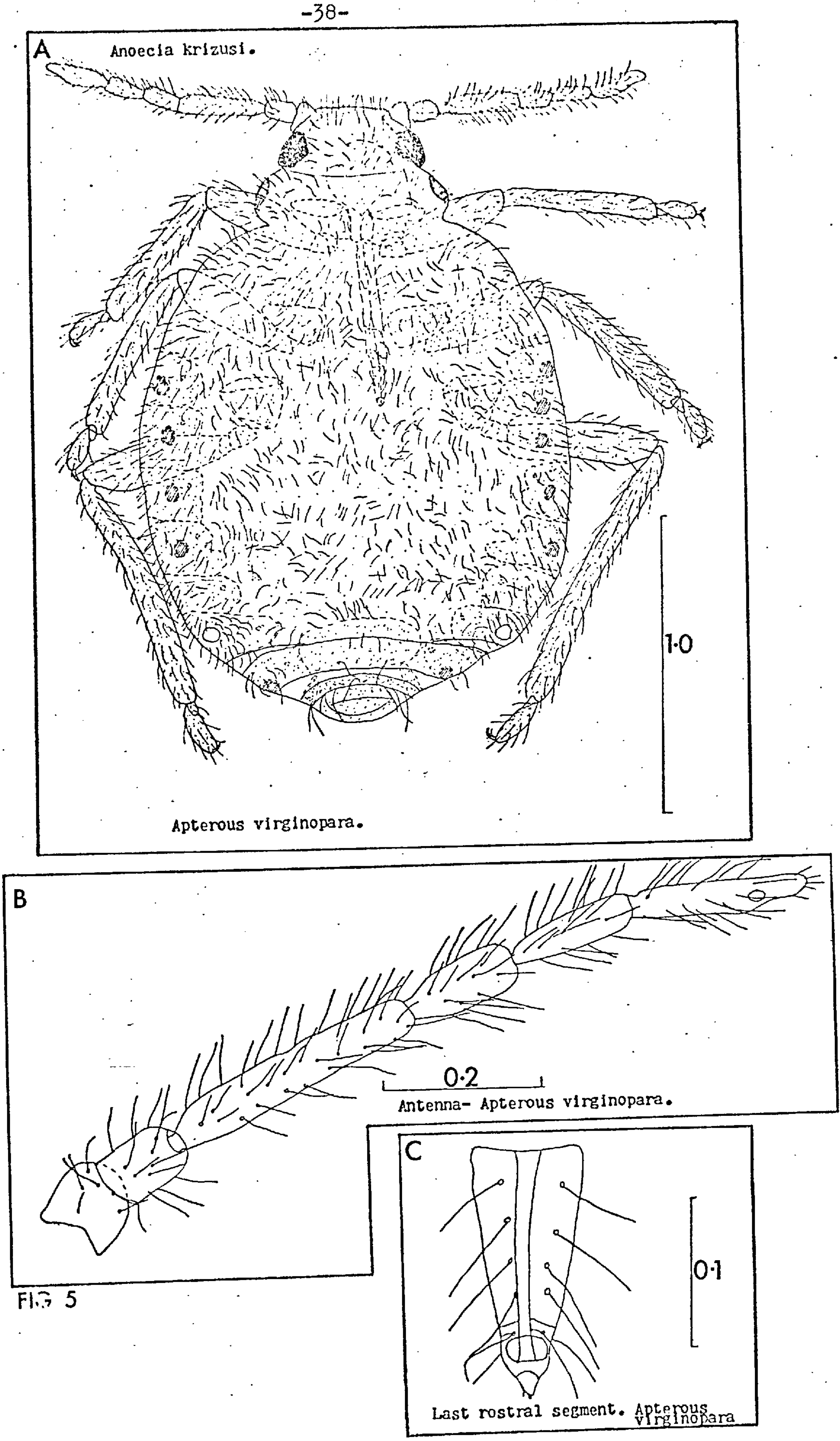


Apterous virginopara.- Antenna.

Apterous virginopara.- Hind Leg.

Apterous virginopara.
Last rostral segment-ventral

FIG 4



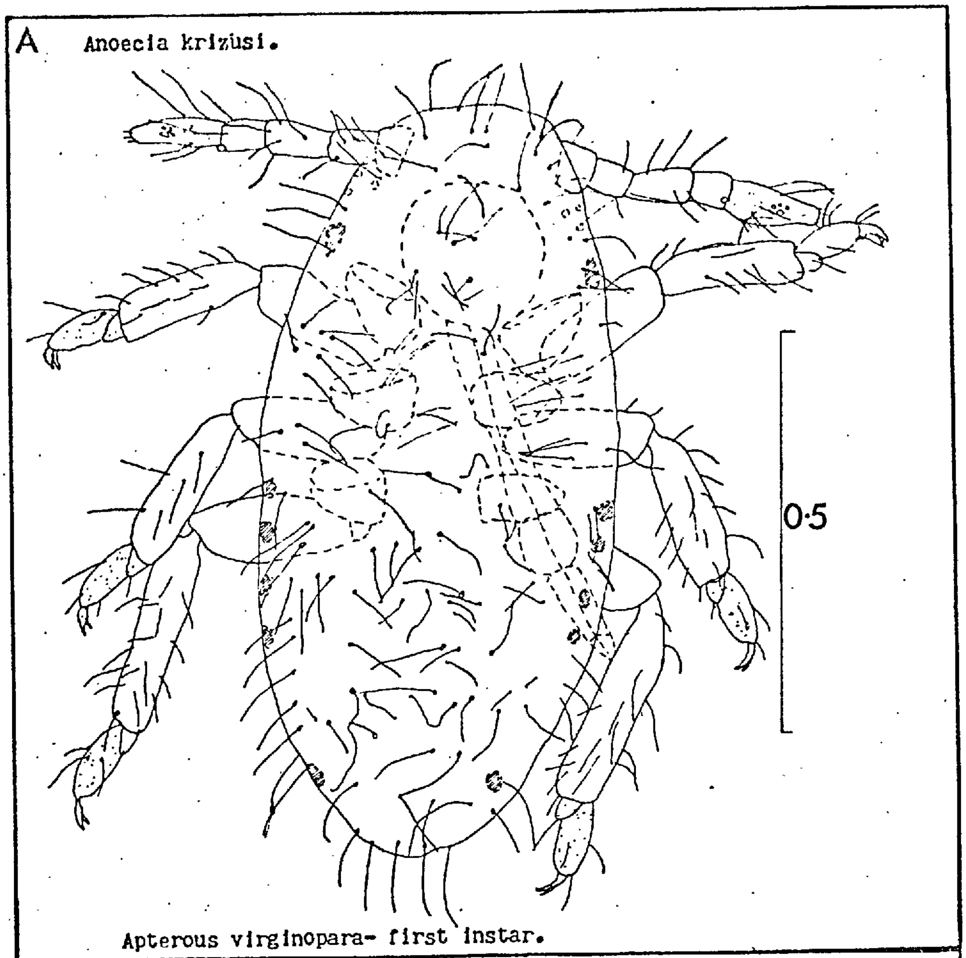
Anoecia krizusi.

Apterous virginopara.

Antenna- Apterous virginopara.

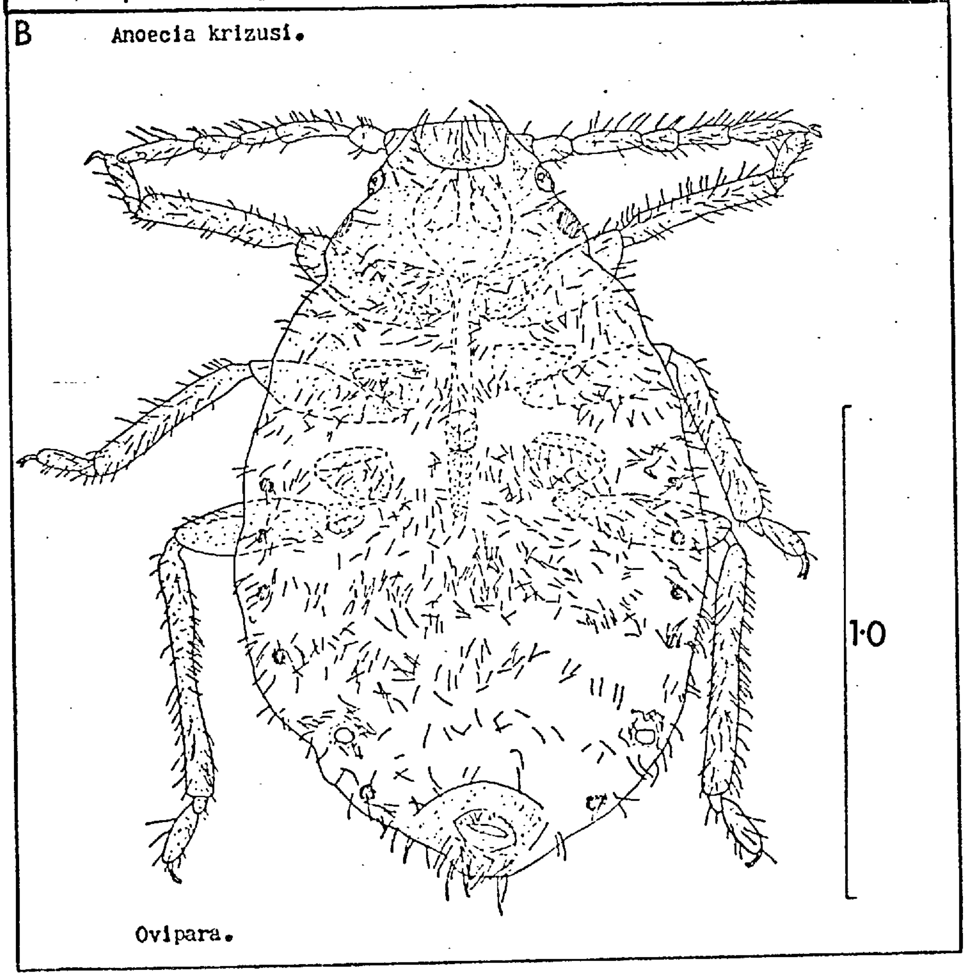
Last rostral segment. Apterous virginopara

FIG 5



Anoecia krizusi.

Apterous virginopara- first instar.



Anoecia krizusi.

Ovipara.

FIG 6

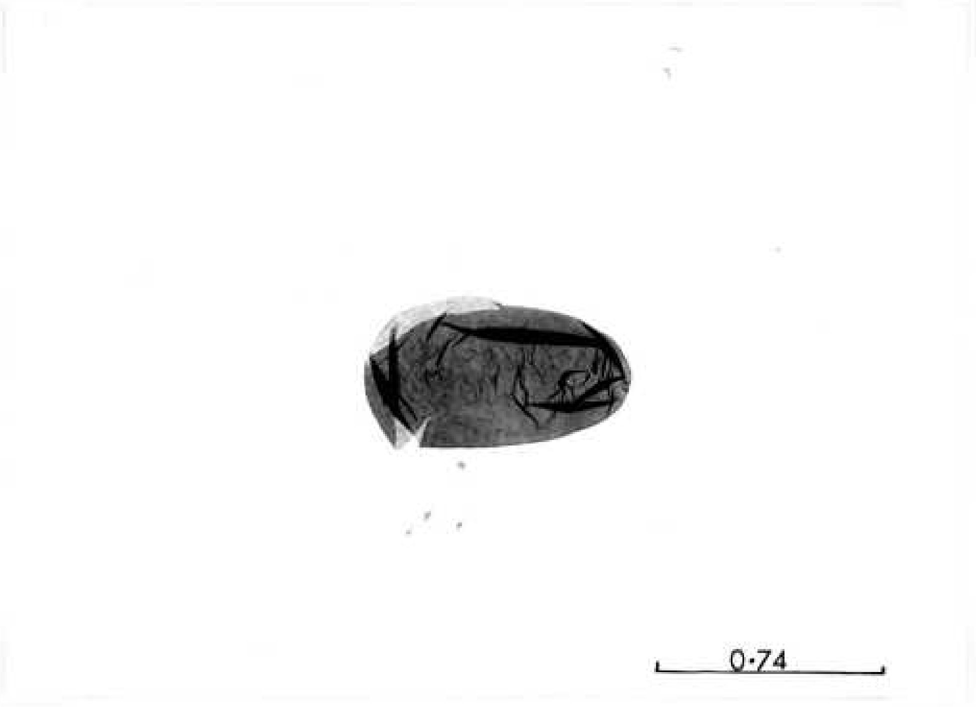


Plate 3. Anoecia zirnitzi. Egg.

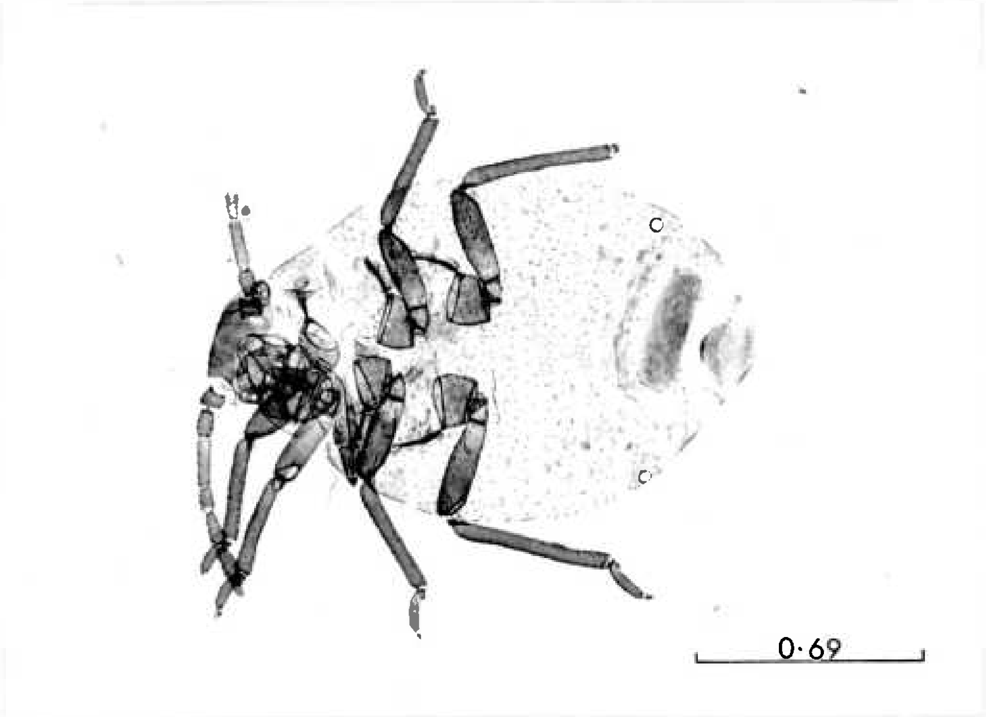


Plate 4. Anoecia zirntizi. Ovipara.

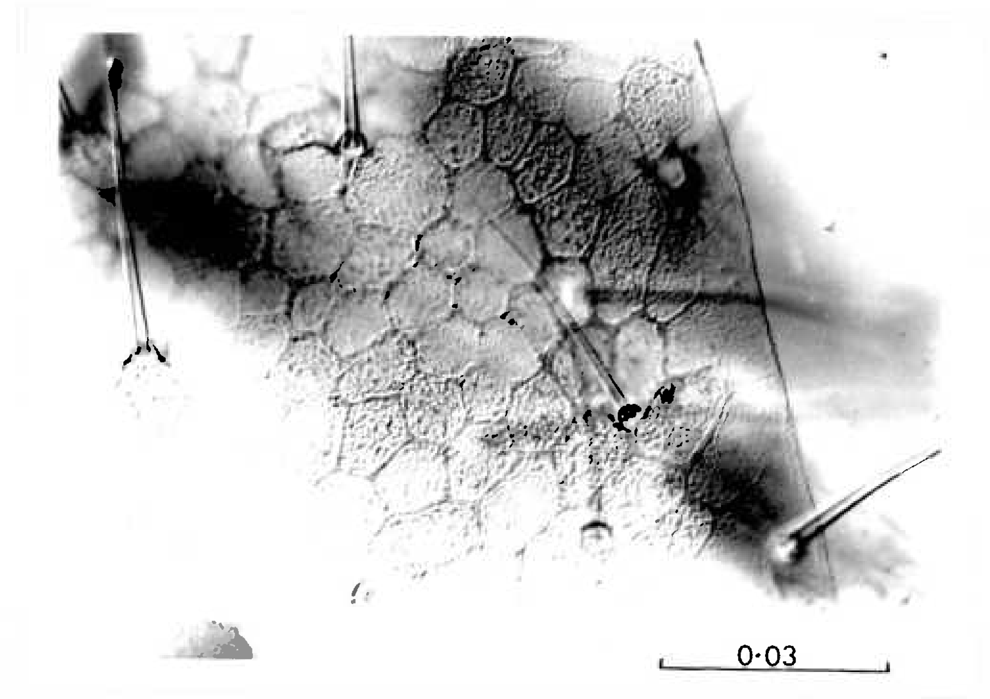


Plate 5. *Anoecia zirnitsi*. Wax gland of ovipara.

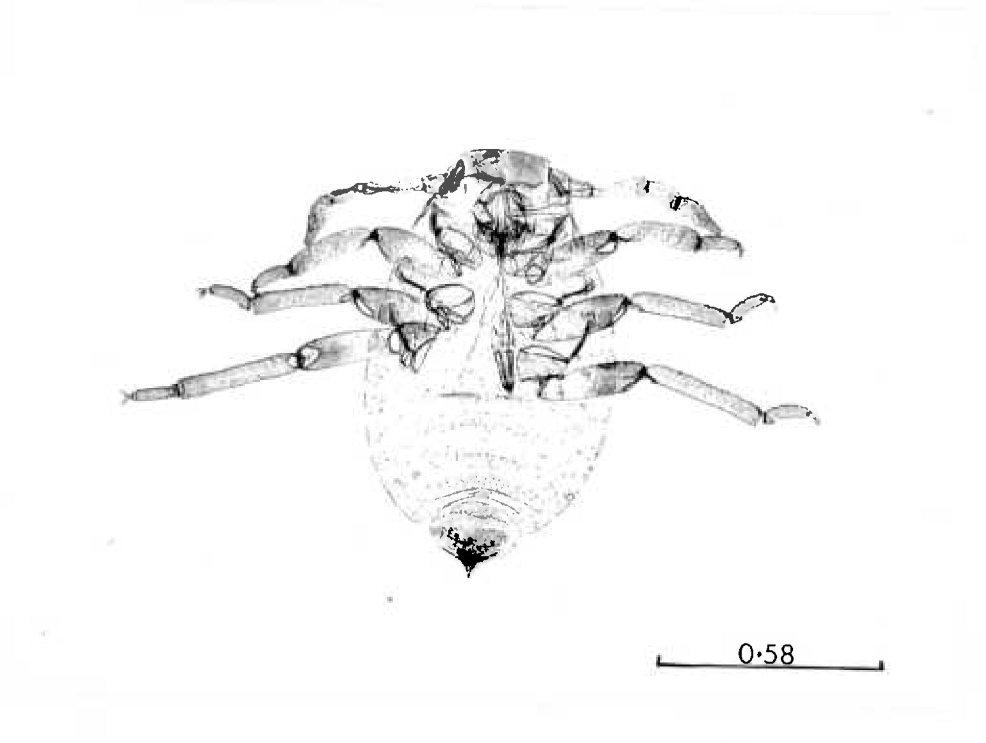


Plate 6. *Anoecia zirnitsi*. Male.

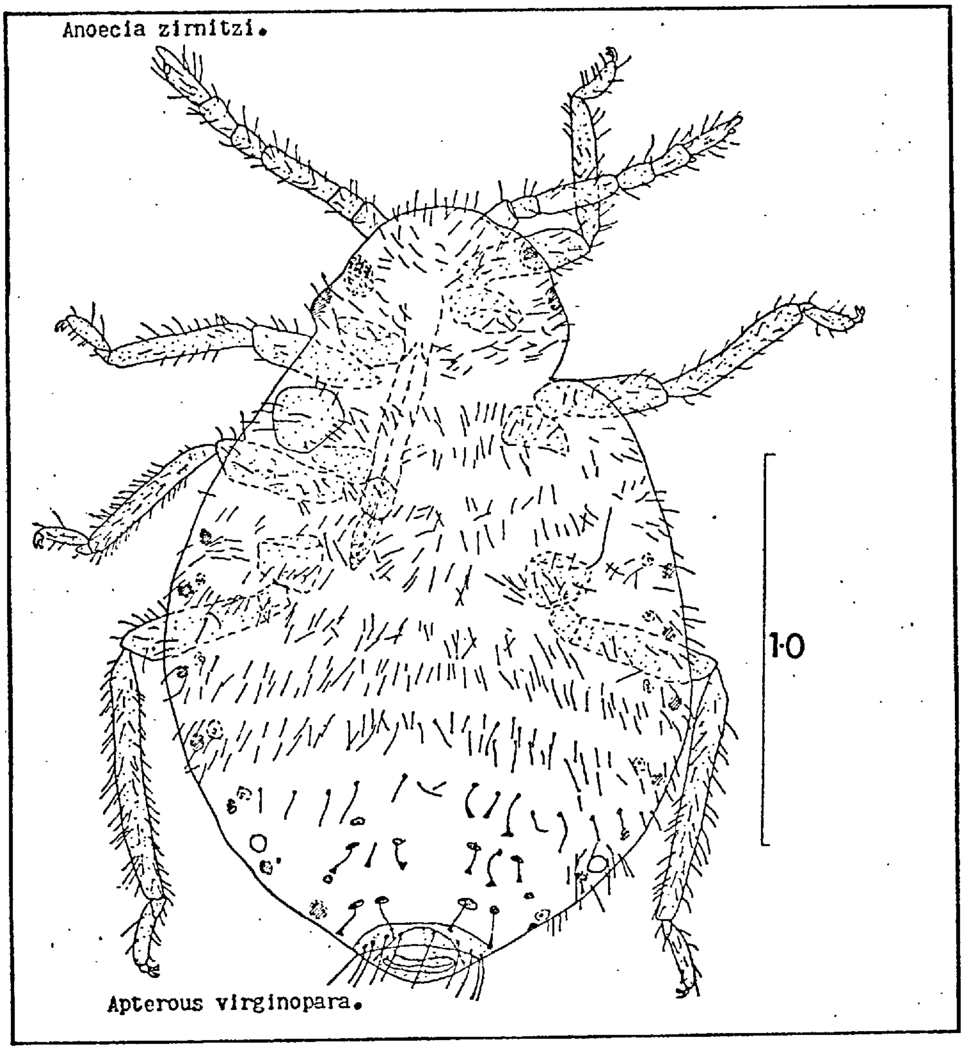


FIG 7

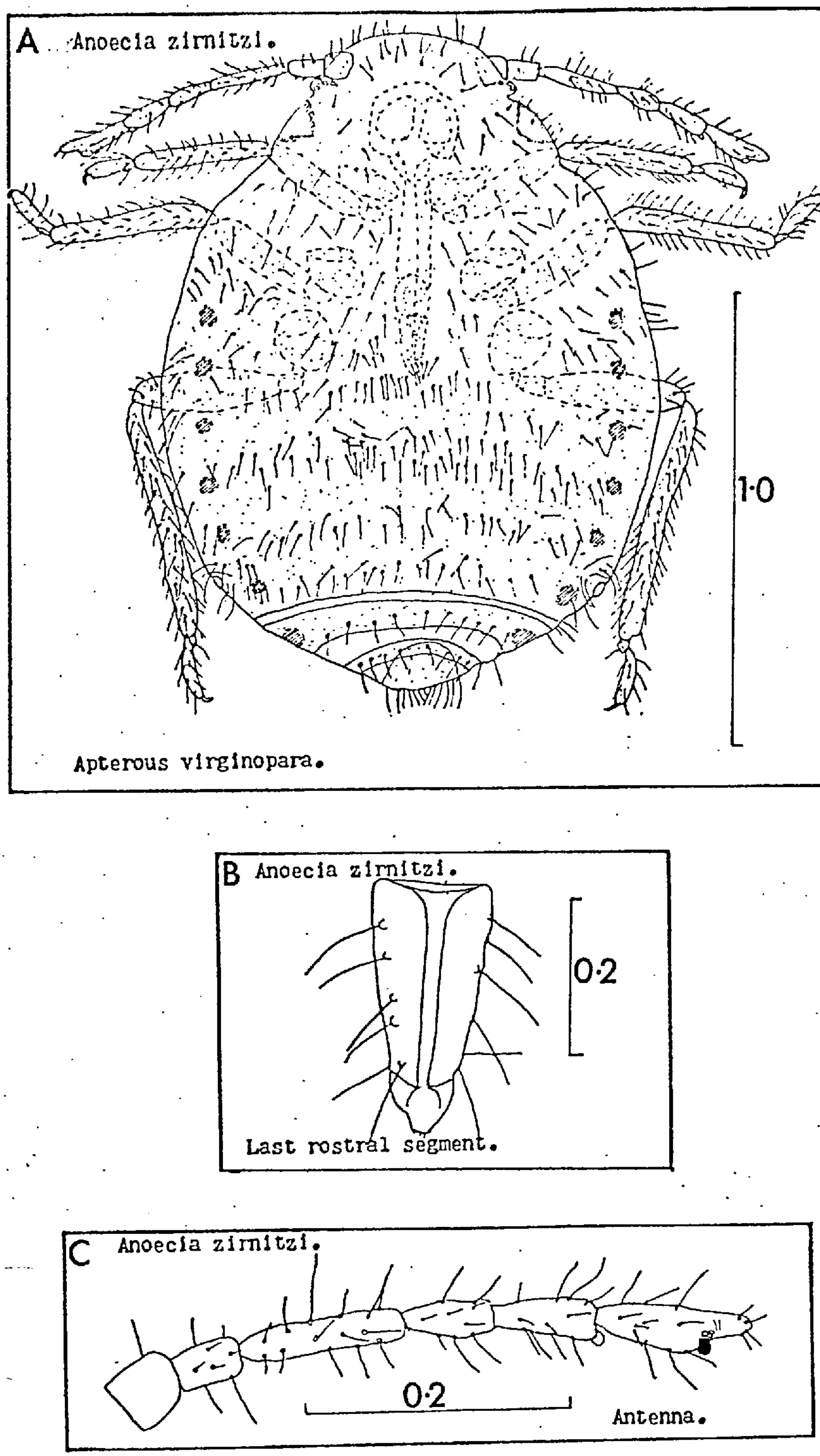
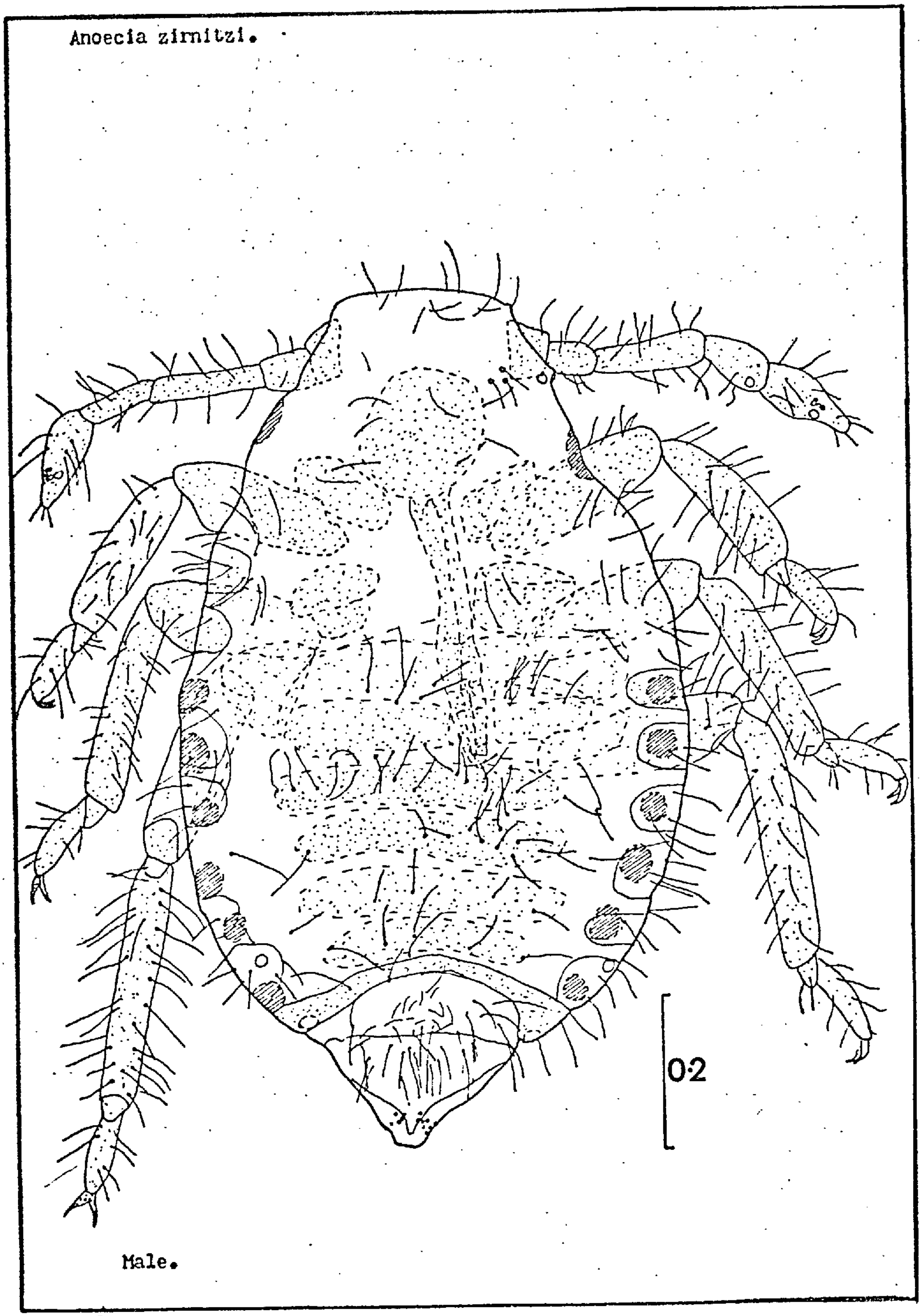

A
Anoecia zirnitzi.
1·0
Apterous virginopara.
B
Anoecia zirnitzi.
0·2
Last rostral segment.
C
Anoecia zirnitzi.
0·2
Antenna.

FIG 8


Anoecia zirnitzi.

Male.

FIG 9

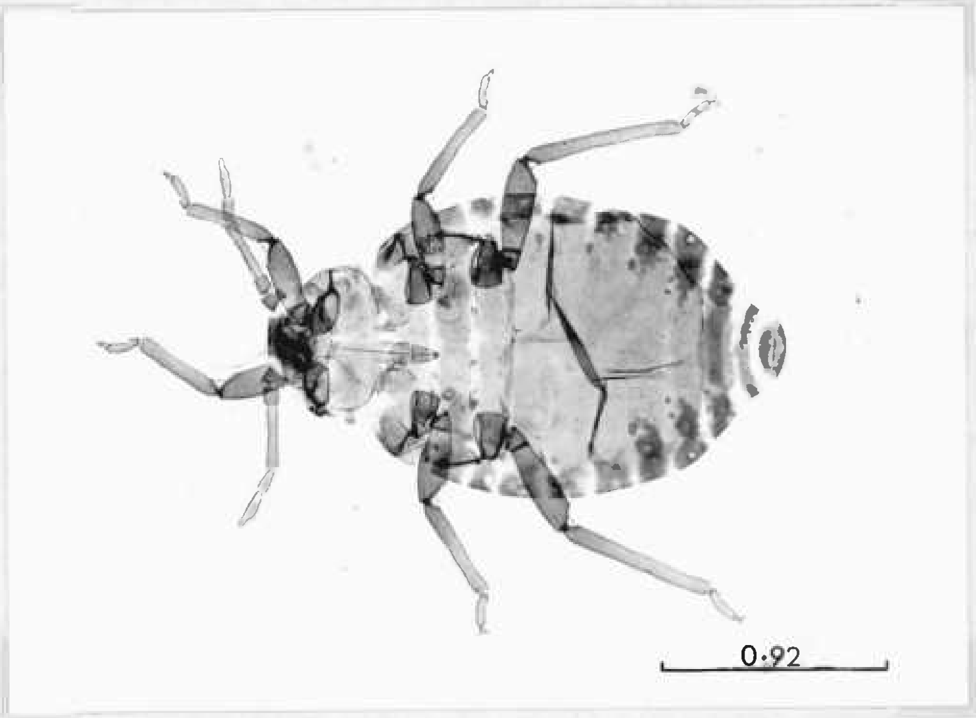


Plate 7. Anoecia corni. Fundatrix.

Plate 8. Anoecia corni. Alate fundatrigenia.

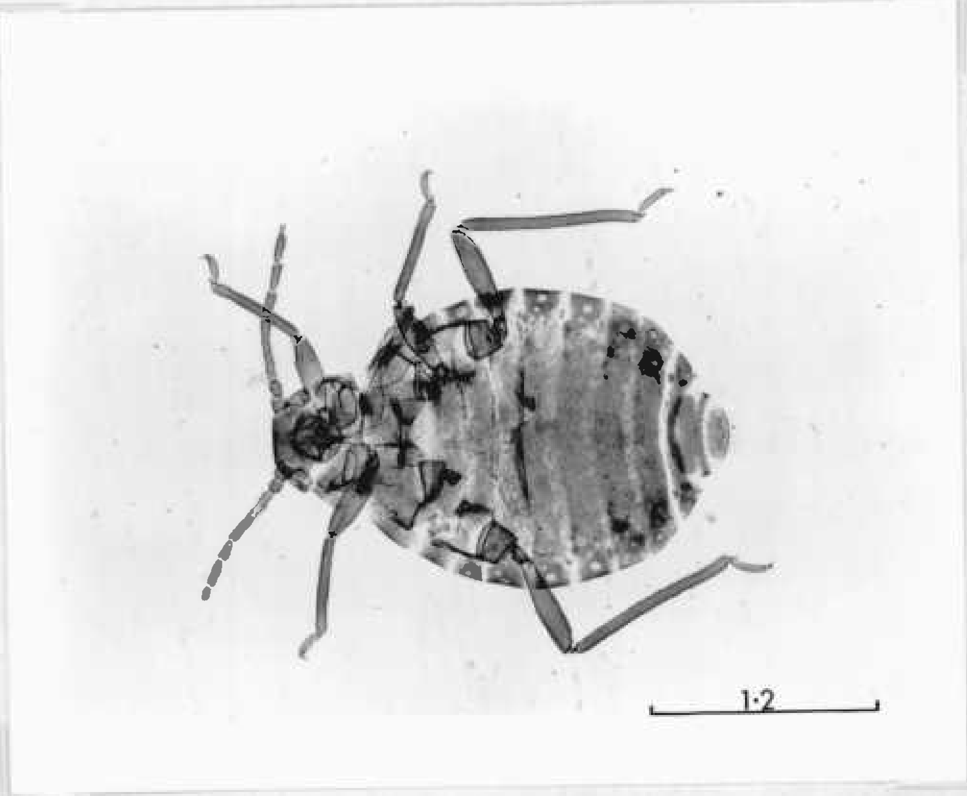


Plate 9. Anoecia corni. Apterous virginopara.

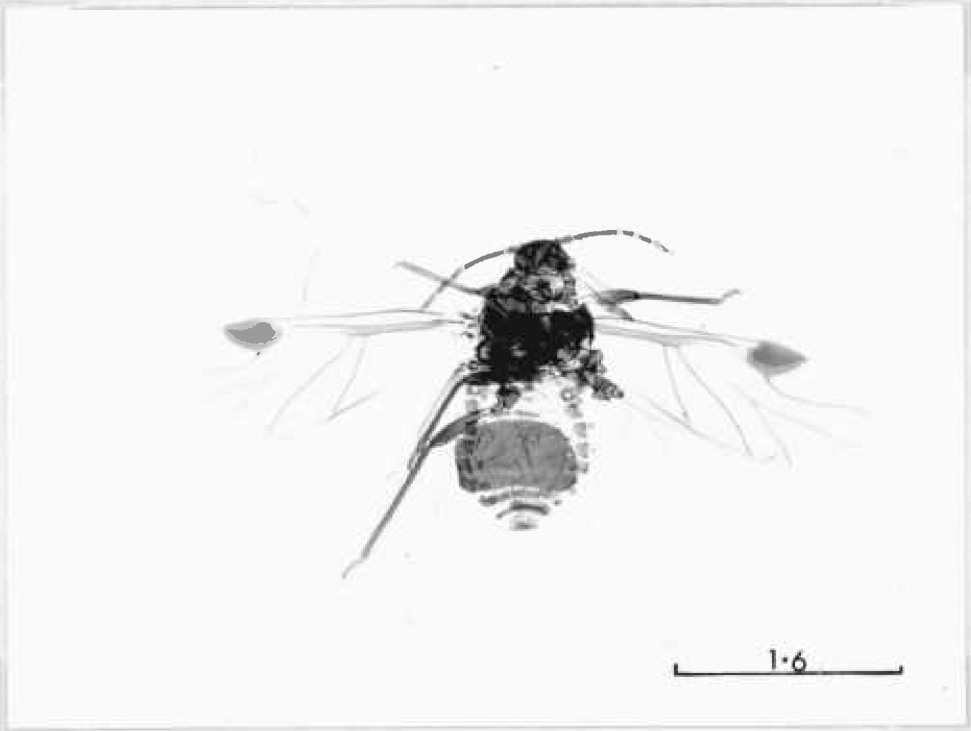


Plate 10. Anoecia corni. Alate virginopara.

Plate 11. Anoecia corni. Sexupara and Sexuales.

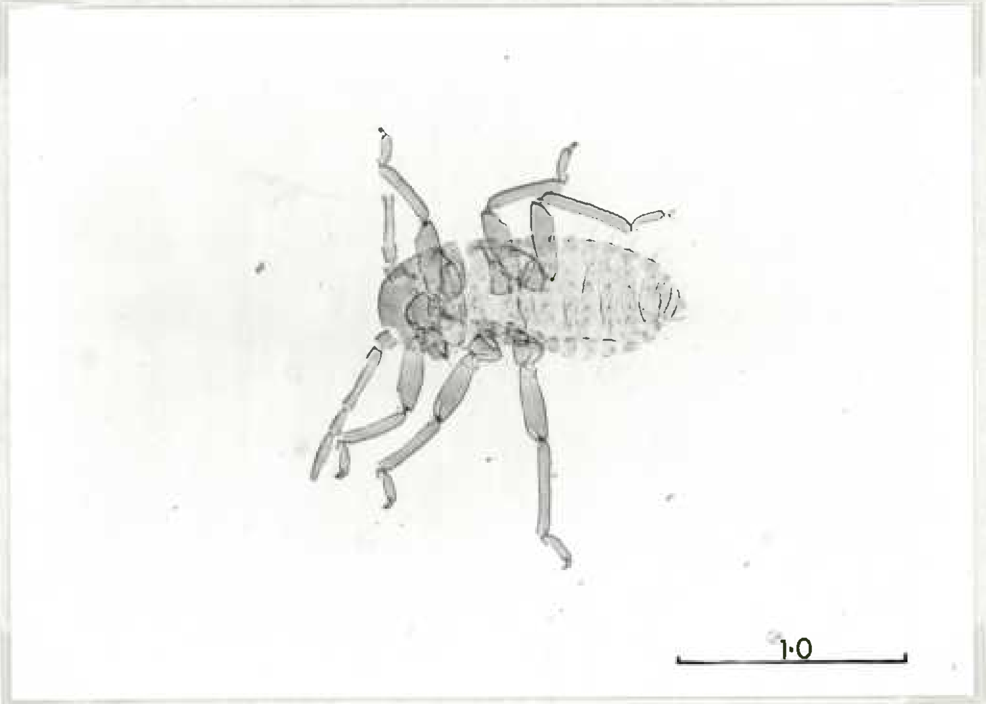


Plate 12. Anoecia corni. Male.

Plate 13. Anoecia corni. Males and Oviparae.

Plate 14. Anoecia corni. Males and Oviparae with white Syrphid egg laid in their vicinity.

Plate 15. *Aphis corniella*. Sexuparae and sexulaes. *Aphis corniella* is found on dogwood at the same time as *Anoecia* species but is distinguished by lacking a pterostigma.

Plate 16. *Aphis corniella*. Sexupara.

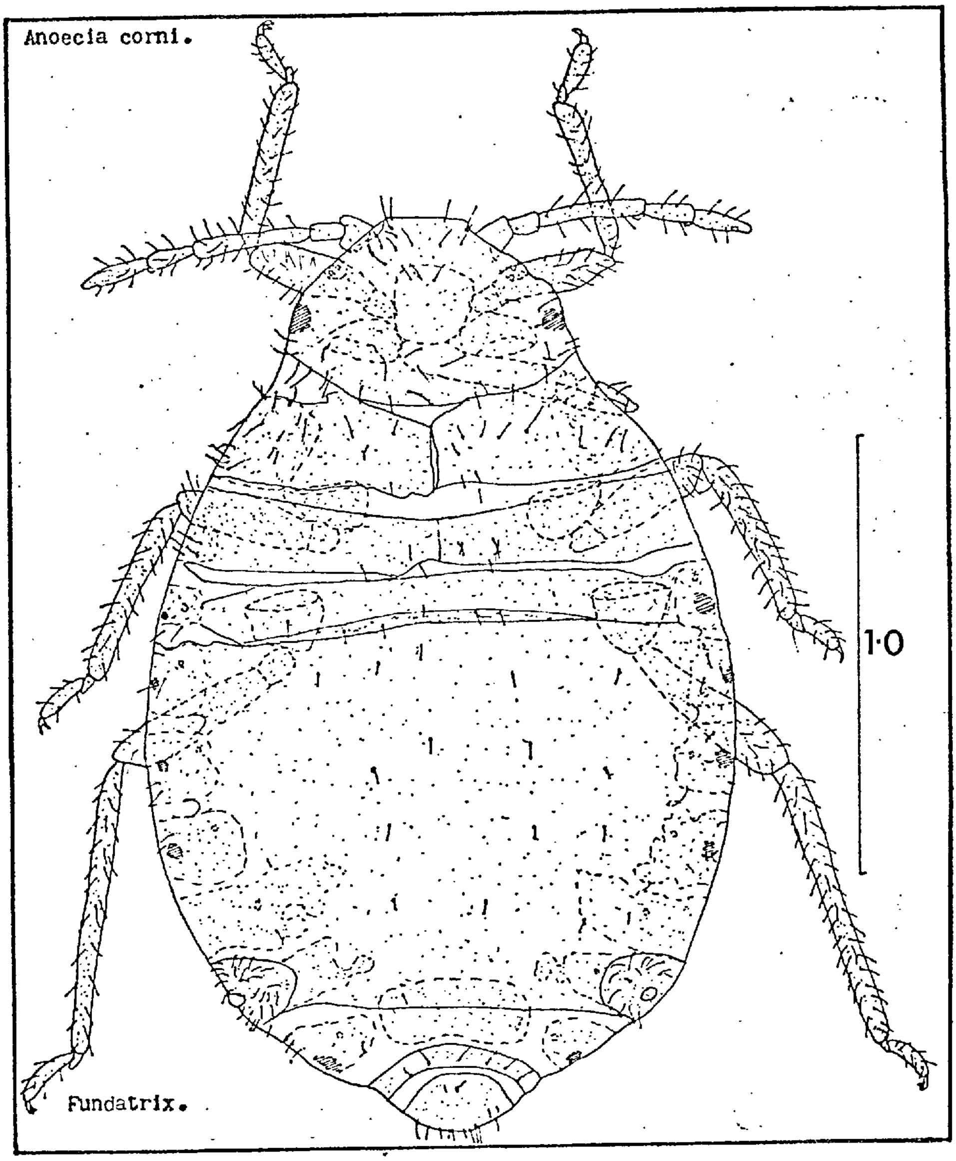


FIG 10

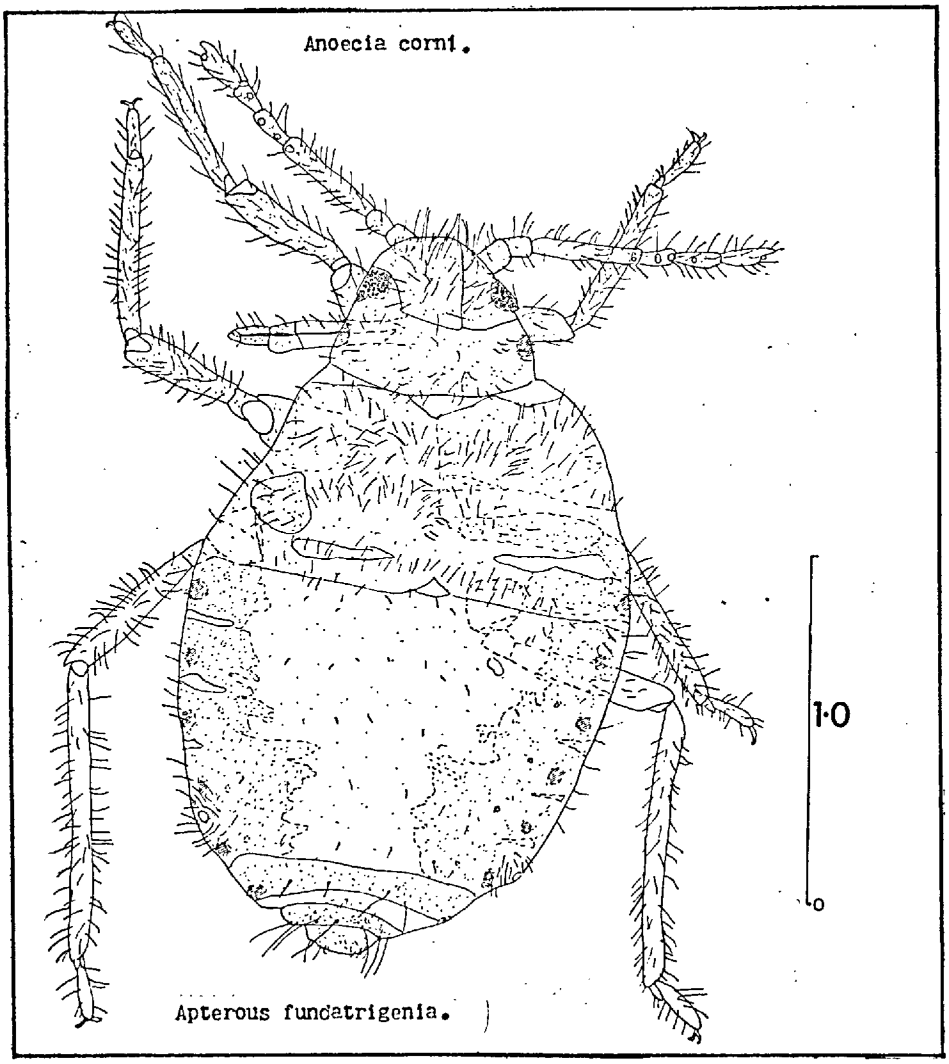


FIG. 11.

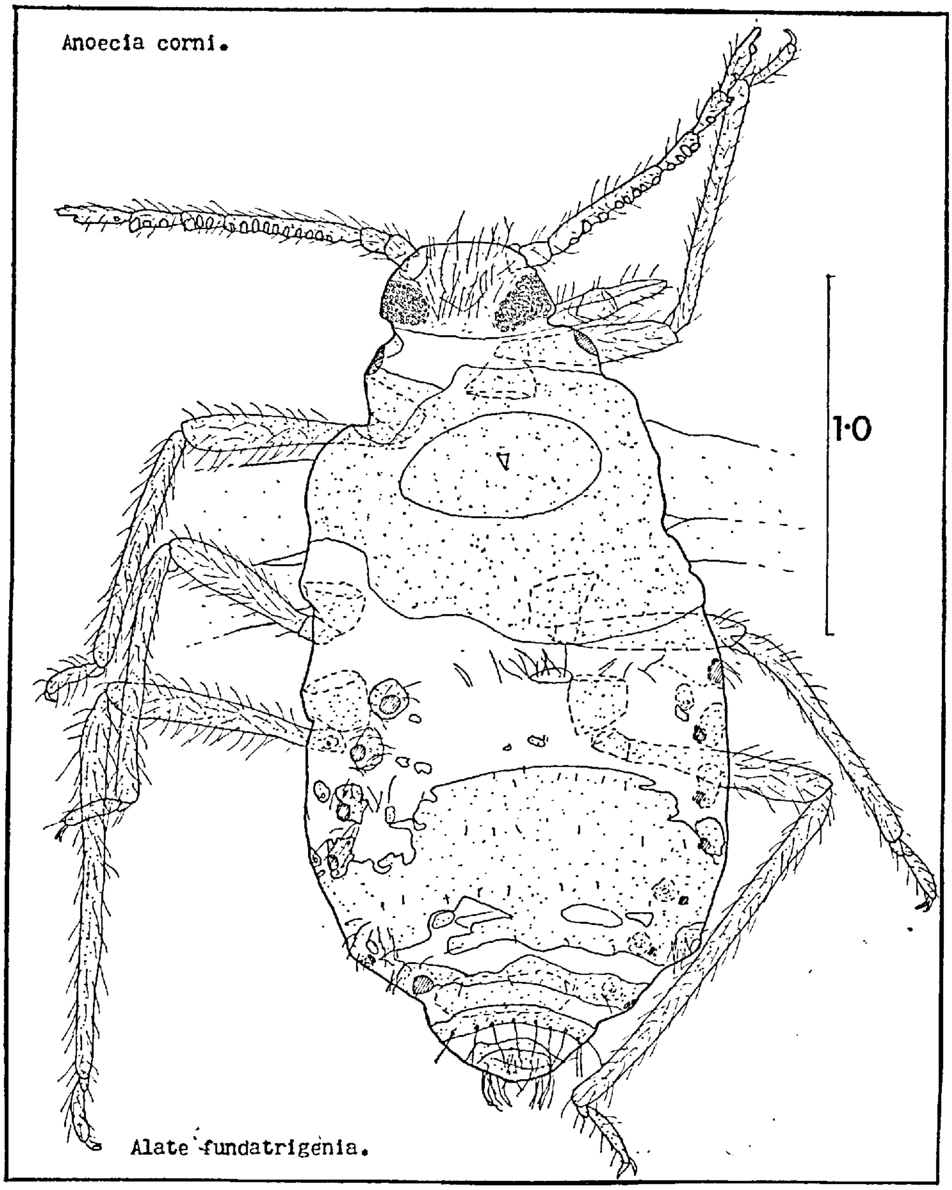
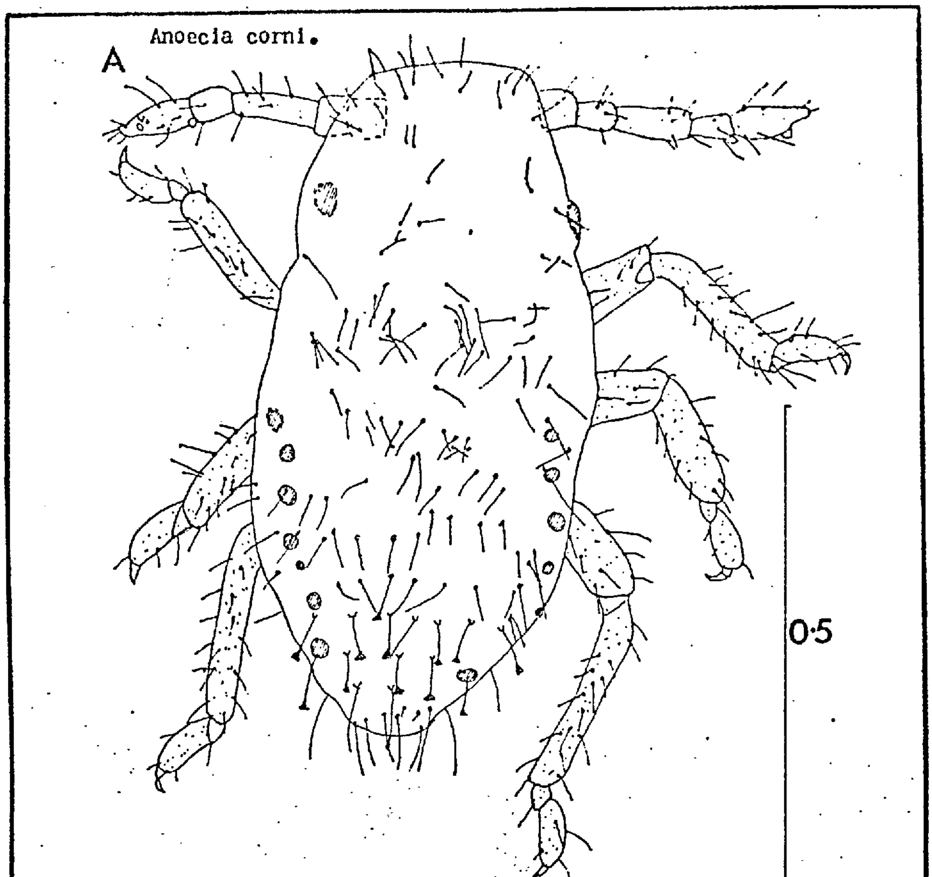
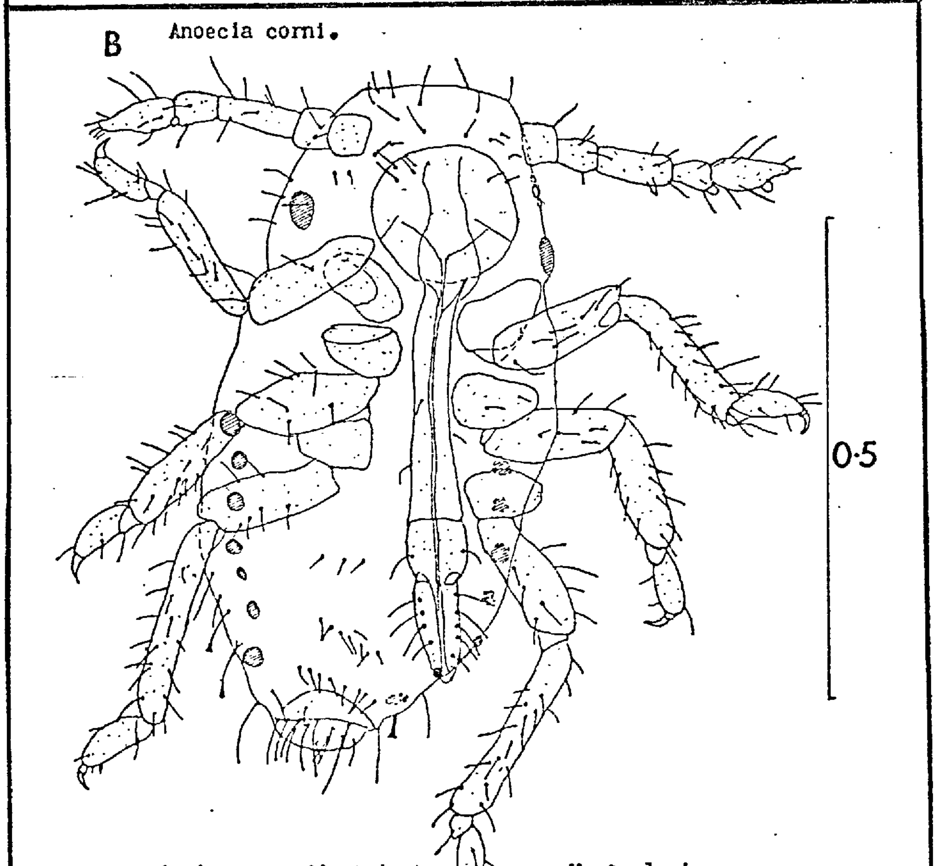


FIG. 12.



Apterous virginopara- first instar. Dorsal view.



Apterous virginopara- first instar Ventral view.

FIG 13

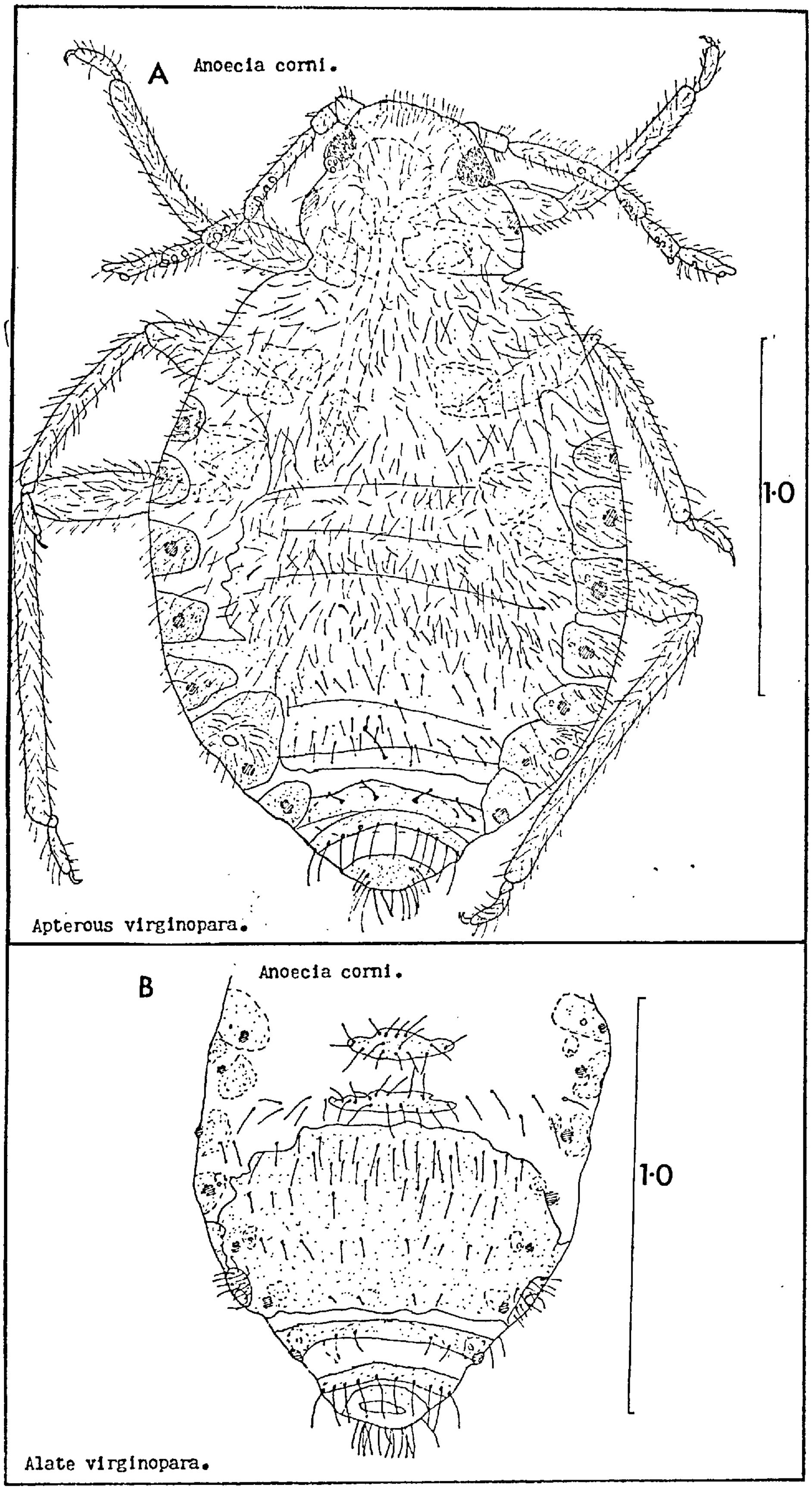
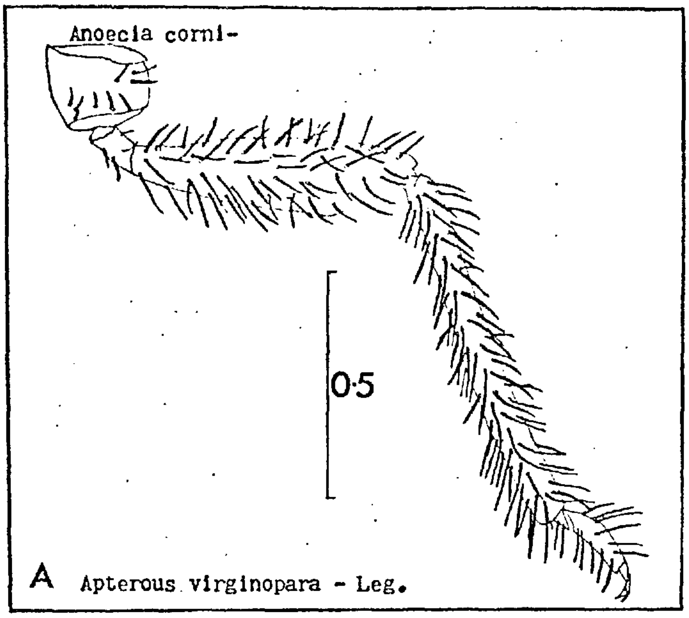
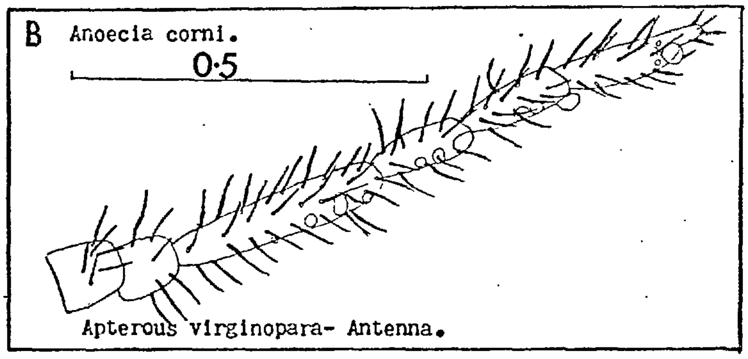

A
Anoecia corni.
1·0
Apterous virginopara.
B
Anoecia corni.
1·0
Alate virginopara.

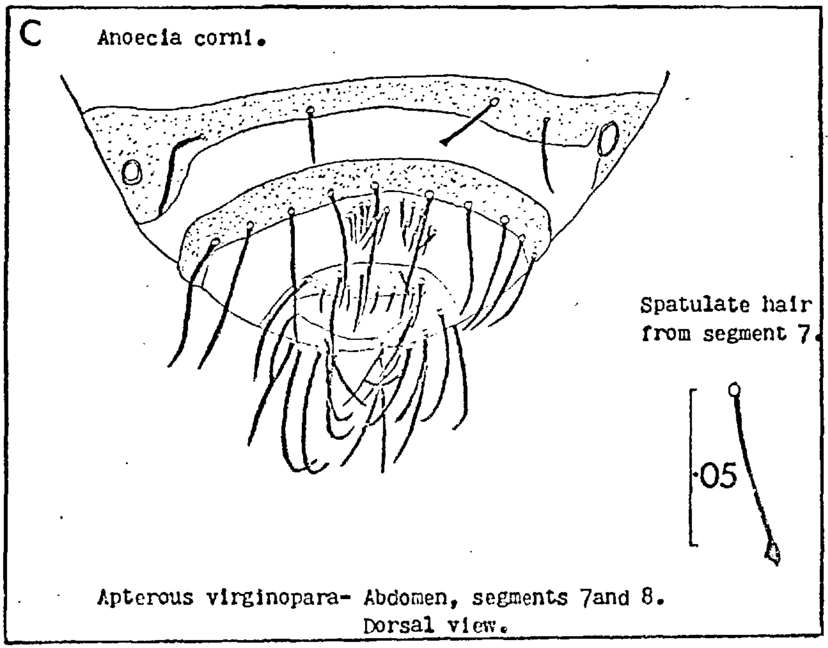
FIG. 14.



Apterous virginopara - Leg.



Apterous virginopara- Antenna.



Apterous virginopara- Abdomen, segments 7and 8. Dorsal view.

FIG 15

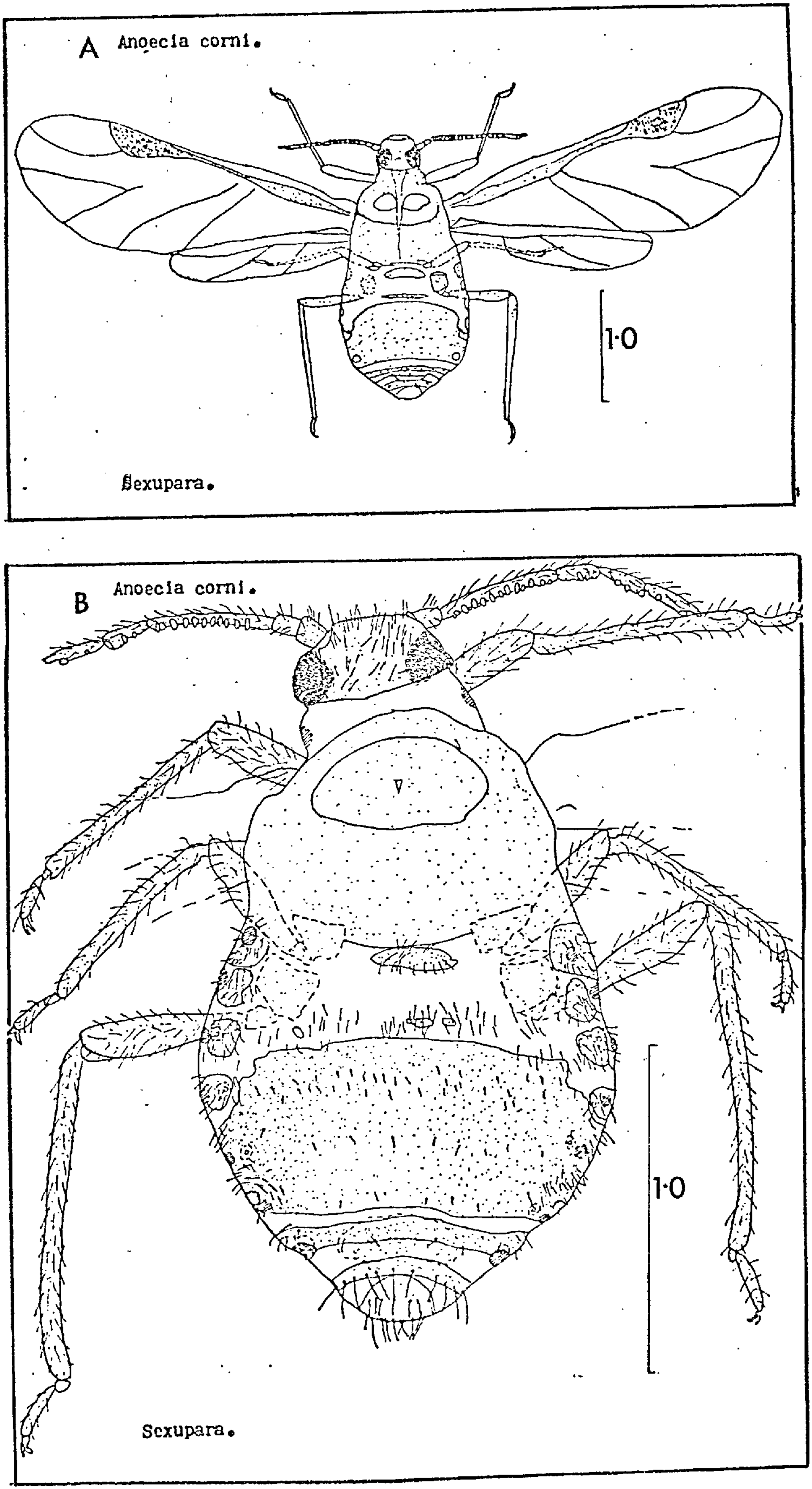


FIG 16

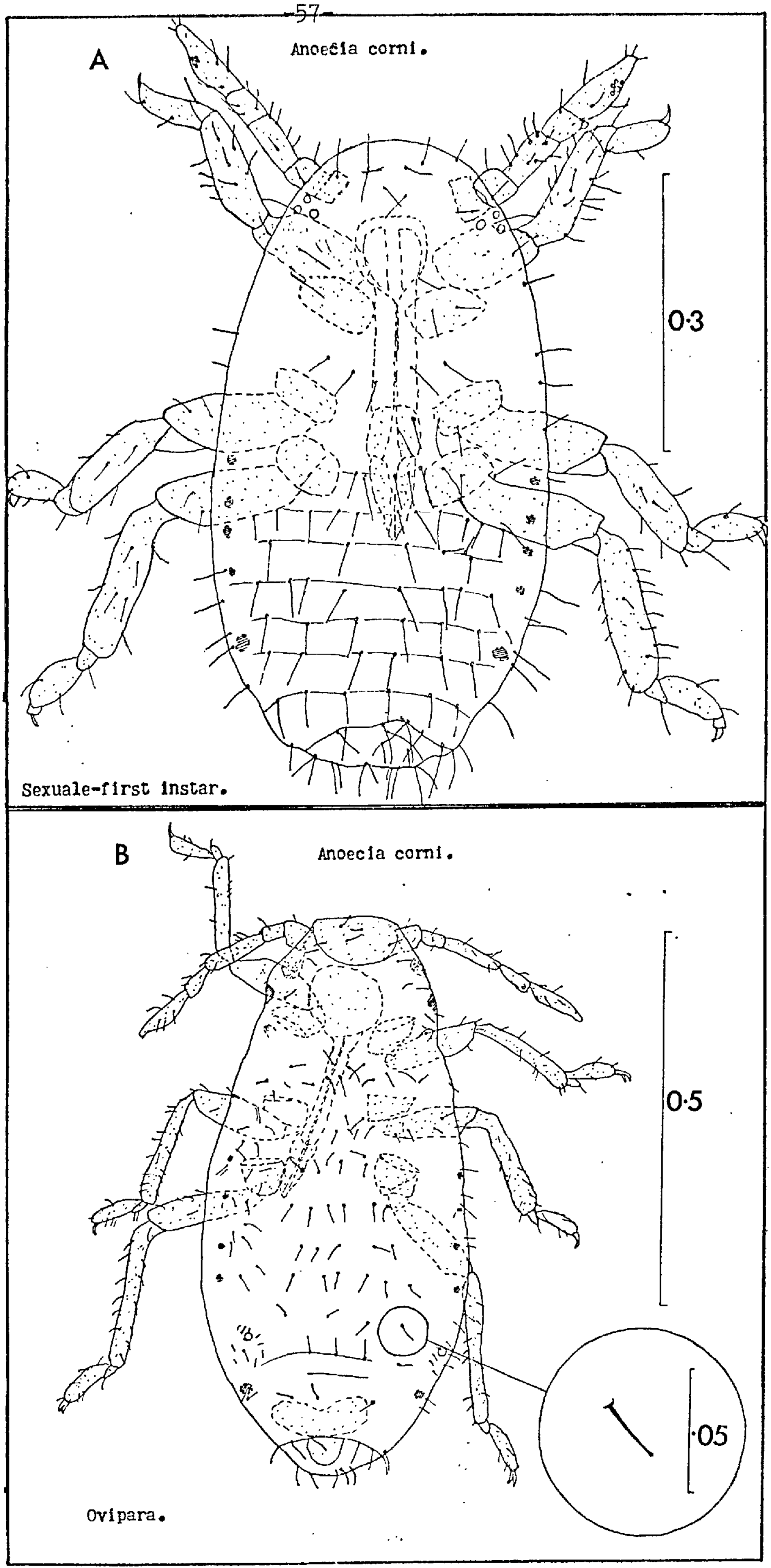

A
Anoecia corni.
0·3
Sexuale-first instar.
B
Anoecia corni.
0·5
·05
Ovipara.

FIG. 17.

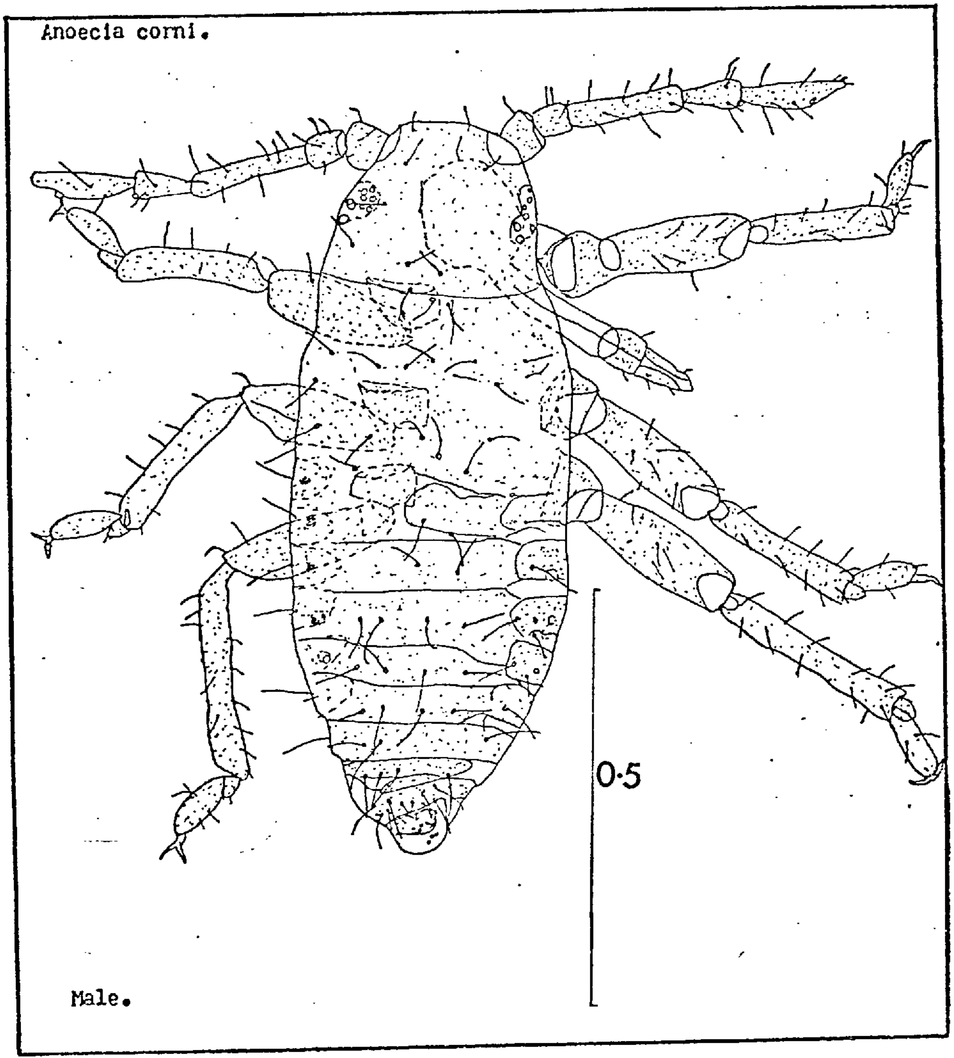
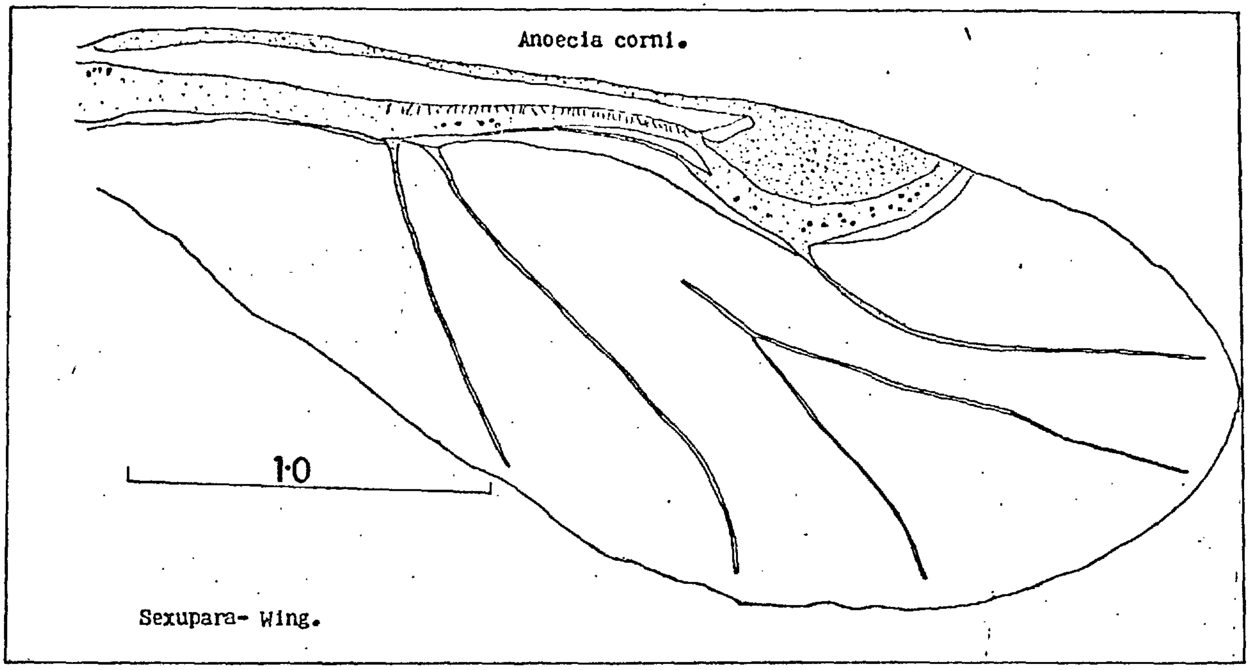
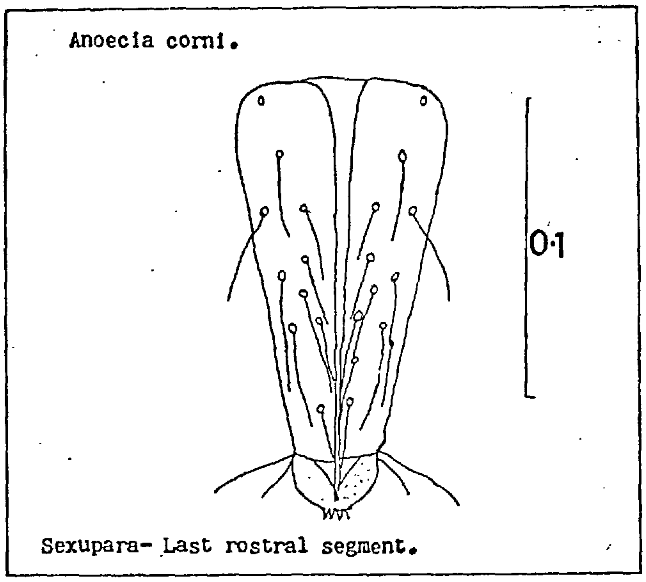


FIG 18



Anoecia corni.

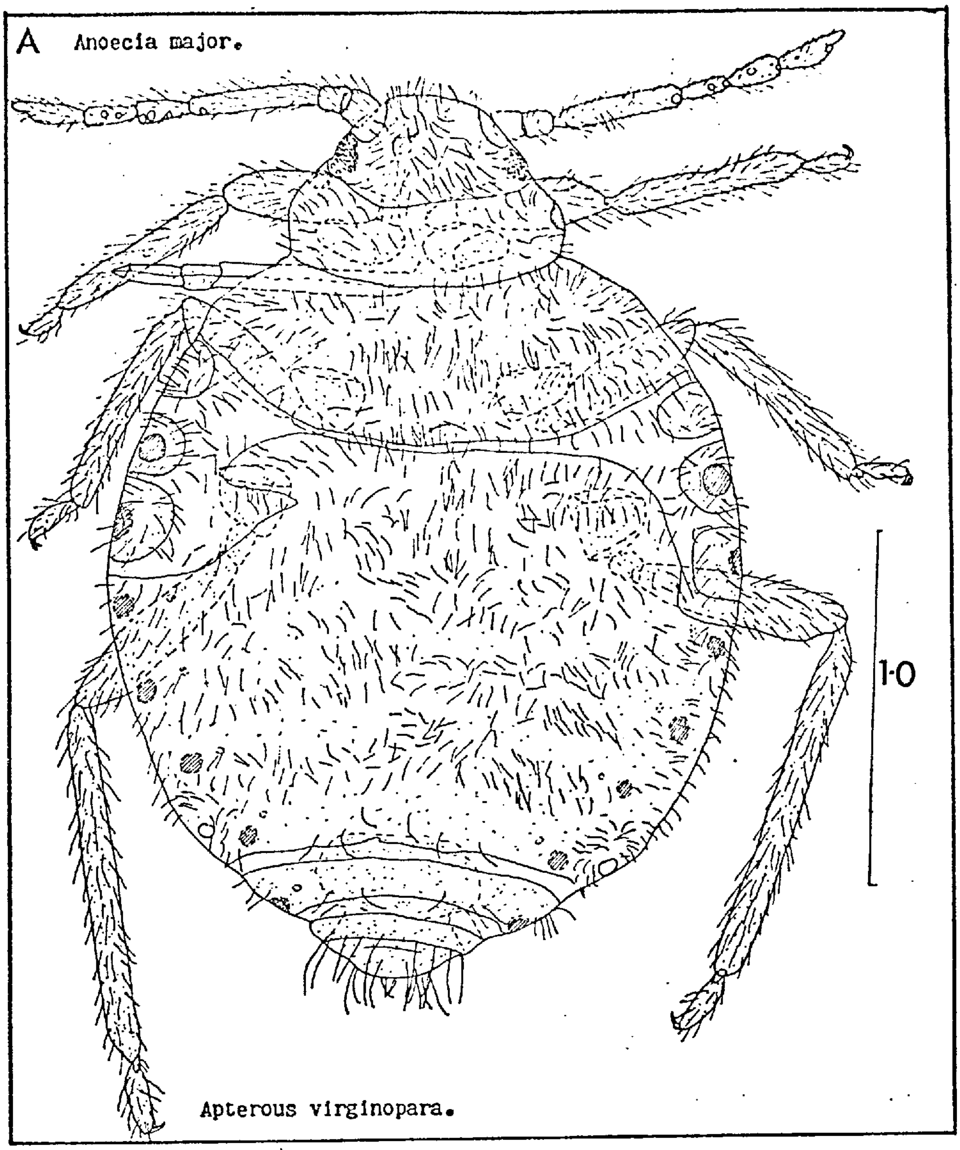
Sexupara- Wing.



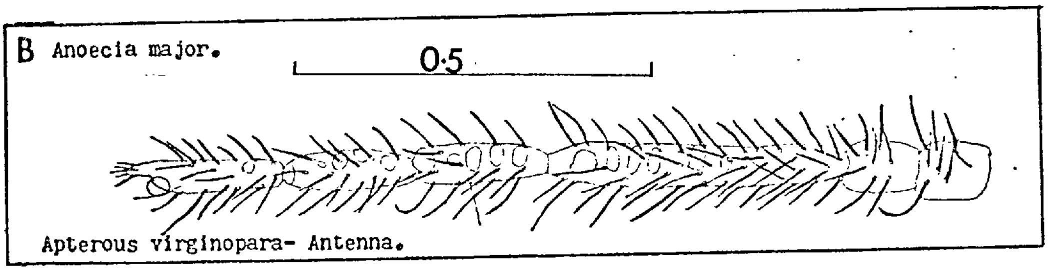
Anoecia corni.

Sexupara- Last rostral segment.

FIG 19

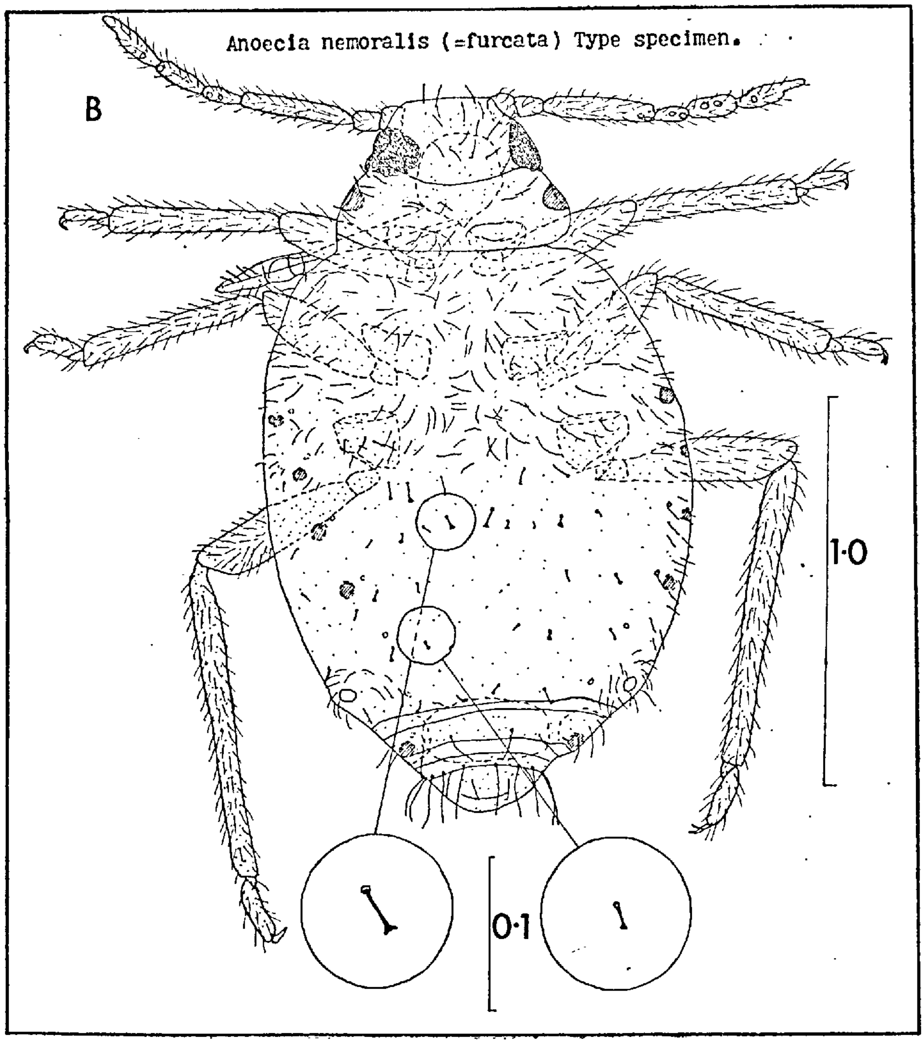


Apterous virginopara.



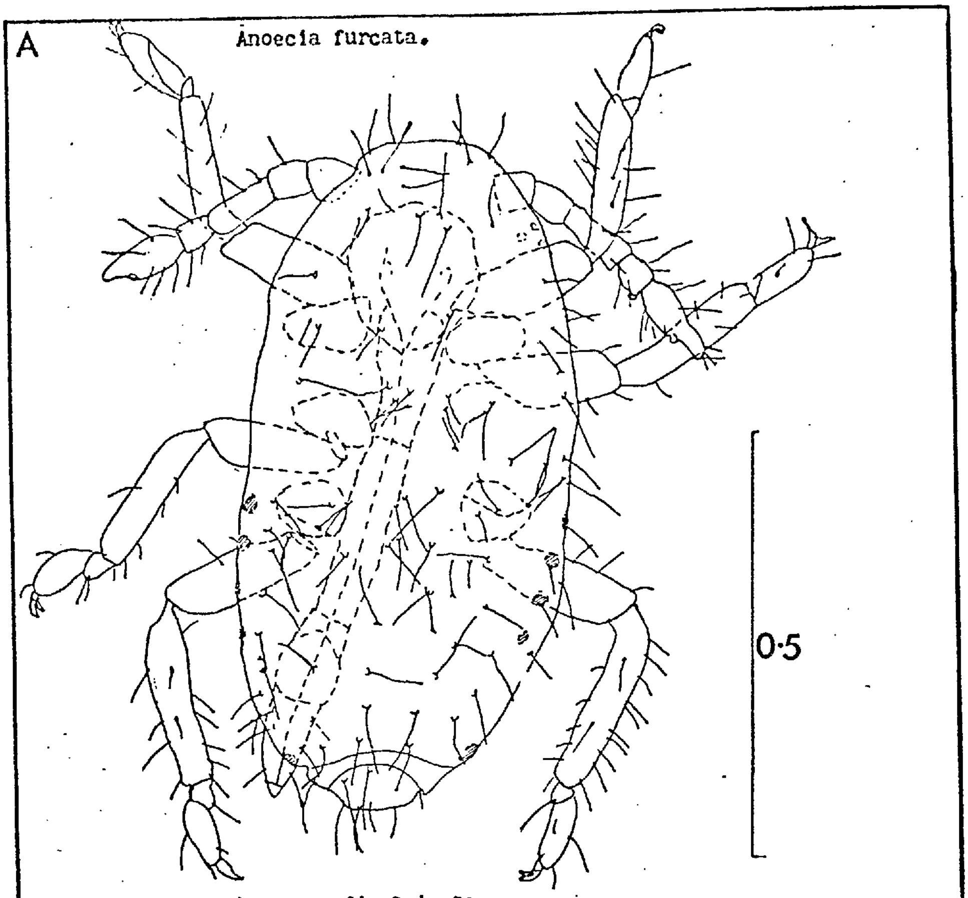
Apterous virginopara- Antenna.

FIG 20



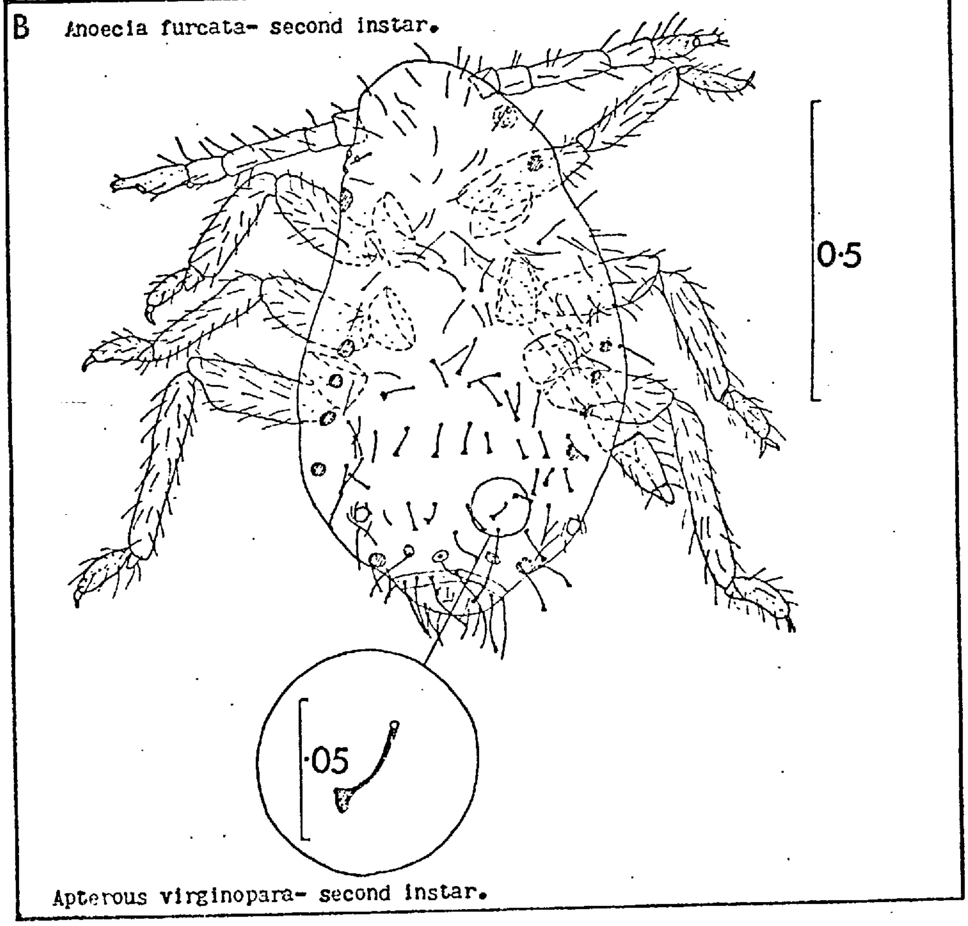
Anoecia nemoralis (=furcata) Type specimen.

FIG. 21.



Anoecia furcata.

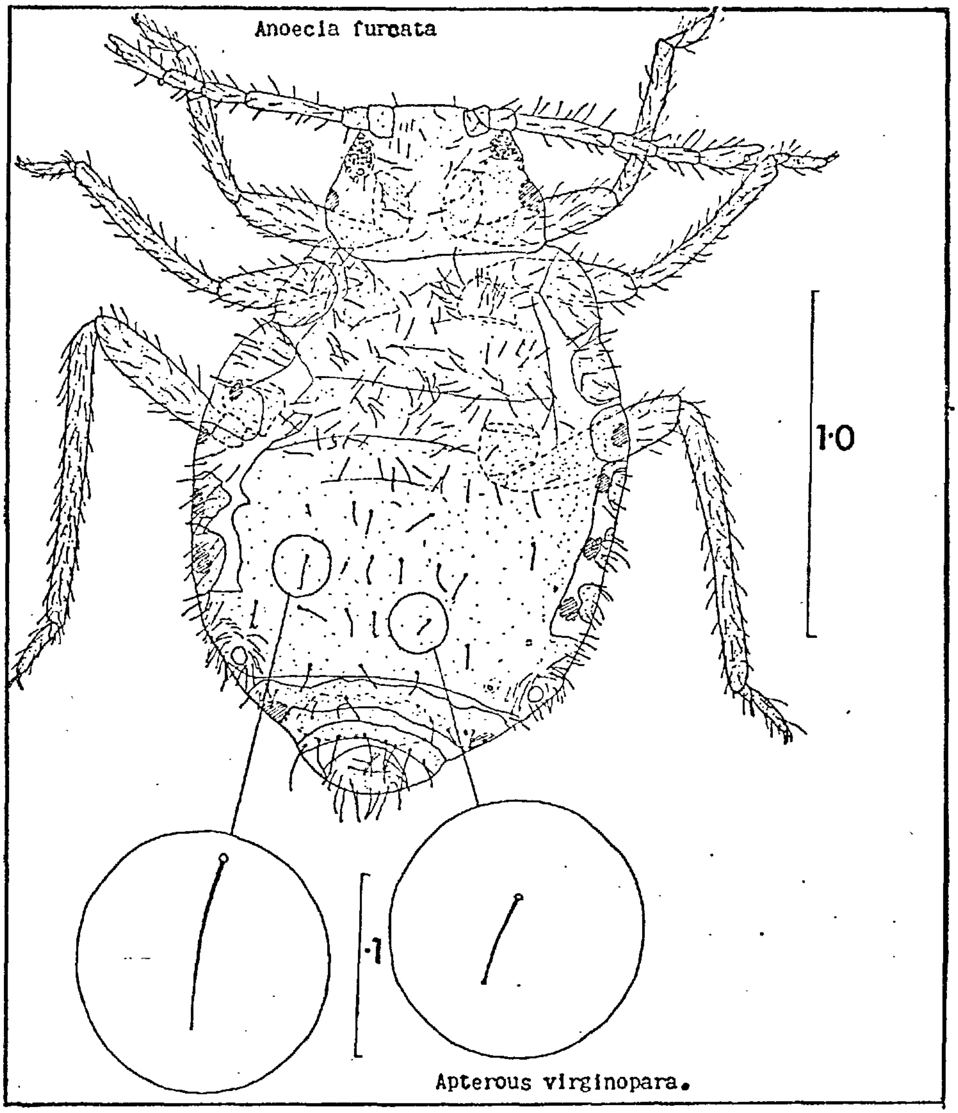
Apterous virginopara- first instar.



Anoecia furcata- second instar.

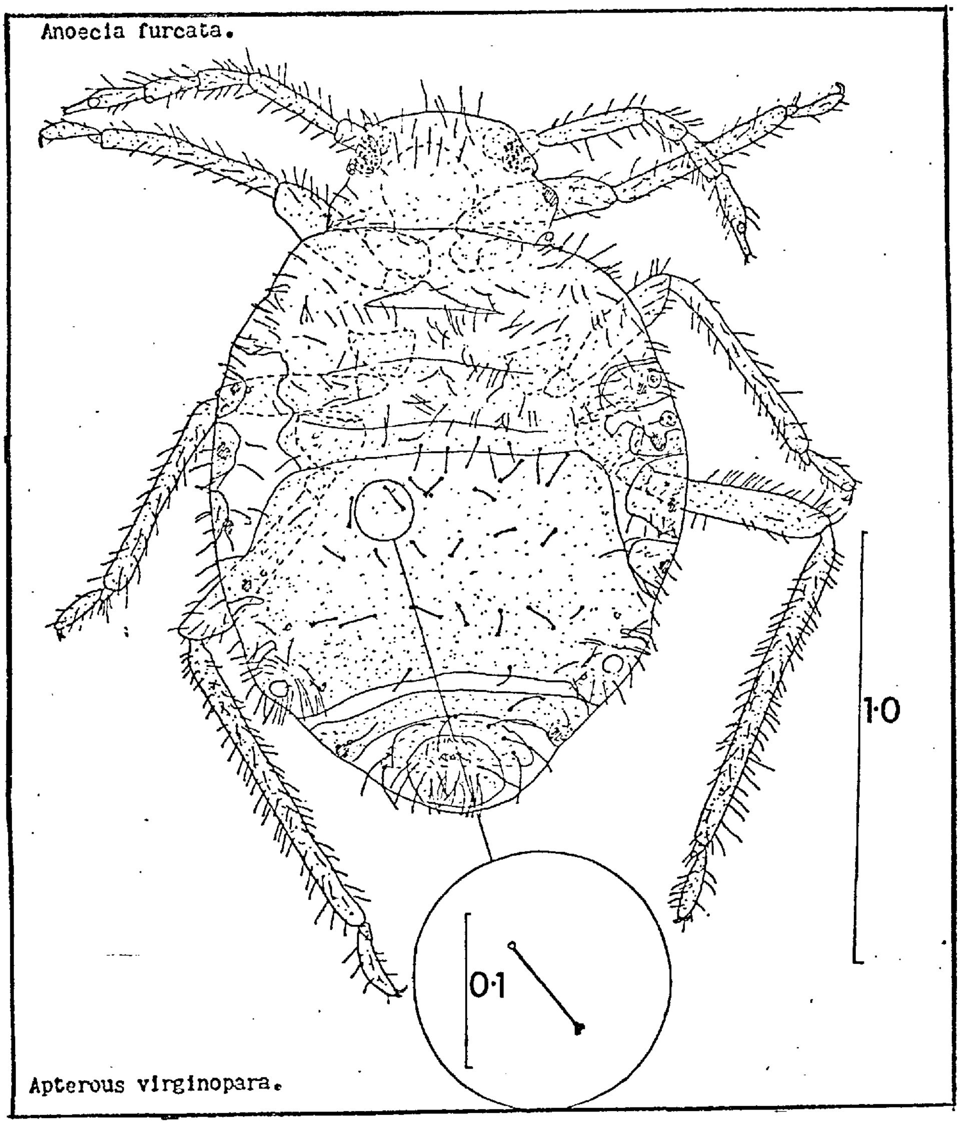
Apterous virginopara- second instar.

FIG 22



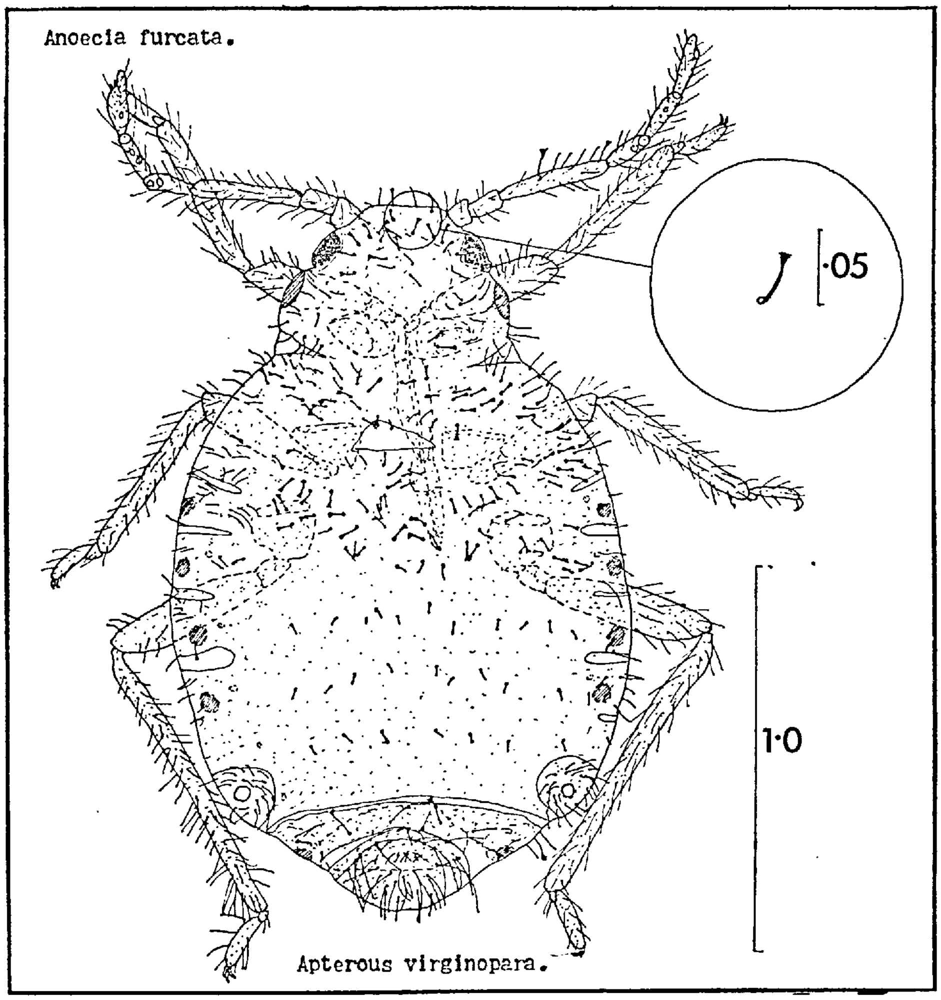
Acute-haired form.

FIG 23



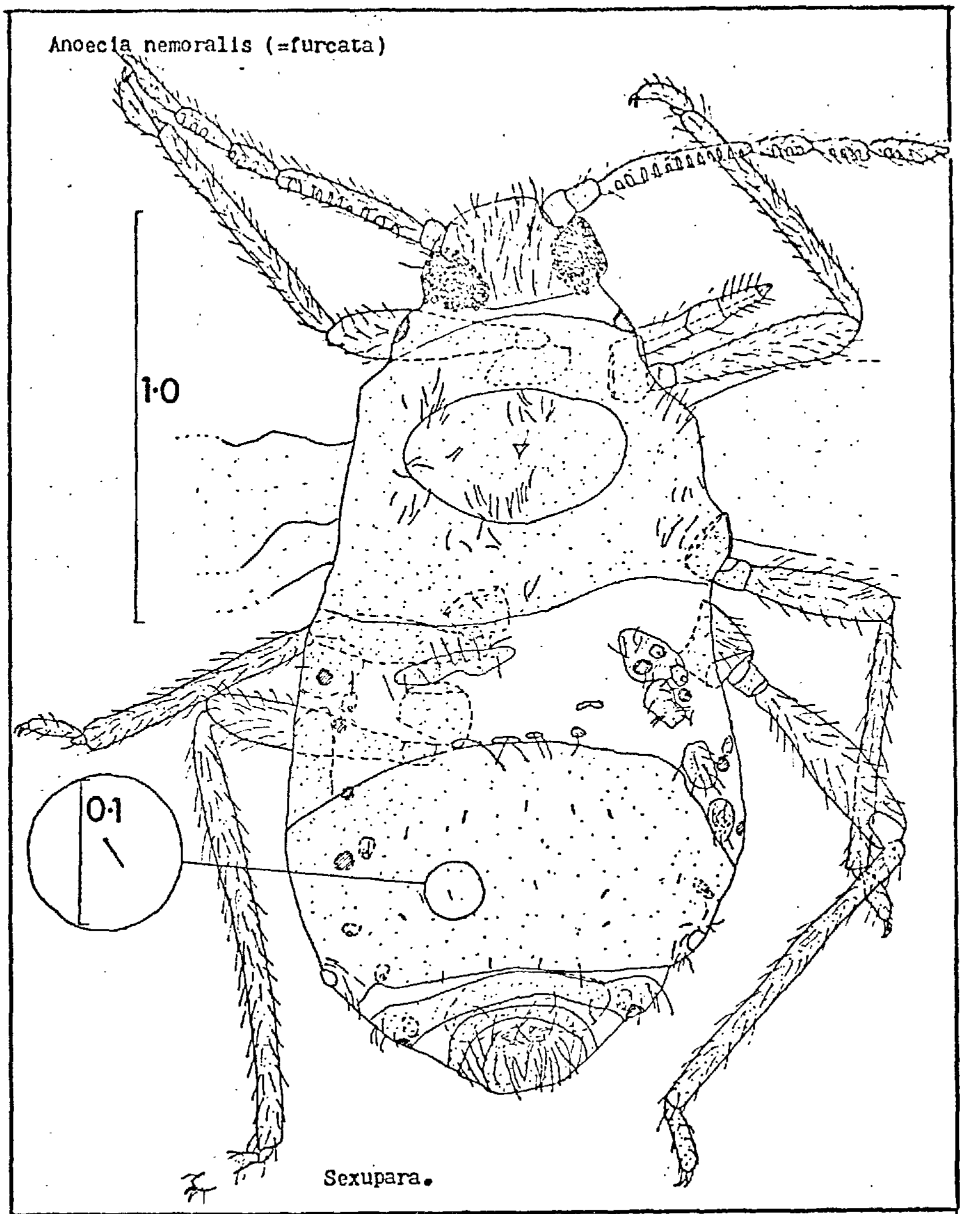
Intermediate form.

FIG 24



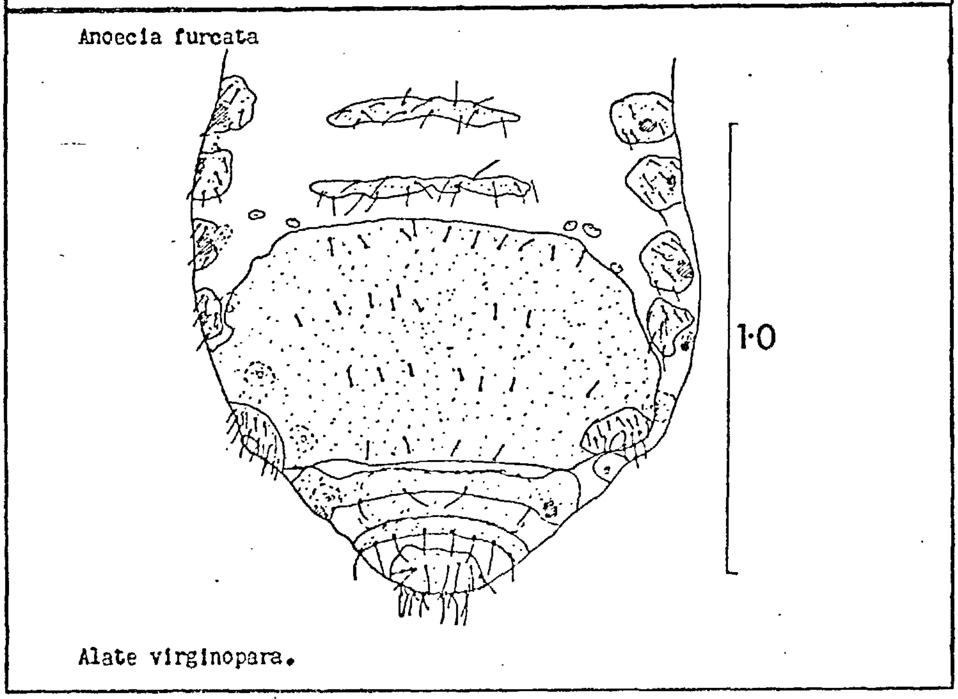
Spatulate-haired form.

FIG. 25.



Anoecia nemoralis (=furcata)

Sexupara.



Anoecia furcata

Alate virginopara.

FIG 26

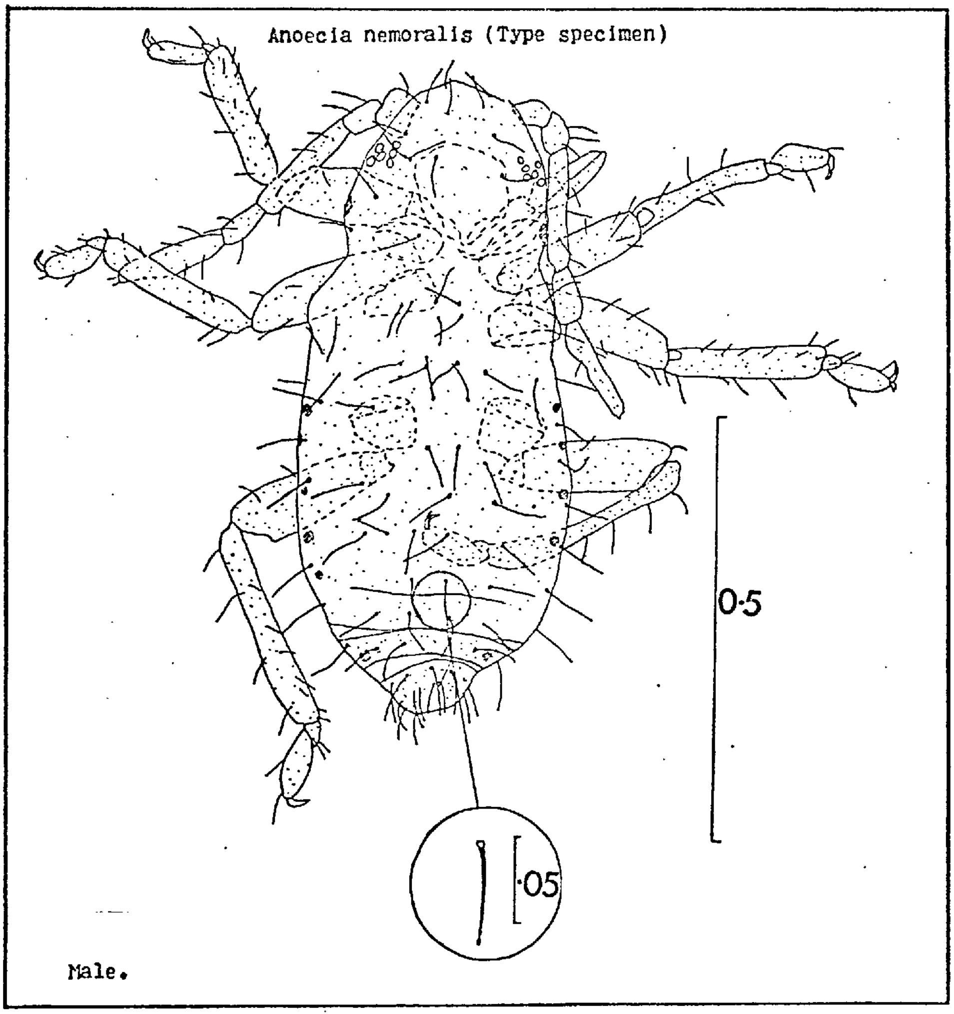


FIG 27

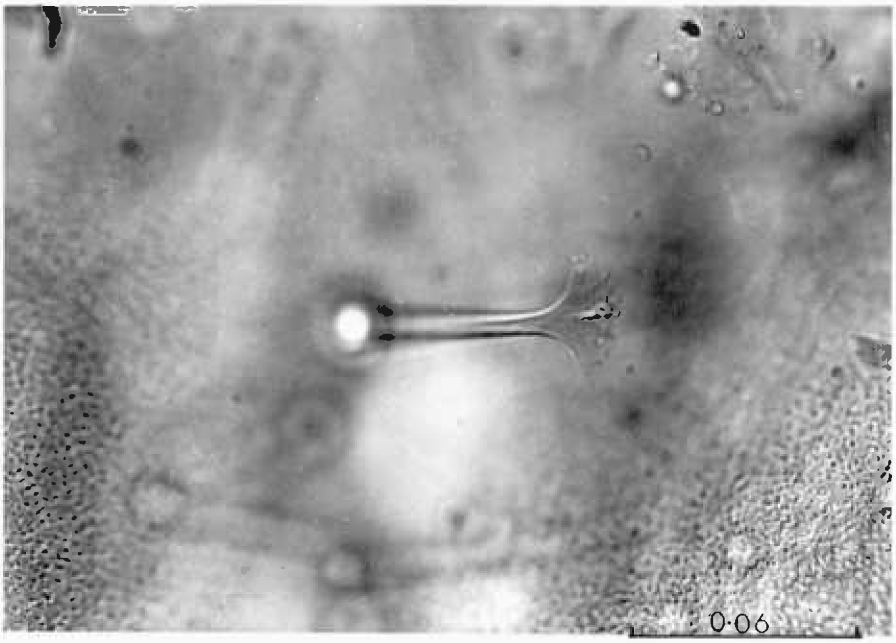


Plate 17. Anoecia furcata. Apterous virginopara, dorsal abdominal spatulate hair.

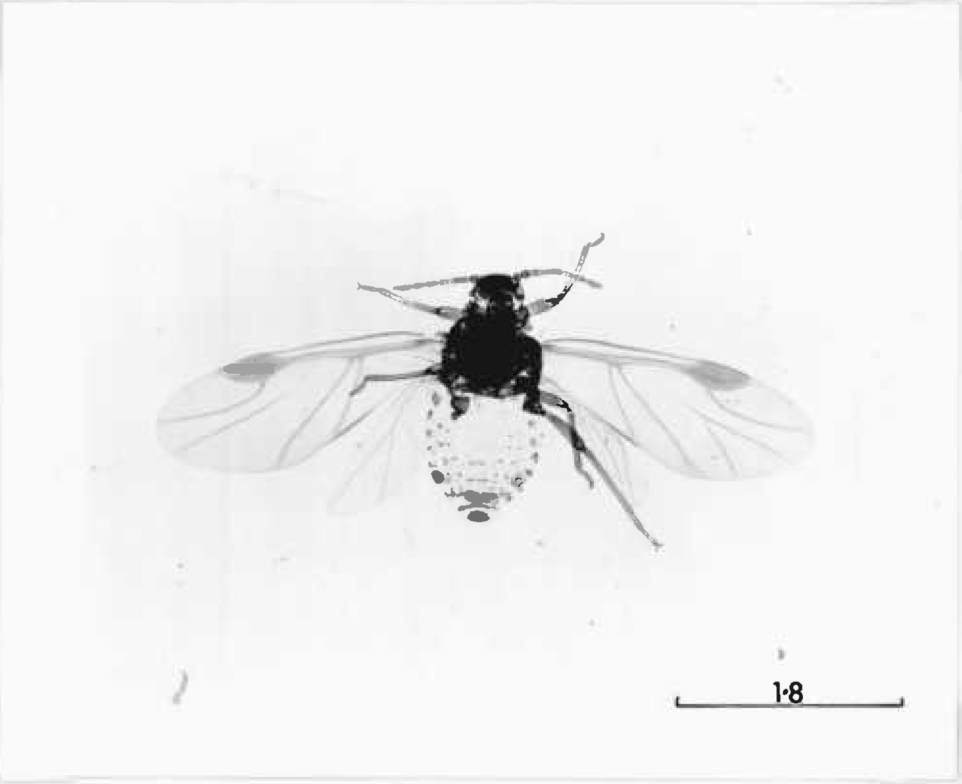


Plate 18. Anoecia vagans. Alate fundatrigenia.

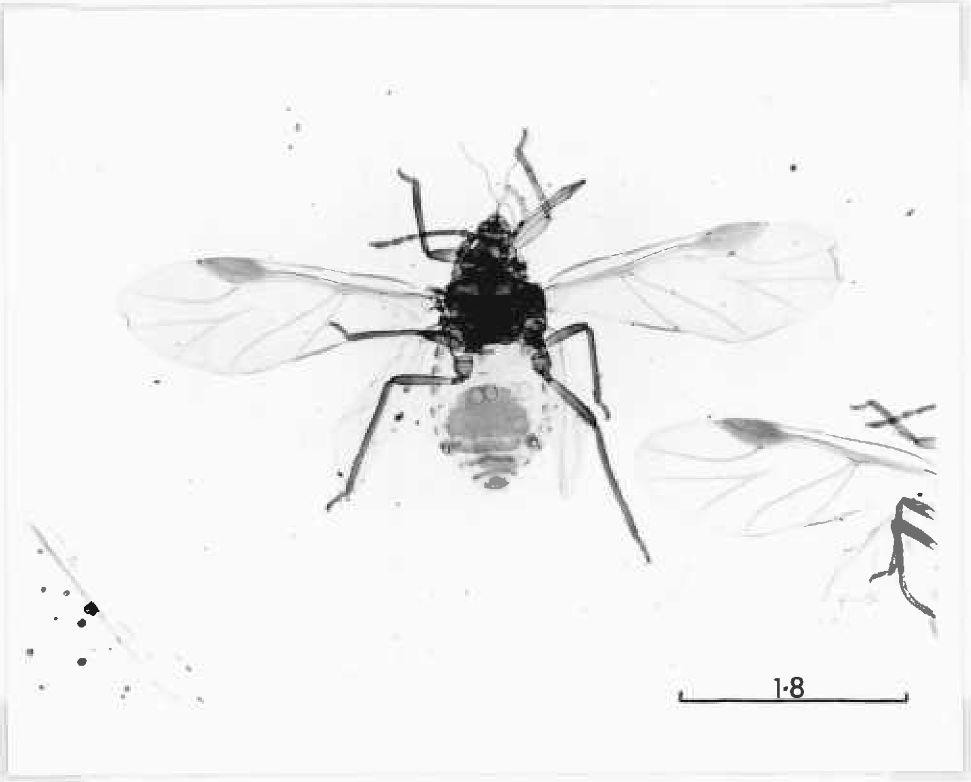


Plate 19. Anoecia vagans. Alate virginopara.

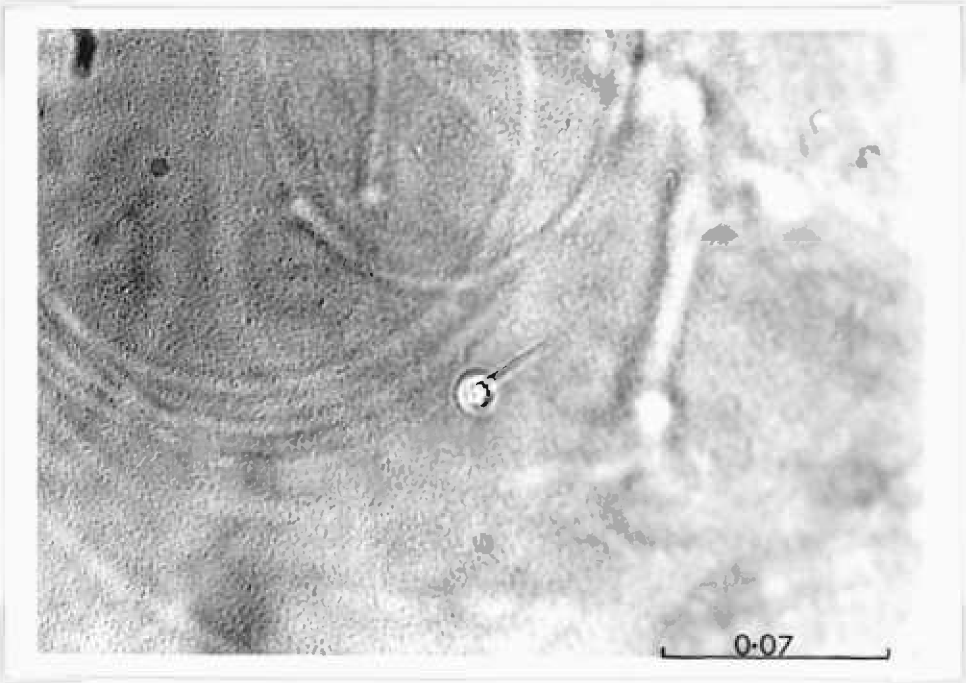
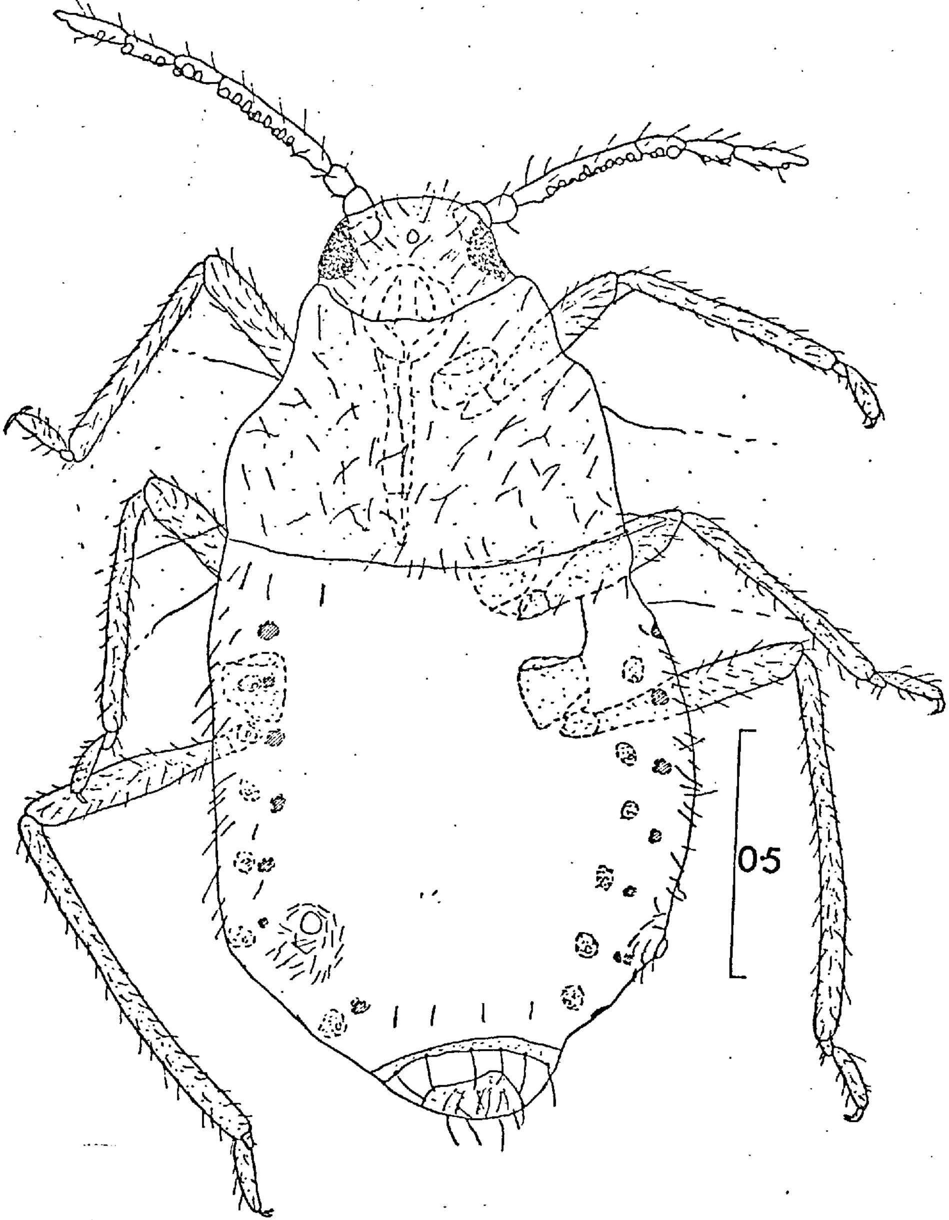


Plate 20. Anoecia vagans. Apterous virginopara,
dorsal abdominal spatulate hair.

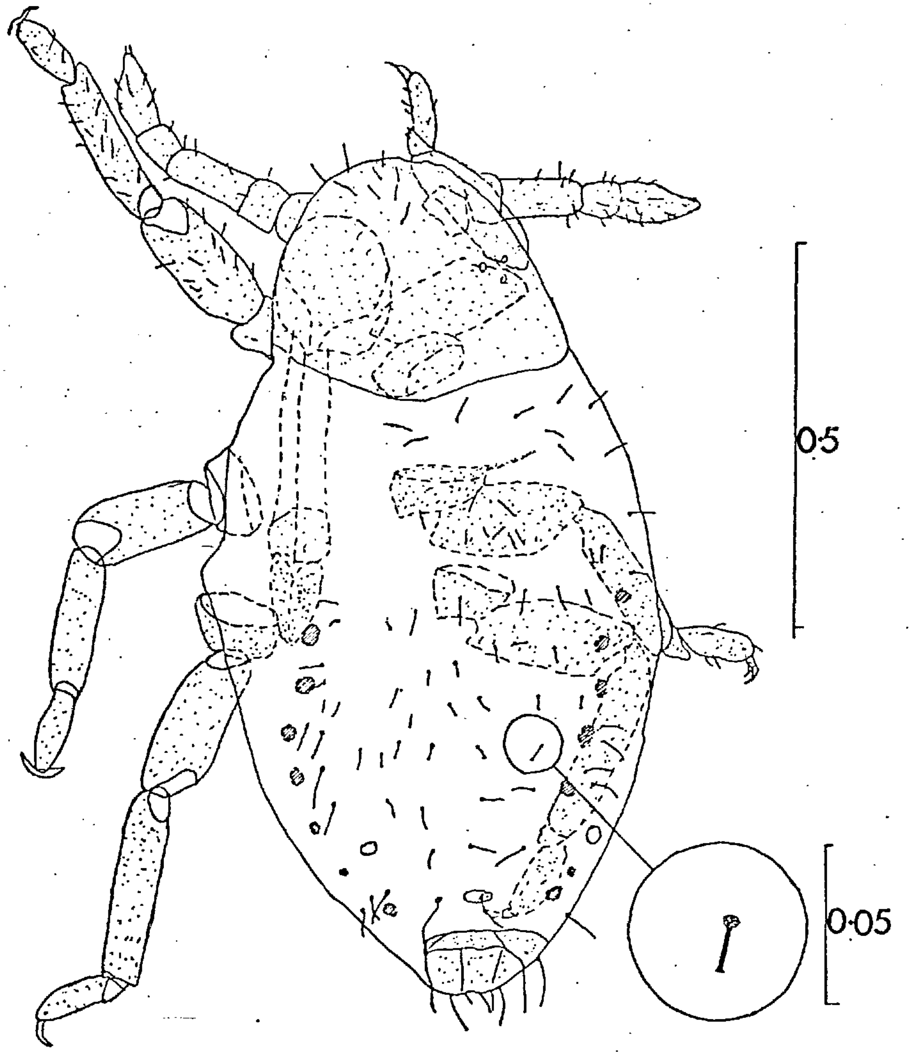
Anoecia vagans.



Alate fundatrigenia.

FIG 28

Anoecia vagans.



Fundatrigenia nymph.

FIG 29

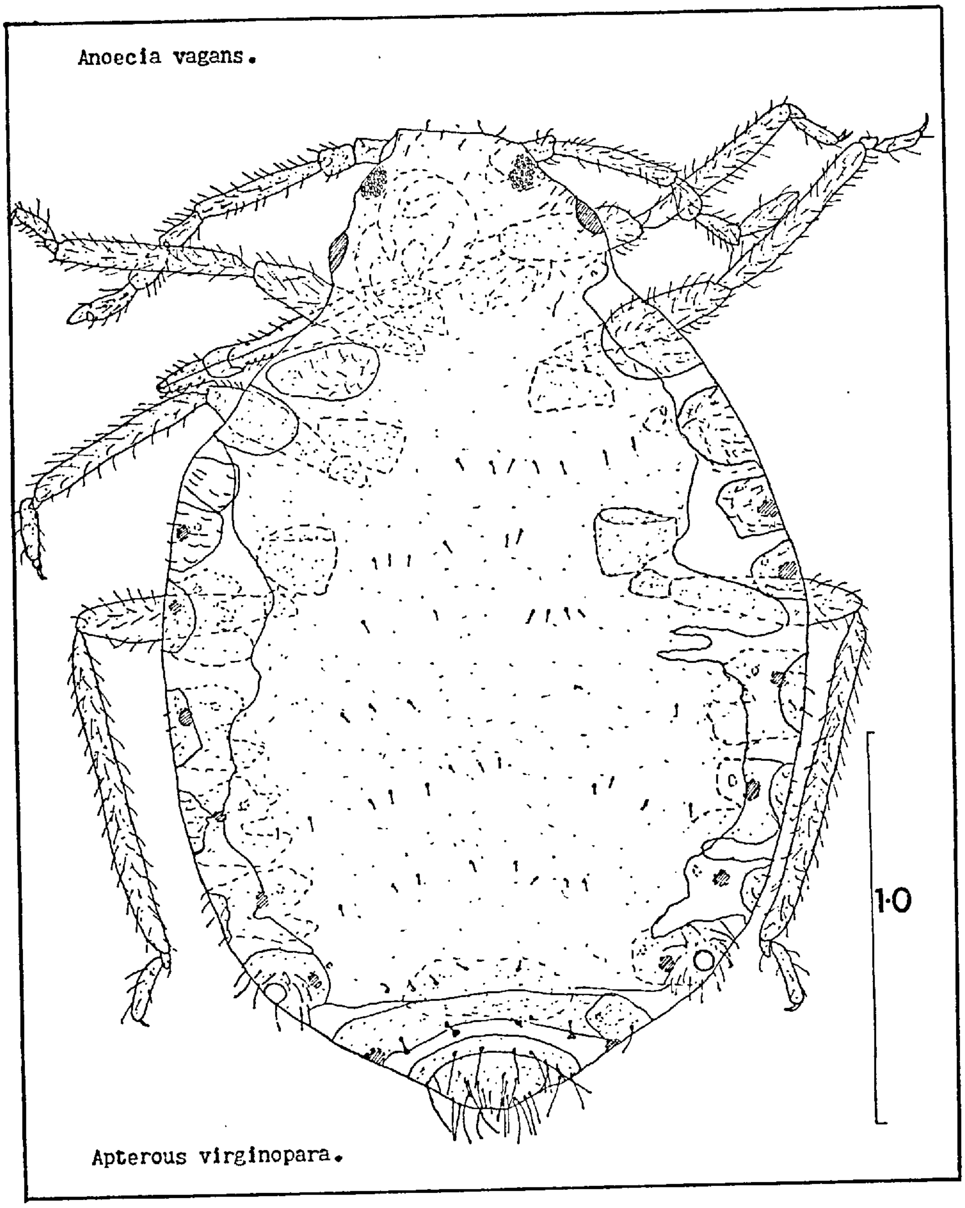


FIG. 30.

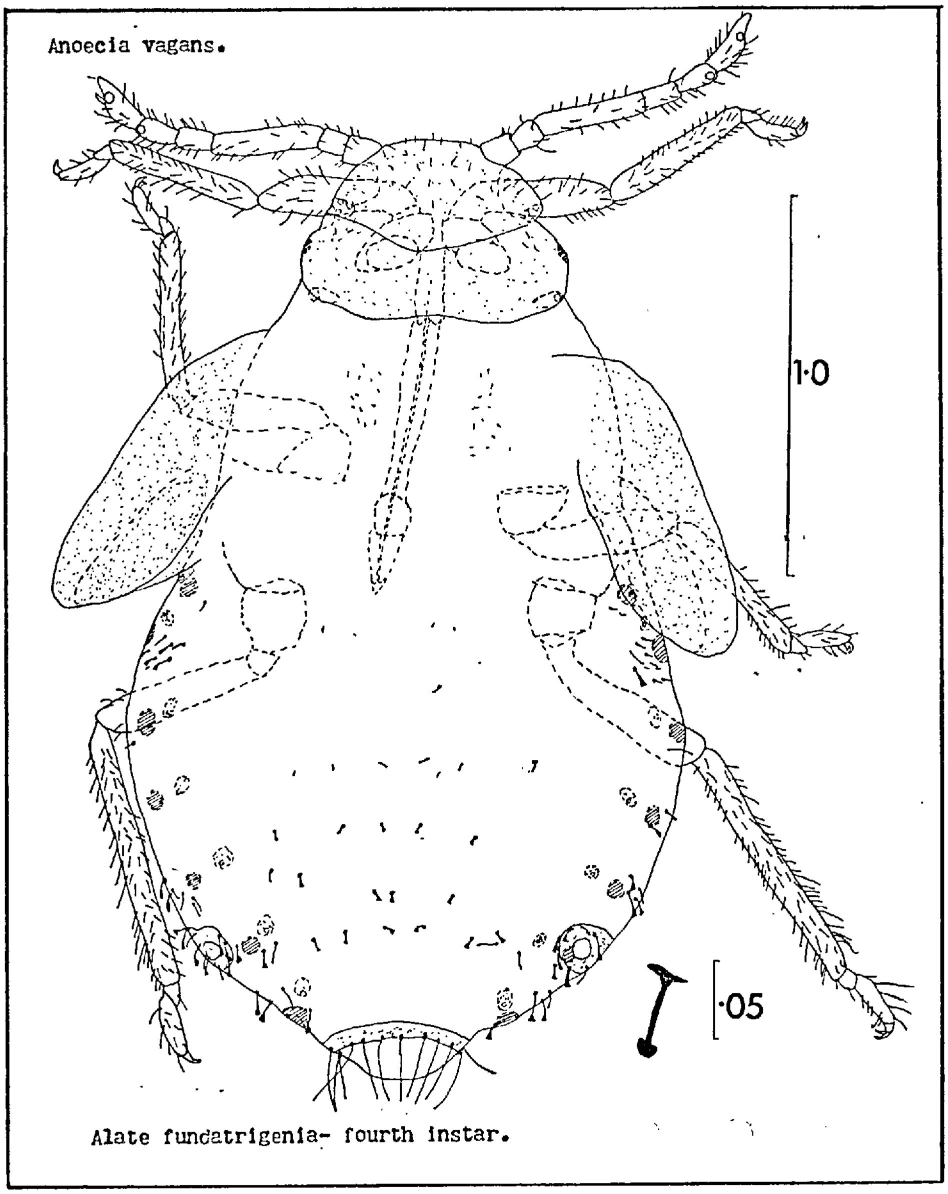
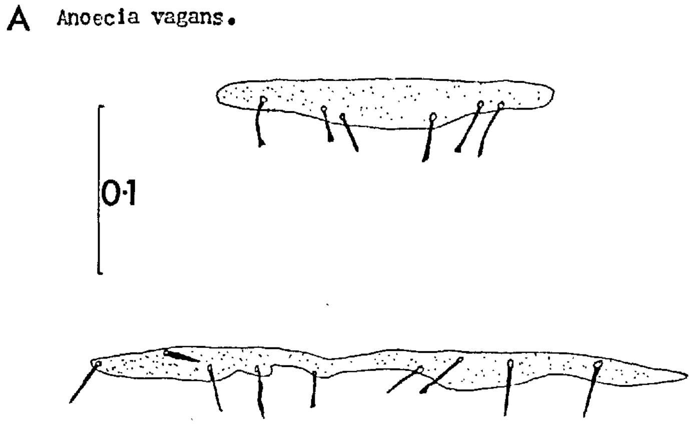
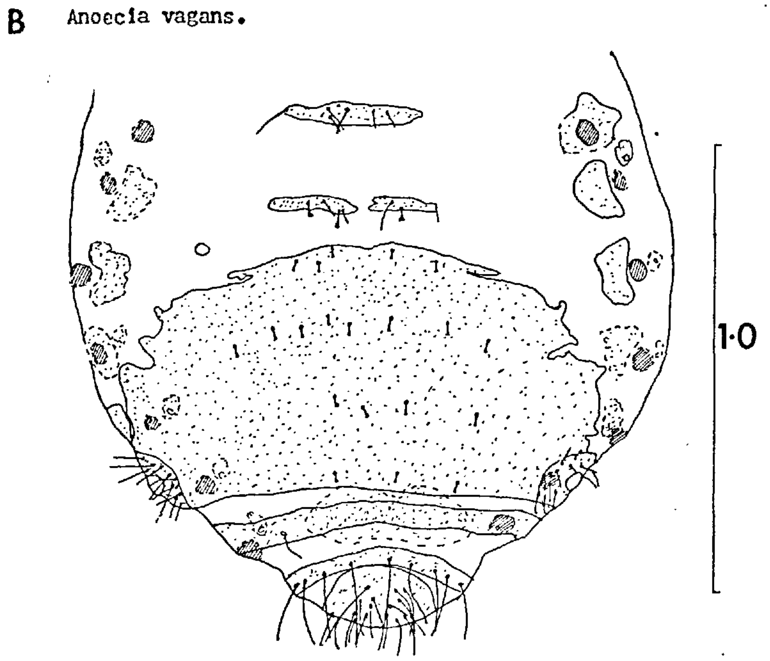


FIG. 31.



Sexupara. Abdominal segments 1 and 2. Dorsal view.



Sexupara. Abdomen. Dorsal view.

FIG. 32.

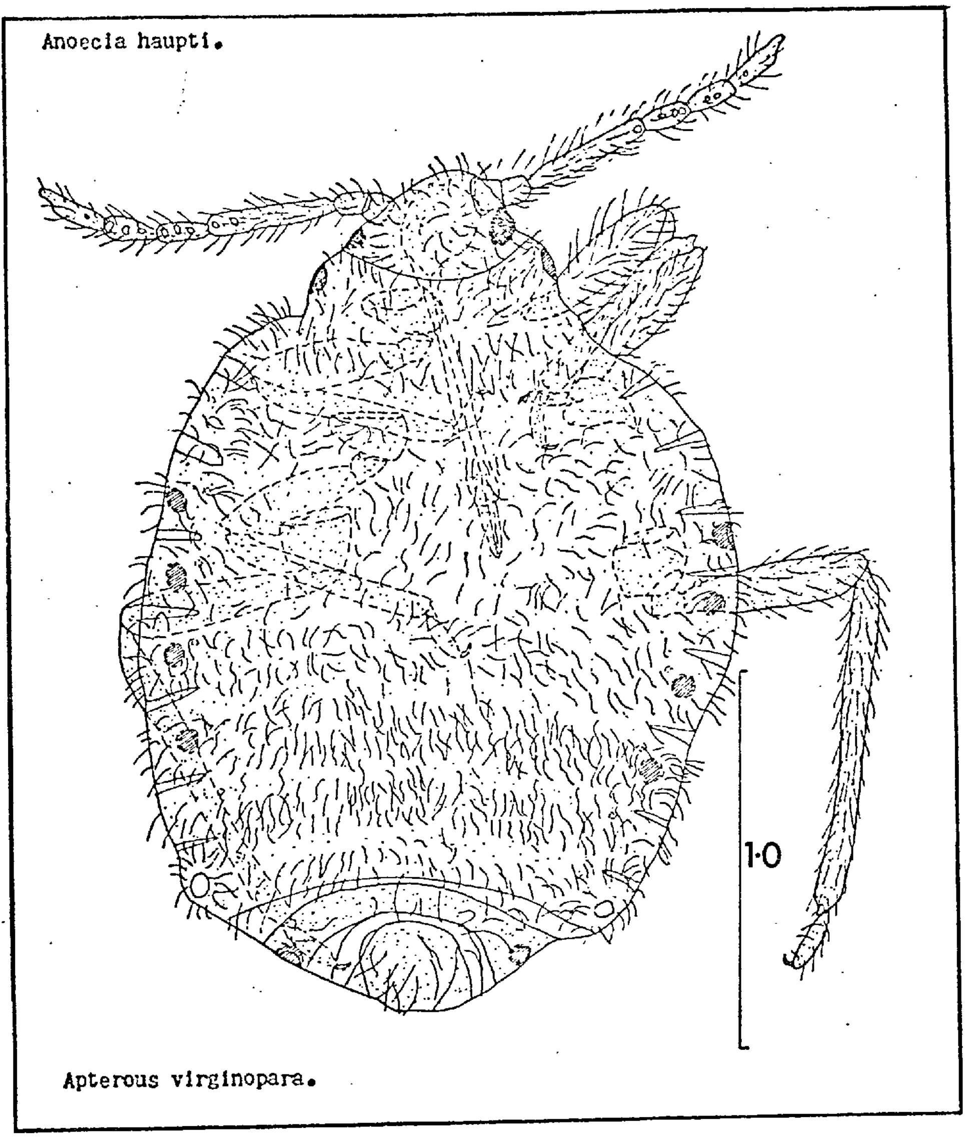


FIG 33

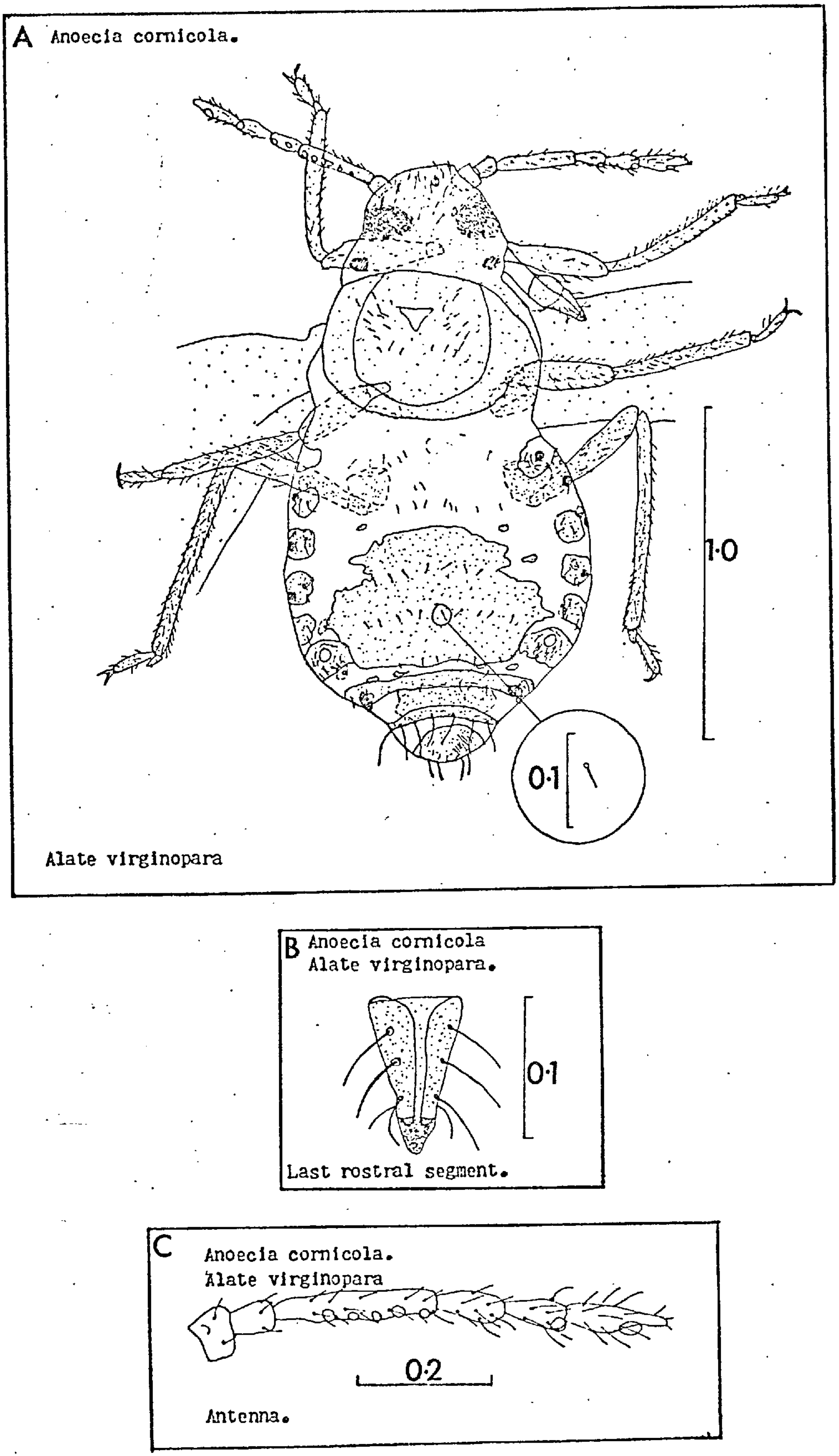

A
Anoecia cornicola.
1·0
0·1
Alate virginopara
B
Anoecia cornicola
Alate virginopara.
0·1
Last rostral segment.
C
Anoecia cornicola.
Alate virginopara
0·2
Antenna.

FIG 34

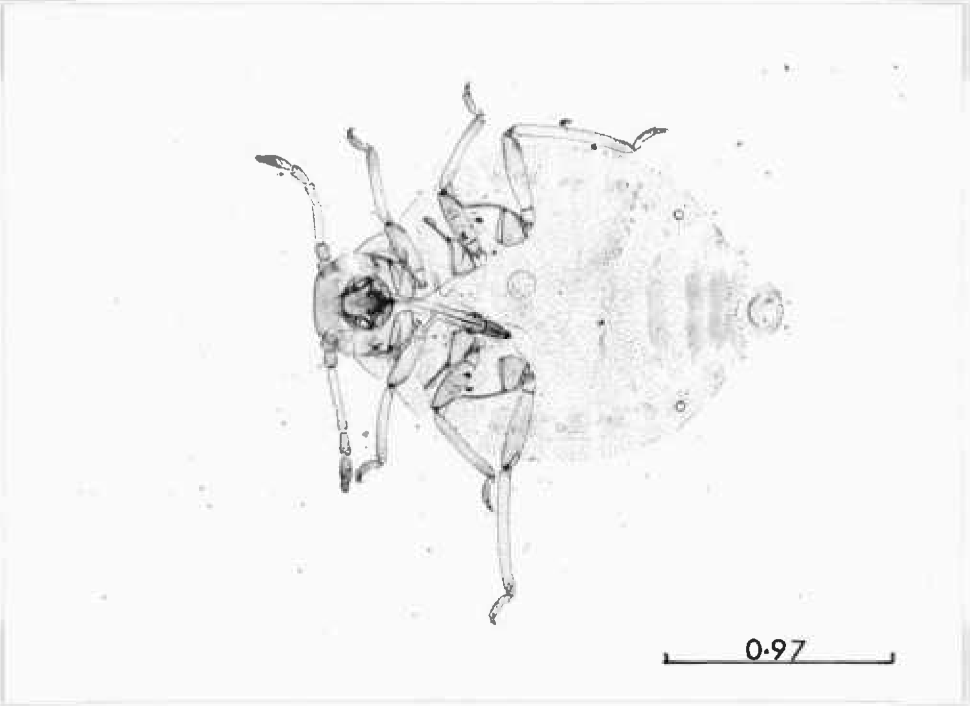


Plate 21. Anoecia setariae. Apterous virginopara.

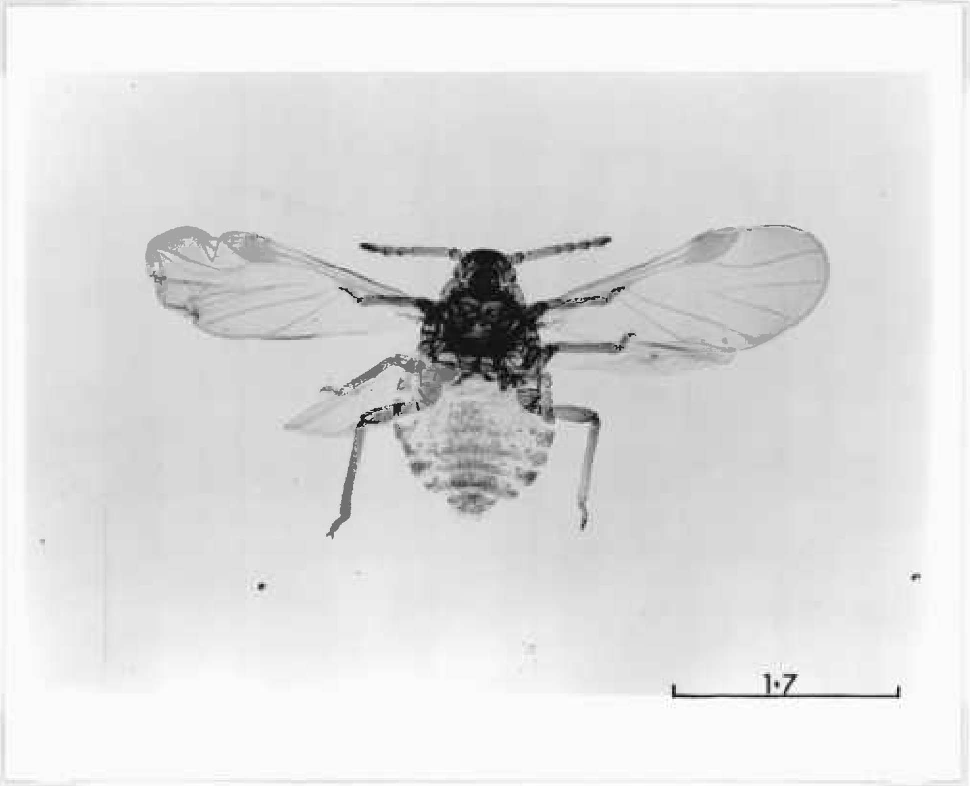


Plate 22. Anoecia oenotherae. Alate virginopara.

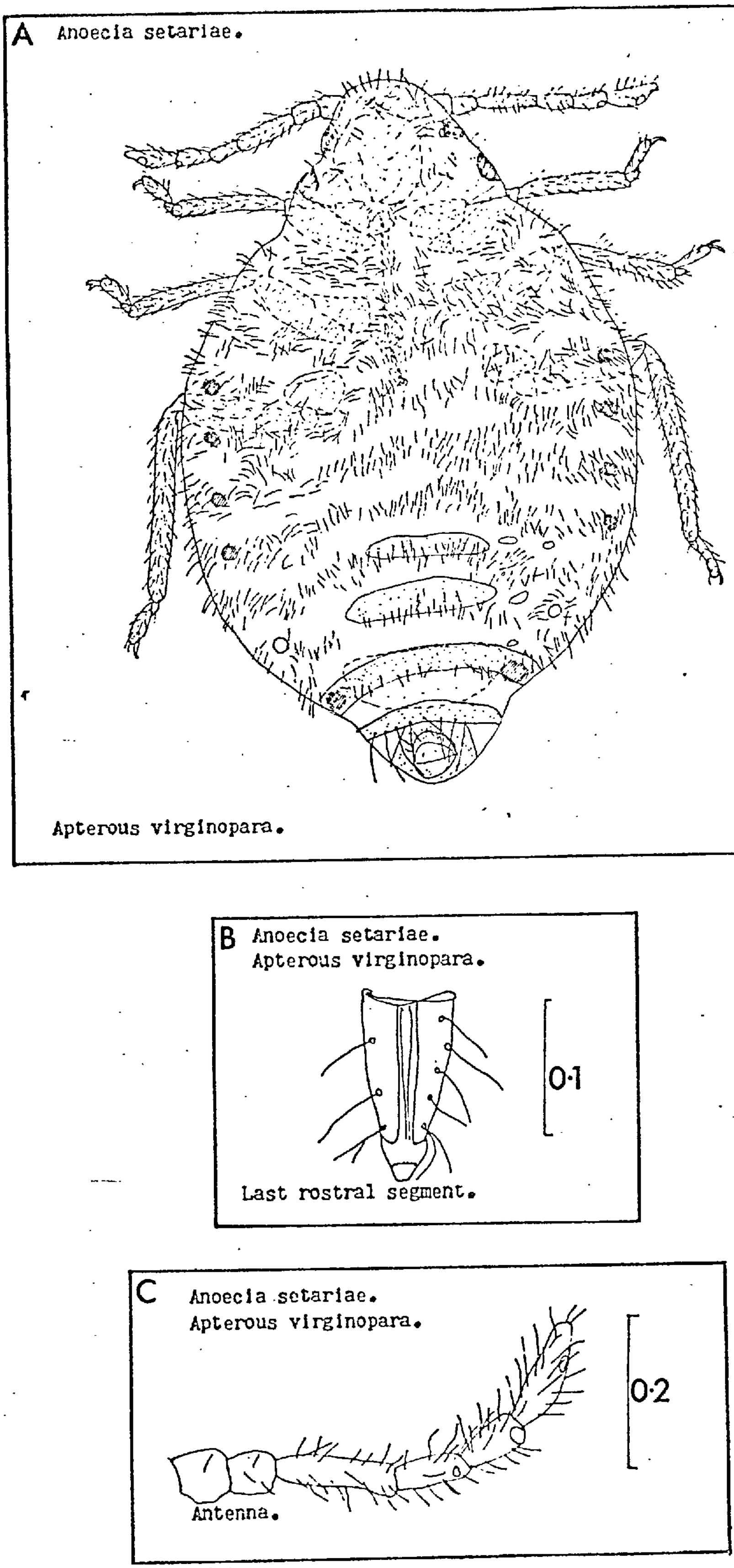
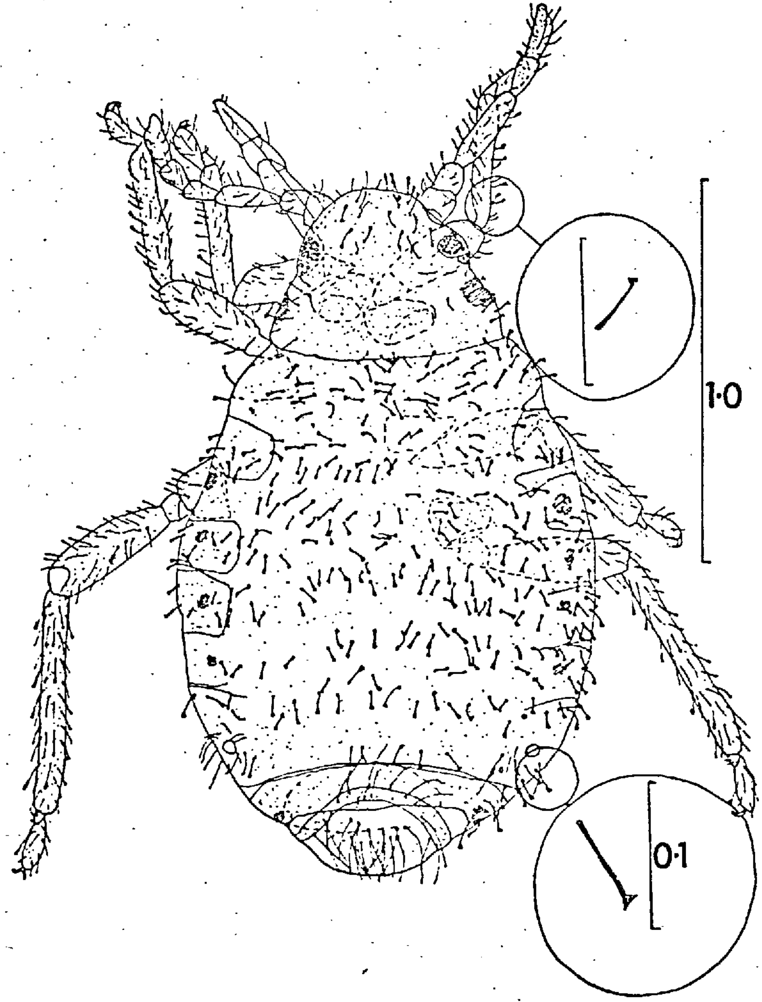

A
Anoecia setariae.
1·0
Apterous virginopara.
B
Anoecia setariae.
Apterous virginopara.
0·1
Last rostral segment.
C
Anoecia setariae.
Apterous virginopara.
0·2
Antenna.

FIG 35

Anoecia graminis (=furcata).



Apterous virginopara.

FIG 36

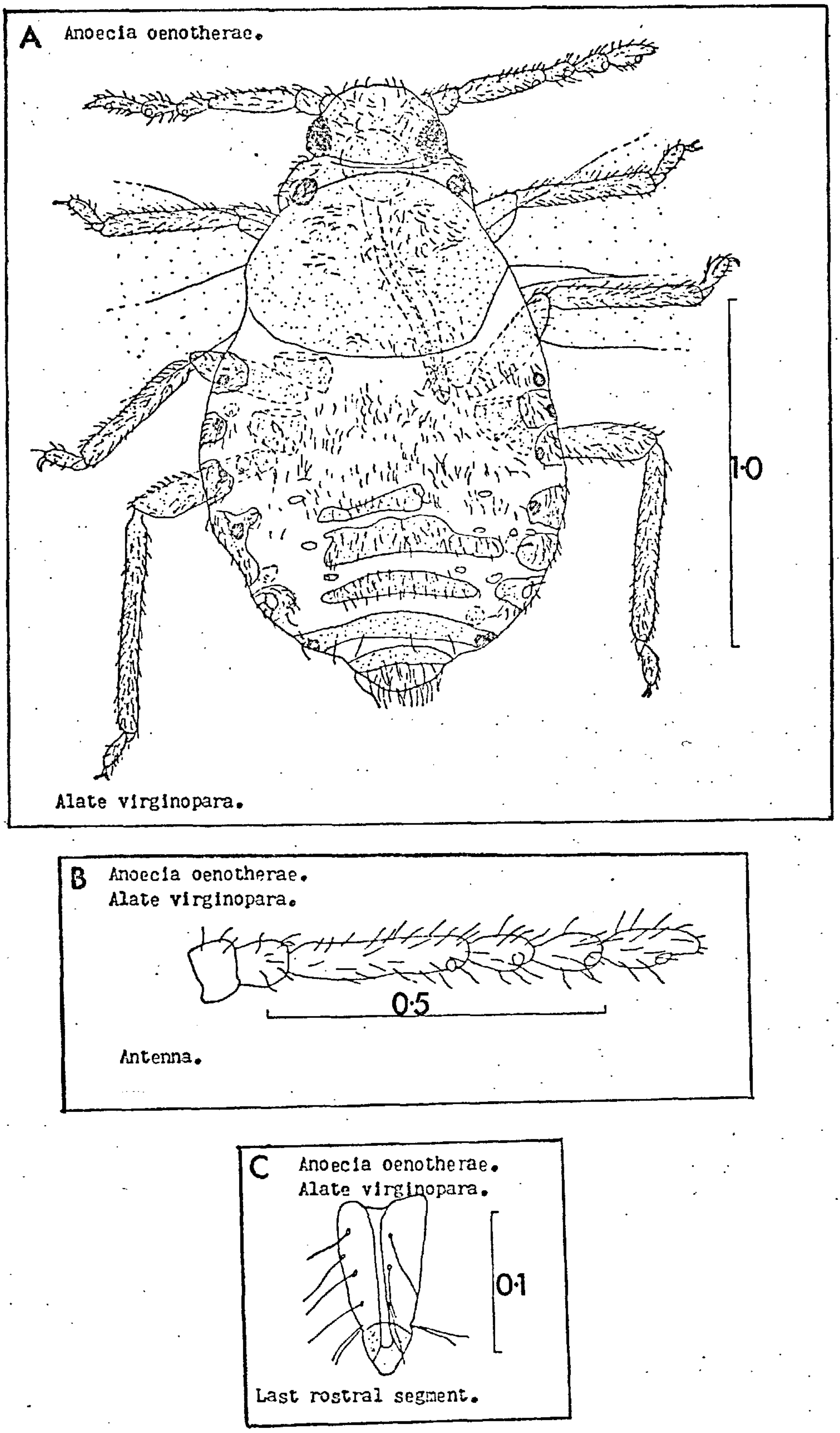

A
Anoecia oenotherae.
1·0
Alate virginopara.
B
Anoecia oenotherae.
Alate virginopara.
0·5
Antenna.
C
Anoecia oenotherae.
Alate virginopara.
0·1
Last rostral segment.

FIG 37

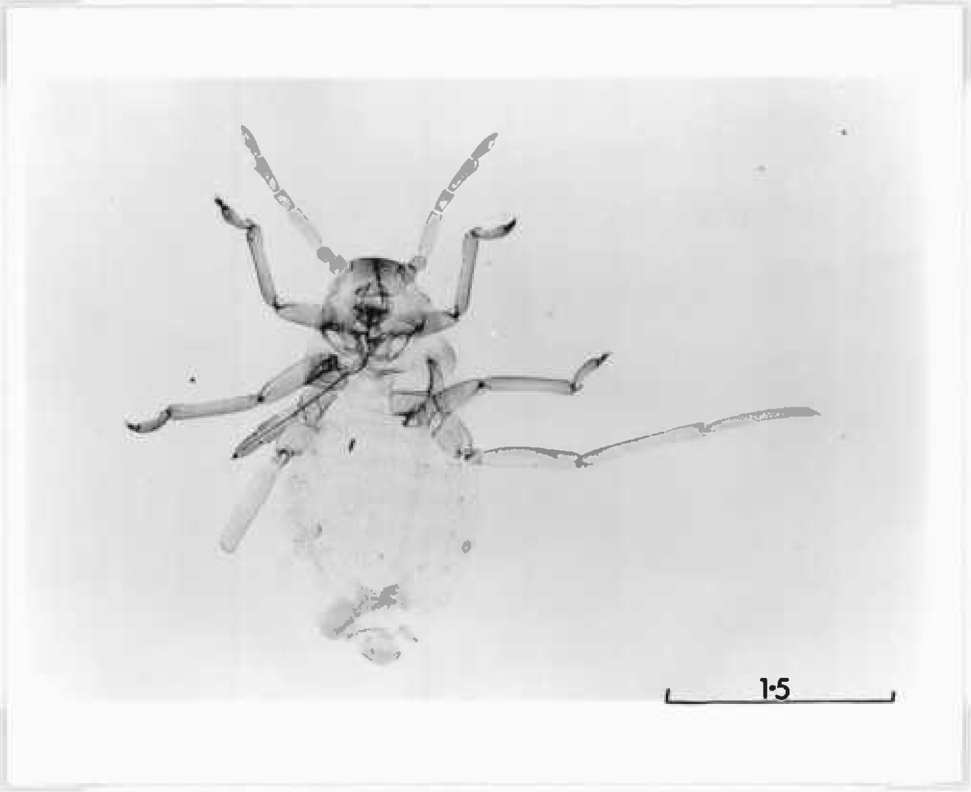


Plate 23. Neotrama caudata. Apterous virginopara.

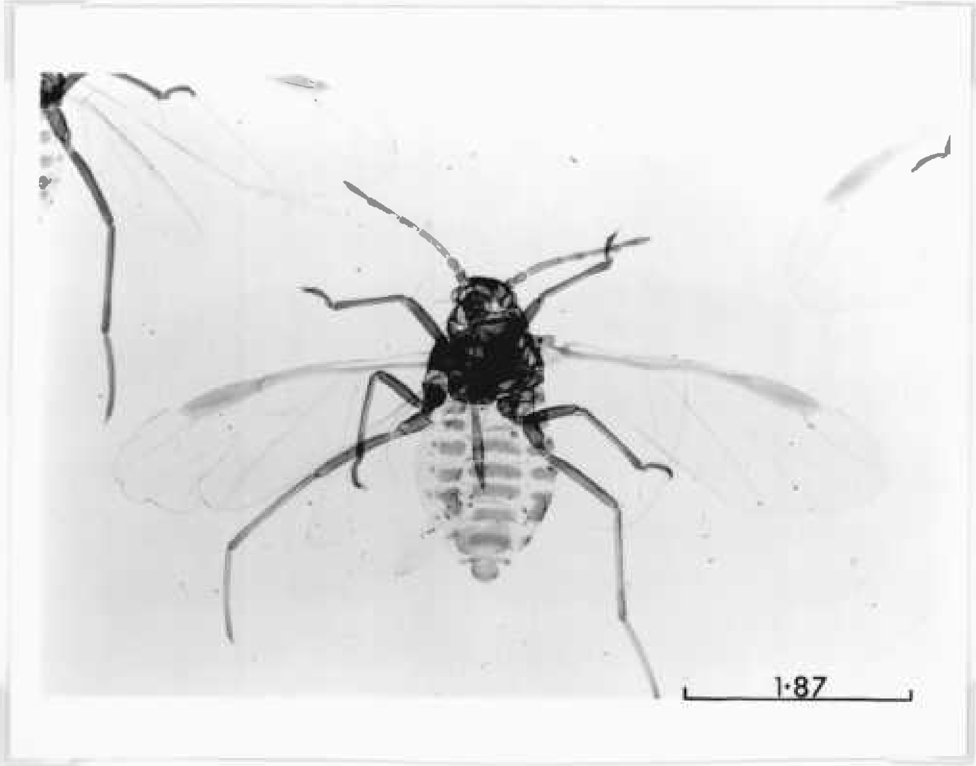


Plate 24. Neotrama caudata. Alate virginopara.

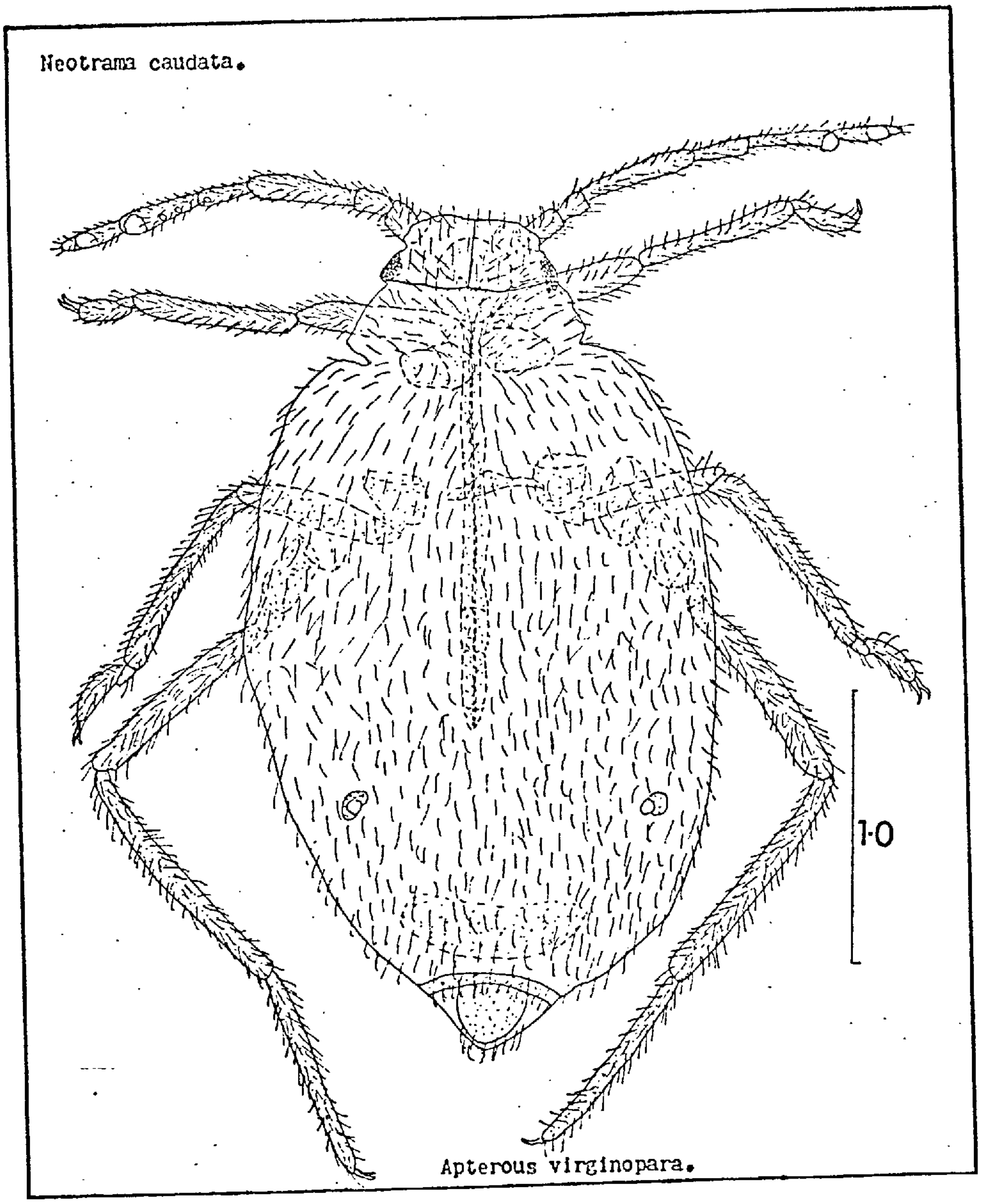


FIG 38

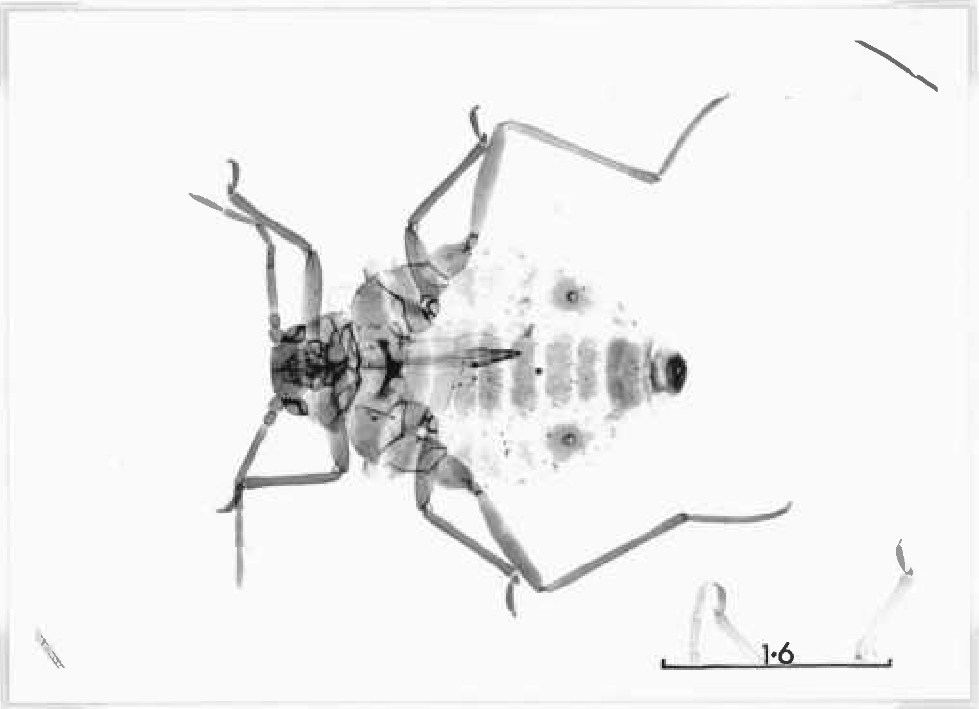


Plate 25. Protrama flavescens. Apterous virginopara.

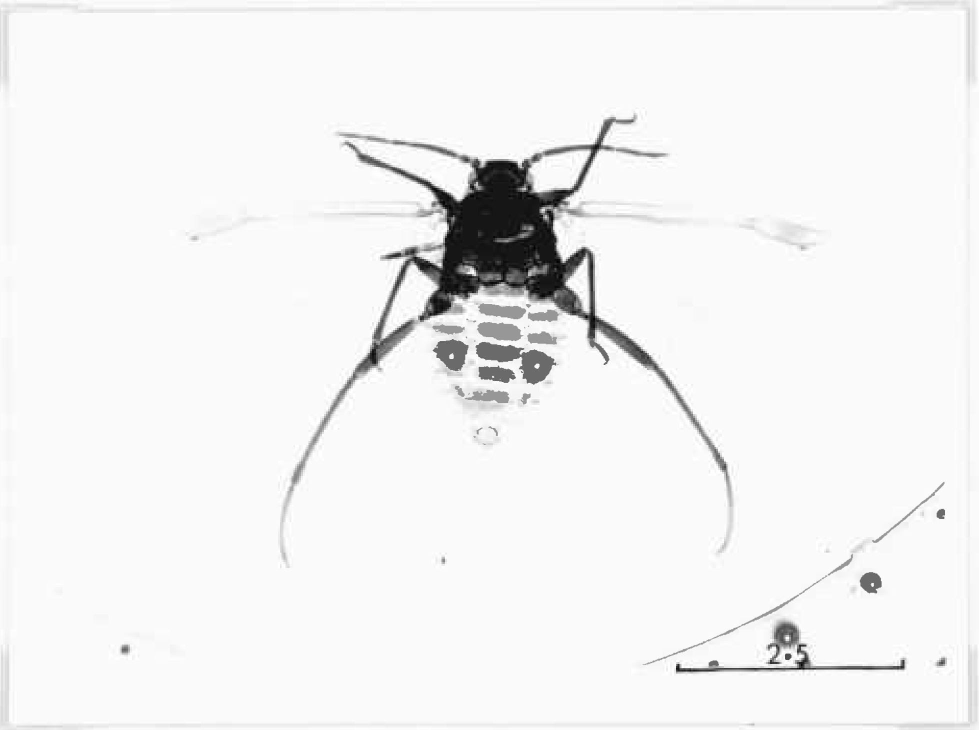


Plate 26. Protrama flavescens. Alate virginopara.

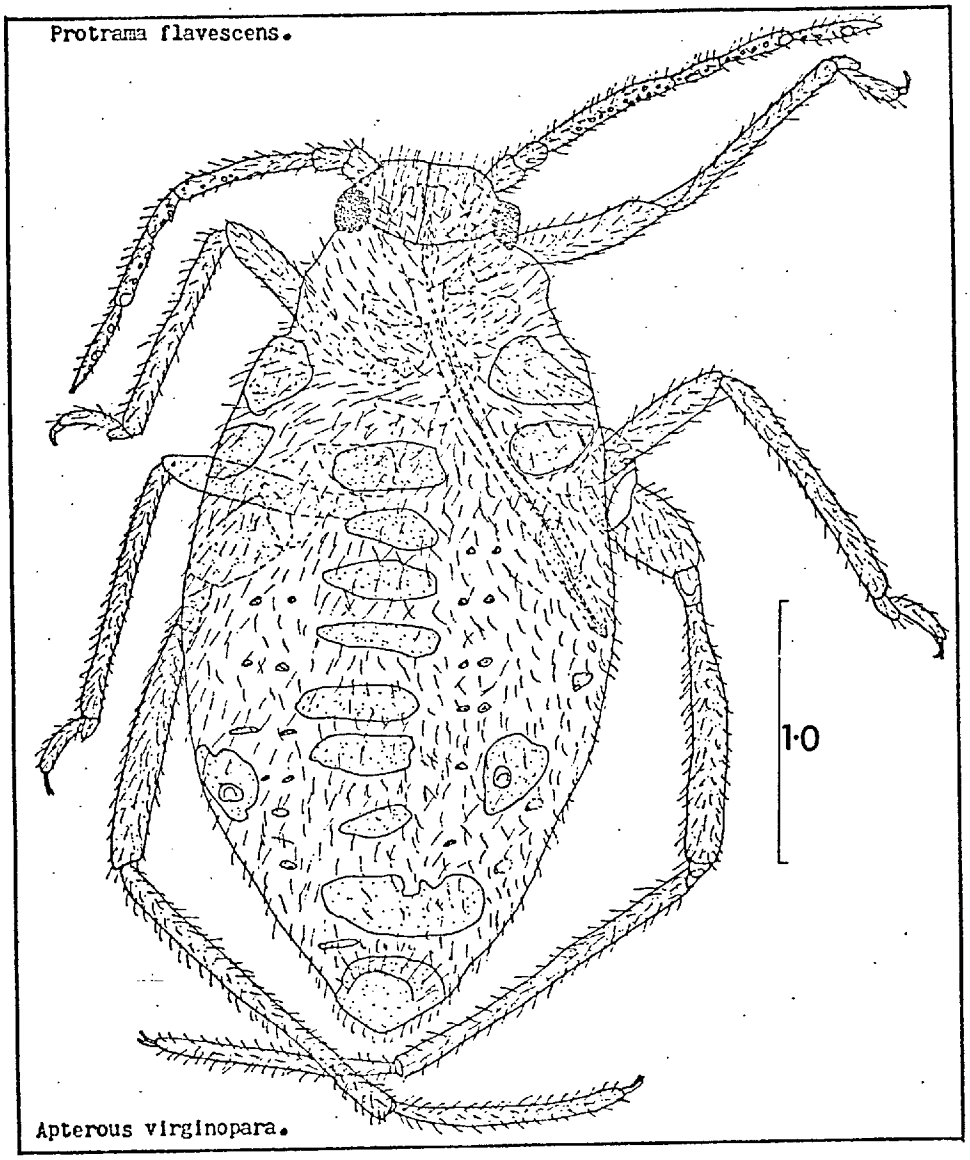


FIG 39

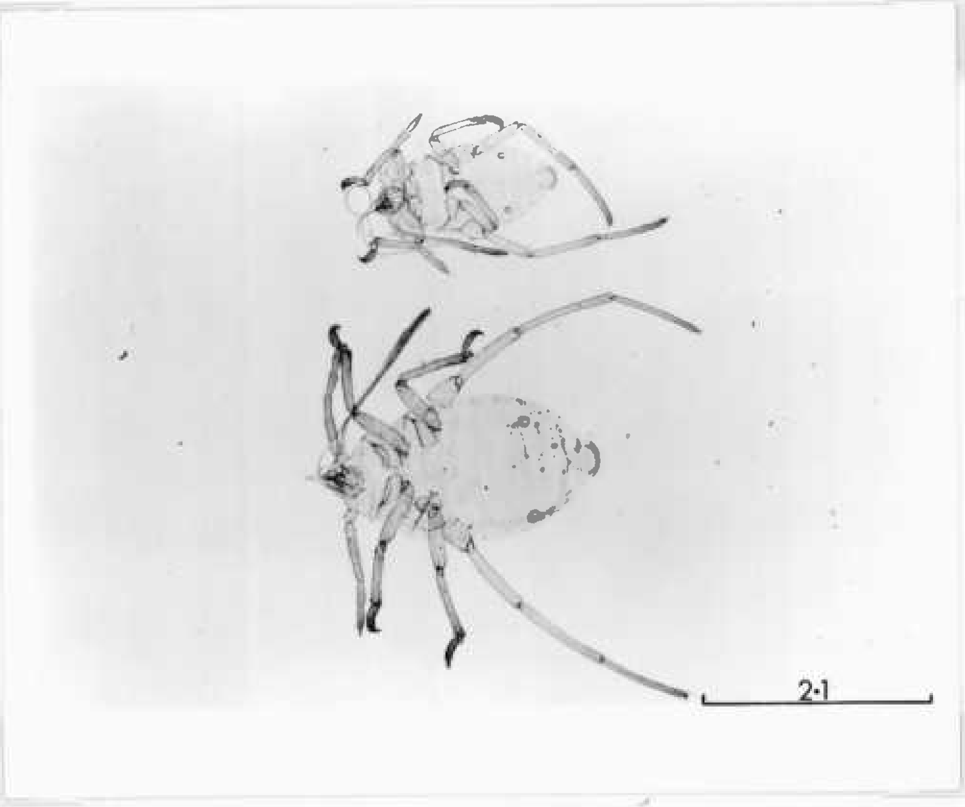


Plate 27. Protrama radicis. Apterous virginopara.

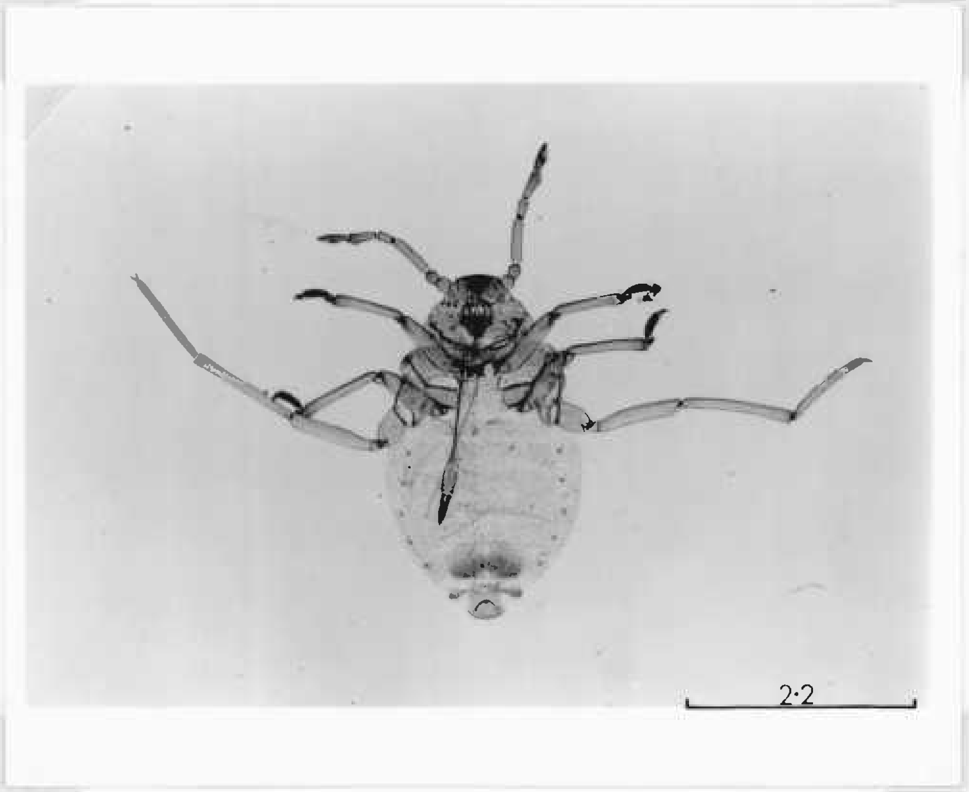
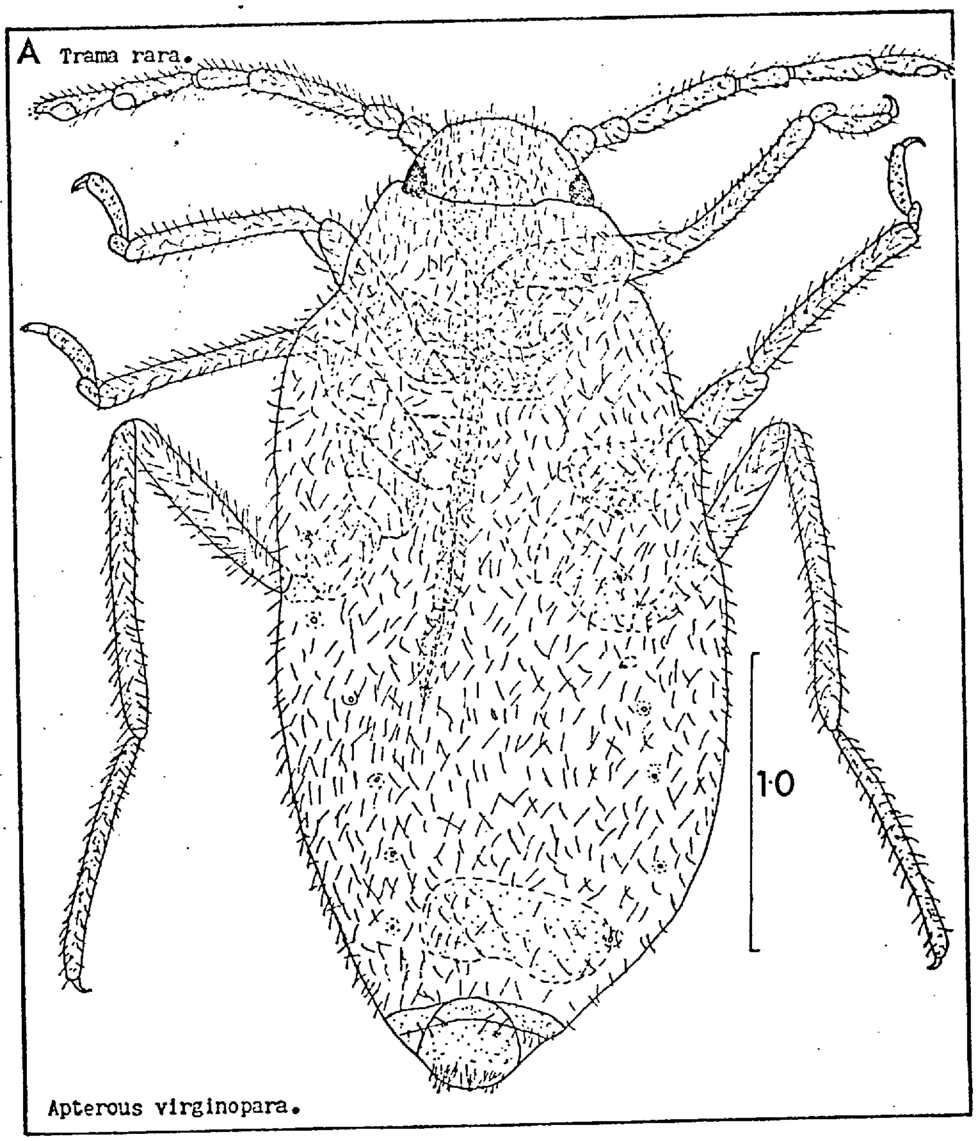
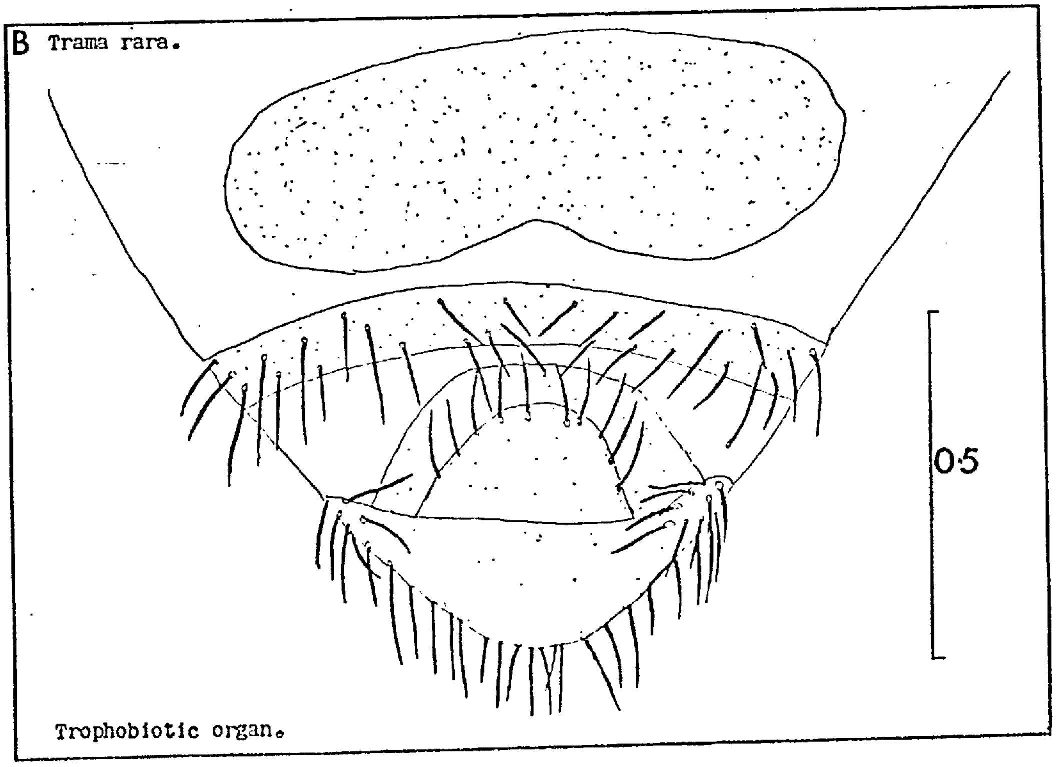


Plate 28. Trama rara. Apterous virginopara.



Trama rara.

Apterous virginopara.

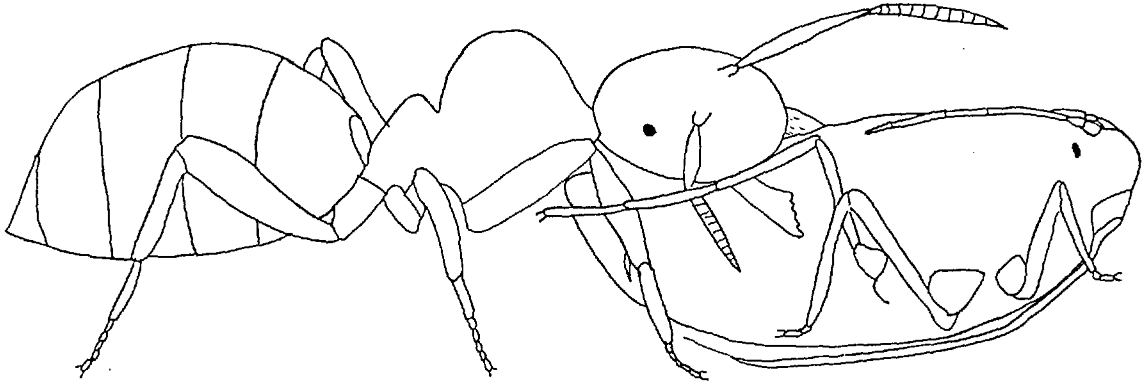


Trama rara.

Trophobiotic organ.

FIG 40

FIG. 41.



Lasius flavus carrying Trama rara.

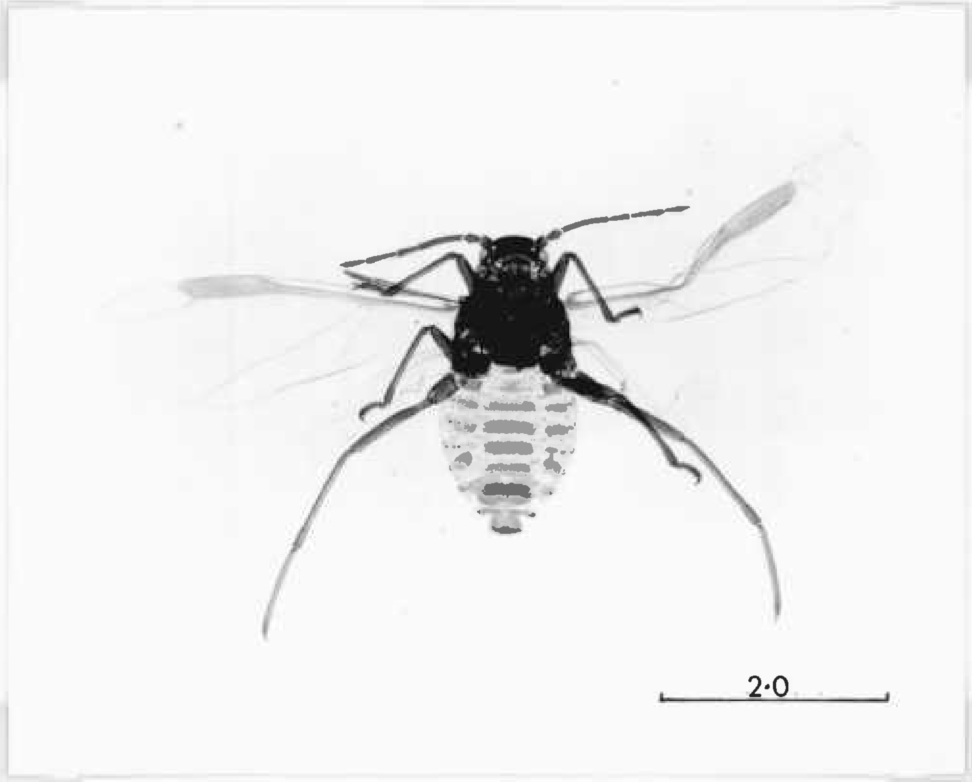
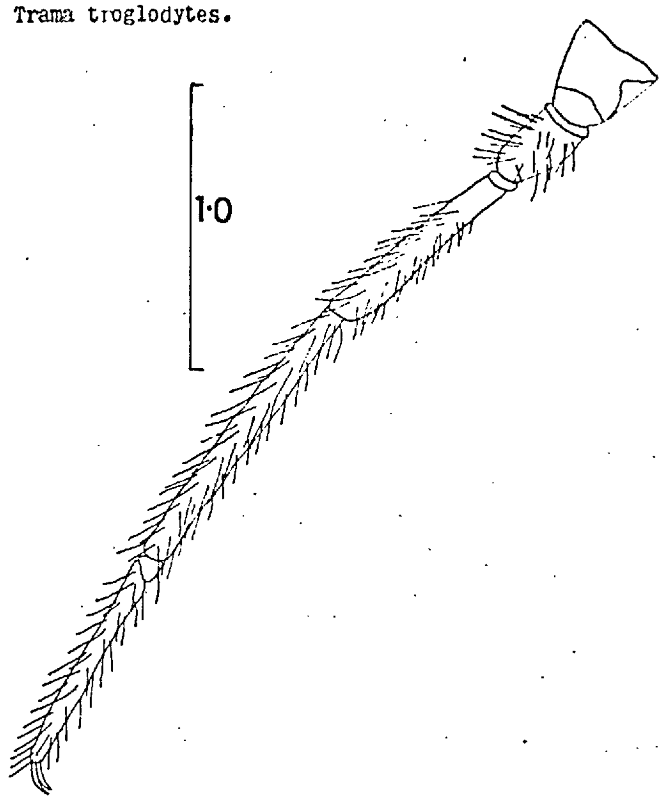


Plate 29. Trama rara. Alate virginopara.

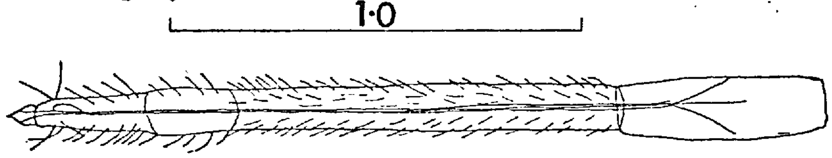
Plate 30. Trama troglodytes. Alate virginopara.

A Trama troglodytes.



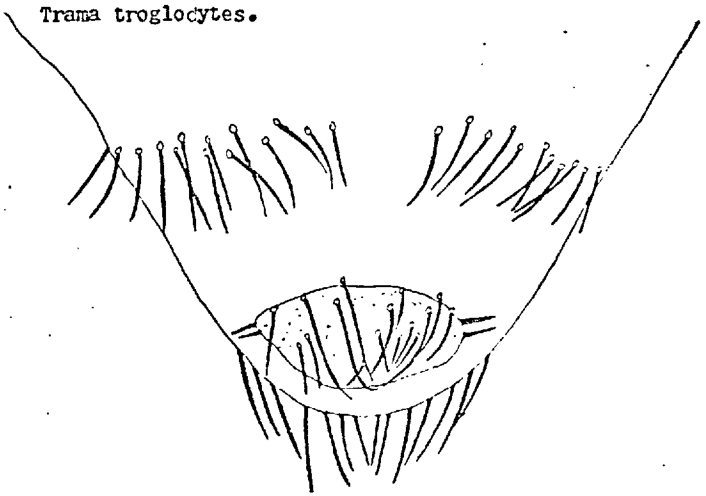
Apterous virginopara. - Hind Leg.

B Trama troglodytes.



Apterous virginopara.- Rostrum.

Trama troglodytes.



C Apterous virginopara.- Trophobiotic organ.

FIG 42

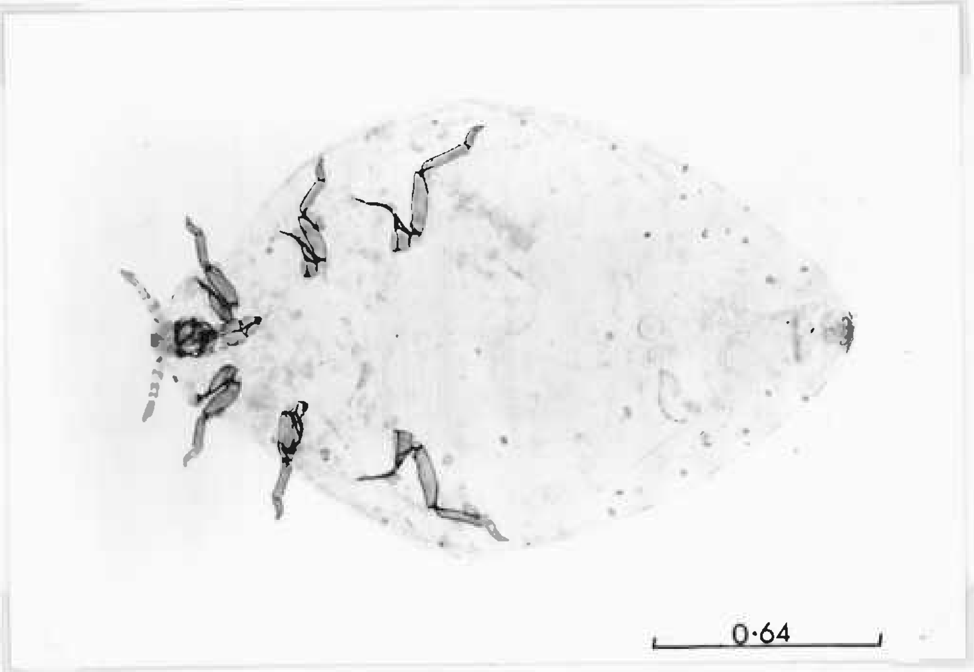


Plate 31. Aploneura lentisci. Apterous virginopara.

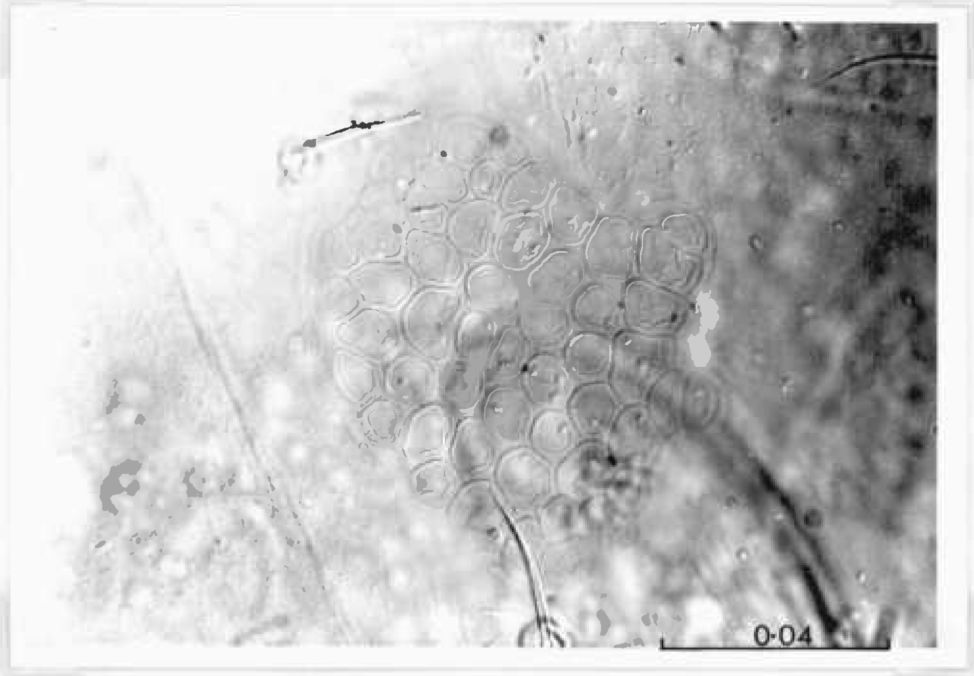


Plate 32. Aploneura lentisci. Wax gland.

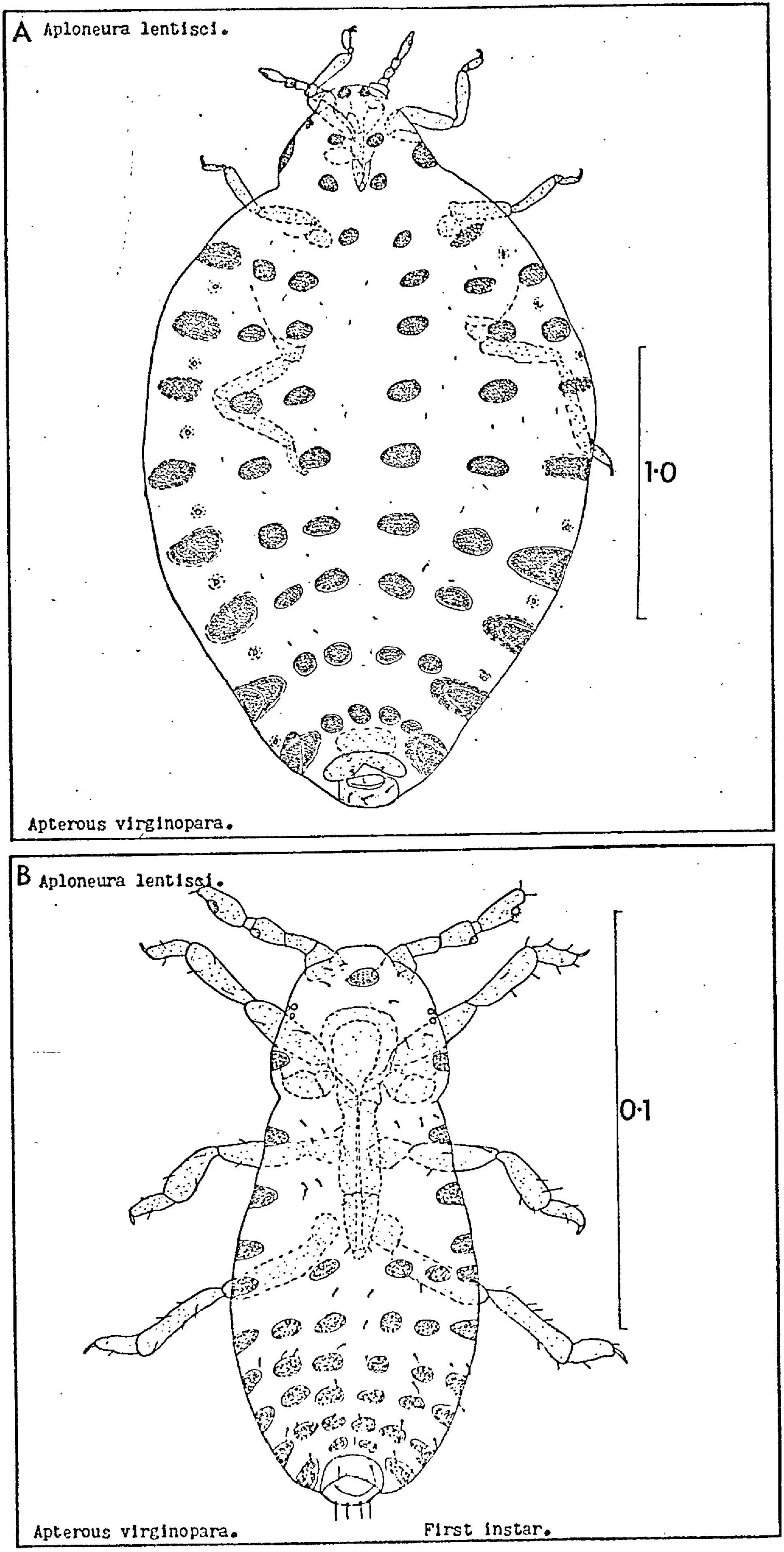
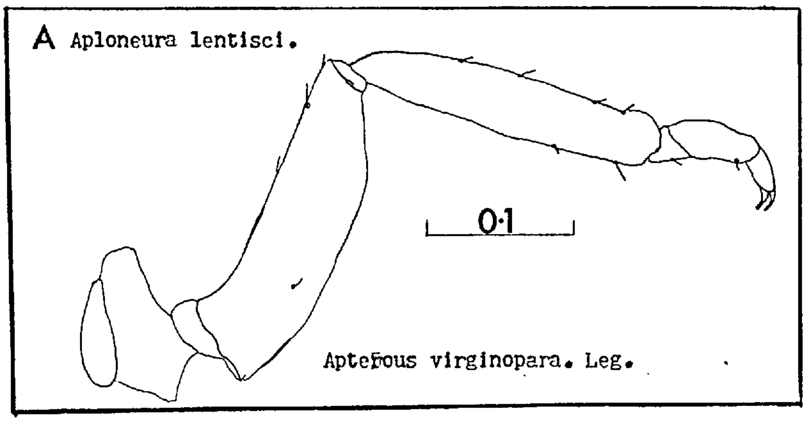
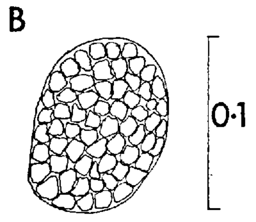

A Aploneura lentisci.
1·0
Apterous virginopara.
B Aploneura lentisci.
0·1
Apterous virginopara.
First instar.

FIG 43

Aploneura lentisci.

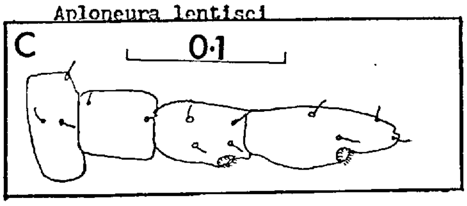


Apterous virginopara. Leg.



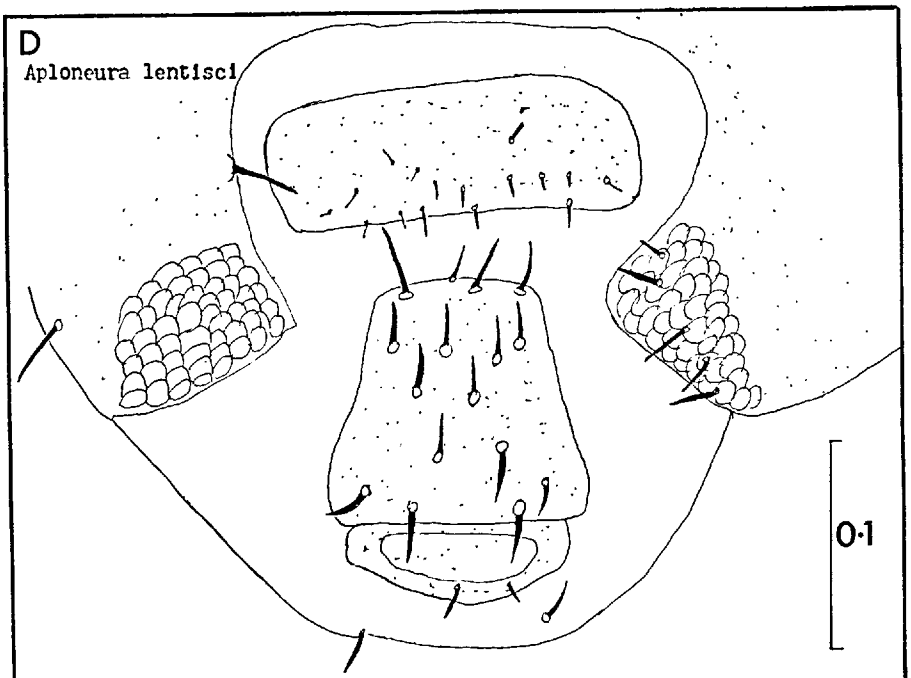
Wax gland.
Apterous virginopara.

Aploneura lentisci



Apterous virginopara.-first instar.
Antenna.

Aploneura lentisci



Apterous virginopara.-Anal region.

FIG. 44.

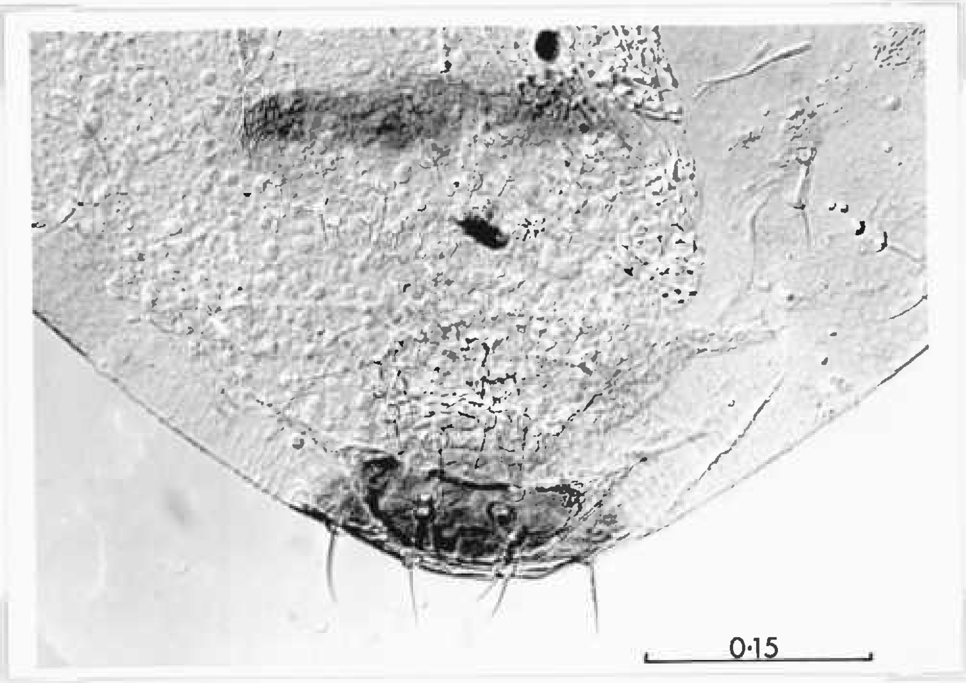


Plate 33. Aploneura lentisci. Apterous virginopara, anal region.

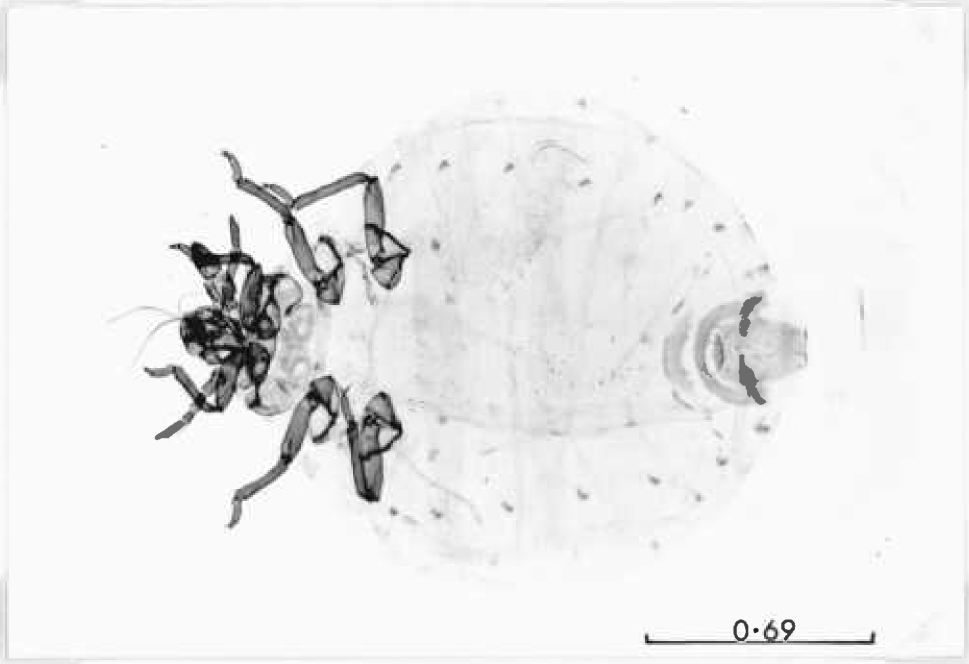


Plate 34. Baizongia pistaciae. Apterous virginopara.

Plate 35. Baizongia pistaciae. Apterous virginopara.

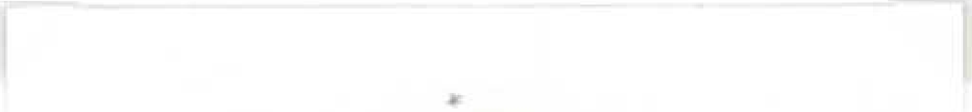


Plate 36. Baizongia pistaciae. Alate virginopara.

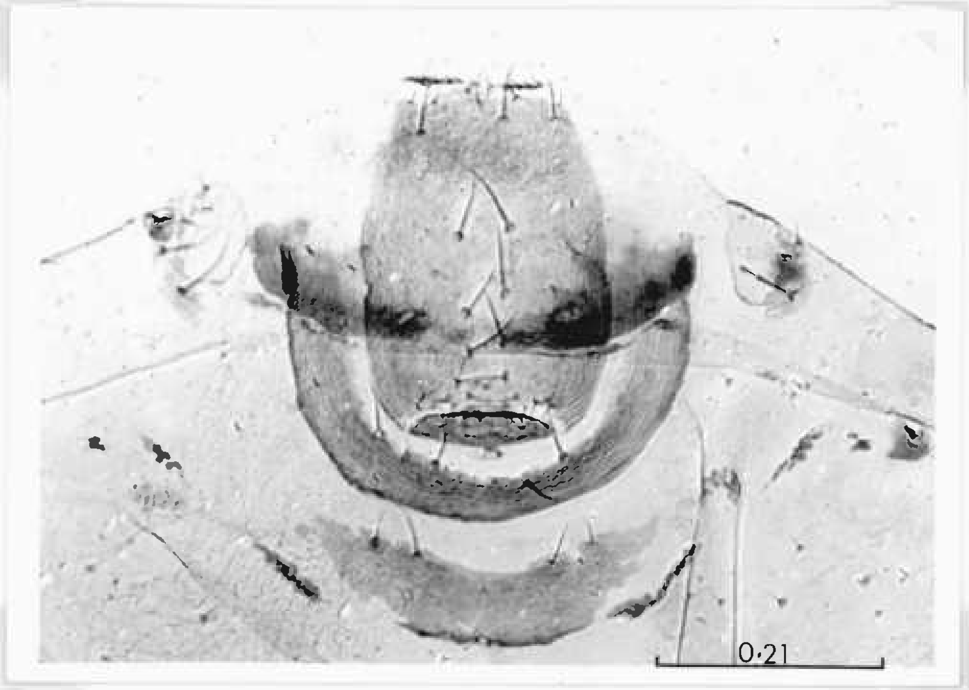


Plate 37. Baizongia pistaciae. Apterous virginopara, anal region.

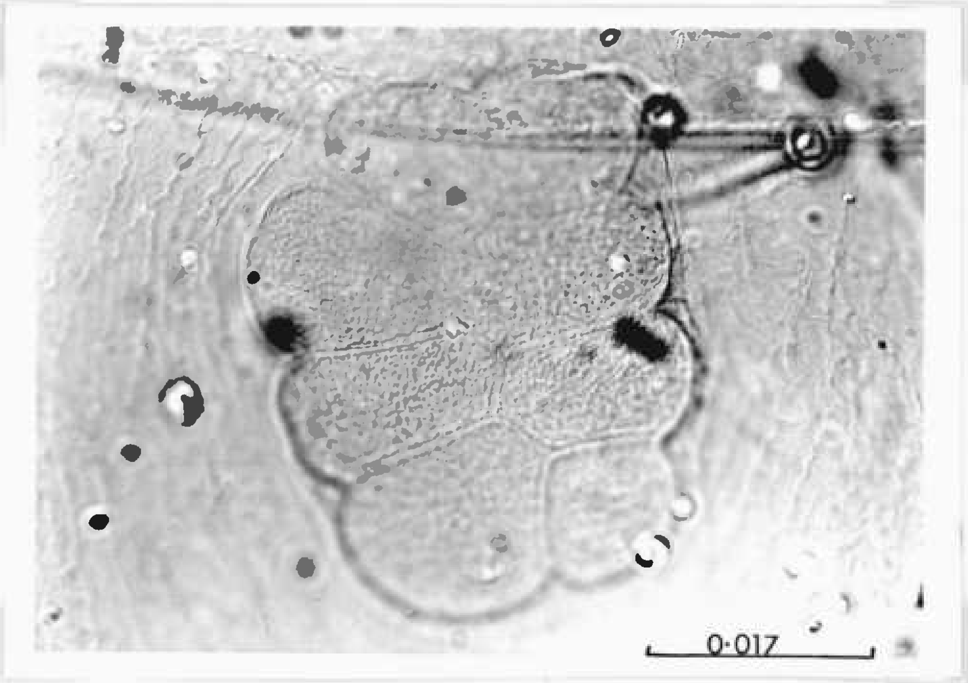


Plate 38. Baizongia pistaciae. Apterous virginopara, wax gland.

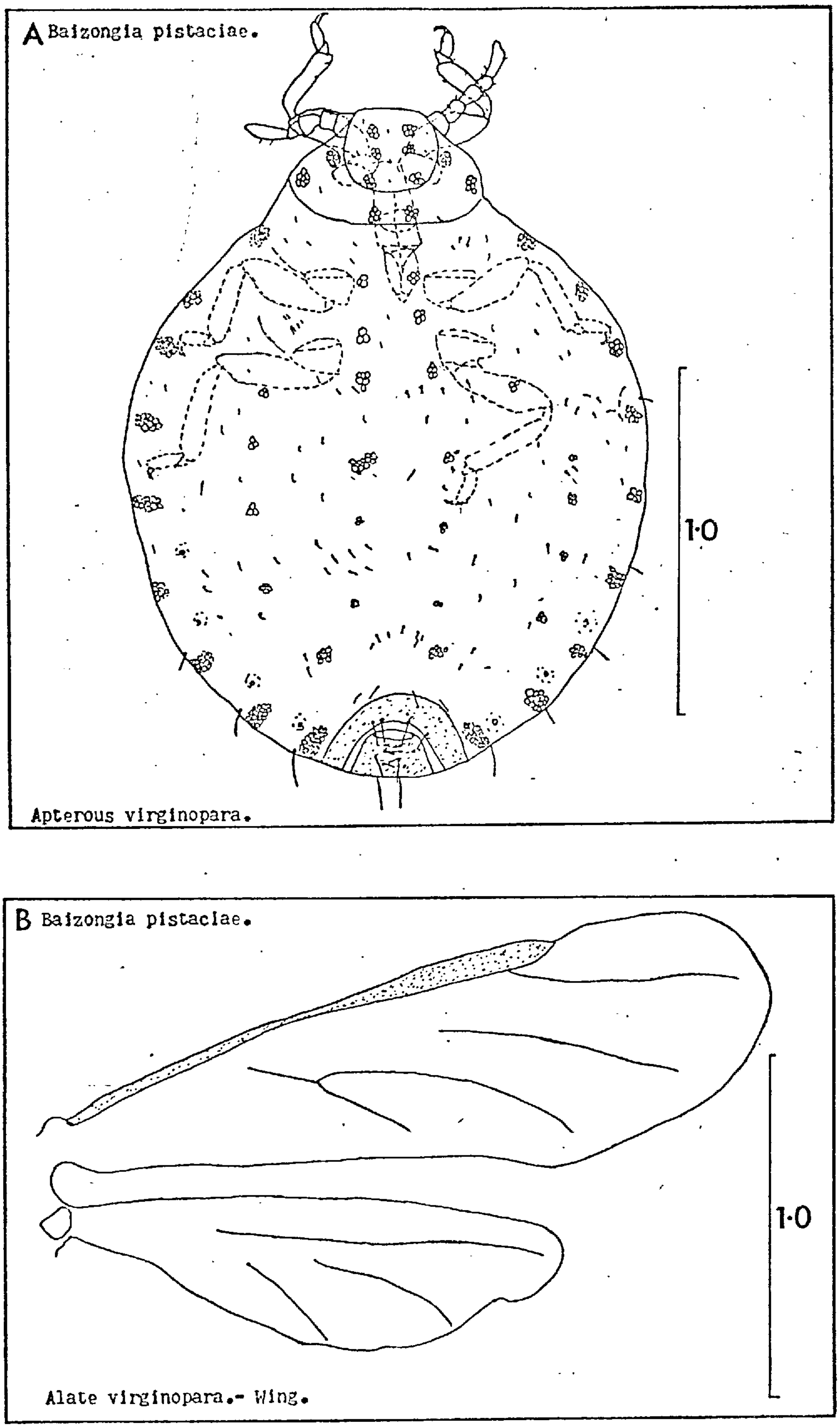
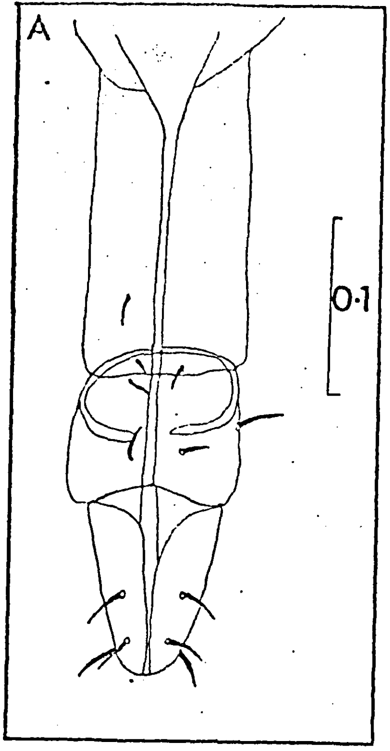
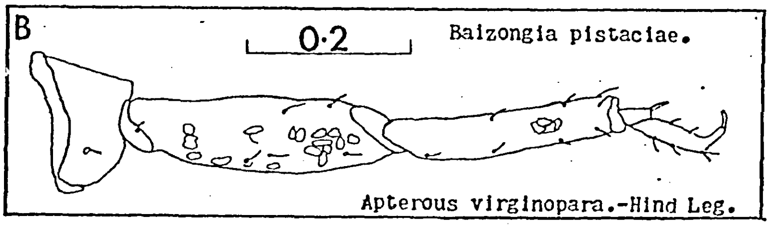

A Baizongia pistaciae.
1·0
Apterous virginopara.
B Baizongia pistaciae.
1·0
Alate virginopara.- Wing.

FIG 45

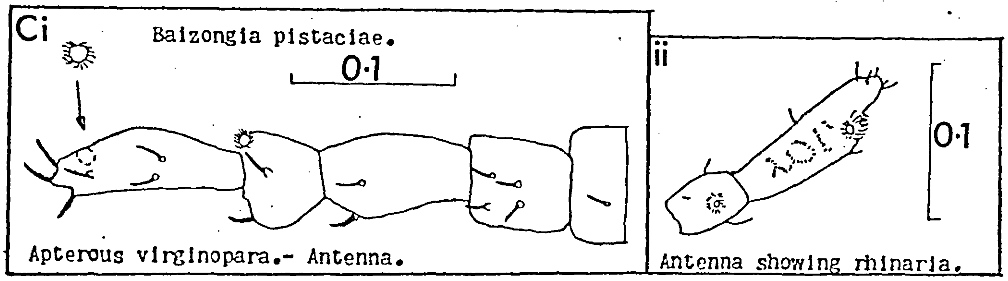


Baizongia pistaciae.
Apterous virginopara.
Rostrum.



Baizongia pistaciae.

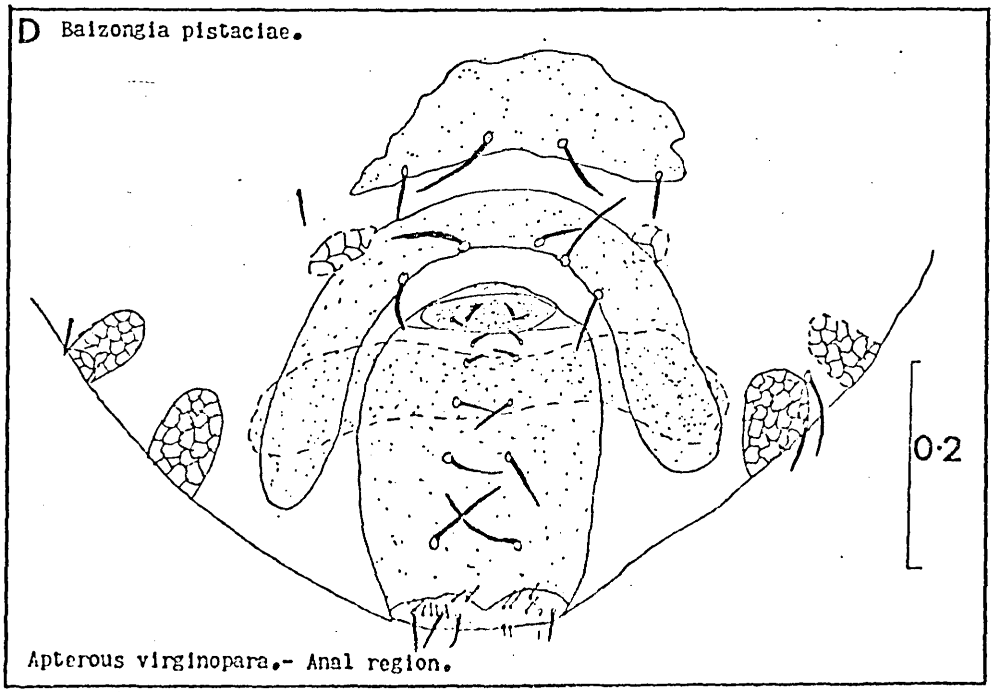
Apterous virginopara.-Hind Leg.



Baizongia pistaciae.

Apterous virginopara.- Antenna.

Antenna showing rhinaria.



Baizongia pistaciae.

Apterous virginopara.- Anal region.

FIG 46

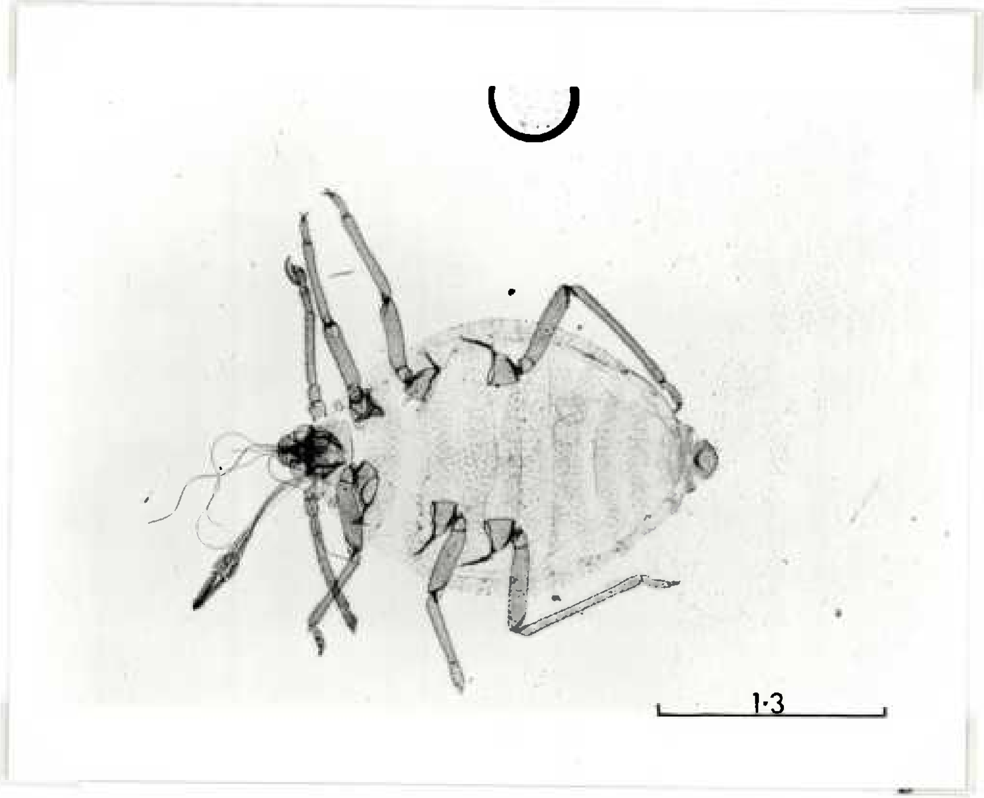


Plate 39. Forda formicaria. Apterous virginopara.

Plate 40. Lasius flavus carrying Forda formicaria.

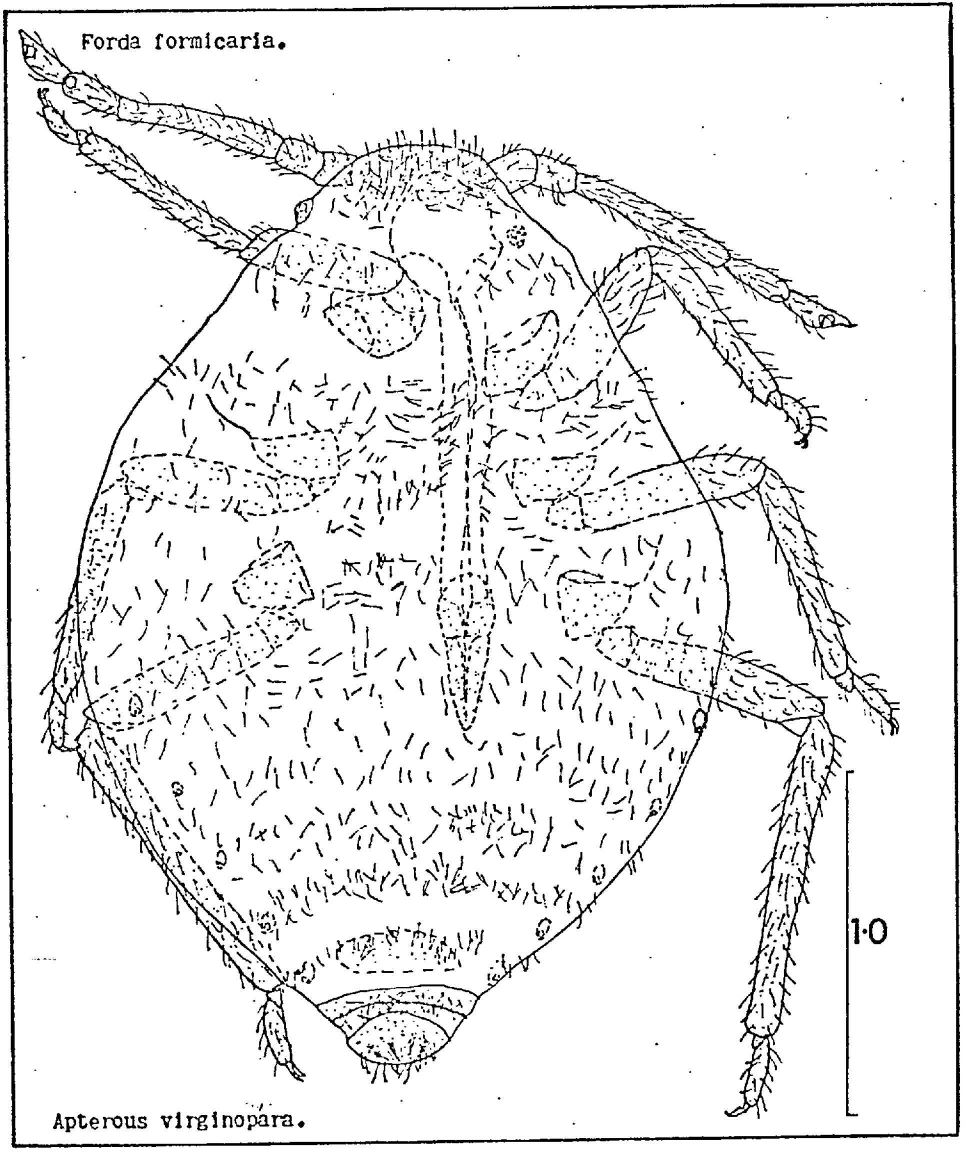


FIG 47

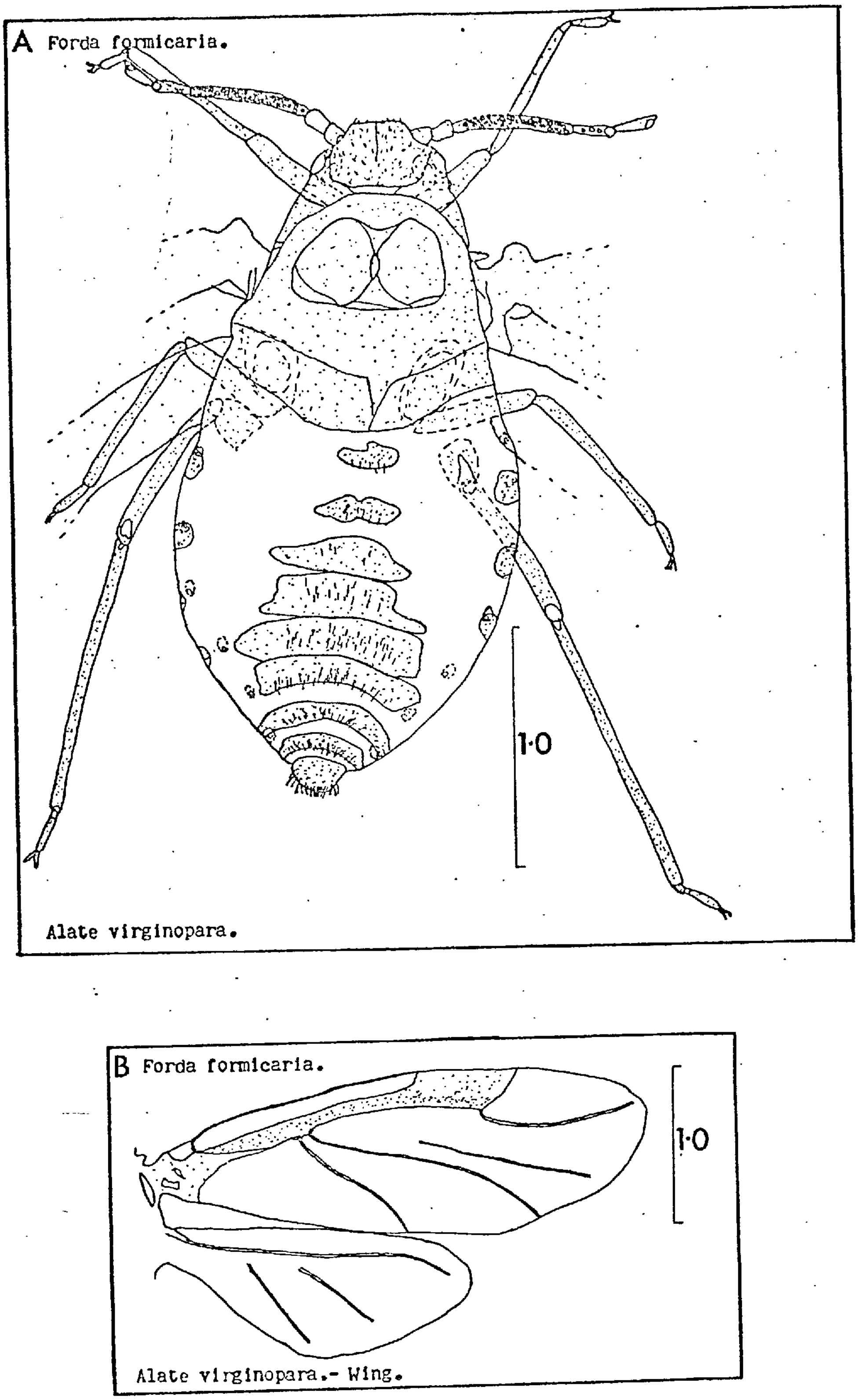
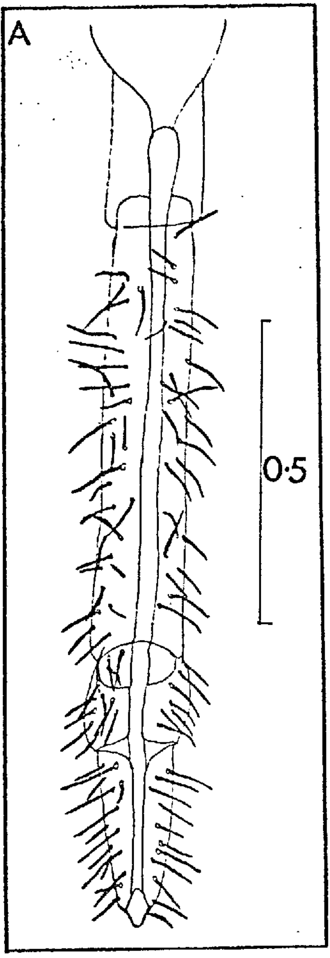
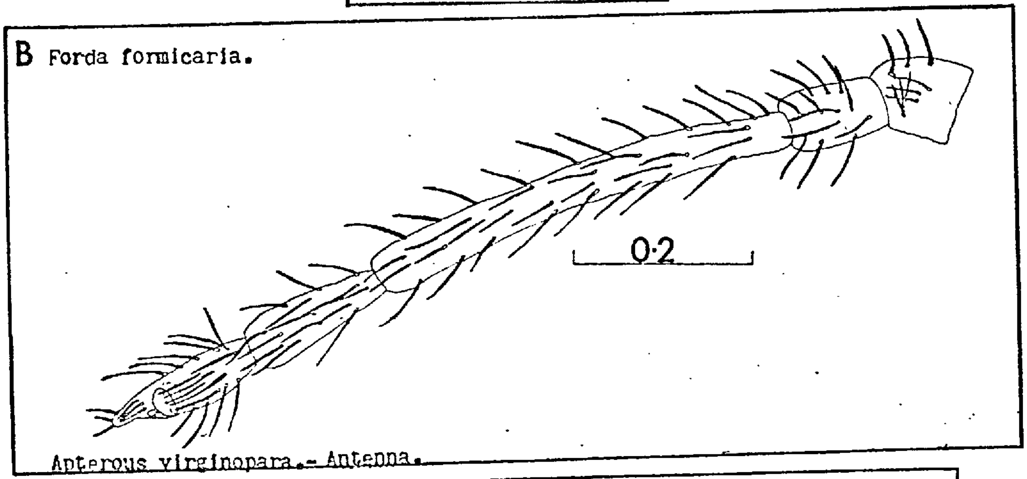

A Forda formicaria.
1·0
Alate virginopara.
B Forda formicaria.
1·0
Alate virginopara.- Wing.

FIG 48

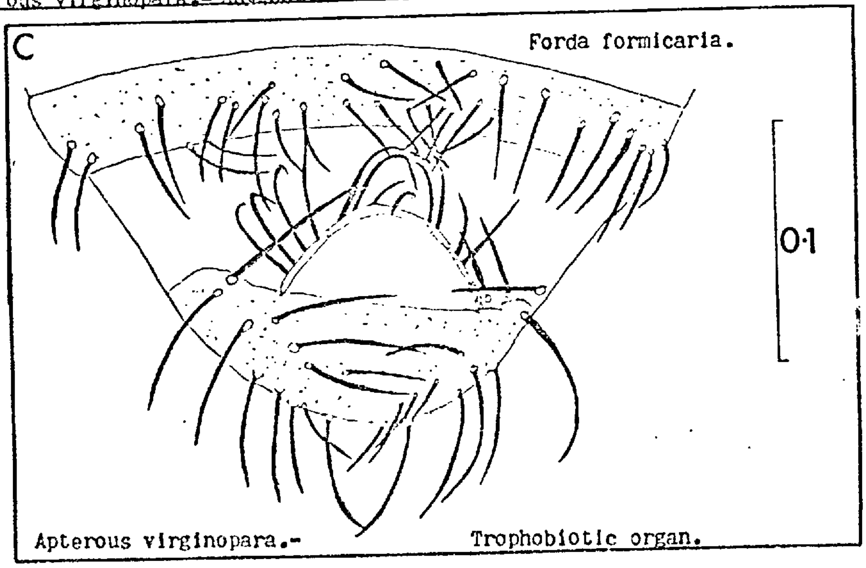


Forda formicaria.
Apterous virginopara.
Rostrum.



Forda formicaria.

Apterous virginopara.- Antenna.



Forda formicaria.

Apterous virginopara.- Trophobiotic organ.

FIG 49

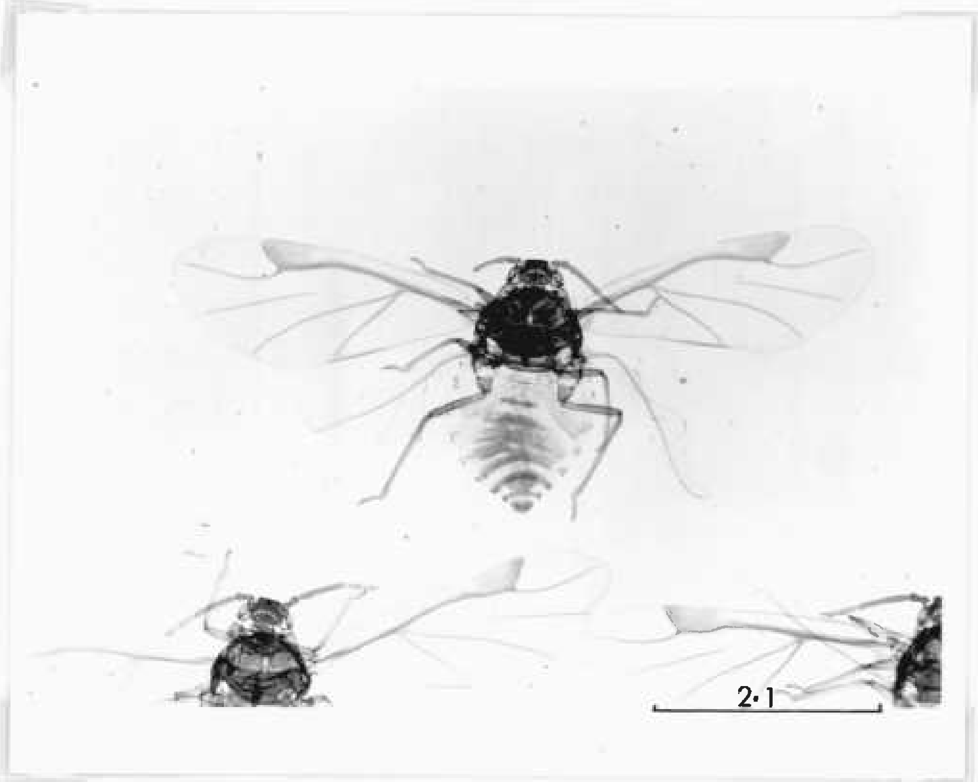


Plate 41. _Forda formicaria_. Alate virginopara.

Plate 42. _Forda marginata_. Alate virginopara.

Plate 43. Forda marginata. Apterous virginopara, last antennal segment.

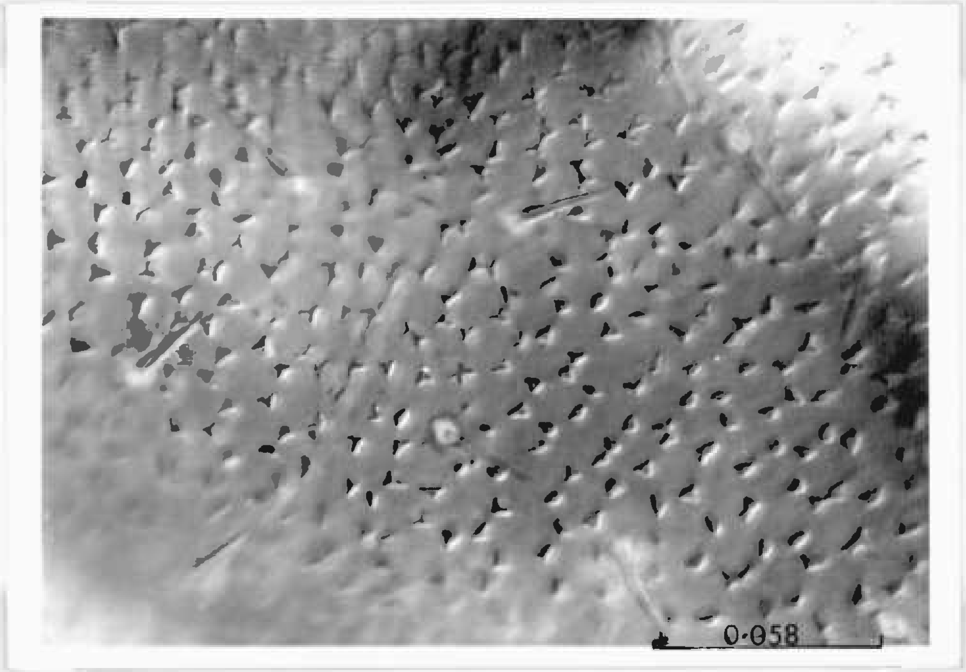


Plate 44. Forda marginata. Apterous virginopara, cuticular sculpturing.

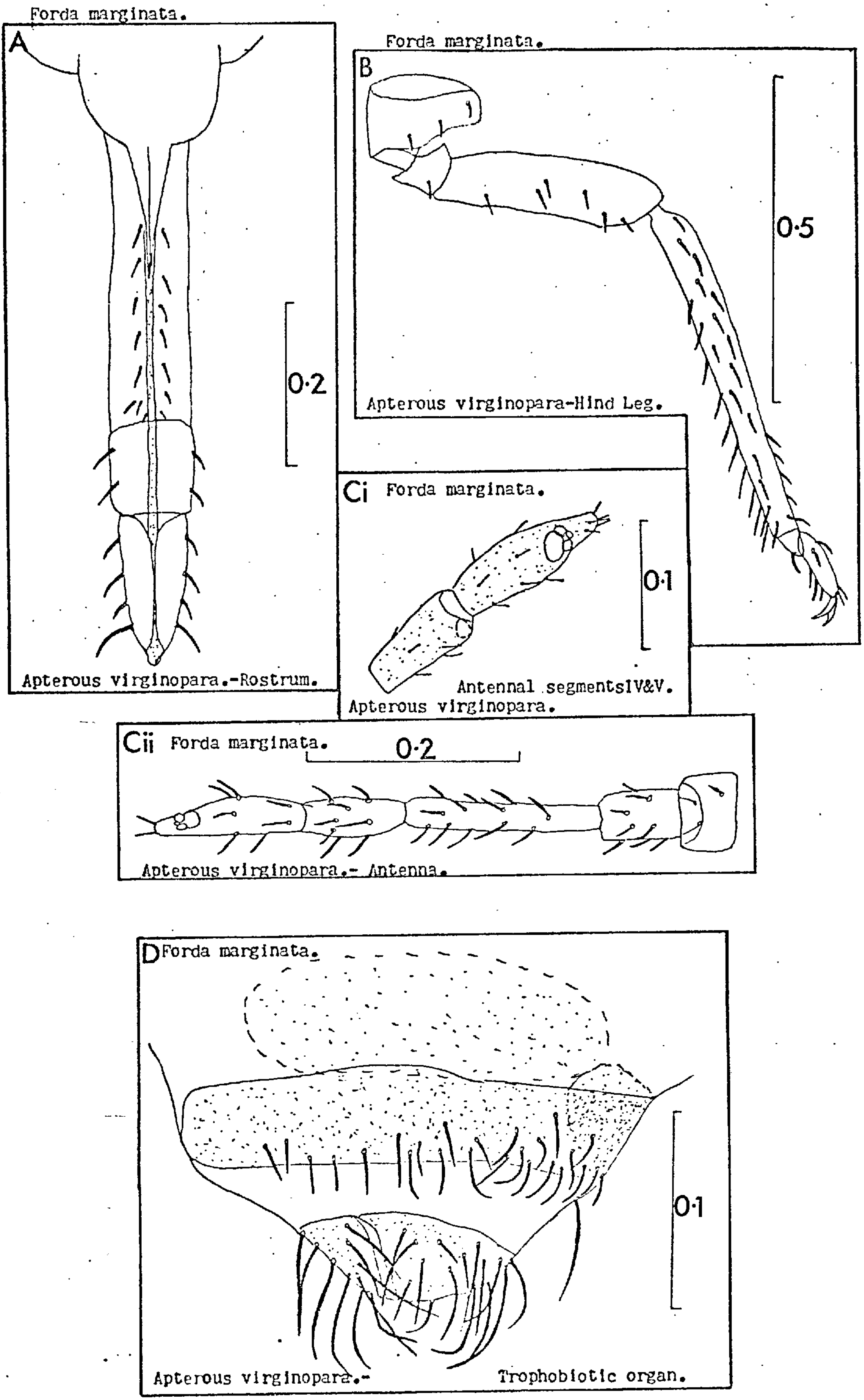

Forda marginata.
A
0·2
Apterous virginopara.-Rostrum.
Forda marginata.
B
0·5
Apterous virginopara-Hind Leg.
Ci
Forda marginata.
0·1
Antennal segmentsIV&V.
Apterous virginopara.
Cii
Forda marginata.
0·2
Apterous virginopara.- Antenna.
D
Forda marginata.
0·1
Apterous virginopara.-
Trophobiotic organ.

FIG 50

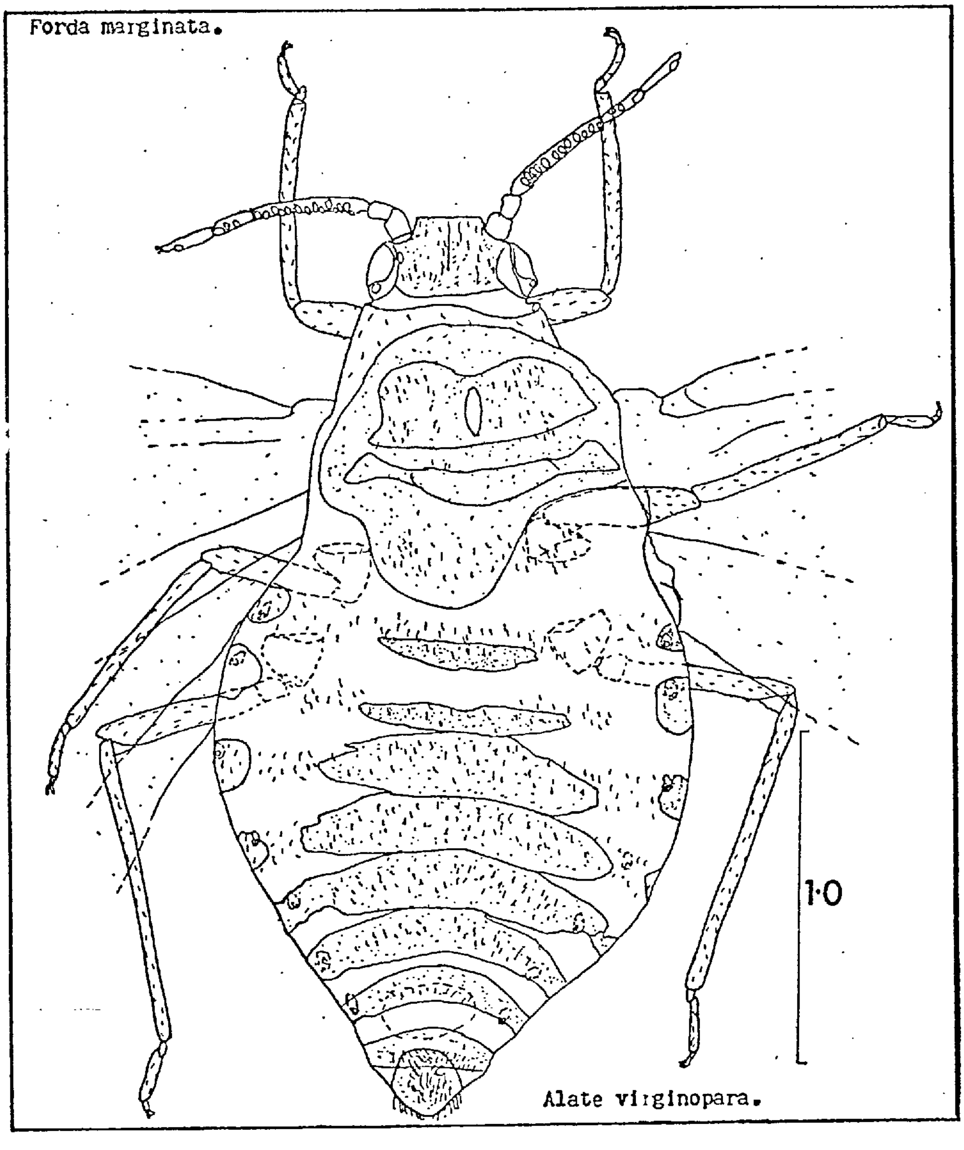


FIG 51

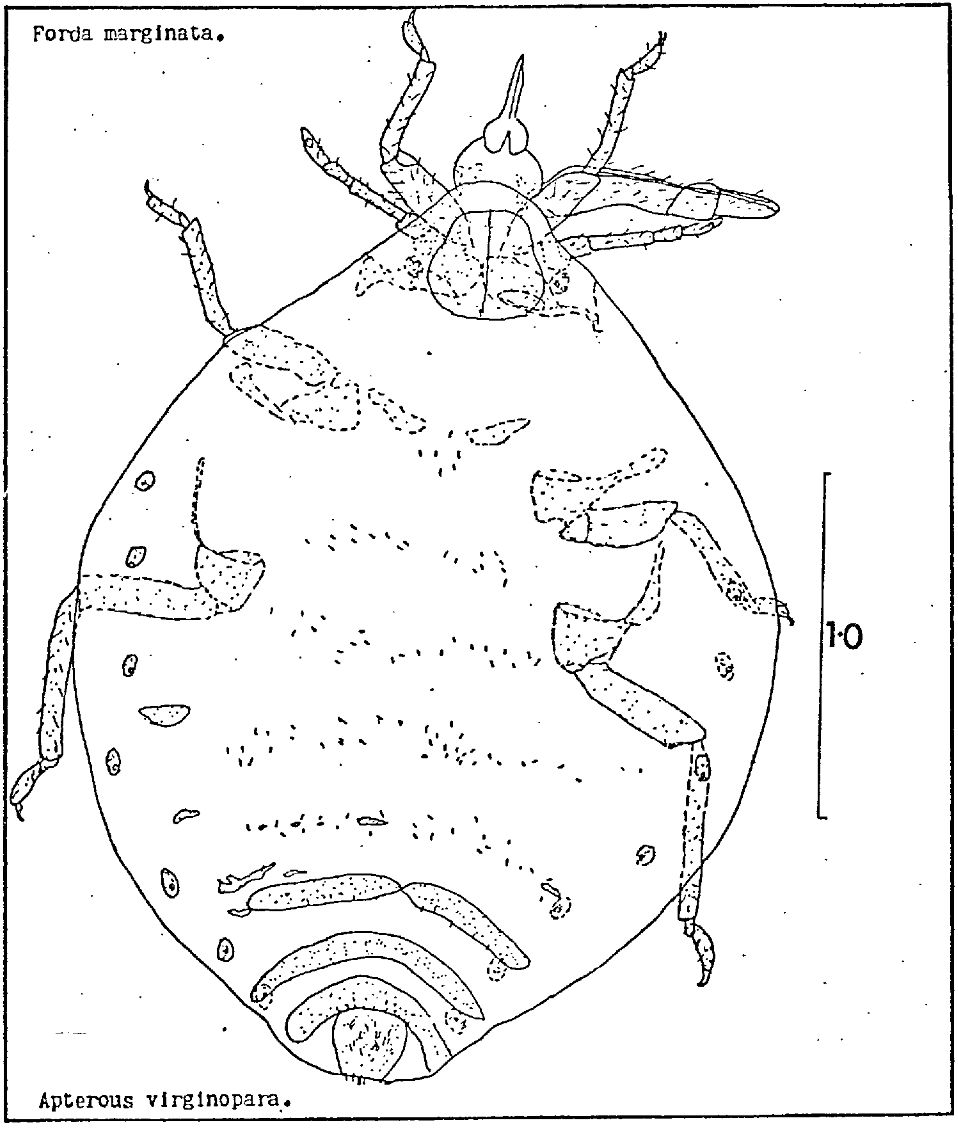


FIG 52

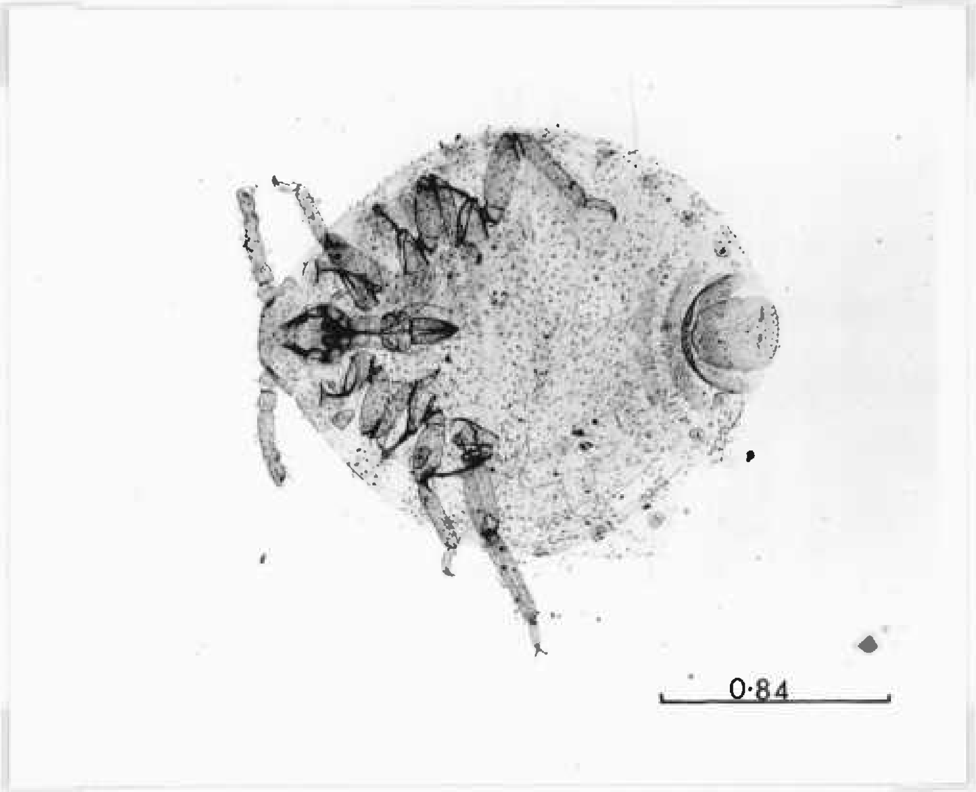


Plate 45. Geoica eragrostidis. Apterous virginopara.

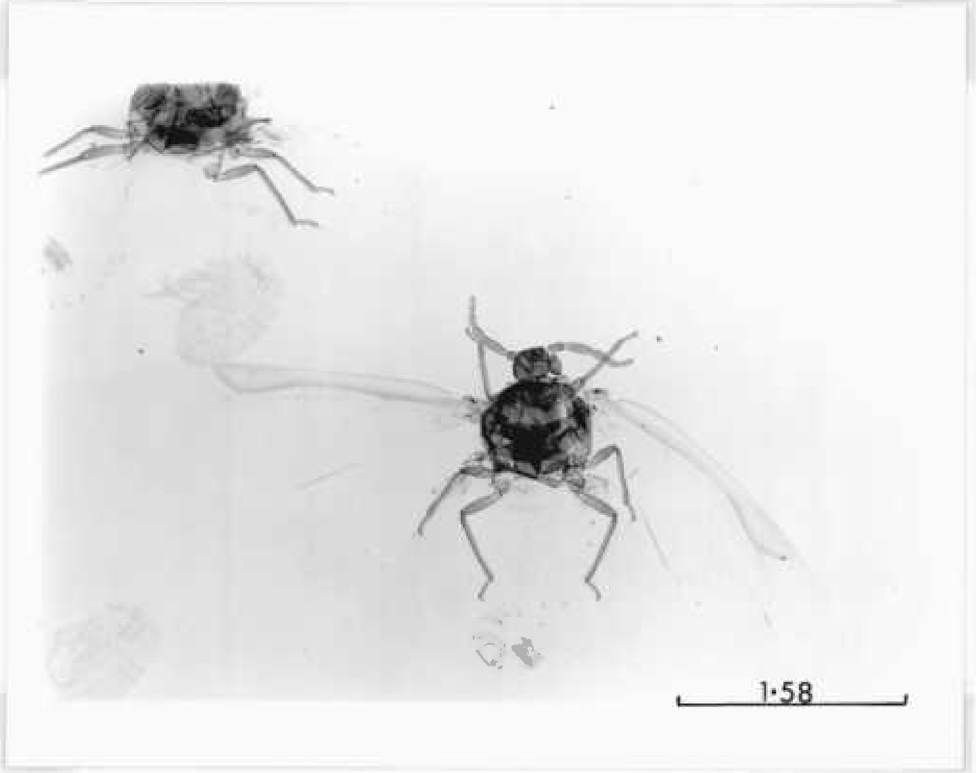


Plate 46. Geoica eragrostidis. Alate virginopara.

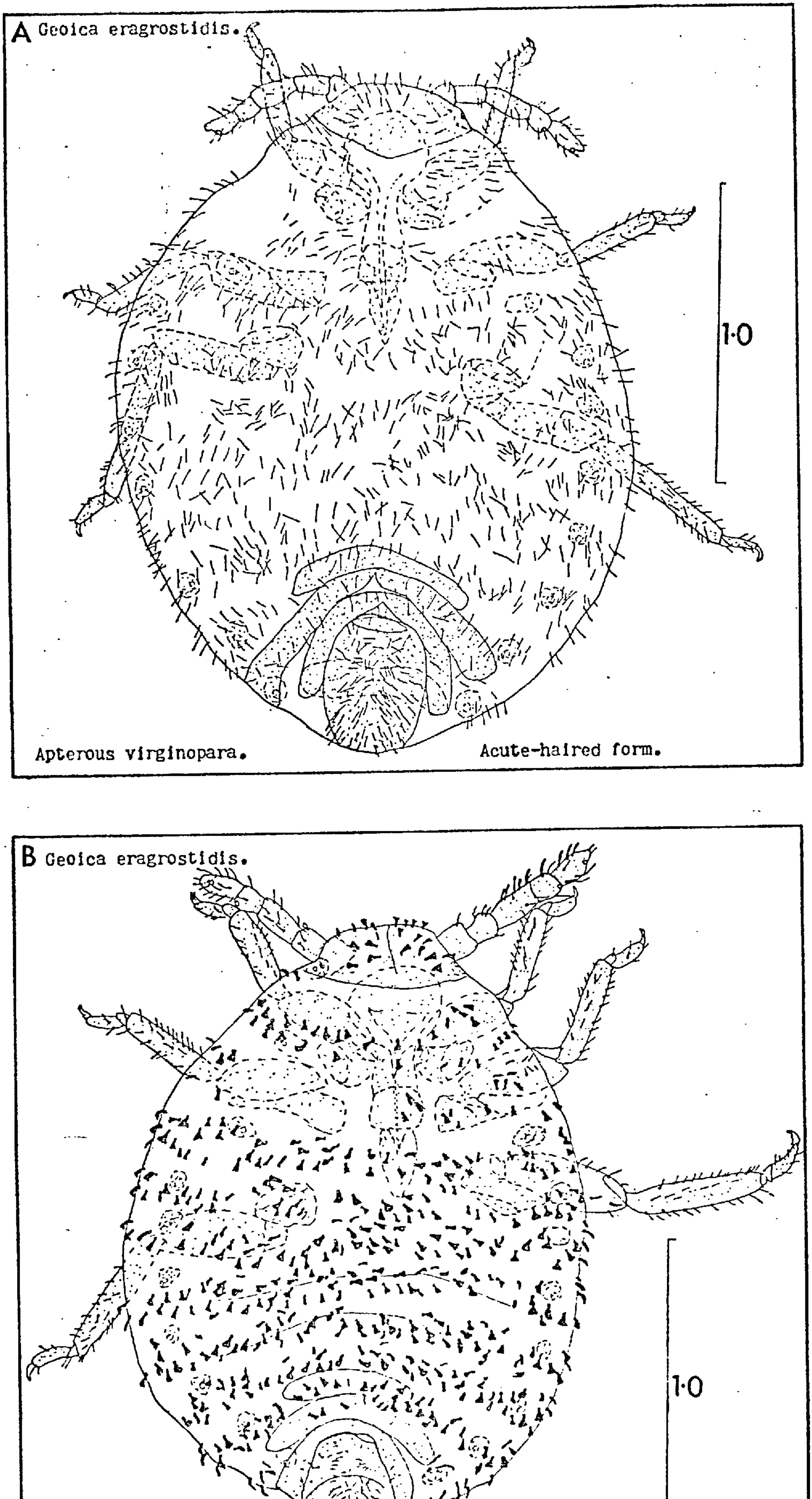

A Geoica eragrostidis.
1·0
Apterous virginopara.
Acute-haired form.
B Geoica eragrostidis.
1·0
Apterous virginopara.
Spatulate-haired form.

FIG 53

Plate 47. Geoica eragrostidis. Apterous virginopara, anal region.

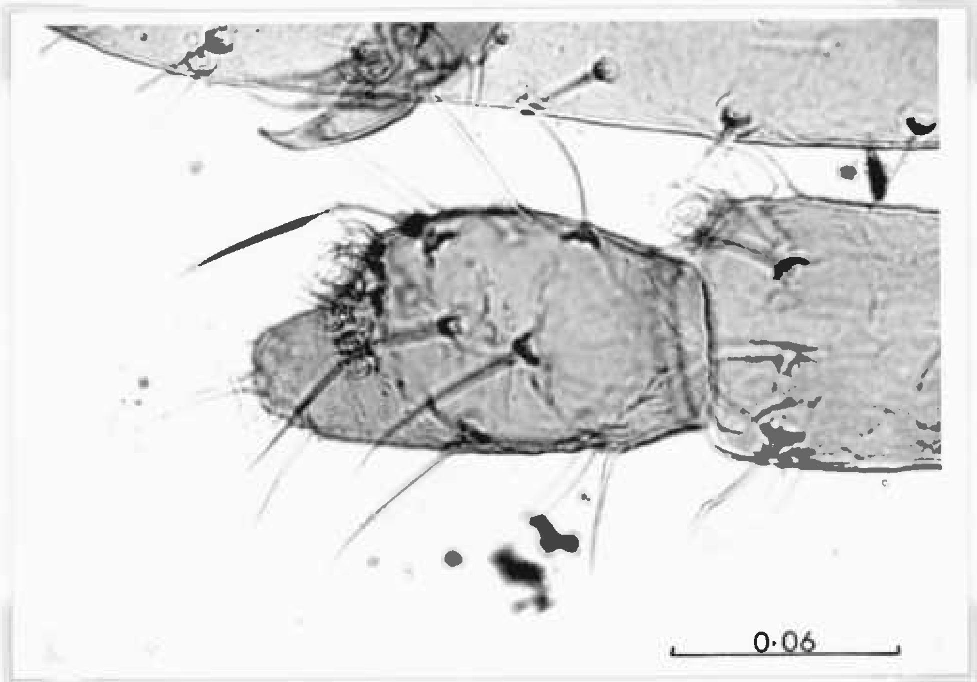


Plate 48. Geoica eragrostidis. Apterous virginopara, last antennal segment.

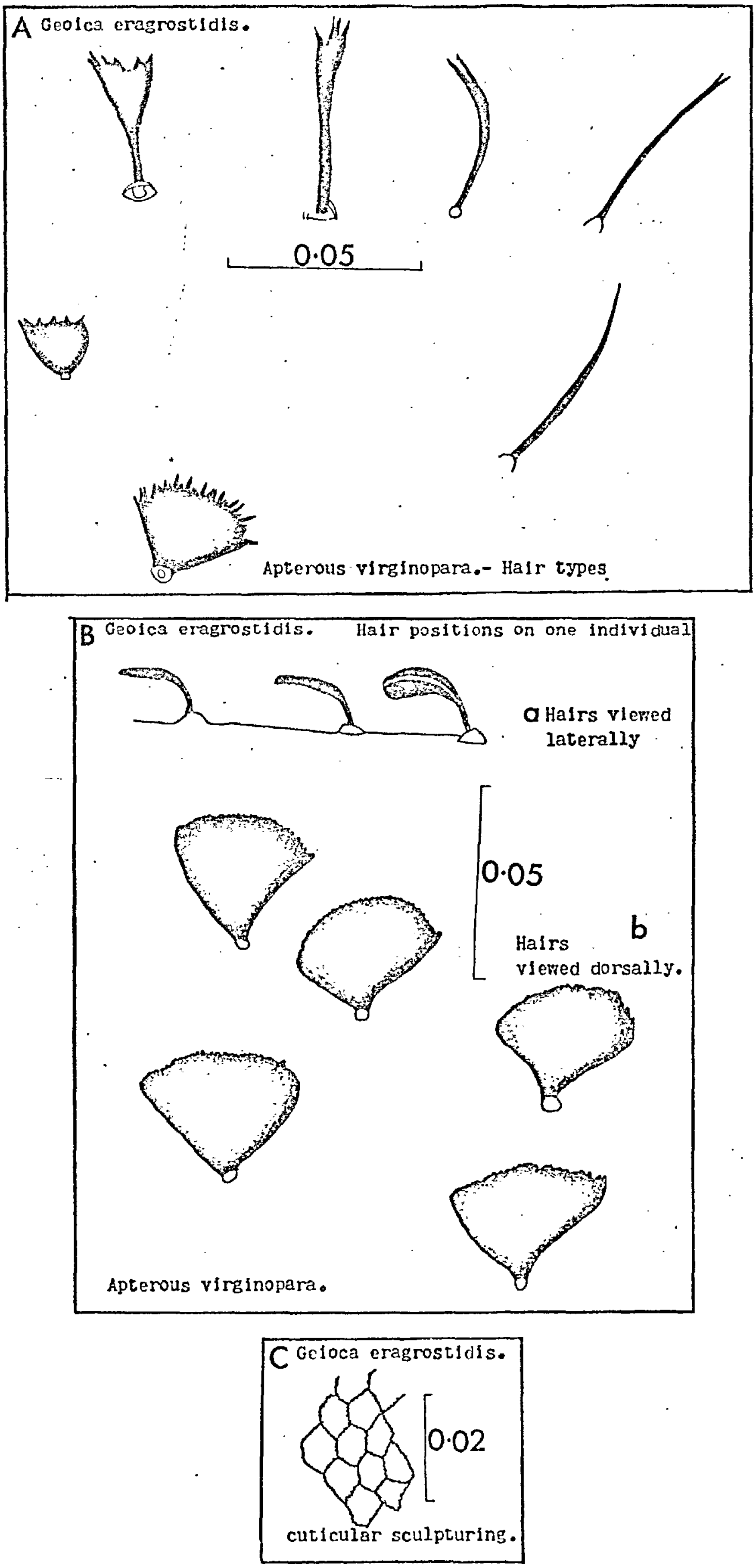

A Geoica eragrostidis.
0·05
Apterous virginopara.- Hair types
B Geoica eragrostidis. Hair positions on one individual
a Hairs viewed laterally
0·05
b
Hairs viewed dorsally.
Apterous virginopara.
C Geioca eragrostidis.
0·02
cuticular sculpturing.

FIG 54

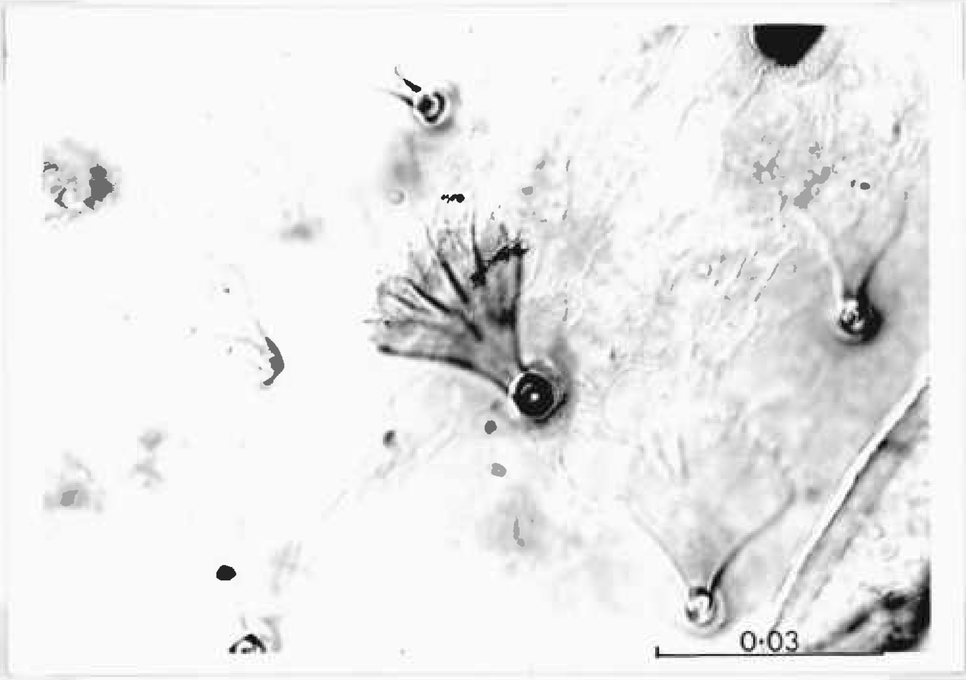


Plate 49. Geoica eragrostidis. Apterous virginopara, spatulate hair.

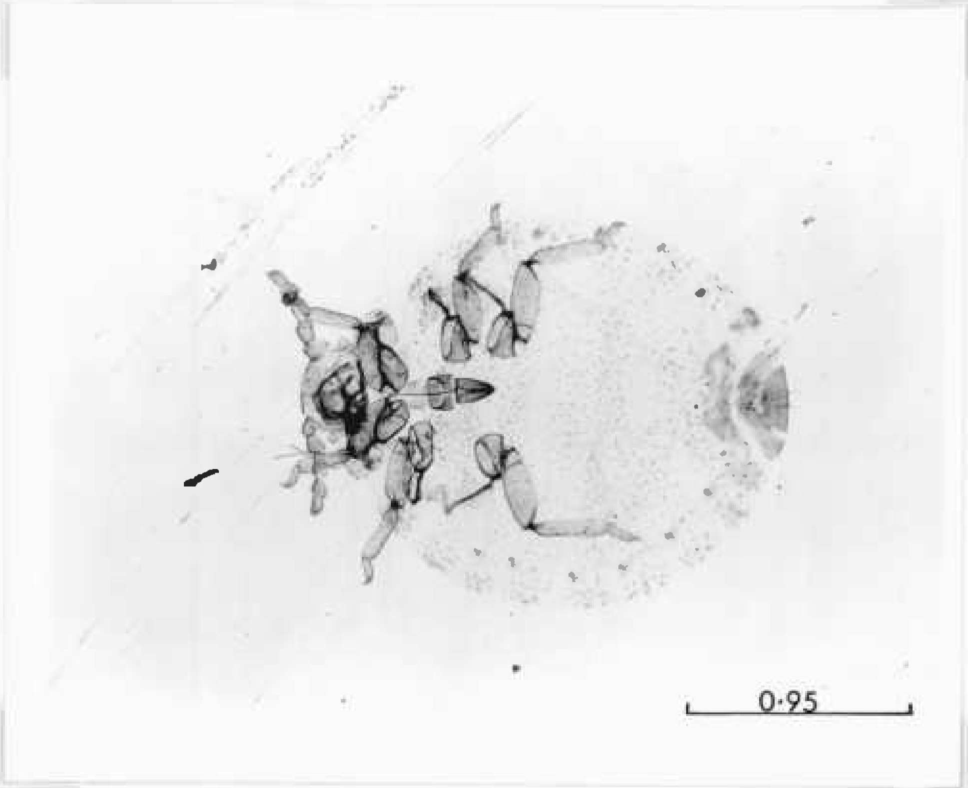
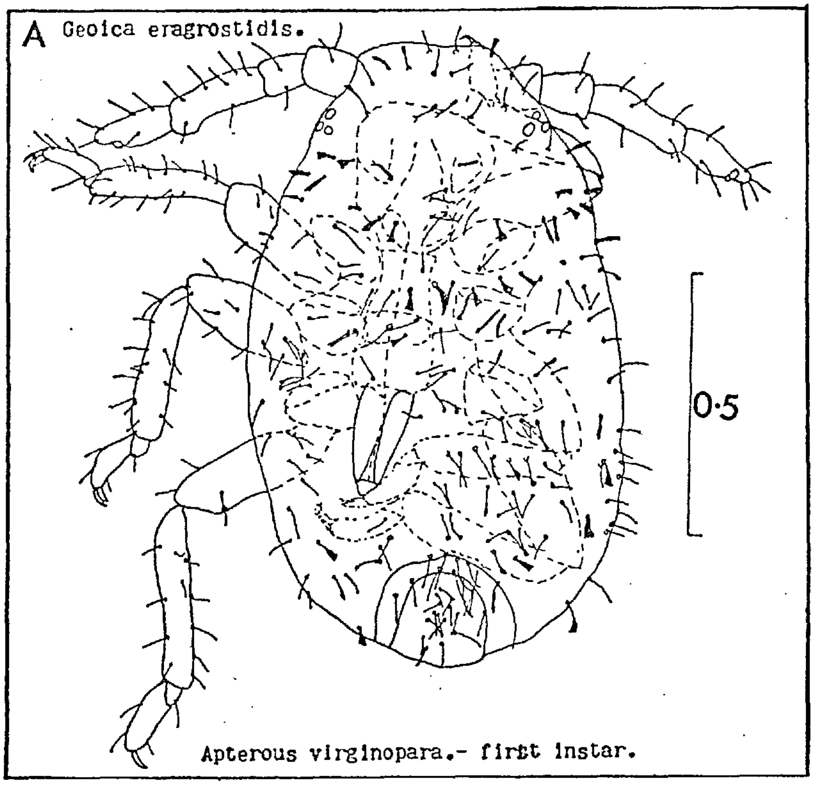
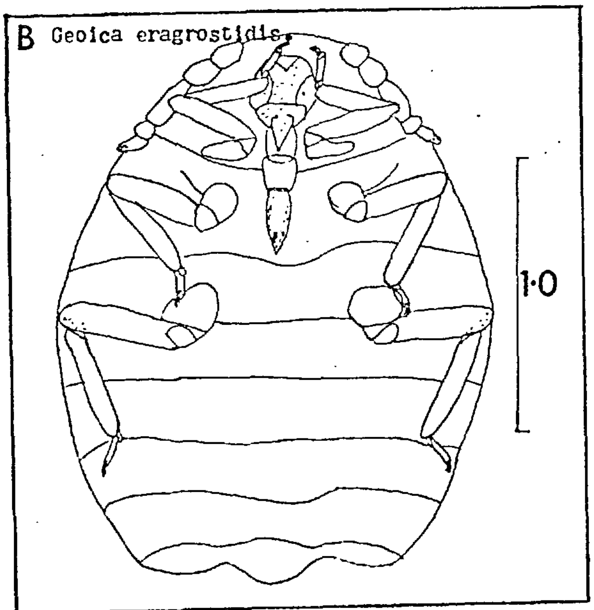


Plate 50. Geoica setulosa. Apterous virginopara.

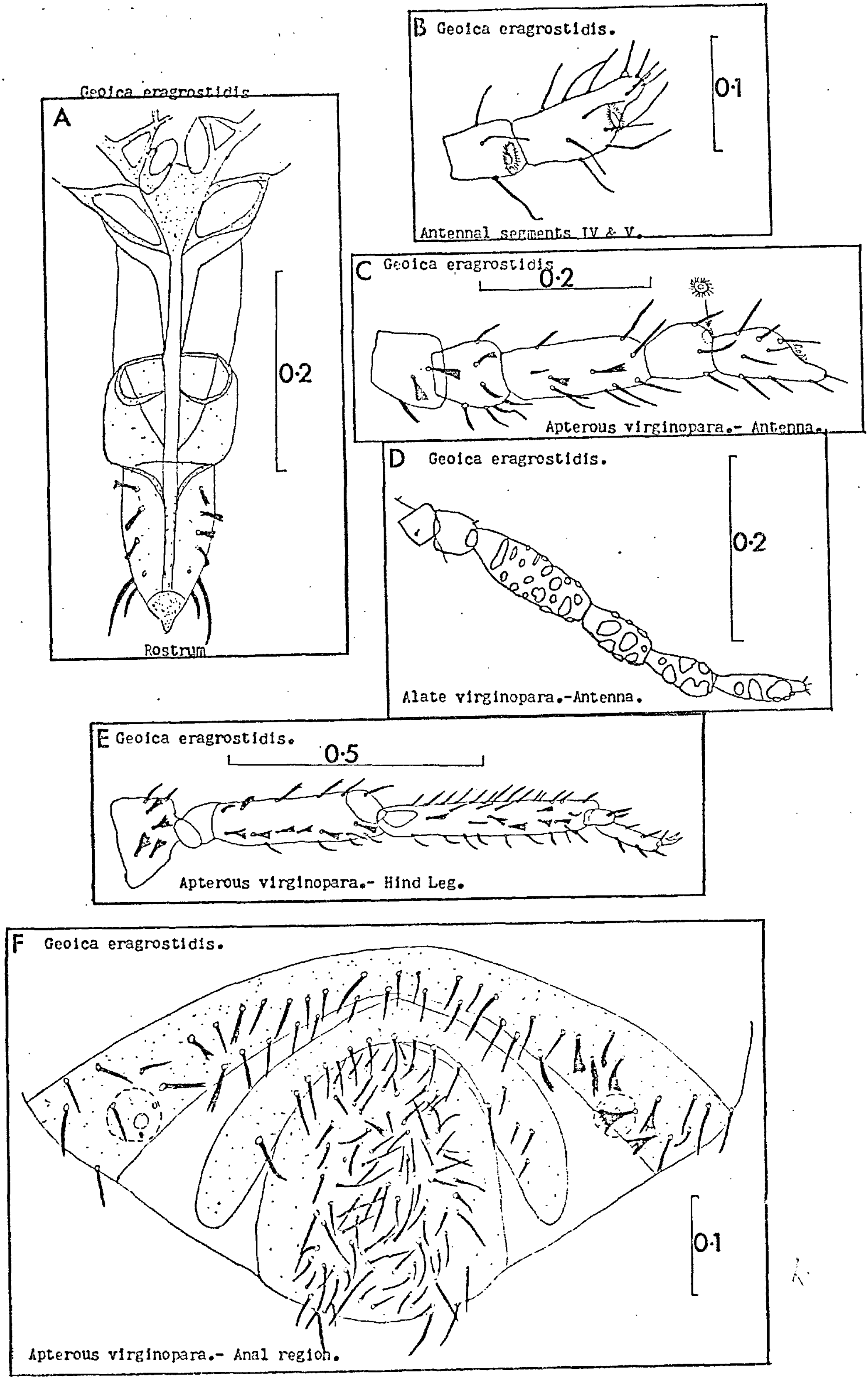


Apterous virginopara.- first instar.



Death-feigning position.

FIG 55



A Rostrum

B Antennal segments IV & V.

C Apterous virginopara.- Antenna.

D Alate virginopara.-Antenna.

E Apterous virginopara.- Hind Leg.

F Apterous virginopara.- Anal region.

FIG 56

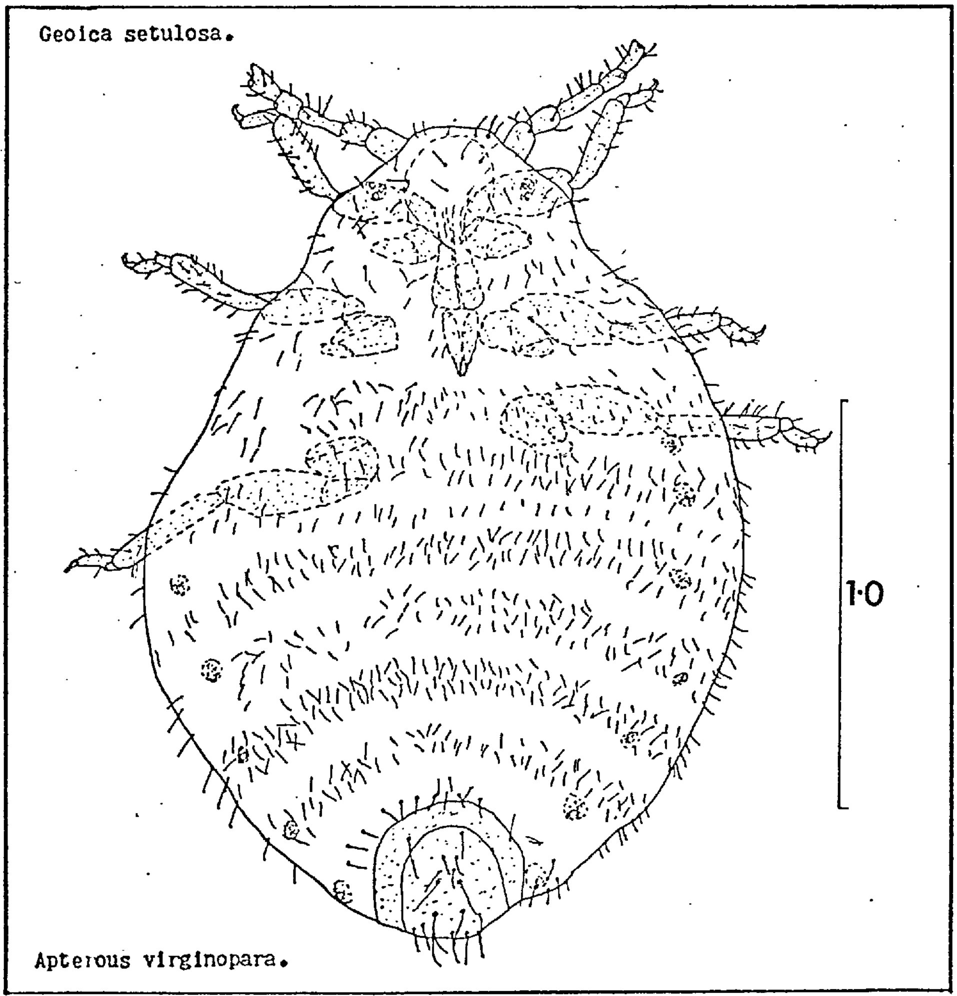


FIG 57

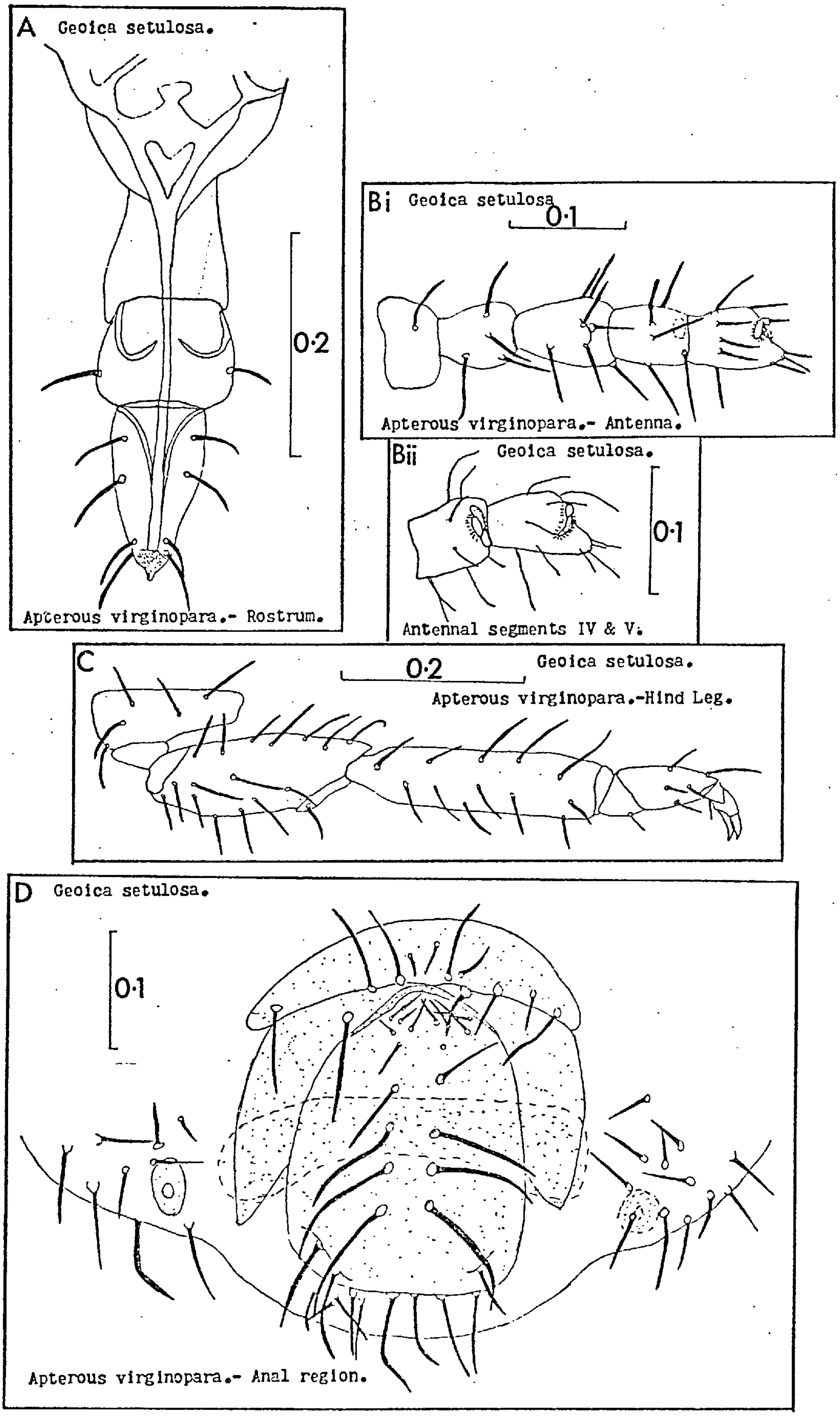
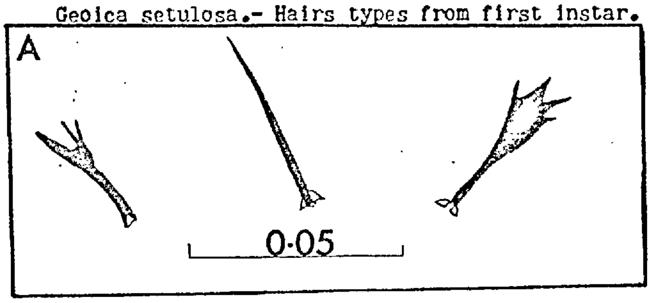
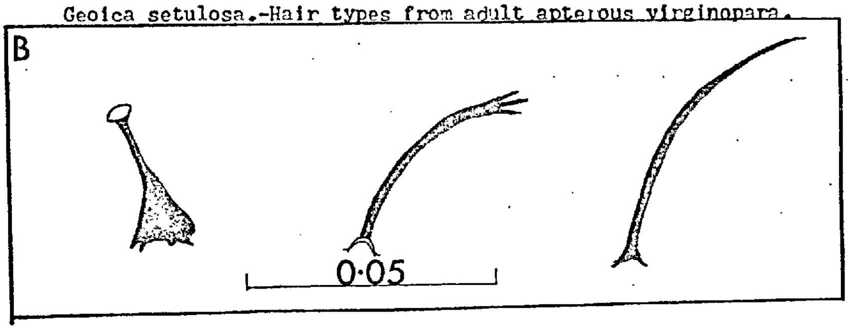

A Geoica setulosa.
0·2
Apterous virginopara.- Rostrum.
Bi Geoica setulosa
0·1
Apterous virginopara.- Antenna.
Bii Geoica setulosa.
0·1
Antennal segments IV & V.
C Geoica setulosa.
0·2
Apterous virginopara.-Hind Leg.
D Geoica setulosa.
0·1
Apterous virginopara.- Anal region.

FIG 58

Geoica setulosa.- Hairs types from first instar.



Geoica setulosa.-Hair types from adult apterous virginopara.



Geoica setulosa.-
Hair types from adult apterous virginopara.

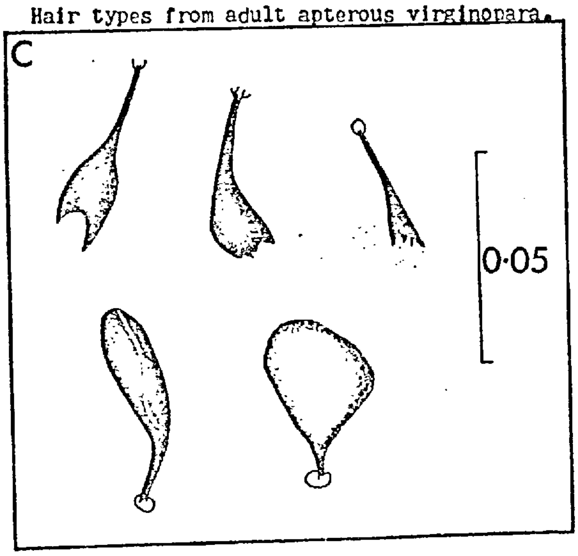
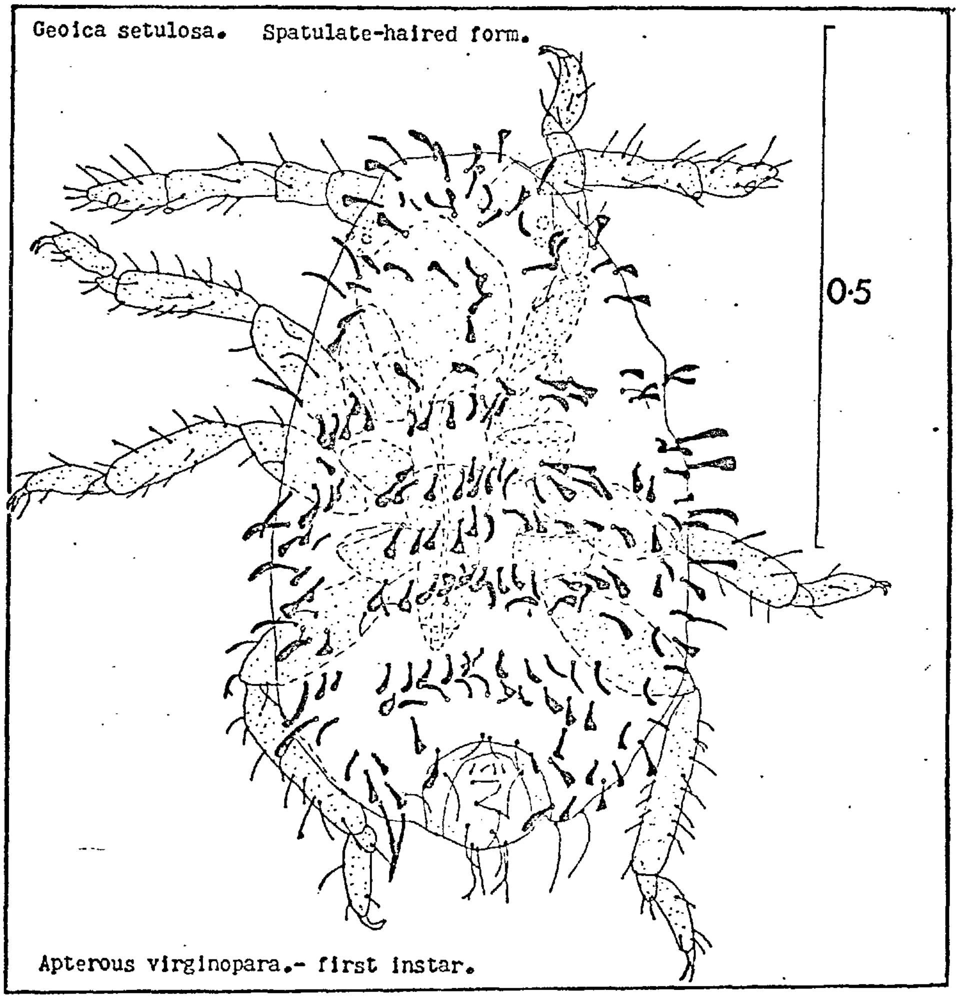
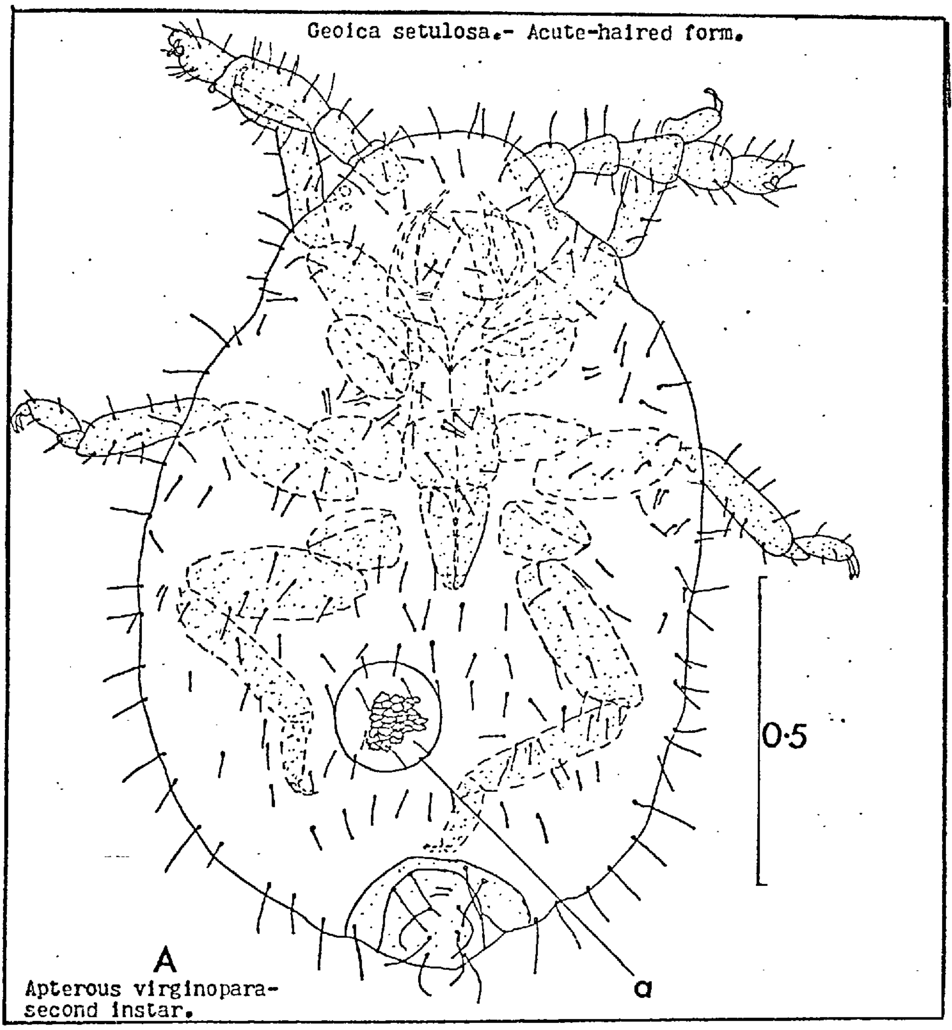


FIG 59


Geoica setulosa. Spatulate-haired form.

Apterous virginopara.- first instar.

FIG 60



Apterous virginopara-second instar.

FIG 61

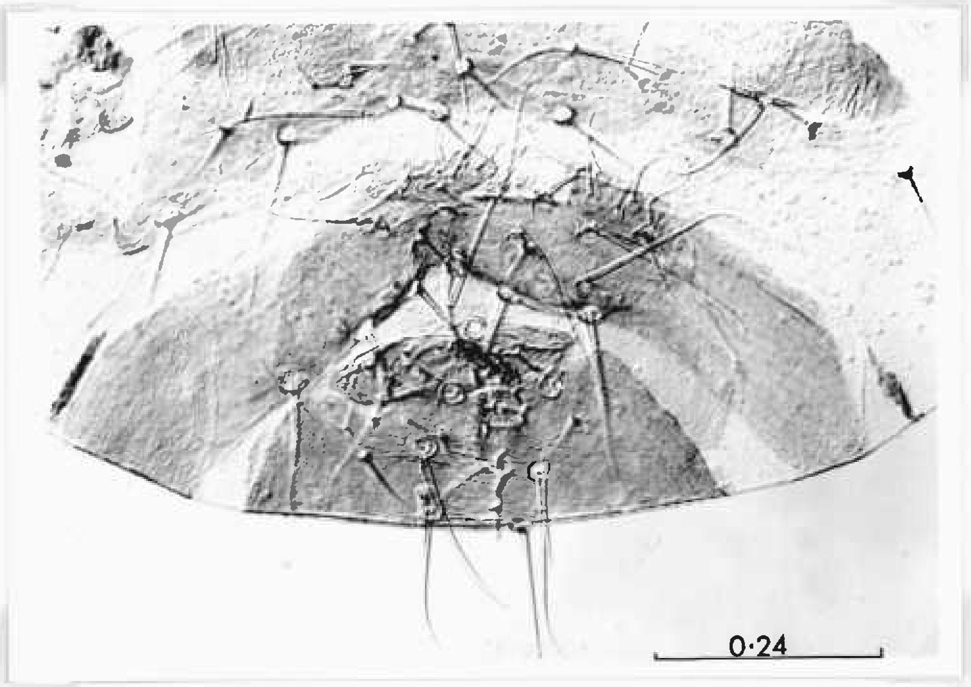


Plate 51. Geoica setulosa. Apterous virginopara, anal region.

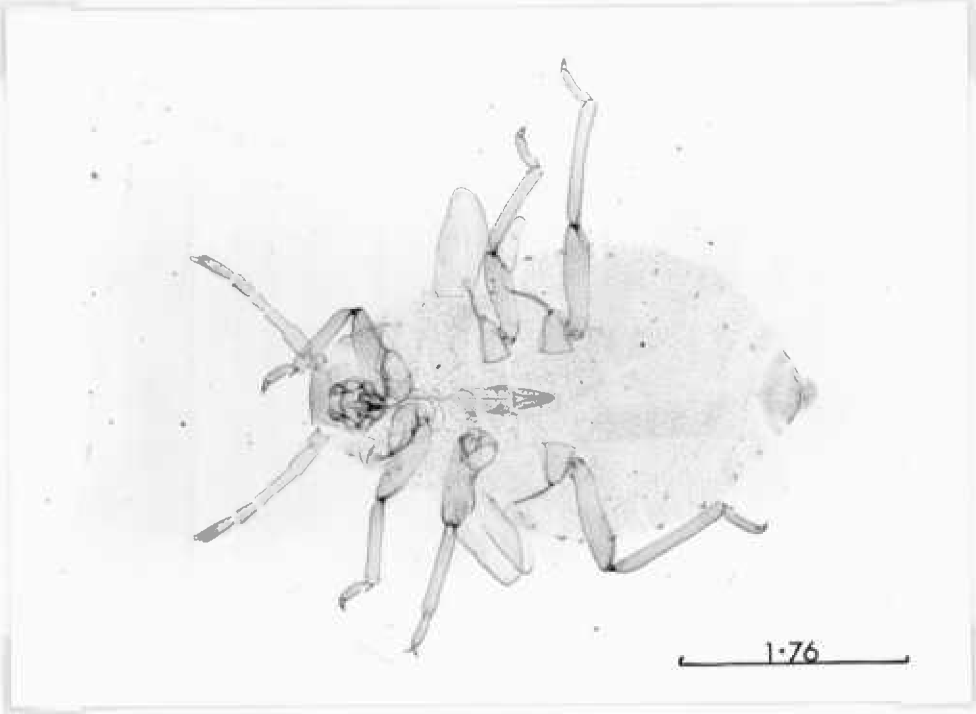


Plate 52. Smynthurodes betae. 3rd. instar alate virginopara.

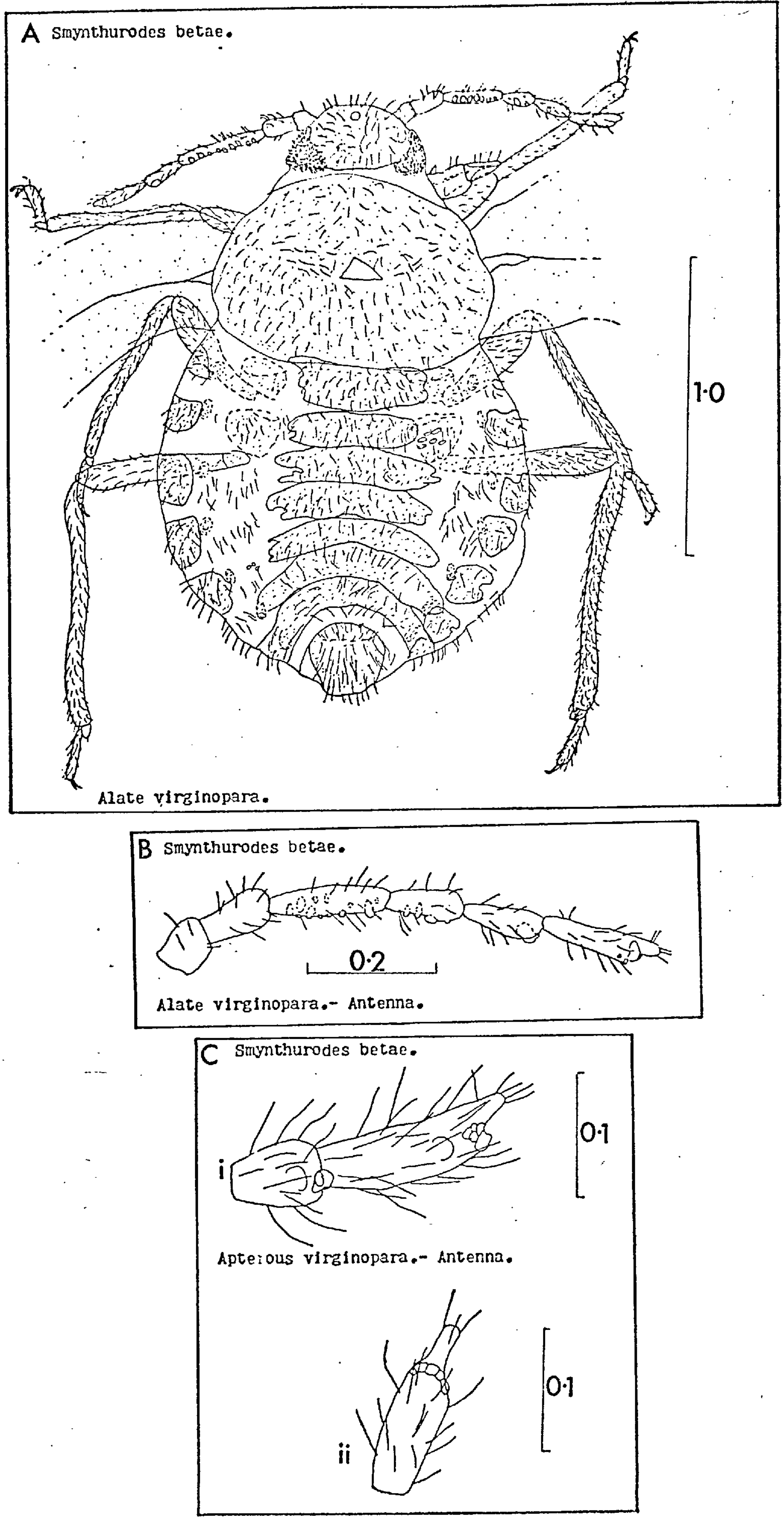
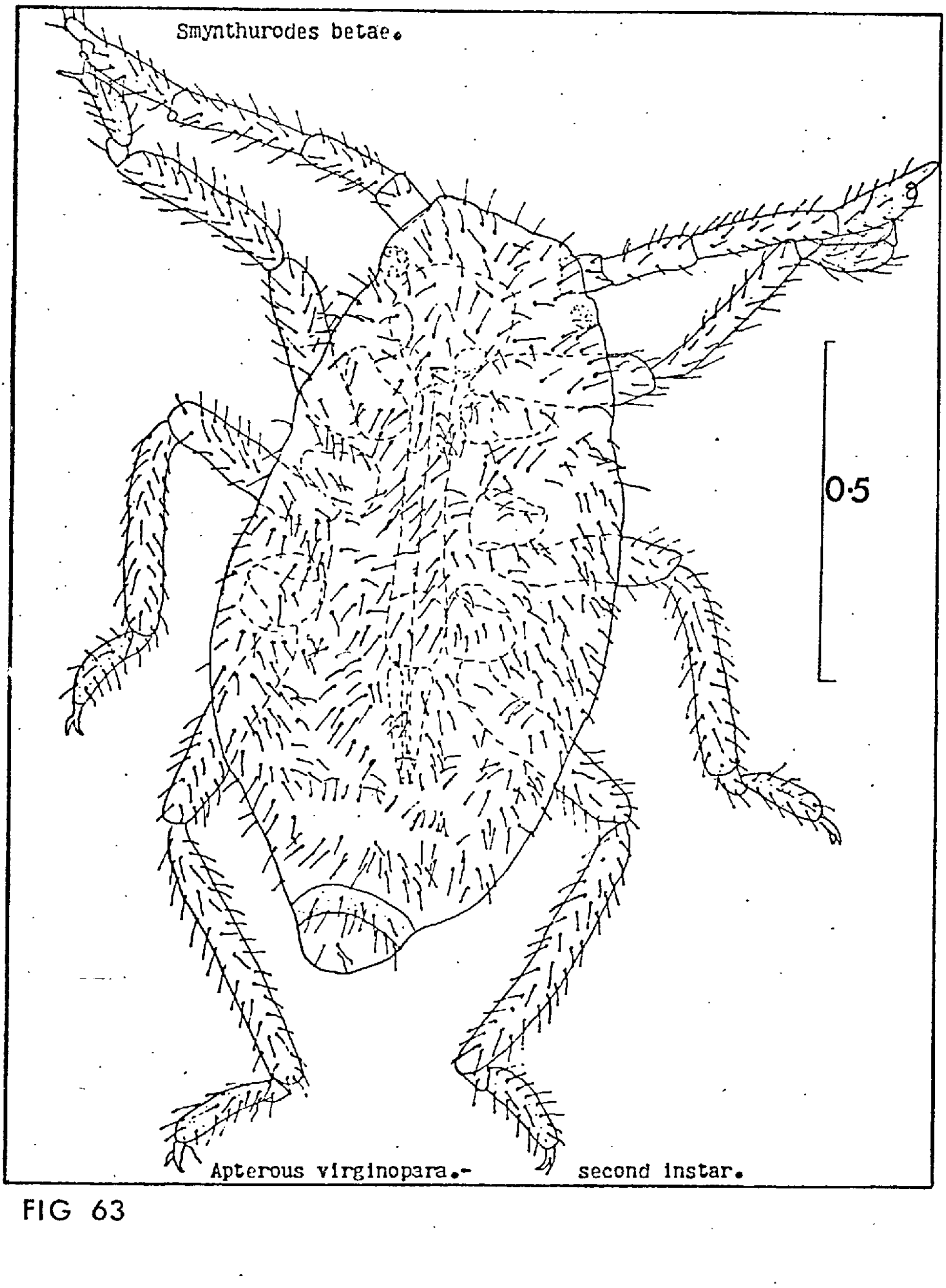

A Smynthurodes betae.
1·0
Alate virginopara.
B Smynthurodes betae.
0·2
Alate virginopara.- Antenna.
C Smynthurodes betae.
i
0·1
Apterous virginopara.- Antenna.
ii
0·1

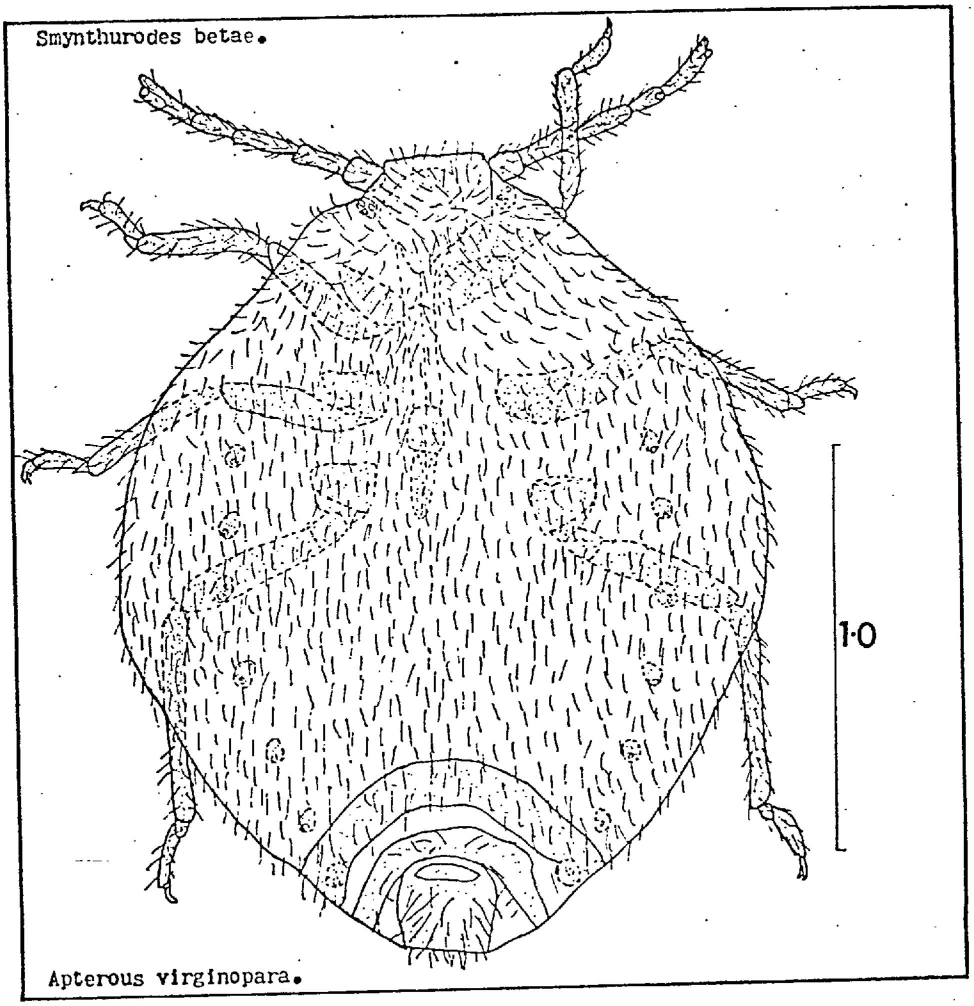
FIG 62



Smynthurodes betae.

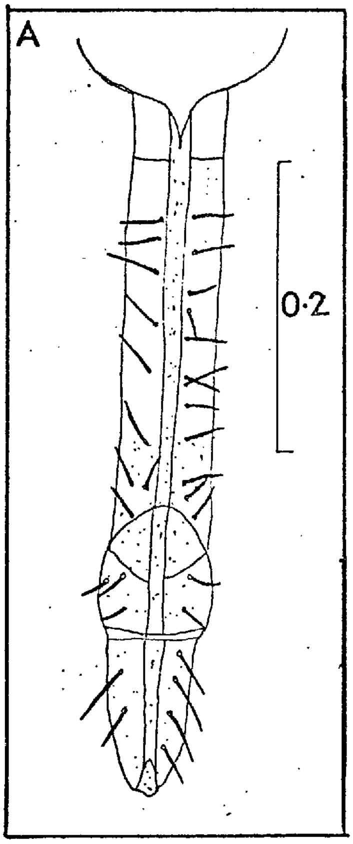
Apterous virginopara.- second instar.

FIG 63

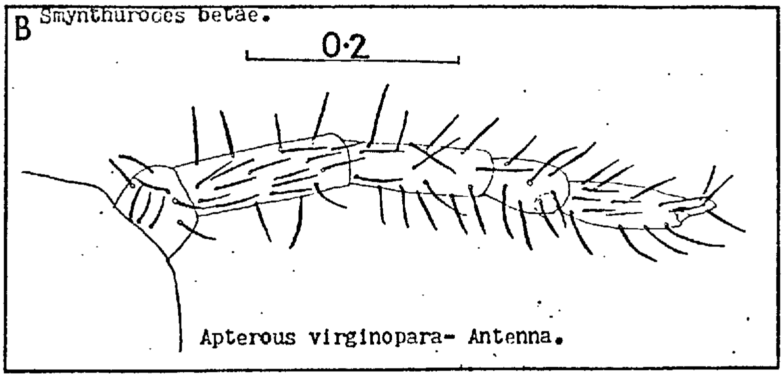

Smynthurodes betae.

Apterous virginopara.

FIG 64

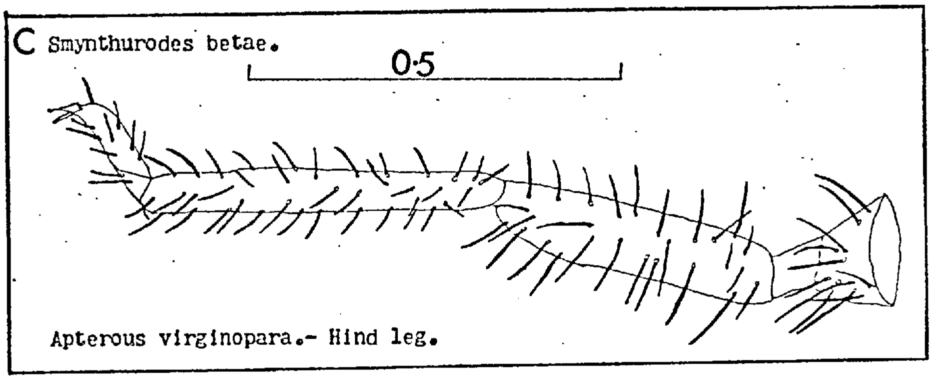


Smynthurodes betae.
Apterous virginopara.
Rostrum.



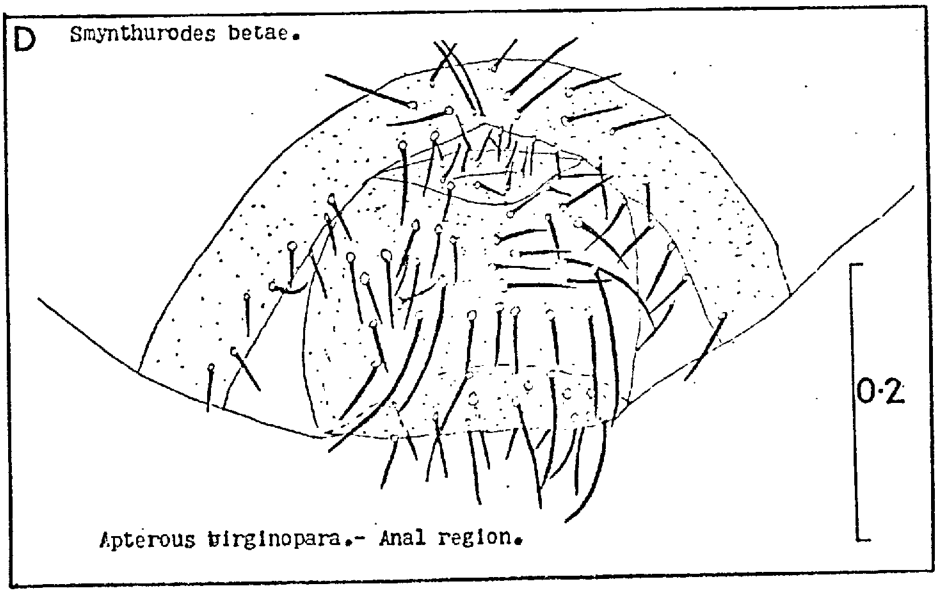
Smynthurodes betae.

Apterous virginopara- Antenna.



Smynthurodes betae.

Apterous virginopara.- Hind leg.



Smynthurodes betae.

Apterous virginopara.- Anal region.

FIG 65

Plate 53. Smynthurodes betae. Alate virginopara.

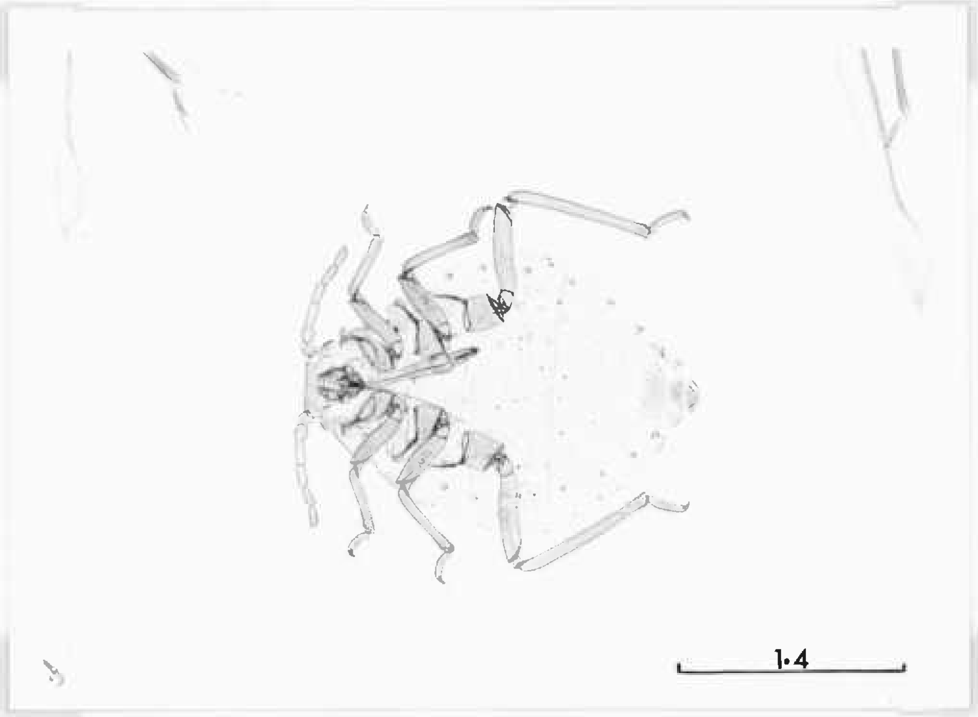


Plate 54. Paracletus cimiciformis. Apterous virginopara.

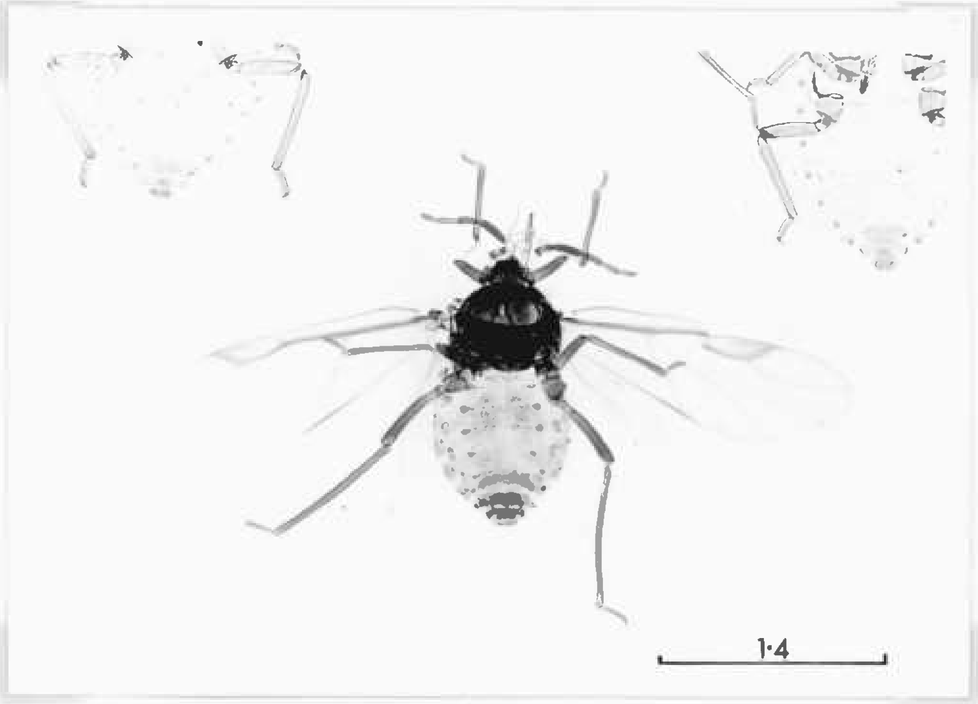


Plate 55. Paracletus cimiciformis. Alate virginopara.

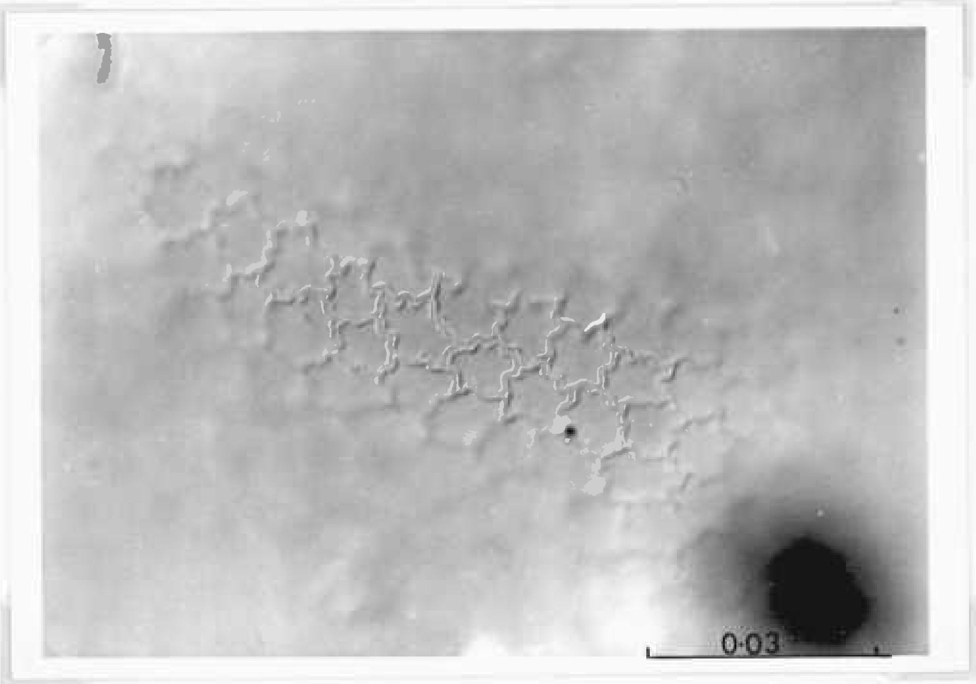


Plate 56. Paracletus cimiciformis. Apterous virginopara, cuticular sculpturing.

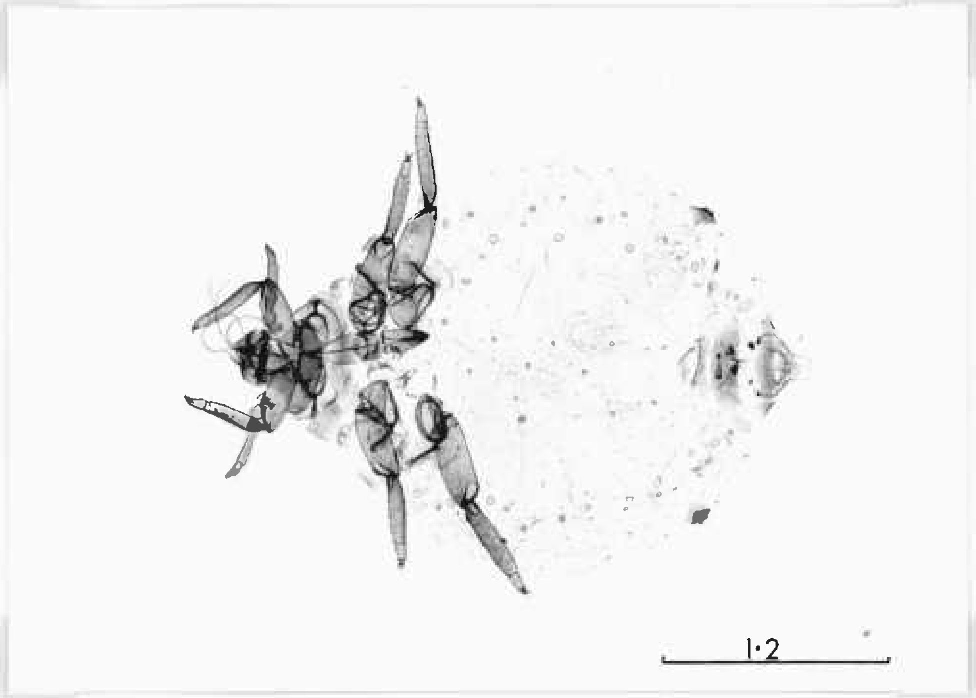


Plate 57. Tetraneura ulmi. Apterous virginopara.

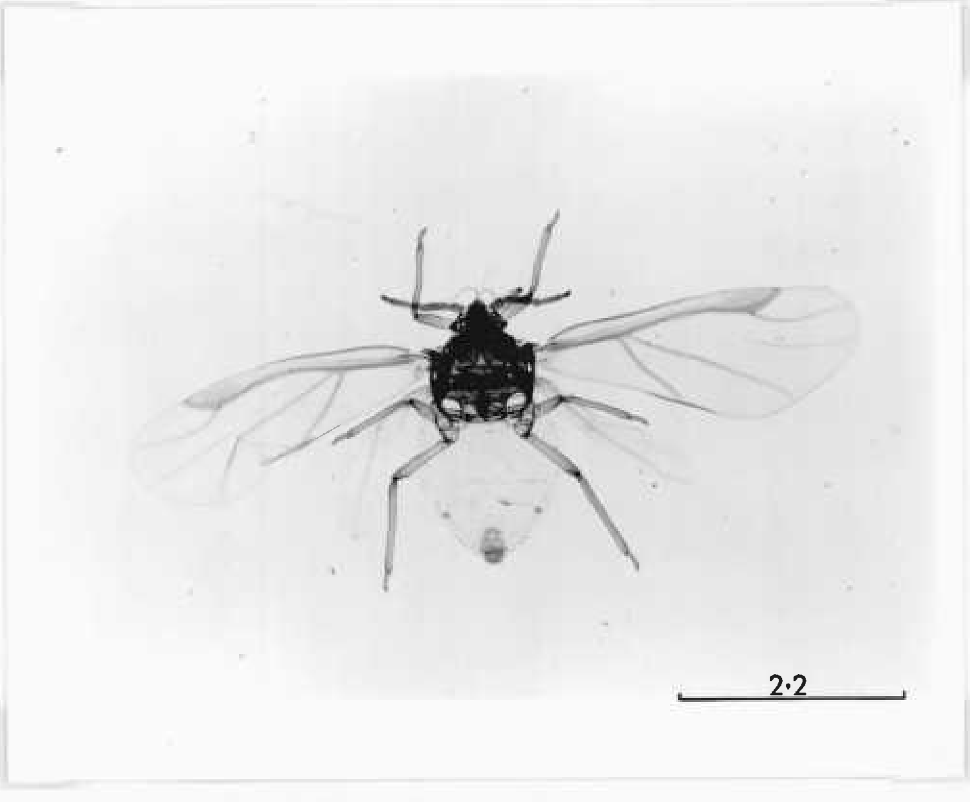


Plate 58. Tetraneura ulmi. Alate virginopara.

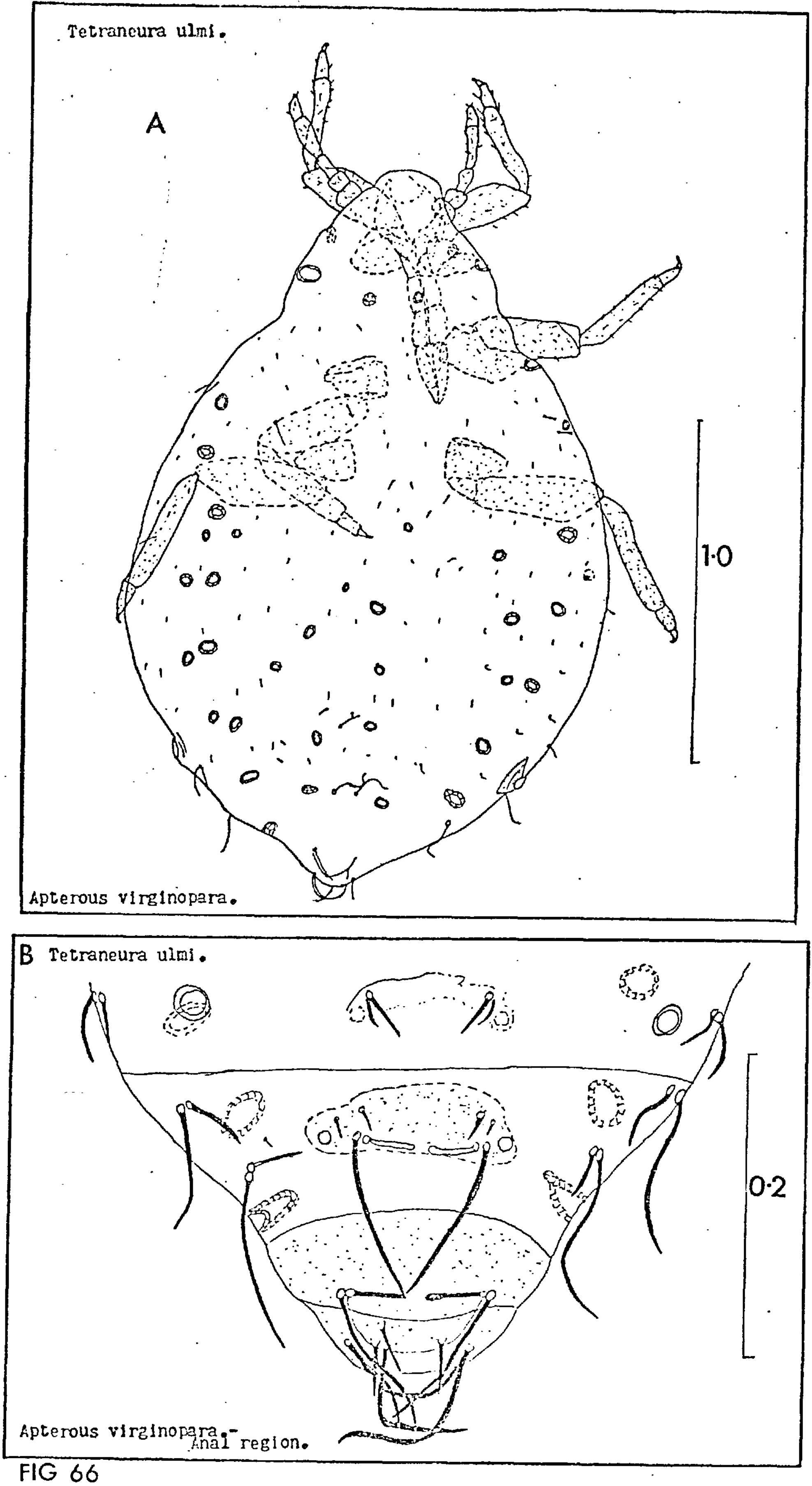
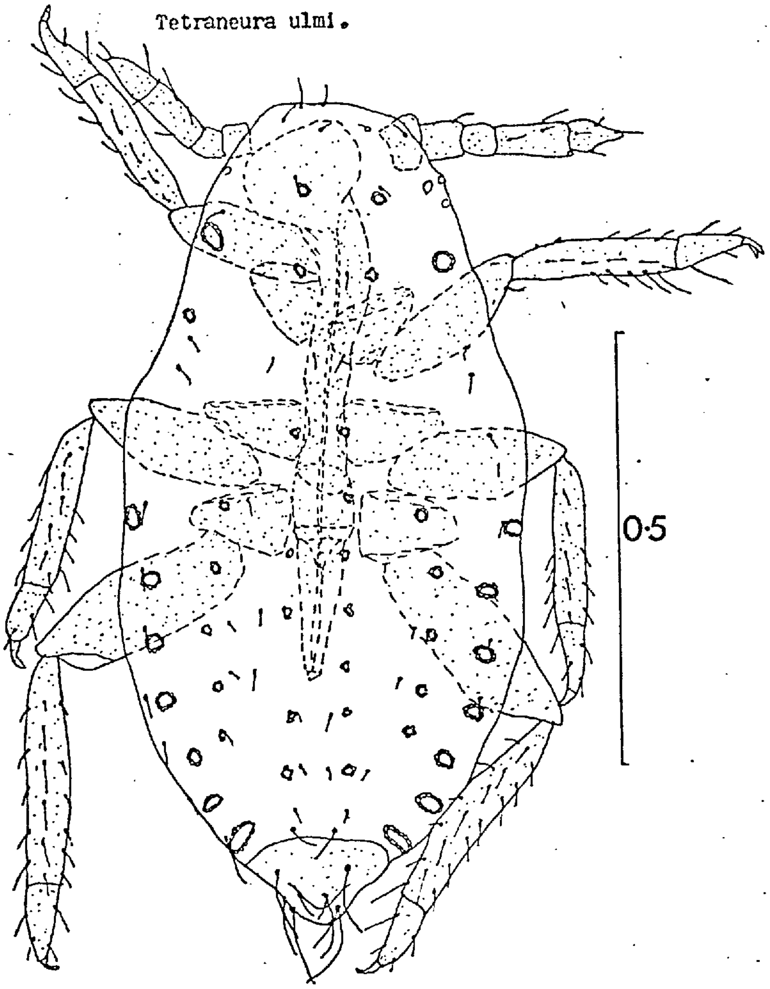

Tetraneura ulmi.
A
1·0
Apterous virginopara.
B Tetraneura ulmi.
0·2
Apterous virginopara.-
Anal region.

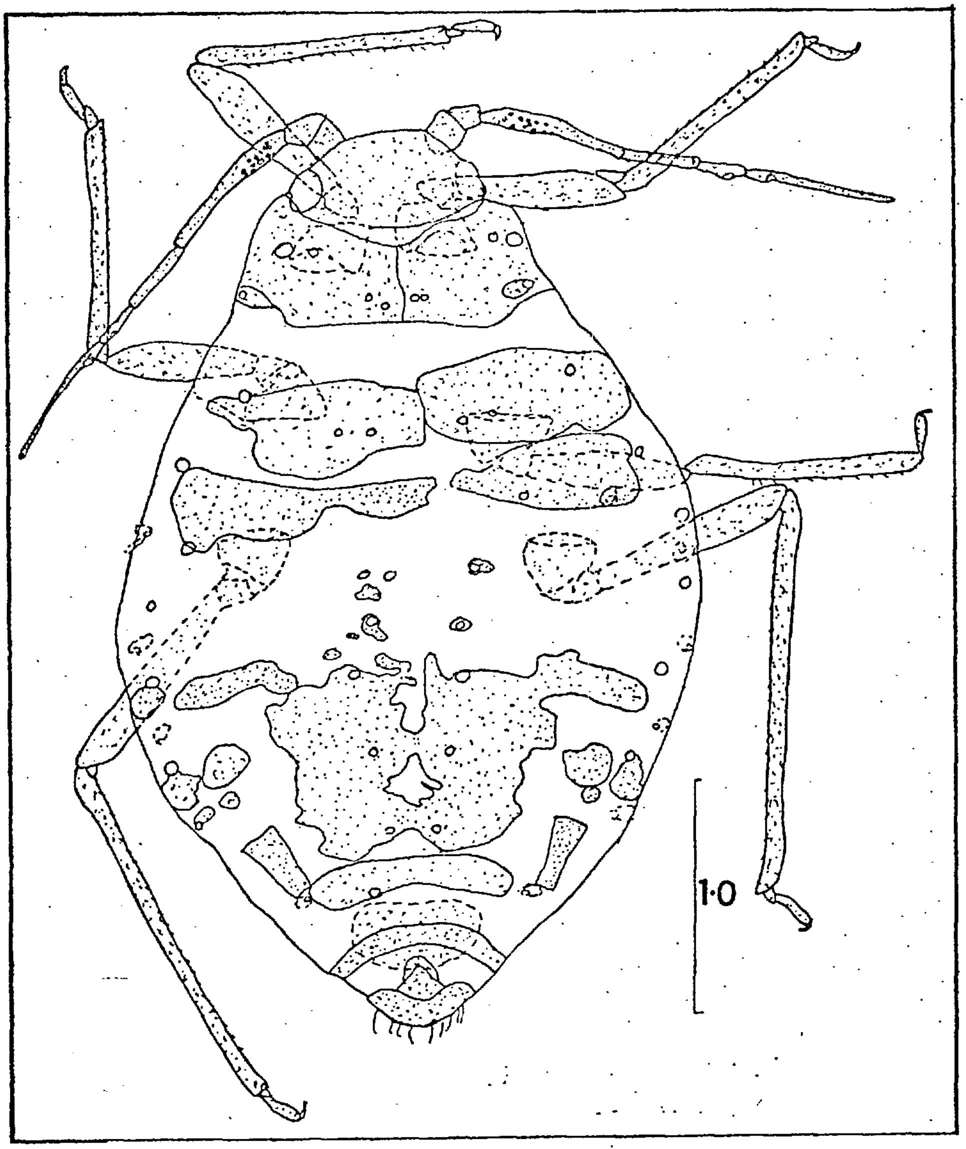
FIG 66

Tetraneura ulmi.



Virginopara.-first instar.

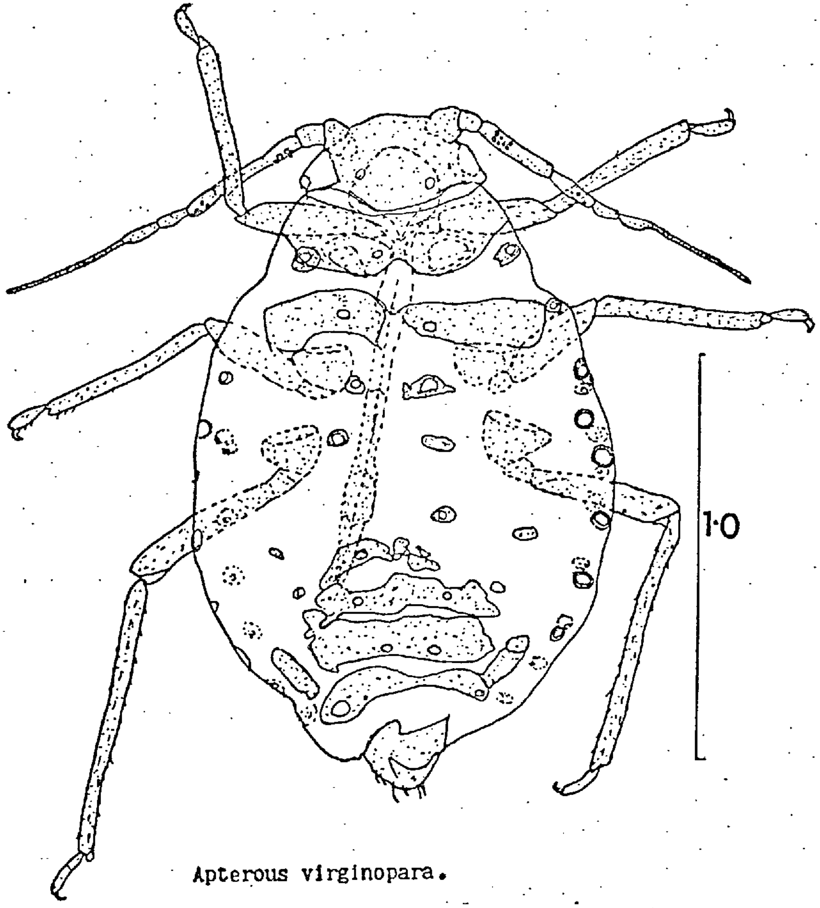
FIG 67



Anuraphis farfarae. Apterous virginopara.

FIG 68

Anuraphis catonii.



Apterous virginopara.

FIG 69

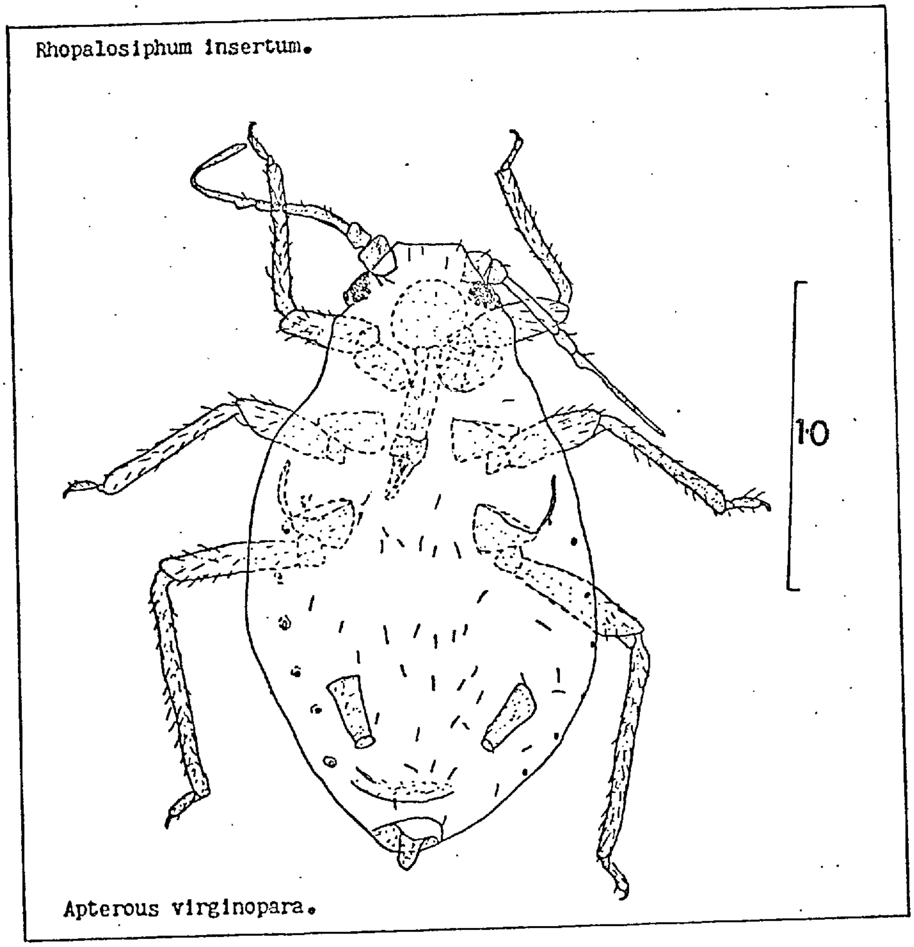
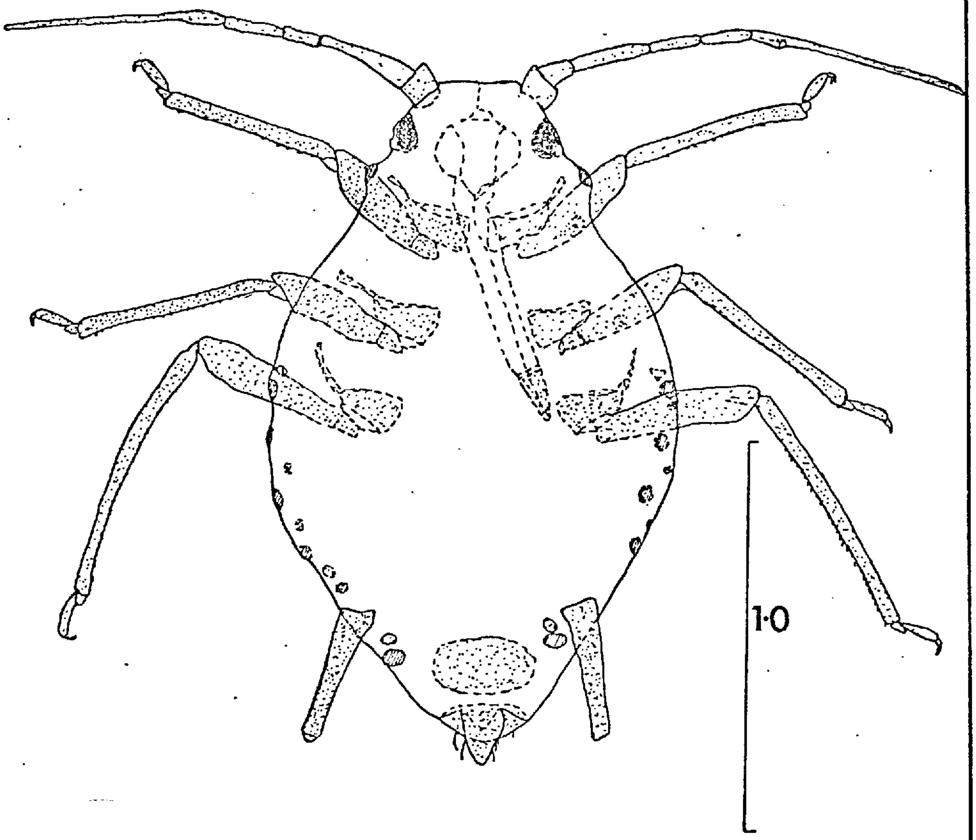


FIG 70

Toxopterina vandergooti



Apterous virginopara.

FIG 71

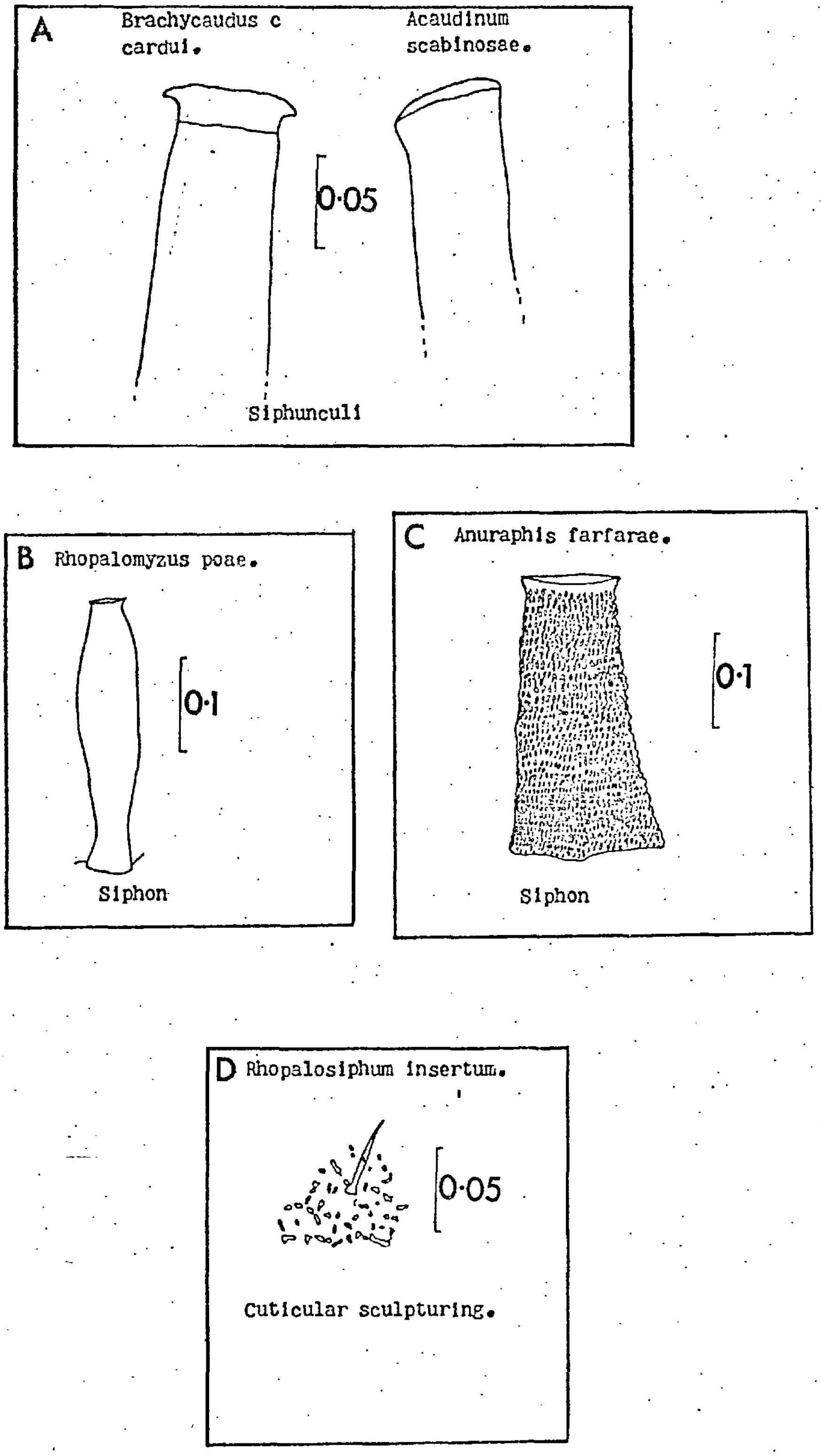

A
Brachycaudus c
cardui.
Acaudinum
scabinosae.
0·05
Siphunculi
B
Rhopalomyzus poae.
0·1
Siphon
C
Anuraphis farfarae.
0·1
Siphon
D
Rhopalosiphum insertum.
0·05
Cuticular sculpturing.

FIG 72

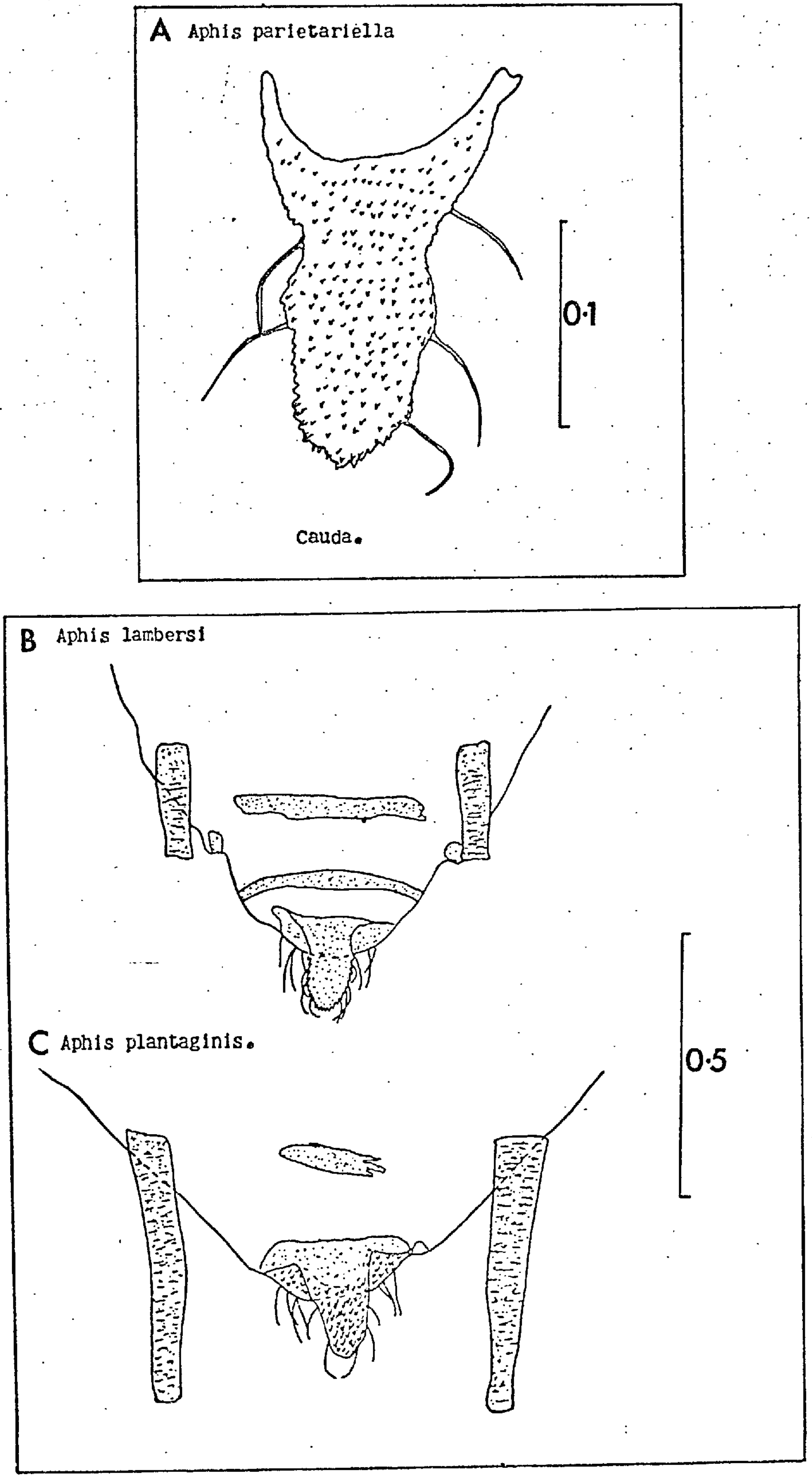

A Aphis parietariella
0·1
Cauda.
B Aphis lambersi
C Aphis plantaginis.
0·5

FIG 73

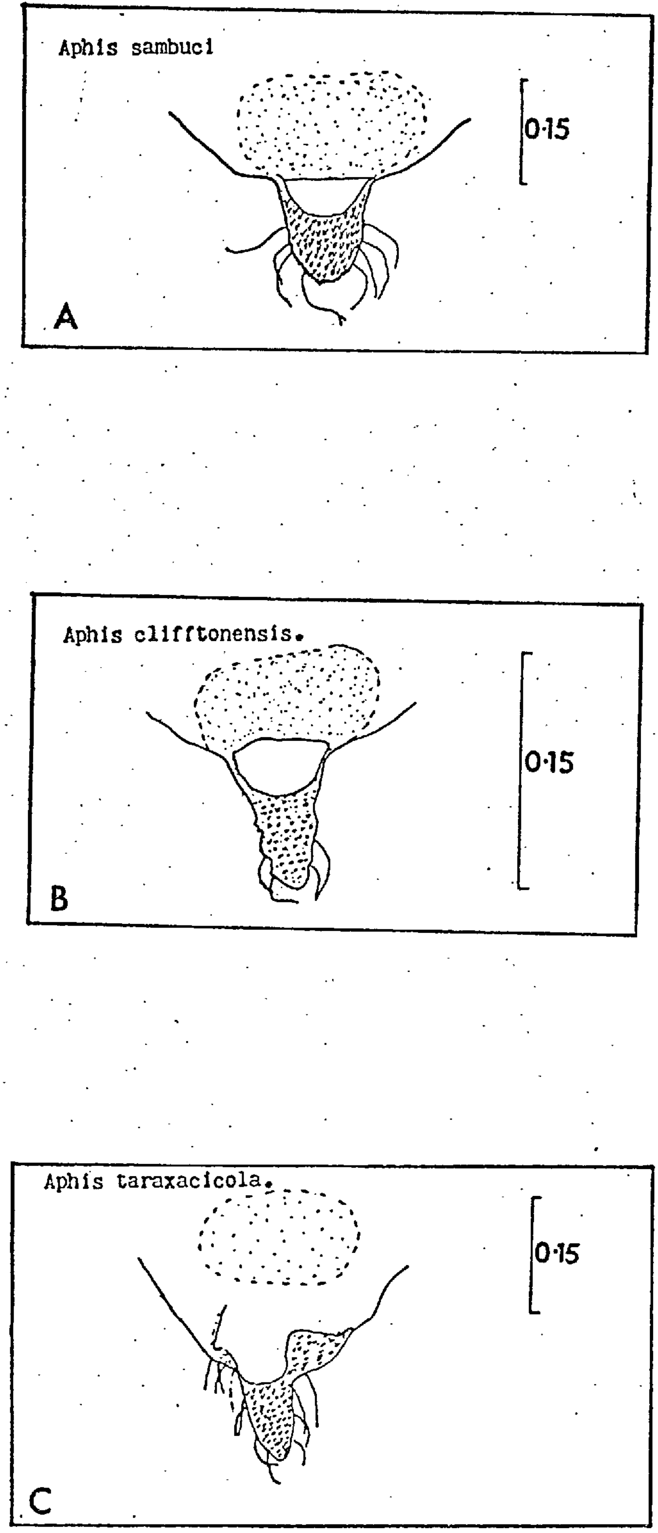

Aphis sambuci
0·15
A
Aphis clifftonensis.
0·15
B
Aphis taraxacicola.
0·15
C

FIG 74

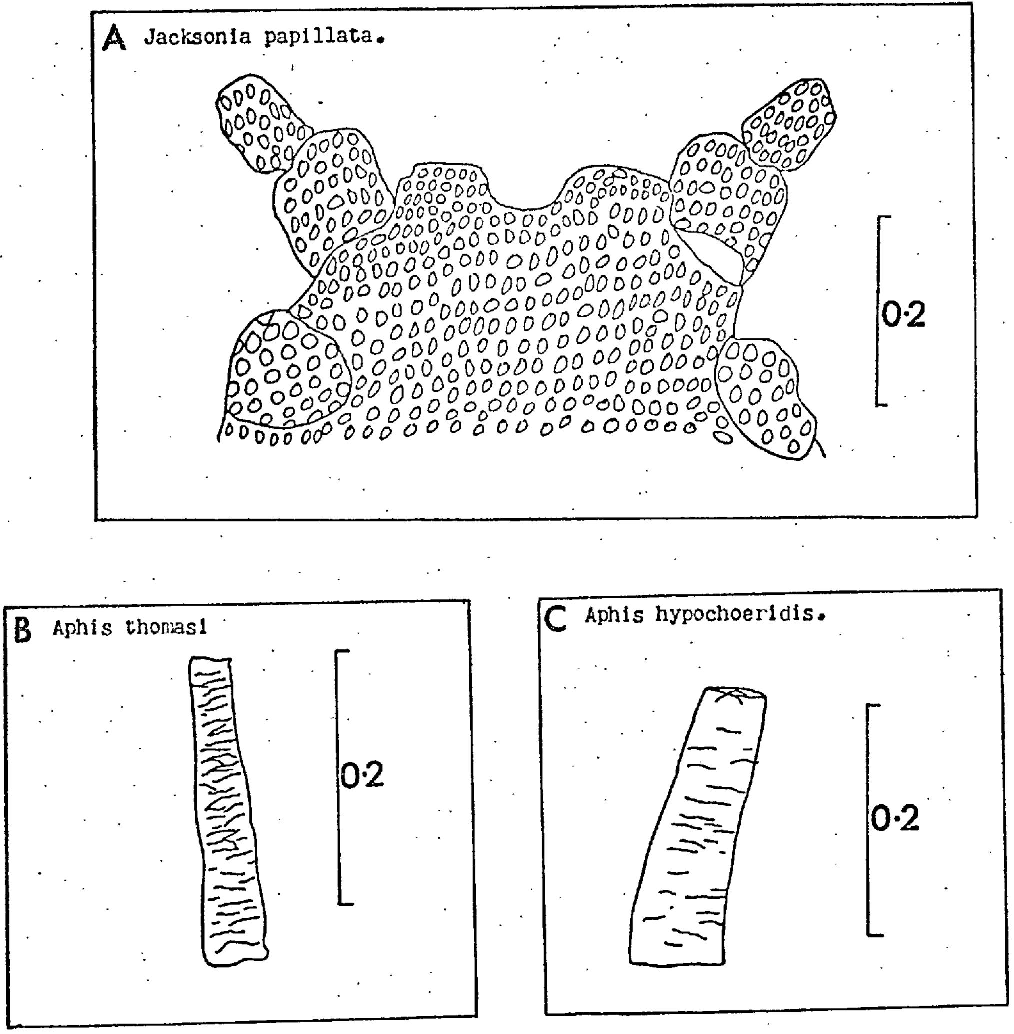
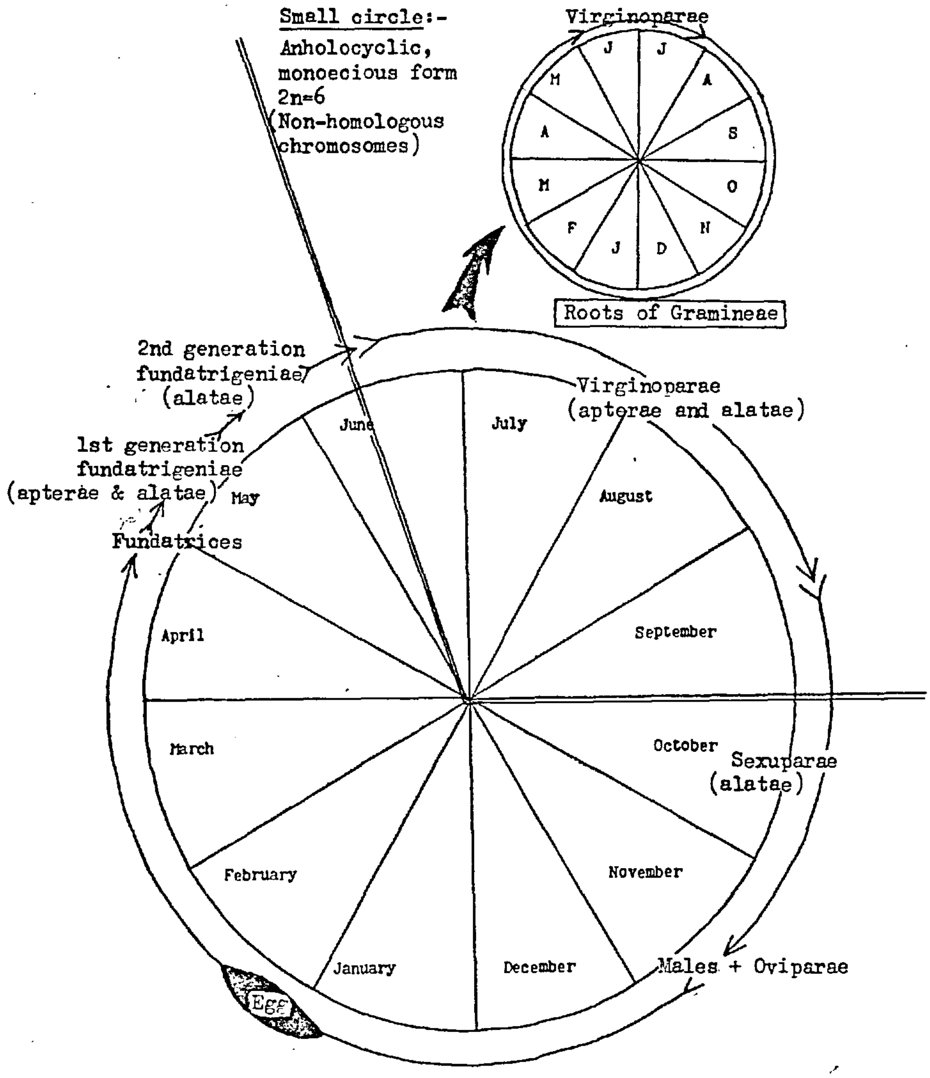

A Jacksonia papillata.
0·2
B Aphis thomasi
0·2
C Aphis hypochoeridis.
0·2

FIG 75

TAXONOMY OF THE SUBFAMILY ANOECIINAE (MORDVILKO) TULLGREN.

Rhinaria are not fringed. The hairs of the dorsum of first instar larvae are usually in single rows. The antennae of young larvae are 5-segmented, those of the adult are 6-segmented. Siphunculi which are flat , cone-shaped and ringed with hairs are lacking in first instars. The sides of the prothorax and the abdominal paratergites bear flat lateral tubercles. These may be missing from abdominal paratergites 5 and 6. Facetted wax glands are absent except in some oviparae. A trophobiotic organ (which probably holds drops of honeydew while ants imbibe them) is present. This organ consists of a distal border of long lash-like hairs on abdominal segment 8, and stiff curved hairs on the cauda and anal plate, all of which point towards the anal opening.

All the secondary host forms are attended by ants. Secondary hosts are roots of Gramineae and Cyperaceae. Primary hosts are the Cornaceae and (if Aiceona truly belongs in the Anoeciinae) the Lauraceae.



Small circle:-
Anholocyclic,
monoecious form
2n=6
(Non-homologous
chromosomes)

Cornus spp.

(The bold arrow indicates
probable line of evolution)

Large circle:-
Holocyclic, dioecious forms
2n=6 and 2n=8.
(Homologous chromosomes)

FIG 76 LIFE CYCLES IN ANOECIA CORNI.

PHYLOGENY OF THE ANOECIINAE.

It is suggested that within the Anoeciinae the genus Paranoecia has evolved farther from the ancestral stock than Anoecia, and within the genus Anoecia the subgenus Neanoecia has evolved farther than the subgenera Anoecia sensuo stricto and Subanoecia.

The genus Paranoecia and subgenus Anoecia (Neanoecia) are monoecious and holocyclic on grass roots. The large size of the oviparae (almost as large as virginoparae) distinguishes them from Anoecia s.s. and Anoecia (Subanoecia) in which the oviparae are dwarf, and perhaps indicates that they are secondarily evolved from virginoparae. Paranoecia pskovica has a very short processus terminalis compared with Anoecia which is a derived character.

Subgenus Anoecia sensuo stricto.

Anoecia corni and A. major seem closely related because they are morphologically very similar. The characters which separate them (see descriptions) are all related to size. The anholocyclic A. corni, holocyclic A. corni and A. major form a natural group.

Subgenus Subanoecia.

A. vagans and A. furcata both have chromosome numbers of 2n=12 (A. furcata also has a population with 2n=13) They have the same number and configuration of accessory rostral hairs and have a similar distribution of spatulate hairs although these are longer on the abdomen of A. furcata. The only major character in which they differ (apart from life cycle) is the number of lateral tubercles, A. furcata has 5 abdominal pairs and A. vagans has 7. They are therefore regarded as a subgenus, Subanoecia.

A. vagans and A. furcata seem to represent a divergence from a common ancestor which is now taking place within Anoecia corni where the holocyclic and anholocyclic forms, although separate, have more morphological similarities.

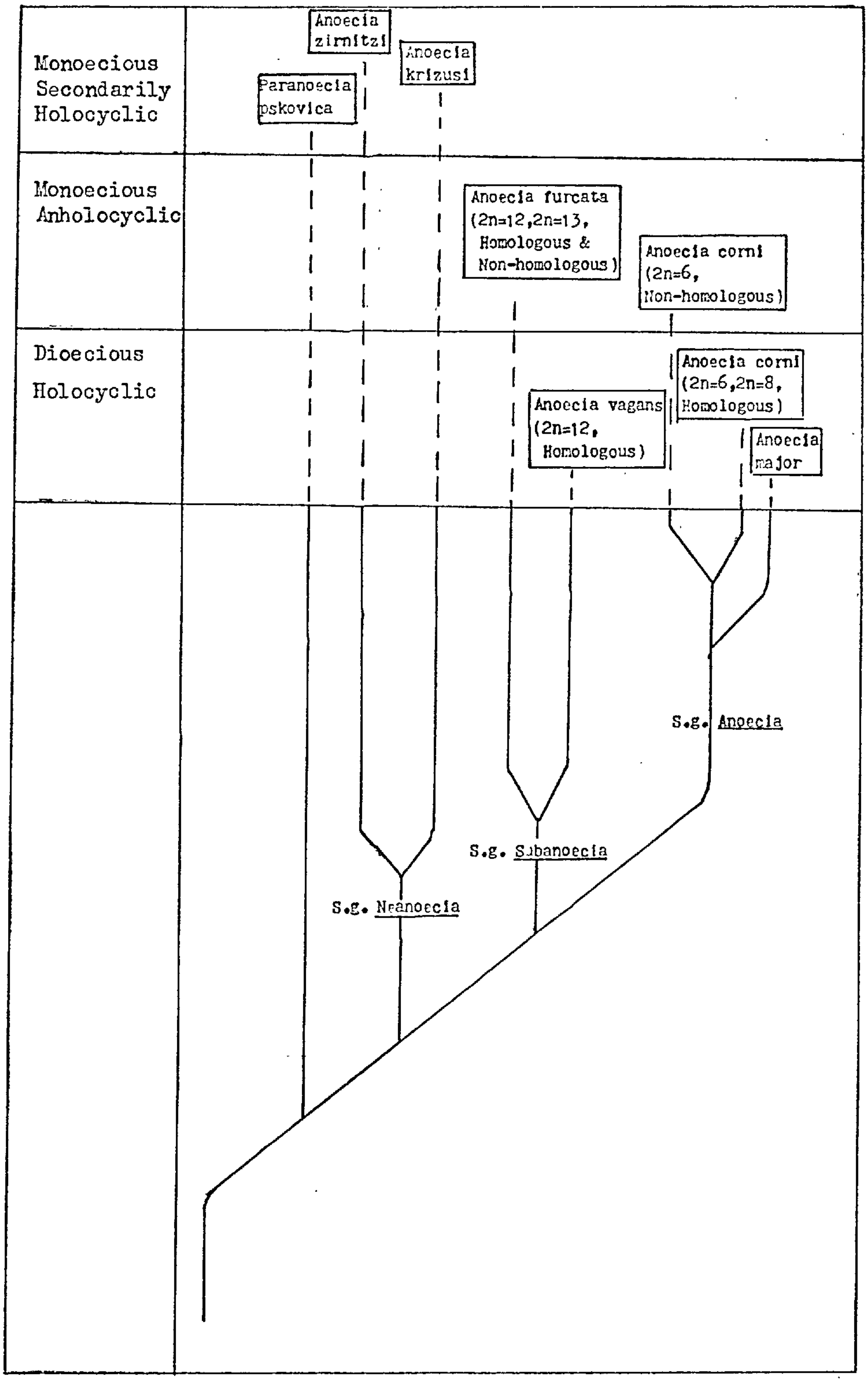


FIG 77 PHYLOGENY OF THE ANOECIINAE

Genus *Anoecia* Koch 1856.
Type species:- *Aphis corni* Fabricius,1775.
Synonyms :- *Schizoneura*: Passerini, 1863,nec. Hartig,T. 1839.
Neanoecia: Borner, 1950, *Subanoecia*: Borner 1950.

Either holocyclic and dioecious, migrating between Cornaceae and roots of grasses or anholocyclic and monoecious on roots of grasses. In the subterranean part of the life cycle they are always found with ants. On Cornaceae they may or may not be attended by ants. The holocyclic dioecious forms lay their eggs in soil beneath Cornaceae, the holocyclic monoecious forms lay their eggs in or near, ants' nests.

The adult virginoparae of most species are grey in colour and are fairly mobile when disturbed. Larval instars of virginoparae are either white or cream and unsclerotized. Most adult virginoparae have a strongly sclerotized 'discoidal plate' stretching from abdominal segments 2 or 3 to 6. Except for *Anoecia zirnitzi* all virginoparae have compound eyes. The processus terminalis of the last antennal segment is finger-shaped and at least one quarter of the length of the whole of the last segment. In the subgenus *Anoecia* ,fundatrices, oviparae and males have 5-segmented antennae, all other adult forms have 6-segmented antennae. Oviparae and males are both dwarf, males are smaller than oviparae. In the subgenus *Neanoecia* ,fundatrices and oviparae have 6-segmented antennae and and oviparae are of normal size. The males are dwarf and have 5-segmented antennae.

Subgenus *Anoecia* s.str. Börner 1952.
Type species: *Anoecia corni*.

The subgenus *Anoecia* s. str. contains *A. corni* and *A. major*. Börner (1952) defined the subgenus by the fact that fundatrigeniae possess a discoidal plate. In addition the present work shows that the dorsal abdomen is clothed in irregular acute hairs except for segment 6 and 7 (sometimes also 5) which bear single rows of hairs, some of which may be spatulate. Virginoparae have 8-17 accessory rostral hairs in two parallel rows, always with at least one hair displaced laterally from each row.

Anoecia corni Fabricius I775.

Synonyms :- agrostidis, Borner I950; corni, Hartig I84I (Schizoneura); disculigera, Borner I950; graminis, del Guercio, I895 (Schizoneura), obscura, Walker, I852 (Schizoneura).

Fundatrix. (Fig.10) (Plate 7).

The antennae are sparsely clothed in acute hairs. Primary rhinaria are small and no secondary rhinaria are present. There are 5 accessory rhinaria clustered around the distal primary rhinarium . The second antennal segment is longer than the first. The legs are clothed in acute hairs and no compound eyes are present, only triommatidia. The last rostral segment has four accessory hairs. Head and thorax bear acute hairs but an occasional spatulate hair is present. These hairs are not as dense as in the apterous virginopara. Abdominal tergites I-7 bear single rows of short (c. 0.0I4) spatulate hairs. The abdomen is sclerotized around the lateral abdominal tubercles. Lateral abdominal tubercles are present on the prothorax and on abdominal segments I-4 and 7. They are usually missing on segments 5 and 6.

In life either dark grey and shiny or if dusted with white wax then light grey. Fourth instars have grey heads and thoraces while the abdomen is mottled greenish brown.

Apterous Fundatrigeniae. (Fig. 11).

Antennae usually 6-segmented. Occasionally the third and fourth segments are not fully differentiated. Secondary rhinaria are present on segments III, IV, V and VI. Antennae and legs are clothed in acute hairs which are more densely placed than in the fundatrix but less densely than in the apterous virginopara. Compound eyes (c. 40 facets) are present as well as triommatidia. The last rostral segment bears 7-8 accessory hairs. The head and thorax are densely clothed in acute hairs. The abdominal tergites bear one row of short(c. 0.0I8) spatulate hairs per segment and the paratergites bear dense acute hairs. Lateral abdominal tubercles are present on the prothorax and abdominal segments I-7. They may be missing from either segment 5 or 6. The dorsal surface of the abdomen is not heavily sclerotized but ventrally the margins are irregularly sclerotized giving rise to serrated darkened margins.

In life the first instars are light grey on the head and prothorax. The meta- and mesothoracic segments and the abdomen are light green mottled with russet brown. Antennae and legs are clear and unsclerotized. Later are nymphs are brown on the abdomen and greenish on the head and thorax.

Alate Fundatrigenia. (Fig. 12) (Plate 8)

Characters as in the alate virginopara except that:-

I. There are not more than 8 accessory hairs on the last rostral segment.
2. The single rows of short acute hairs on the abdominal tergites extend from segments 3-7 instead of from 4-7.
3. Lateral abdominal tubercles on abdominal segments 5 and 6 are often reduced or missing.

In life the adults range from light brown in unsclerotized parts of the abdomen to light grey in sclerotized parts, or in more heavily pigmented specimens from light grey in unsclerotized parts to black in sclerotized parts.

Apterous virginopara. (Fig. 14 A)

Antennae are clothed in dense irregular acute hairs which are about twice as long as the basal diameter of antennal segment III. The distal primary rhinarium on antennal segment VI at the base of the processus terminalis is protuberant and has a group of 5 accessory rhinaria around it. The processus terminalis is finger-shaped and more than 0.25 times the length of the base of segment VI. The legs are clothed in dense irregular acute hairs about as long as the antennal hairs. The hind leg is from I.65 to 2.0I long. The first tarsal segments have 5 hairs on the first leg, 5 or 6 on the second leg and 6 or 7 on the third. Compound eyes have 35- 8I facets. The rostrum is 0.59- 0.85 long. Last rostral segment is 0.I4-0.I7 long. The ultimate rostral segment bears 9-I3 accessory hairs distributed in either 4 parallel rows or in 2 main rows with at least one hairs offset from each row. The head is clothed in dense irregular acute hairs and is more or less fused to the prothorax bears a pair of large (0.075 in diameter) lateral tubercles.

p 55
fig 15

?

?

Abdominal segments I & II bear broad sclerotized strips. Segments 3 to 6 have a central sclerotixed discoidal plate. Segments I-7 have lateral sclerotized paratergites and segments 7 and 8 bear narrow transverse sclerotized strips.

Siphunculi are cone-shaped rings surrounded by 3 or 4 rings of acute hairs. The abdomen is clothed in irregular dense acute hairs (approximately 2 times the basal diameter of antennal segment III) except for segments 6 and 7 (occasionally also 5) which have more regularly arranged hairs, often in a single row, often these hairs are spatulate. Segment 7 has 4 hairs in a single row while segment 8 carries 9-I2 long bristles which curve towards the anal opening. The cauda and anal plate also carry stout inward curving bristles. (The stout hairs on segment 8, the cauda and the anal plate constitute the trophobiotic organ). Lateral tubercles occur on abdominal segments I-7, those on the prothorax and abdominal segments I-7 are the largest while those on segments 5 and 6 are often reduced, occassionally missing. Gonapophyses are indistinct.

In life the abdomen is light greenish grey except for the sclerotized margins, cauda, sub-genital plate and anal plate which are dark grey. The dorsal abdomen, thorax and head are all sclerotized and dark grey.

Distinguished from Anoecia vagans by possessing long irregular acute hairs on the dorsal surface of abdominal segments I-5. Anoecia vagans has single rows of short hairs with incrassate or spatulate apices.

Apterous virginopara first instar. (Fig. 13)

Antennae are 5-segmented and sparsely haired with acute hairs. Primary rhinaria are present with a cluster of 5 accessory rhinaria around the distal primary rhinarium. There are irregular acute hairs on the dorsal surface of the head, thorax and abdominal segments I-4. On abdominal segment 5 one or two of the hairs may be spatulate. On abdominal segments 6 and 7 most of the hairs are spatulate. Siphunculi are absent. Lateral tubercles are present on the prothorax and on abdominal segments I-7.

In life the specimens are pale green in colour.

Alate virginopara. (Fig.14 B.) (Plate 10)

Antennae are 6-segmented with larger primery rhinaria than in the apterae. 5 accessory rhinaria are clustered proximally to the primary rhinarium on segment VI. Transversely elongate secondary rhinaria are present on segments III, IV, V and VI. Antennae are densely covered in acute hairs. There are large compound eyes (80-I20 facets) as well as triommatidia. The rostrum reaches the third pair of coxae. Hairs on the last rostral segment are as in the apterae. The thorax is heavily sclerotized and the legs are clothed in dense acute hairs.

Transverse sclerotized bands are found on abdominal segments I and 2. These are located centrally and extend for about I/5 of the width of the abdomen. They are covered with numerous acute hairs. Abdominal segment 3 has dense acute hairs and segments 4-7 have single rows of very short (0.0I7) acute hairs sometimes spatulate but,as they are so small,the apices are difficult to distinguish. The trophobiotic organ is as in the apterae. The discoidal plate extends to the sides of the abdomen on segment 5 and 6. On segments 3 and 4 there is an unsclerotized gap between the discodal plate and the side of the abdomen. Segments 7 and 8 have sclerotized cross bands. Lateral tubercles are present on the prothorax and abdominal segments I-7. Those on the prothorax and abdominal segments I and 7 are the largest. Those on segments 5 and 6 are often reduced but not so reduced as in the apterae. Each lateral tubercle has an island of sclerotization densely covered in acute hairs.

Wing venation:- Forewing, the pterostigma is large and distinctive, the radial sector is curved and the proximal third of the once forked media is missing. CuI and Cu2 are clearly separated at the base and diverge outwards. Gonapophyses are indistinct.

Hind wing, CuI and Cu2 are widely separated at the base and diverge outwards.

In life the underside of the abdomen is light grey. The underside of the metathorax and mesothorax is black and the underside of the prothorax is light grey. The head, thorax (dorsal) and the antennae are black due to sclerotization. There is a light grey unsclerotized section between the discoidal plate and the thorax with three black cross bands and black sclerotized patches along the side of the abdomen. The discoidal plate is dark grey.

Alate viviparae are distinguished from <u>Anoecia vagans</u> by the dense acute hairs on the sclerotized patches of abdominal segments I and 2. <u>Anoecia vagans</u> has single rows of short spatulate hairs on these sclerotized patches.

<u>Sexuparae</u>. (Figs. 16 & 19)(Plate 11).

Characters are the same as for the alate virginoparae except that there are on average more secondary rhinaria on the third antennal segment(9-I6; mean II.6, SE.± 0.4I) and the eyes are larger than in the alate virginopara (77-II0; mean,I03.6, SE.3.6I). Sexuparae are on average larger than alate virginoparae. Body length 2.I-2.55, (mean,2.36, SE.± 0.05.)

<u>Sexuales, First instar</u>. (Fig. 17 A).

The males are much lighter brown than the adult males but are nevertheless distinguishable from the very pale green oviparae. As development proceeds males become darker and the females become a darker green with a black patch in the centre of the abdomen.

Oviparae. (Fig. 17 B).(Plates 13 & 14)

The antennae are 5-segmented and the legs and antennae are sparsely covered in acute hairs. Compound eyes are absent, only triommatidia are present. The head, thorax and abdomen have acute hairs but not in such distinct rows as in the male and they are somewhat smaller(c. 0.046). The head is slightly sclerotized but the thorax and abdomen are unsclerotized except for the small isolated patches. Even the sub-genital plate and cauda are very lightly sclerotized. Siphunculi are present. Lateral tubercles are present on the prothorax and on abdominal segments 5 and 6. The body is less elongate than in the male and somewhat larger (1.I7). The antennae are shorter than in the male.

In life the legs and antennae are whitish to very pale green and the eyes are black. The abdomen is very pale to pale green except for a central dark patch. Specimens move about,but not as readily or as quickly as the males. As maturity proceeds the entire ovipara darkens and becomes brownish grey in the adult.

Male. (Fig. 18) (Plates 13 & 14)

The antennae are 5 segmented and bear sparse acute hairs. There are primary rhinaria on the ultimate and penultimate antennal segments. The distal primary rhinarium has a cluster of accessory rhinaria. Small compound eyes are present as well as triommatidia (5-I0 facets). The rostrum reaches to the third pair of coxae. The last segment has 6 accessory hairs. Single rows of long (0.052) acute hairs are found, one per segment on the abdomen, thorax and head with 5 hairs in each row. Abdominal tergites are sclerotized in bands with slight unsclerotized intersegmental gaps. Siphunculi are absent. There are lateral tubercles on the prothorax and abdominal segments 1-4 and 7. The body is elongate and dwarf, length c. 0.9. The antennae are longer and the body is more elongate than in the oviparae.

In life the antennae and legs are white, tarsae are black and the eyes dark. The head and thorax are light brown and the abdomen dark brown. Males are active in contrast to oviparae. The end of the abdomen curves underneath with a lobe-like unsclerotized aedeagus.

Biology.

There are at least 3 populations of Anoecia corni. One is anholocyclic on grass roots and has a chromosome number of 2n=6, the other two are holocyclic and dioecious with Cornus spp. as the primary host and roots of grasses as secondary host and have chromosome numbers of 2n=8 and 2n=6. Specimens with chromosome numbers of 2n=7 have been recorded which may represent hybrids between the 2n=6 and 2n=8 forms.

It has been possible to separate the 2n=6 and 2n=8 forms on the basis of size (see appendix) but no morphological characters that are not dependent on size have been found. 34 fundatrices and fundatrigeniae were examined and 18 were found to have a chromosome number of 2n=8, 9 were found to have a chromosome number of 2n=6 and 1 of 2n=7. Six specimens could not be determined.

The anholocyclic populations are infrequent. They have been recorded from Berwick 20/11/47; Knowle 7/11/74; South Kensington 5/2/76; Silwood Park 6/2/76 and 27/2/76and Llanwrtyd Wells 16/2/76.

Life Cycle.

At the end of April the first instar fundatrices of the holocyclic populations emerge from the overwintering eggs which were laid in the soil at the base of dogwood* shrubs. The young fundatrices crawl up into the opening flower and leaf buds. They commence feeding right inside the clustered leaves and flowers and are difficult to find. The first generation of fundatrigeniae contains both apterae and alatae. The apterae continue feeding on the flowers and leaves of dogwood while the alatae migrate to grass roots. Fundatrices and fundatrigeniae were transferred from Cornus sanguinea to Cornus stolonifera. The second generation of fundatrigeniae are all alatae and migrate to grass roots. The migration from dogwood is normally complete by the middle of June but exceptionally fundatrigeniae have been found on dogwood in August.

The progeny of migrants from dogwood reproduce on grass roots and alate virginoparae are produced reaching a peak towards the end of August. Sexuparae begin to appear on dogwood in the second week of September and normally continue to arrive until early November. The sexuparae usually feed on the large veins on the undersides of leaves. Sexuparae may be found feeding singly but they are normally gregarious and as many as 25 may be found on one leaf. When disturbed the sexuparae pivot on the pro- and mesothoracic legs and the rostrum

*Cornus spp.

and waves the abdomen from side to side, causing the wings also to sweep from side to side. If further disturbed they will withdraw their rostra and walk away. In order to locate each other on the leaf the sexuparae must walk around the dogwood, and as the majority of colonies are lower down (approximately within four feet of the ground) they probably alight towards the top of the plant and work their way down. The gregarious behaviour of sexuparae may serve two purposes. Firstly, it ensures that males and oviparae from different individuals are close to each other and the chances of cross fertilisation are increased. Secondly, aggregating in colonies makes it more likely that ants will find the honeydew and attend the aphids. Only about a third of the colonies found were attended by ants, either Lasius niger or Myrmica rubra. Spring colonies have been found attended by Formica rufa (Pontin pers. comm.).

Virginoparae of A. corni on grass roots were never observed to eject honeydew even those kept in the absence of ants always extruded drops which were held at the anus by the trophobiotic organ. Sexuales however are able to expel drops of honeydew to some distance by a contraction of the rectum. This suggests that colonies on dogwood are not attended sufficiently often for them to rely on ants for the removal of honeydew and are adapted to remove honeydew for themselves. They were subject to predation by an unidentified Syrphid larva and ants may provide some protection. White syrphid eggs (Plate 14) were found on the underside of leaves in close proximity to aphid colonies The larvae which emerged were found to feed voraciously on Anoecia corni. After settling on dogwood, sexuparae rapidly produce both males and oviparae. Embryos within sexuparae which have arrived at dogwood are all at about the same stage of development. 117 males and 496 oviparae were taken from 36 leaves.

The sexuales also feed on the large leaf veins and tend to cluster about the sexuparae. The males have 2 larval instars and the oviparae have 3 larval instars. As development proceeds the males, which have relatively longer antennae than the oviparae and have compound eyes, become more active than the oviparae and mating takes place on the leaf. Mature oviparae in which the two dark overwintering eggs can be seen, walk down the dogwood stems and lay their eggs in the soil. Mature oviparae have a circle of wax strands around the anus. The eggs are shiny black and elongate oval in shape.

Host plants.

Gramineae:-Found twice on Agropyron repens; Dactylis glomerata x 50+; Festuca sp. x 2; Festuca rubra x3; Holcus lanatus x6; Holcus sp.x1; Hordeum sp.x1; Poa sp. x1; Molina caerulea x1; Agrostis sp. x1.

Cornaceae:- Cornus sanguinea x 29; C. stolonifera x16; C. mas x2; C. glabrata x2; C. amomum var. augustifolium x2; C. walteri x2; C. rugosa x1 ; C. alba var. sibirica x1; C. alba var. gouhault x1; C. obliqua x1; C. stolonifera var. flaviramea x1; C. officinalis x1; C. australis x1.

A. corni apterae were successfully transferred from Dactylis glomerata to Phragmites communis on 19/8/75 and were still feeding by 27/8/75.

Relationship with ants.

On Gramineae:-Lasius flavus 8 records; L.niger x12; Myrmica rubra x30+; L. alienus x1.

On Cornaceae:- Formica rufa x1(Pontin pers comm.); L.niger x20+; Myrmica rubra x20+; Formica fusca x1.

One spring population attended by Formica rufa was found by Dr. A.J. Pontin (Pers. comm.)in Shrubbington Wood, Berkshire. In the present study about 1/10 of the spring populations were attended by Lasius niger and one population was found with Formica fusca.

About 1/3 of the autumn colonies found on dogwood on chalk downland were attended by Lasius niger and Myrmica rubra in approximately equal numbers. Autumn colonies found on clay or sandy soils, if attended, were attended by Lasius niger.

Populations on grass roots were always found with ants. Anholocyclic poulations on grass roots were found with Lasius niger and in mounds of Lasius flavus.

Predators and Parasites

Aclitus obscuripennis Forst (Braconidae) was reared from the 2n=8 form of A. corni feeding on Dactylis glomerata at Denham, Bucks. 30/7/76.

Habitats.

Grass roots.

On canal banks, lawns gardens, commons, disused railways, in rough grass in either chalky or sandy conditions. On grass growing on sandy beaches and on mountain sides up to 1000 feet.

Cornus spp.

On chalk downland, in low hedges, on canal banks and anywhere where small thickets of Cornus sanguinea occur. On Cornus stolonifera in wetter habitats, bogs, and banks of streams and lakes.

Anoecia major Börner 1950. (Fig. 20)

Synonyms :- ? *Schizoneura obscura* Walker 1852.

Apterous virginoparae.

Similar to *A. corni* except for the following characters associated with greater size:-

(a) Body length is greater, 2.46-2.8(mean 2.58 SE.± 0.046.)

(b) Rostrum length is greater 0.28- 0.38 (mean, 0.87 SE. ± 0.038)

(c) The rostrum/body length ratio is also greater, 0.28-0.38, (mean,0.34, SE.±0.02). For data relating to *A. corni* see table

Alate virginopara.

Specimens collected by Dr.V.F.Eastop and Dr.D.Hille Ris Lambers (from *Phalaris arundinacea*, Wageningen, Netherlands, 29/9/71),now in in the collection of the British Museum(Natural History) appear to be alate virginoparae and not sexuparae. They are not significantly smaller than sexuparae transferred from *Phalaris arundinacea* to *Cornus alba* by Dr. H.L.G.Stroyan (pers. comm.) but have a smaller mean number of secondary rhinaria on antennal segment III(13-15, mean, 15.5 SE.± 0.31. In other characters they resemble the sexuparae.

Sexuparae.

Similar to *A.corni* except for the following characters:-

(a) Body length is greater,2.34-2.69 (mean 2.56 SE. ±0.046.)

(b) Rostrum length is greater,0.74-1.0 (mean 0.86 SE.± 0.039).

(c) Number of secondary rhinaria is greater,16-21 (mean 18.9 SE.±0.44).

Biology.

The secondary host is stated by Börner(1948) and Zwölfer (1957) to be *Phalaris arundinacea*. In Britain it has been taken from *Phalaris arundinacea* and possibly *Calamagrostis* sp. Börner(1948) gives the primary host as *Cornus sanguinea*. Stroyan (Pers. comm.) transferred sexuparae of *A. major* from *Phalaris arundinacea* to *Cornus alba*.

Distribution.

Recorded from England, France, Hungary, Netherlands, and Germany.

Taxonomic Status.

All the characters which separate *A. major* from *A. corni* can be related to greater size. It is possible that this is an effect of the host plant, *Phalaris arundinacea* on *Anoecia corni*. Unfortunately as no *Anoecia* were found on *Phalaris arundinacea* during the course of this study it was not possible to attempt a transfer of *A. major* to other grass roots.An attempt to transfer *Anoecia corni* to *Phalaris arundinacea* was unsuccessful.

Subgenus *Subanoecia* Börner 1952.

Type species: *Anoecia vagans*.

Börner (1952) defined the subgenus *Subanoecia* by the fact that the alate fundatrigeniae lack a discoidal plate. Evidence from morphology and cytogenetics in the present work suggests that *A.vagans* and *A.furcata* are closely related and *A. furcata* is therefore included in the subgenus *Subanoecia*.

Morphology:-

Both species possess a similar number of accessory rostral hairs.

	A.vagans.	*A.furcata*.
Apterous virginoparae:	4-7(m.5.8,SE ±0.44)	6-8(m.7.5,SE±0.2)
Alate virginoparae:	6-7(m.6.14,SE ±0.14)	6-8(m.7.0,SE±0.37)

The accessory rostral hairs are in two parallel rows and do not have any hairs displaced from the row. Apterous virginoparae of both species possess spatulate hairs which in some forms are found over the whole dorsal surface.

Virginoparae of both species have a small number of secondary rhinaria on the third antennal segment (compared with *Anoecia* s. str.).

	A.vagans.	*A.furcata*.
Apterous virginoparae:	0-4(1.58,SE± 0.4)	0-5(m.0.79±0.32)
Alate virginoparae:	7-10(m.7.9,SE±0.38)	6-10(m.8.5±0.15)
	A.corni.	
Apterous virginoparae:	0-11(m.3.7,SE±0.28)	
Alate virginoparae:	9-12(m.9.9,SE±0.31)	

The few specimens of *A. disculigera* that it has been possible to examine are morphologically similar to *A. vagans* except for the possession of larger lateral tubercles, and it is included in *Subanoecia*.

Anoecia vagans/(Koch 1856) (Schizoneura). (Figs. 28-32)(Plates 18-20) ?

Synonyms :- cerealium Szanislo, 1880/1 (Schizoneura), kochii Lichtenstein 1885(Schizoneura), ? radicicola Mokrzecky, 1903(Schizoneura), rossica Cholodkovsky 1897 (Colopha), venusta Passerini 1860 (Schizoneura), viridis Borner and Blunck, 1916,willcocksi Theobald, 1915.

Alate fundatrigeniae/ (Fig. 28) (Plate 18) ?

Secondary rhinaria are present on antennal segments III and IV. The distal primary rhinarium has four accessory rhinaria. The antennae are sparsely clothed in acute hairs (c.0.065). Compound eyes with about 45 facets are present. The rostrum reaches to the third pair of coxae and the last rostral segment bears four accessory hairs. Head and thorax bear long acute hairs (c. 0.069). The abdomen bears single rows of acute hairs (0.052), one row per segment and is unsclerotized except for occasional small patches around hair bases. Lateral tubercles are present on the prothorax and abdominal segments 1-7. The longest are approximately 0.04 in diameter (compared with c. 0.14 in alate fundatrigeniae of Anoecia disculigera).

In life the head and thorax are light grey and the abdomen is green. Nymphs of alate fundatrigeniae are green.

Apterous virginoparae/ (Fig. 30)(Plate 20) ?

Antennae are 6-segmented and clothed in a mixture of spatulate and acute-ended hairs (c. 0.081). Secondary rhinaria present on antennal segments III, IV and more rarely on V and VI. Compound eyes are present (30-40 facets). The rostrum is 0.7-0.83,(mean 0.77 SE.±0.02) and the last rostral 4-7 accessory hairs. The head and thorax are clothed in a mixture of short spatulate hairs (c.0.015) and long acute hairs (c.0.055). The abdomen has one row of very short spatulate hairs (0.006) per segment from abdominal segments 1-6. Abdominal segment 7 has a row of 4 larger (0.029) spatulate hairs. The trophobiotic organ is as in Anoecia corni. The sclerotized discoidal plate extends over most of the abdomen but there is a lateral unsclerotized gap between it and the paratergites. Lateral tubercles are present on the prothorax and on abdominal segments 1-7. In life sclerotized areas are light grey and unsclerotized areas are light green. Legs and antennae are blackish.

Alate virginoparae (Plate 19)

The distal primary rhinarium is accompanied by a group of 5 accessory rhinaria. Secondary rhinaria are present on segments III, IV and more rarely on V and VI. Antennae are clothed in acute hairs (c. 0.067) which are less densely packed than in *Anoecia corni*. There are approximately 30 hairs on antennal segment III. Large compound eyes (c. 130 facets) are present in addition to the triommatidia. The rostrum length is 0.63-0.82,(mean 0.71 SE.±0.025) and the last rostral segment bears 6-7 accessory hairs. The head and thorax bear acute-ended hairs which are less densely placed than in *Anoecia corni*. The dorsal surface of abdominal segments 1 and 2 is narrower than the one on segment 1. These bands bear a mixture of acute-ended and spatulate hairs. Segments 3-6 each bear a single row of spatulate hairs. Segment 7 bears a row of longer (c. 0.063) acute hairs. Trophobiotic organ is as in *Anoecia corni*.

Sexuparae. (Fig. 32)

Characters as for the alate virginopara but sexuparae have a greater number of secondary rhinaria on the third antennal segment(11-15, mean 12.75 SE.±2.7). In alate virginoparae there are 6-10 (mean 7.92± 0.38)

Sexuales.

Embryos from *A. vagans* sexuparae were not separable from embryos of *A. corni* sexuparae. It seems likely that the morphology of the adults of the two species is very similar.

Biology.

Anoecia vagans is holocyclic with Cornaceae as the primary host and grass roots as the secondary host. No populations have been found to overwinter parthenogenetically. *A. vagans* constitute only about 4%(9 out of 211) of the sexuparae collected from *Cornus stolonifera* and *C. sanguinea* from 7 sites (*C. stolonifera*,Hampstead Heath 5/9/75; Hampstead Heath 8/9/75; Silwood Park, Berks. 10/9/75; Temple Balsall,Warks.14/9/75; *C.sanguinea*, Reigate,Surrey 17/9/75; Box Hill, Surrey, 9/9/75; Kenilworth, Warks. 19/10/75).

Fundatrigeniae of *Anoecia vagans* were found on *Cornus sanguinea* on 21/5/76 at Box Hill and are easily distinguishable from *A. corni* by their green colour. Suction trap catches show that alate fundatrigeniae begin to fly in the third week of July. Alate virginoparae production reaches a peak at the end of August and sexuparae were first found on dogwood on the 9th of September. The return migration to dogwood ceases in the first week in November. The sexuales of *Anoecia vagans* could not be distinguished from those of *Anoecia corni* and the egg laying site is unknown, though it is possible that it is in the soil as with *A. corni*.

Habitats.

On the secondary host *A. vagans* was found on canal banks and in rough grassland. On the primary host, it was only found on *Cornus sanguinea* growing on chalk downland. Suction trap catches for 1975 and 1976 suggest that *A. vagans* may be restricted in its range by the availability of dogwood as no alates were taken in suction traps north of Edinburgh where dogwood is uncommon (map 121). It may also be restricted by temperature as these areas also have a mean daily temperature (1941-70) of less than 9°C.

Distribution.

Recorded from England, Germany, Italy, Korea, Switzerland, Egypt, South Africa, Turkey.

Anoecia disculigera. Börner 1950.

Fundatrices.

The antennae are 5-segmented and there are no secondary rhinaria or compound eyes. The dorsal surface of the abdomen is sparsely covered in blunt-ended or acute hairs. The abdomen is sclerotized.

Fundatrigeniae, first instars.

The antennae are 5-segmented and the primary rhinarium on the last antennal segment has 6 accessory rhinaria clustered around it. The rostrum reaches to the tip of the abdomen. Siphunculi are not developed but lateral tubercles are found on the prothorax and abdominal segments 1-7. No part of the specimen is heavily sclerotized. It is clothed in long acute hairs.

Alate fundatrigeniae.

The antennae are 6-segmented. Secondary rhinaria are present and are round to oval in shape. Compound eyes of about 60 facets are present. The abdomen is unsclerotized as in *Anoecia vagans* but the lateral tubercles are larger in diameter (c.0.138). The dorsal surface of the abdomen has very sparse blunt or acute-ended hairs.

Biology.

This species has not been found in Britain. Börner (1952) found fundatrices and fundatrigeniae on *Cornus sanguinea* in Germany. Zwölfer (1957) records one population of virginoparae from *Cynosurus cristatus* and two populations from *Agrostis tenuis*. I have examined the specimens from *Cynosurus cristatus* and consider them to be *A. corni*.

Distribution.

Recorded from Switzerland and Germany.

Anoecia furcata. (Theobald)1915 (Forda) (Figs.21-27)

Synonyms:- haupti, Börner 1950, nemoralis Börner 1950, graminis, Gilette and Palmer 1924.

Apterous virginoparae. (Figs. 21-25)(Plate 17)

Secondary rhinaria are present on antennal segments III, IV, V and VI. Antennae are less densely clothed in acute hairs (c.20 on antennal segment III) than Anoecia corni. Compound eyes are present (24-70 facets, mean 46.2 SE.±4.15). Rostral length 0.52-0.82, mean 0.62 SE±0.025. There are 6-8 (mean 7.5 SE.±0.27) accessory hairs on the last rostral segment. The ratio of spatulate to acute-ended hairs on the head, thorax and abdomen is variable. In extreme spatulate-haired forms, the abdominal rows of hairs(one per segment) are all spatulate and many of the irregular hairs on the thorax and head are spatulate, the remainder being acute. In these forms some of the hairs on the antennae and legs may also be spatulate. At the other extreme there are forms in which the rows of hairs on the dorsal surface of the abdomen are only just discernable as having spatulate ends. In these forms there are no spatulate hairs on the head, antennae legs, or thorax. All intermediate forms exist. An abdominal sclerotized discoidal plate is present. Lateral tubercles are present on the Prothorax and abdominal segments 1-4 and 7. In life, virginoparae vary from olive-green or brownish green on the dorsal surface, to almost black. The discoidal plate is darker than less heavily sclerotized parts of the dorsal surface. The ventral surface is light to dark grey in colour. Nymphs are pale green to cream.

Alate virginoparae. (Fig. 26 B.)

On average there are fewer secondary rhinaria on antennal segment III than in alate virginaparae of A. corni. (A. corni, 7-12, mean 9.94 SE.± 0.31: A. furcata 6-10, mean 8.53 SE.± 0.15). Compound eyes are present(60-80 facets, mean 71.8 SE. ± 2.27. Rostral length is 0.53-0.71, mean 0.576 SE.±0.02 and there are 6-8(mean 7.0 SE.±0.37) accessory hairs on the last rostral segment. The head and thorax are clothed in acute hairs. The dorsal surface of the first and second abdominal segments bear narrow sclerotized bands each with about 12 hairs in irregular lines. Most of the hairs are acute but a few may be spatulate.

The discoidal plate which extends from segments 3 to 6 bears single transverse rows, (one per segment) of short (c. 0.017) spatulate or blunt-ended hairs.

Lateral tubercles are present on the prothorax and abdominal segments 1-4 and 7. In life sclerotized areas vary from dark grey to black and unsclerotized areas are light grey.

Sexuparae. (Fig.26 A)

Sexuparae resemble alate virginoparae but possess more secondary rhinaria on antennal segment III (8-12, mean 10.0 SE.±0.31). Large numbers of embryos are present of roughly equal size and which resemble the sexuales embryos of Anoecia corni. They do not possess rows of spatulate hairs which characterize embryos of virginoparae.

Sexuales.

Sexuales have not been found on dogwood but embryos from sexuparae suggest that they resemble those of Anoecia corni and A. vagans. One of the type specimens is a male (Fig. 27) (held by the Deutsches Entomologisches Institut) but there is no aspect of its morphology to distinguish it from males of A.corni.

Biology.

In Britain A. furcata is either completely monoecious and anholocyclic on grass roots or infrequently holocyclic with the Cornaceae as primary host and Graminae as secondary hosts. Specimens are found throughout the year reproducing parthenogenetically on grass roots. Alate virginoparae first begin to fly at the beginning of June, numbers reach a peak at the end of July and the beginning of August. Sexuparae have been recorded in October in suction traps but none have been taken from dogwood. Sexuparae can be recognized because they contain numerous embryos of equal size and the embryos do not bear spatulate hairs unlike the embryos of virginoparae. Alate virginoparae cease flying by the end of October or beginning of November.

Host Plants.

Gramineae:-Recorded from Poa subcaerulea once; Festuca rubra x2; Poa annua x7; Agropyron repens x2; Festuca ovina x3; Poa trivialis x1; Poa sp. x1; Poa pratensis x1; Panicum antidotale x1; Deschampsia caespitosa x1; Agrostis stolonifera x1; Corynephoris canescens x1; Hieracium sp. x1; Dactylis glomerata x1; Festuca sp. x2; Arrhenatherum elatius var. bulbosum x1.

Relationship with ants.

Anoecia furcata has been recorded with the following ants:- Lasius flavus 15 times; L. niger x6; Myrmica sp. x3; M.rubra x1; M. ruginodis x1.

No population of A.furcata has been found without ants.

Overwintering populations were found both in mounds of L. flavus and outside ants' nests but with ants in attendance.

Distribution.

Recorded from Cyprus, England, France , Greece, Italy, Norway, Wales, Scotland, Japan, Turkey, Yugoslavia.

Discussion of the synonyms of A. furcata.

As defined by Börner(1950) and Zwölfer(1958) the nemoralis group within Anoecia contains the following species, all with pairs of lateral tubercles on abdominal paratergites 1-4 and 7 (missing om 5 and 6):- A. haupti, A. nemoralis, and A. furcata. The separation of these species is based on the distribution of spatulate hairs. Zwölfer(1958) defines the species as follows:- Adults of A. haupti have only acute hairs although the first instars have spatulate hairs on abdominal segments 7-5.

The winter form of A. nemoralis has spatulate hairs on abdominal tergites 7-3(2). The summer form also has spatulate hairs on abdominal tergite 1 and on the metathorax.

A. furcata has spatulate hairs on abdominal segments 7-1, the meta-, meso-, and prothoracic segments and head. Often also on the legs and antennae.

Specimens have been found from one colony some of which fall clearly within Zwölfer's definition of A. furcata, some within A. nemoralis and some are intermediate in that they have spatulate hairs on the meso- or prothorax but not on the head. Specimens have also been found with spatulate hairs on the head but not on the thorax.

The distinction between A. haupti and A. nemoralis is blurred as specimens from one colony were found, some of which have no spatulate hairs and some of which have spatulate hairs on abdominal tergites 7-3. Specimens which fit morphologically into Zwölfers (1958) descriptions of both A. haupti and A.furcata were found to have chromosome numbers of 2n=12 and 2n=13. In view of the presence of intermediates between A. furcata and A. nemoralis and between A.nemoralis and A. haupti. A. nemoralis and A. haupti are here treated as synonyms of A. furcata.

The specimens examined of the American species, Anoecia graminis conform morphologically to A. furcata with spatulate hairs on the whole dorsum, head, legs and antennae. The species is also treated as a synonym of A. furcata.

Names as used by Borner(1950 and Zwolfer (1958).	Number of segments with spatulate hairs	Head	Pro-thorax	Meso-thorax	Meta thorax	Abdominal Segments 1	2	3	4	5	6	7
A. furcata	10		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
A. furcata	10	Y	Y	Y	Y	Y	Y	Y	Y		Y	Y
A. furcata	9			Y	Y	Y	Y	Y	Y	Y	Y	Y
A. furcata	7					Y	Y	Y	Y	Y	Y	Y
A. furcata	7		Y	Y	Y	Y	Y	Y			Y	
A. furcata	7					Y	Y	Y	Y	Y	Y	Y
A. furcata	6			Y	Y	Y	Y	Y				Y
A. furcata	6		Y	Y	Y	Y	Y		Y			
A.furcata.	8			Y	Y	Y	Y	Y	Y	Y	Y	
A.furcata	6				Y	Y	Y	Y	Y	Y		
A.nemoralis summer form	3					Y	Y	Y				
A.nemoralis winter form	3								Y	Y	Y	
A.nemoralis summer form	2					Y	Y					
A.nemoralis winter form	1						Y					
A. haupti	0											
A. haupti	0											

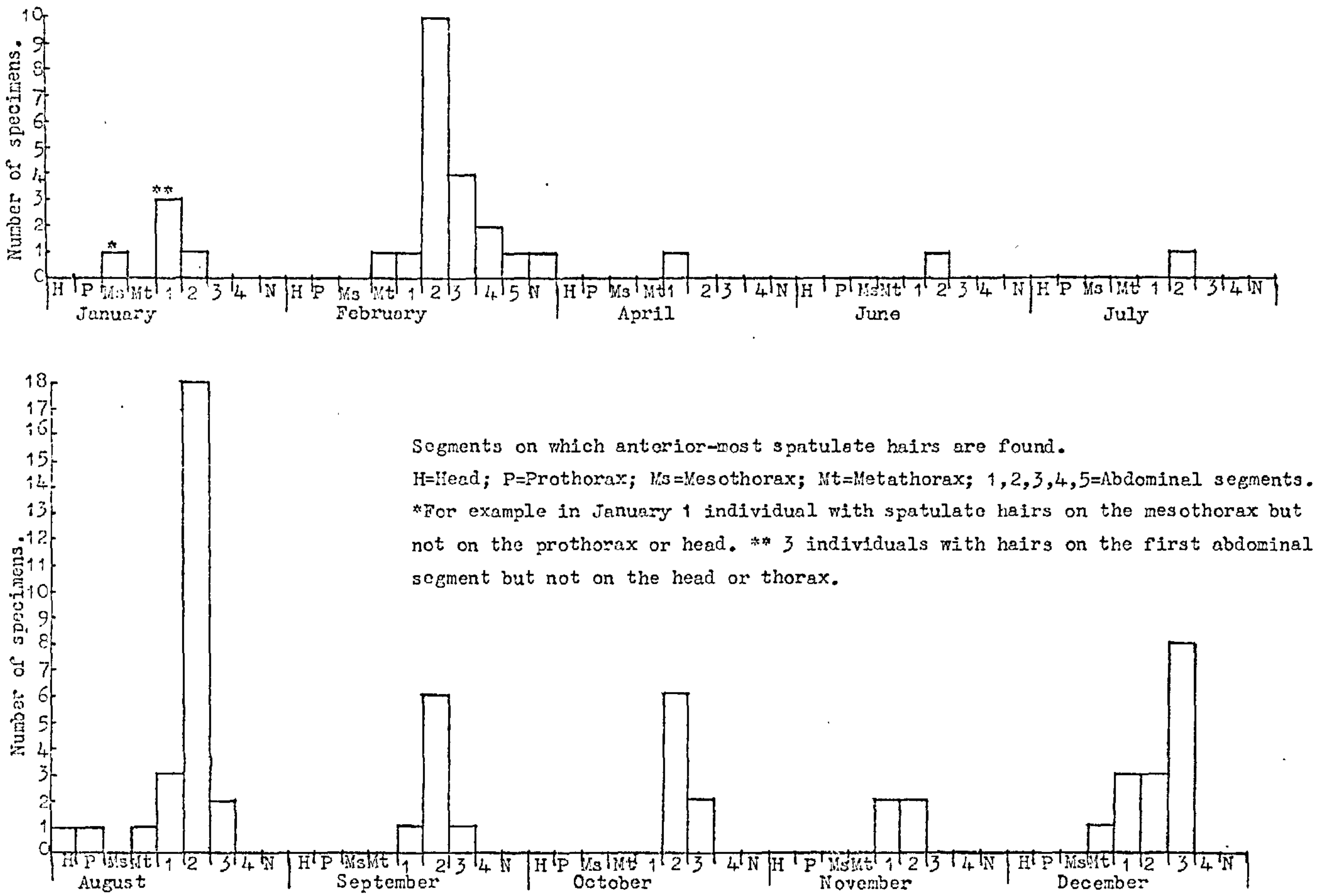
Distribution of spatulate hairs in 16 specimens of *Anoecia furcata* selected to show the range of variation. Each horizontal column represents one specimen.

Y At least one spatulate hair present.

FIG 78 HAIR POLYMORPHISM IN ANOECIA FURCATA THEOBALD.

FIG 79.

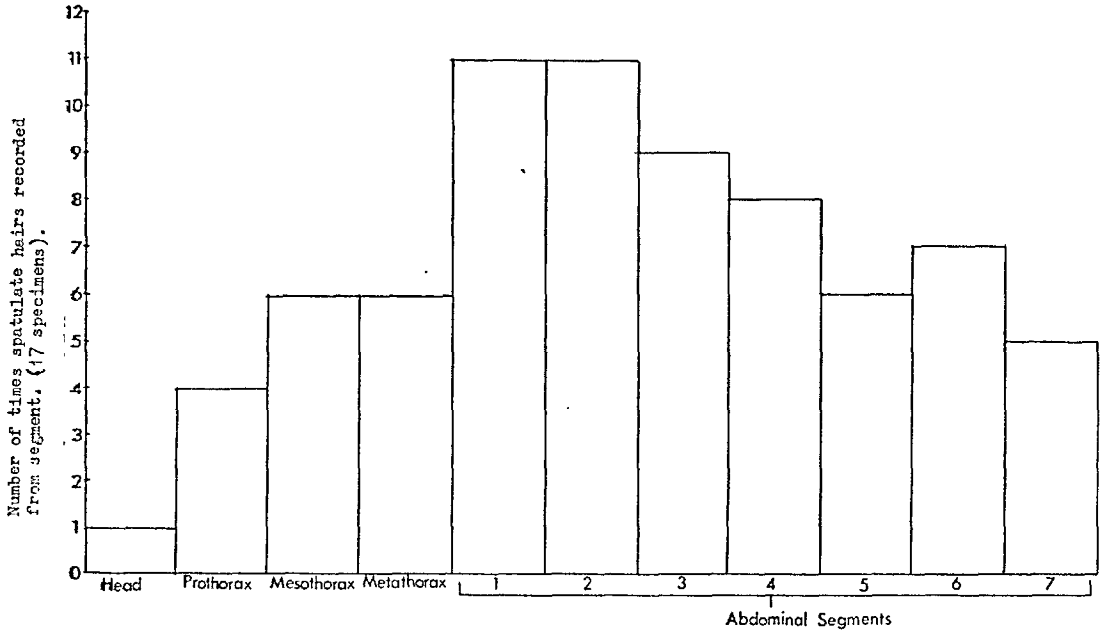
SEASONAL VARIATION OF SPATULATE HAIRS IN ANOECIA FURCATA.



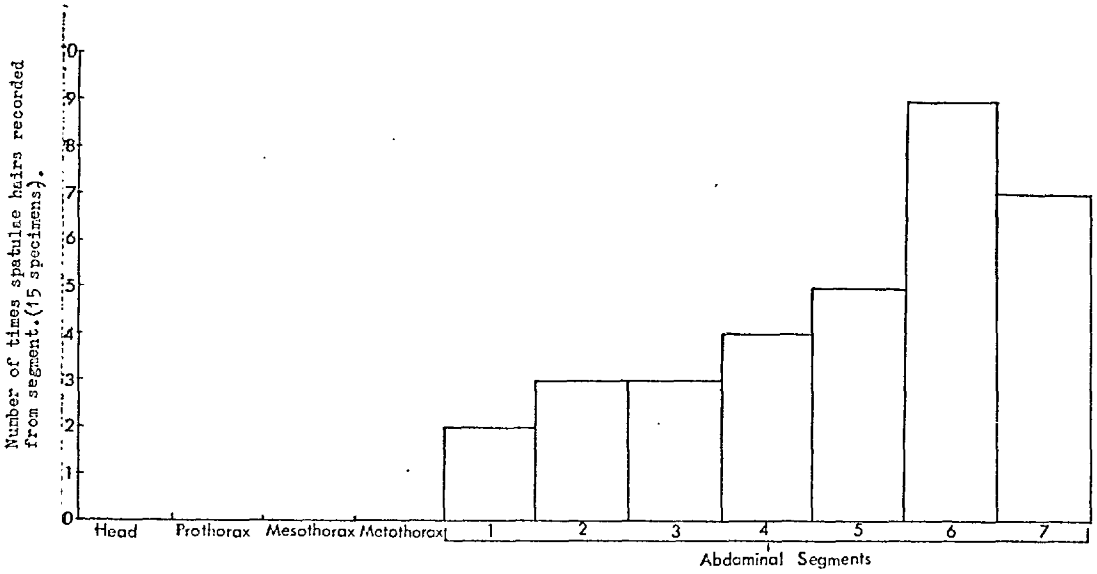
Segments on which anterior-most spatulate hairs are found.

H=Head; P=Prothorax; Ms=Mesothorax; Mt=Metathorax; 1,2,3,4,5=Abdominal segments.

*For example in January 1 individual with spatulate hairs on the mesothorax but not on the prothorax or head. ** 3 individuals with hairs on the first abdominal segment but not on the head or thorax.



DISTRIBUTION OF SPATULATE HAIRS IN ANOECIA FURCATA.



DISTRIBUTION OF SPATULATE HAIRS IN ANOECIA CORNI.

FIG 80

Anoecia oenotherae Wilson 1911. (Fig. 37) (Plate 22).

Alate virginoparae.

Antennae clothed in dense irregular acute hairs (0.04). The distal primary rhinarium at the base of the processus terminalis is slightly protuberant, but not as protuberant as in A. corni. The proximal primary rhinarium at the base of antennal segment V is slightly protuberant.

The legs are clothed in dense irregular acute hairs (0.063). The first tarsal segment of the prothoracic leg bears 5 hairs, of the mesothoracic leg bears 5 hairs and of the metathoracic leg bears 5 hairs.

Compound eyes of 80 facets are present. The rostrum length is 0.43-0.62 and there are 6-8 accessory hairs on the last rostral segment.

The head, thorax and abdomen are clothed in stout acute hairs (0.046). Abdominal segments 1,2 and 3 are more or less unsclerotized. Segments 4,5 and 6 bear spinal sclerotized strips. Segments 8 and 9 have continuous sclerotized strips. Lateral tubercles are present on the prothorax and abdominal segments 1-4 and 7. The largest is on the prothorax and the second largest on abdominal segment 7. Siphunculi are cone-shaped rings surrounded by about 20 hairs. Abdominal segment 8 bears 9 large (0.115) bristles which curve towards the anus. The cauda and anal plate also carry stout hairs curving towards the anus.

Distinguished from other Anoecia except A.zirnitzi and fundatrigeniae of A. vagans by the lack of a continuous discoidal plate; instead there are spinal bands of sclerotization. Distinguished from A. zirnitzi by the presence of large compound eyes and from A. vagans by lacking lateral tubercles on abdominal segments 5 and 6.

Distribution.

Specimens seen from North America:- Manitoba, Minnesota, Ohio and Wisconsin.

Anoecia cornicola. (Walsh 1863) (Eriosoma) (Fig.34)

Synonyms:- eleusinis Thomas,1878 (Rhizobius); fungicola Walsh 1863 (Eriosoma); panicola Thomas 1879 (Schizoneura); querci auct. nec. Fitch 1859 (Eriosoma).

Alate virginopara.

The antennae are clothed in fairly dense acute hairs. Secondary rhinaria are round and have a largest diameter of 0.023. The last rostral segment bears six accessory hairs. The legs are clothed in long acute hairs. A discoidal plate is present on abdominal segments 3,4,5 and 6 and bears single rows of short acute hairs (0.023). There are pairs of lateral tubercles on the prothorax and abdominal segments 1-4 and 7. Abdominal segments 1 and 2 each bear a small central sclerotized patch on the dorsal surface.

Biology.(From Cutright 1925)

There is a holocyclic dioecious population and an anholocyclic monoecious population in the soil.

Host Plants. (From Cutright 1925).

Primary hosts:- *Cornus florida*; *C.stolonifera*; *C. amomum*; *C. paniculata*; *C. sanguinea*; *Diospyros virginiana*.

Secondary hosts:- *Digitaria sanguinalis*; *Setaria glaucia*; *S. viridis*; *Panicum capillare*; *P.virgatum*; *Aster ericoides*; *A. novae-angeliae*; *Solidago graminifolia*; *Polygonum erectum*; *P. hydropiper*; *Poa pratensis*; *Andropogon scoparius*; *Zea mays*; *Sorghum halepense*; *Muhlenbergia mexicana*; *Phleum pratense*.

Distribution.

Specimens seen from Brazil; North America; New York, Ohio, Oklahoma, Utah and Washington.

Anoecia setariae.Gilette and Palmer 1924.

Synonyms:- *cornicola* in Mordvlko 1935.

Alate virginoparae.

A small discoidal plate covers abdominal segments 3,4,5 and 6 but does not quite reach the paratergites laterally even on segment 6. Segments 1 and 2 each bear a small central sclerotized patch on the dorsal surface. There are pairs of lateral tubercles on the prothorax and abdominal segments 1-4 and 7. The dorsal abdomen bears single rows of short (0.02) acute hairs. Compound eyes of about 65 facets are present. Secondary rhinaria are oval.

Apterous virginoparae.

Compound eyes are small, about 13 facets. There are lateral tubercles on the prothorax and abdominal segments 1-4 and 7. The dorsal surface of the abdomen is covered with irregular fine acute hairs (Length 0.073). There is no discoidal plate. The last rostral segment bears 8 hairs excluding the terminal hairs.

Biology.

Specimens have only been taken on the secondary host.

Host Plants.

Roots of Setaria sp. and Equisetum laevigatum

Distribution.

Specimens seen from North America:- Manitoba, Minnesota, Ohio, Wisconsin.

Subgenus Neanoecia (Borner) 1950.

The genus Neanoecia was errected by Borner in 1950 include N. krizusi (the type species) and N. zirnitzi. The genus was defined by the fact that the species are secondarily holocyclic on Gramineae with fundatrices and oviparae which resemble virginoparae in size and in having six antennal segments. In Anoecia oviparae are dwarf and both fundatrices and oviparae only have 5 antennal segments. As Stroyan (1964) points out:- "In the Aphidinae, the existence of secondarily monoecious species in originally heteroecious genera has not been considered satisfactory grounds for splitting such genera, even where the fundatrices and sexuales are closer to the normal viviparae than to the equivalent morphs of the heteroecious species". There is no morphological character which unites A. zirnitzi and A. krizusi and distinguishes them from other Anoecia and so they are included in Anoecia, and Neanoecia is retained as a subgenus in reoognition of the differences in the life cycle.

Anoecia zirnitzi. Mordvilko 1931. (Figs.7-9) (Plate 3-6)

Fundatrix.

The fundatrix is not separable morphologically from the virginoparae.

Apterous virginoparae. (Figs. 7 & 8)

Occasionally antennal segments III and IV are not completely separated. Antennal segment II is longer than segment I. Segment III is proportionally shorter than in Anoecia corni . The ratio of segments II/III is 0.4-0.49 (mean 0.43 SE.±0.01).The last rostral segment bears 7-10 (mean 8.13 SE.±0.61) accessory hairs. Legs, antennae head and thorax are covered in long fine acute hairs (0.086). The abdomen bears irregular long fine acute hairs except for segment 7 which has a single row. In some specimens acute hairs on the abdomen are replaced in part by spatulate. When spatulate hairs replace acute hairs single rows of mixed spatulate and acute hairs may extend from segment 7 to 5.

Lateral tubercles are present on the prothorax and abdominal segments 1-7. Those on segments 5 and 6 show less reduction in diameter than in Anoecia corni. The largest is on the prothorax (diameter 0.098). The abdomen is often completely unsclerotized, sometimes there are small islands of sclerotization. Compound eyes are either not developed or usually less than 10 facets, occasionally up to 20 (mean 4.7 SE.± 0.94). There are no secondary rhinaria but 6 accessory rhinaria cluster around the distal primary rhinarium.

In life colour varies from grey-green through brownish green to olive brown depending on the degree of sclerotization.

Oviparae. (Plate 4 & 5)

Resemble the apterous virginoparae but sometimes two dark eggs can be seen in the abdomen. Small ventral wax glands are found on the ventral side of the abdomen in two fields centering around the margins of the sixth abdominal segment. The diameter of the facets is 0.009.

Male. (From one specimen). (Fig. 9) (Plate 6)

Antennae 5-segmented. The second antennal segment is the same length as the third. The distal primary rhinarium has 4 accessory rhinaria clustered around it. The antennae, legs, head and thorax are clothed in long(0.045) acute hairs. There are no compond eyes, only triommatidia. The rostrum is 0.36 long, reaching just beyond the third pair of coxae. The last rostral segment bears 6 accessory hairs.

The dorsal surface of the abdomen is unsclerotized but the ventral surface bears one thick sclerotized band per segment. Each abdominal segment bears one row of long acute hairs. There are no spatulate hairs. The abdomen ends in a pointed down curved aedeagus enveloped in a fold of unsclerotized integument bearing very small hairs. Siphunculi are present, though small (diameter 0.015). Lateral tubercles are present on the prothorax and abdominal segments 1-7. The largest lateral tubercles are on the prothorax(diameter 0.073). The abdominal lateral tubercles are also comparatively large (diameter 0.044).

Eggs. (Plate 3)

Eggs measure about 0.78 by 0.5 and are shiny black in colour.

Biology.

Anoecia zirnitzi is holocyclic and monoecious on grass roots. In spring, the eggs which have been cared for by ants over the winter (always Lasius flavus) hatch and the first instar fundatrices probably find their own way to grass roots. Eggs were found in nests of Lasius flavus on 11/4/75 at Englefield Green, Surrey; they hatched in the laboratory at room temperature on 15/4/75 and the first instar fed on Poa annua but did not survive. Reproduction proceeds parthenogenetically throughout the summer and colonies are invariably attended by L. flavus. Oviparae were found in early November. They produce 2 overwintering eggs which are laid in the soil. The eggs are gathered by ants and may be found in groups of 100 or more. Lasius flavus was observed to carry eggs in the laboratory. A male found by Dr. A.J. Pontin at Wytham Park in Berkshire 7/11/56(Pontin 1960b) was referred to as Neanoecia krizusi. Dr. Pontin has kindly allowed me to examine his specimens and I have also found the following specimens which were referred to in his paper as Neanoecia krizusi to be Anoecia zirnitzi:-

(a) A slide containing four first instar fundatrices reared ex ova, Upperseeds, Wytham, Berks. 17/4/56.

(b) A slide of an adult fundatrix reared ex ova, Upper Seeds, Wytham, Berks. 1/3/56.

Zwölfer(1958) suggests that as he did not find any males of Anoecia zirnitzi the oviparae might produce eggs parthenogenetically but he was unable to prove this in the laboratory. The discovery of a male makes it unnecessary to postulate parthenogenetic egg production.

Habitats.

In Britain Anoecia zirnitzi has been collected from grass roots in mounds of Lasius flavus on sandy and calcareous soils.

Distribution.

Recorded from England, Scotland, Germany, and Sweden.

Anoecia krizusi. (Börner) 1950 (Neanoecia).

(Material examined:- 4 slides from Börners collection.).

Fundatrix first instar.

Identical to the first instars of virginoparae.

Apterous virginoparae.

The whole dorsum is strongly sclerotized. Lateral tubercles are present on the prothorax and abdominal segments 1-4 and 7. The head, thorax and abdominal segments 1-5 are clothed in irregular dense acute hairs. On abdominal segments 6 and 7 there are single rows of acute hairs. There are no spatulate hairs.

Virginoparae first instar.

Length 0.8-0.96. Lateral tubercles as in the adult. Only acute hairs are present; on the mesothorax and metathorax and on the abdominal tergites usually in a long row. Rostrum (length 0.45-0.55) reaches to about the third abdominal segment.

Oviparae.

Abdomen membranous, only head, thorax and anal region are strongly sclerotized. Lateral tubercles present on the prothorax and abdominal segments 1-4 and 7. Hair distribution is as in the adult virginoparae. Compound eyes are lacking. Antennae are 6-segmented. No ventral wax gland field was visible in these specimens, perhaps due to their strong maceration.

Biology.

Anoecia krizusi is stated by Börner (1950) to be holocyclic and secondarily monoecious on roots of Agropyron spp.

Distribution.

A. krizusi has not been recorded in Britain. Specimens referred to by Pontin(1960b) have been identified as A. zirnitzi (see biology of *A. zirnitzi*), a virginopara of *A. furcata*, Upper Seeds, Wytham Berks. 1/3/56 and a virginopara and two larvae of *A. corni*, Upper Seeds, Whytham, Berks. 3/9/56.

Börner (1950) records *A. krizusi* from Naumburg in East Germany.

Genus *Paranoecia*. Zwölfer 1958. (Figs. 3 & 4)(Plates 1 & 2)

Type species: *Anoecia pskovica* Mordvilko 1916.

The only known species is *P. pskovica* which is holocyclic and monoecious on roots of *Carex* spp. The processus terminalis is not finger-shaped and is only about 1/10th of the length of the last antennal segment . The facets of the ventral wax glands of oviparae are very small (diameter 0.004-0.007).

The eggs, which are laid in the soil, are tended by ants during the winter.

Fundatrix, first instar. (Plate 1)

Antennae are 5-segmented. The primary rhinaria on the ultimate and penultimate antennal segments project forwards. Sclerotization, lateral tubercles and hairs distribution are as in the first instar apterous virginoparae. Body length is 1.05-1.3 (mean 1.3 SE.±0.043.). Antenna length is 0.54-0.64(mean 0.58 SE.±0.022). Body width is 0.55-0.66(mean 0.62 SE.±0.015) Rostrum length is 0.82-0.88(mean 0.8 SE.±0.03).

Fundatrix.

Morphologically identical with the apterous virginoparae.

Apterous virginoparae, first instar.

Antennae are 5-segmented. Processus terminalis of last antennal segment is slightly longer in proportion to the base than in the adult (about 1/5th of the base of the last antennal segment). Lateral tubercles are present on the prothorax and abdominal segments 1-7. Siphunculi are not yet developed.

Legs, antennae head and abdomen (except for segment 7) are covered with irregular acute hairs. Abdominal segment 7 has a single row of acute hairs. Acute hairs have very fine curved tips as in the adults.

In life, whitish due to wax.

Apterous virginoparae. (Figs. 3 & 4) (Plate 2)

Secondary rhinaria are often lacking and when present they are very small. There are no accessory rhinaria. The antennae are clothed in acute hairs. The second antennal segment is slightly longer than the first. Primary rhinaria are slightly oval and project distally from the distal end of segment V and the base of the processus terminalis on segment VI. Compound eyes are absent or of less than 5 facets. The head, thorax and legs have dense acute hairs. The abdomen bears densely packed acute hairs on segments 1-5; segment 6 has a double row of acute hairs and 7 has a single row of acute hairs. The sclerotized band on segment 8 carries about 12 long (0.134) hairs. Lateral tubercles are present on the prothorax and abdominal segments 1-7. The lateral tubercles on the prothorax are very large (diameter 0.184). Other lateral tubercles are also large(0.104 in diameter) compared with those of *A.corni*. The rostrum reaches to the third pair of coxae, length 0.91-1.1(mean 1.05 SE.±0.068). The body hairs are extremely fine and the ends recurved(length, 0.088). There are 13-21 (mean 16.8 SE.±0.65) accessory rostral hairs. They are distributed in two dorsal and two ventral rows. There is no discoidal plate, the mesothorax. and abdomen are unsclerotized except for small isolated patches. The prothorax, legs and antennae are slightly sclerotized.

In life apterous virginoparae are dirty white-grey in colour(Zwölfer 1958).

Oviparae (From Zwölfer 1958)

Resemble the virginoparae. They differ simply in their relatively short antennae and rostrum and in the presence of two very large wax gland fields on the ventral side of the abdomen. These are roundish to oval and reach from the 4th to the 8th sternite and from the lateral tubercles to the middle of the sternites. The facets of the gland field are very small(Diameter 0.004-0.007) and very numerous. In mature females both large dark eggs show through the integument. Living specimens have a white wax secretion on the underside and flanks of the abdomen.

Body length :2.35-3.0	Ant.Seg I :0.095-0.13	Secondary rhinaria
Body width: 1.35-1.8	" " II :0.095-0.145	on:-
Rostrum length:1.05-1.4	" " III:0.41-0.49	III:0-2
Antenna length:1.1-1.4	" " IV :0.13-0.18	IV :0-2
	" " V :0.13-0.195	V :0-2+1
	" " VI :0.165-0.21	VI :0+1

Males (From Zwölfer 1958).

Colour whitish grey. Long thin body shape; specimens appreciably smaller than the female. End of abdomen bent under itself. Body either often unarmoured or only weakly sclerotized. Lateral tubercles are small but distinct on the prothorax and paratergites 1-7. Only acute hairs are present (0.06-0.12) and these are in single rows on tergites 8 and 7, otherwise the hairs are not uniform but weakly ordered. Antennae are 5-segmented. Primary rhinaria are normal. There are only triommatidia, no compound eyes. There are no siphunculi.

Body length :1.5-2.6	Ant. Seg. I :0.082-0.098	No secondary rhinaria.
Body width :0.65-0.75	" " II :0.082-0.098	
Rostrum length :0.65-0.82	" " III :0.29-0.33	
Antenna length :0.73-0.8	" " IV :0.13-0.145	
	" " V :0.145-0.165	

Biology.

Paranoecia pskovika is holocyclic and secondarily monoecious on grass roots. The overwintering eggs are laid in the soil in autumn, collected by ants (Lasius flavus)and cared for over the winter. Pontin (1961) found eggs in Lasius flavus mounds on the 17/4/56 and 10/3/59. He found that L.flavus licked the eggs and that this maintained their condition. If the ants were removed the eggs became shrivelled and mouldy. Zwölfer(1958) on the other hand states that ova are not often found in ants' nests but individually scattered in waxy coatings. Pontin (1961) states that the young aphids, on hatching in artificial nests,were seldom carried by ants and were not transferred to chambers containing food plants but were set down in chambers with the ant's brood. Groups of ants were in constant attendance around young aphids, which walked about the nests for several days even in the absence of food. He considers it unlikely that ants assist aphids in finding their food plants as this would involve discrimination by the ants both of aphid species and of their food plants, with correct association of the two.

According to Zwölfer (1958) oviparae possess ventral wax glands for coating the eggs.

Host Plants.

Paranoecia pskovica feeds almost exclusively on roots of *Carex* spp. It has been recorded from *Carex panicea*, *C.flacca* and *Brachypodium pinnotum*.

Relationship with ants.

P.pskovica is almost invariably recorded with *Lasius flavus*. Zwölfer (1958) also records it on two occasions with *L. niger*.

Habitats.

In Britain *P. pskovica* has been recorded from both cliff sites (Dorset, Dr. V.F.Eastop 6/9/50; Mumbles Head, Dr. H.L.G. Stroyan 1/6/67, 12/9/67) and wet localities inland.

CHROMOSOME NUMBERS IN ANOECIA CORNI, A. VAGANS AND A. FURCATA.

INTRODUCTION.

Chromosome squashes were done using Blackman's technique (Blackman and Takada, 1975) which is described in the materials and methods section. Chromosomes were photographed and measured from photographic prints using a map measuring instrument.

The following chromosome numbers were found:-

	Specimens from roots of Graminae.	Specimens from *Cornus* spp.
A. corni.	2n=6(Non-Homologous)	2n=6(Homologous)
	2n=6(Homologous)	2n=8(Homologous)
	2n=7(Non-Homologous)	2n=7(Males)
	2n=8(Homologous)	
A. vagans.	2n=12(Homologous)	2n=12(Homologous)
A. furcata.	2n=12(Homologous)	
	2n=13(Non-Homologous)	

In order to simplify discussion of possible dissociations and fusions, chromosomes have been ranked by length, and the numbers given in the text refer to the tables, where percentage lengths are given.

COMPARISON OF THE CHROMOSOMES OF THE 2n=6 AND 2n=8 FORMS OF ANOECIA CORNI. (Table 1 and Fig.81)

It was found that chromosomes 3 and 4 of the homologous 2n=6 form were not significantly different (at p=0.1) in percentage length from chromosomes 3 and 4 plus 7 and 8 of the 2n=8 form. It was also found that chromosomes 1 and 2 plus 5 and 6 of the 2n=6 form were not significantly different in percentage length (at p= 0.1) from 1 and 2 plus 5 and 6 of the 2n=8 form.

Thus 5 and 6 of the 2n=6 form may have dissociated and a portion fused with 1 and 2, the remainder going to form 5 and 6 of the 2n=8 form. Alternatively 1 and 2 of the 2n=8 form may have dissociated, one part forming 1 and 2 of the 2n=6 form, and another fusing with 5 and 6 of the 2n=8 form to give 5 and 6 of the 2n=6 form.

It was found (Table 1.) that there is no significant difference between the chromosomes of grass root-feeding specimens and their morphological equivalents collected from Dogwood. It is

CHROMOSOME LENGTHS, given in percentages.

Specimens collected from grass roots.

A. corni.	1.	2.	3.	4.	5.	6.	7.	8.
(2n=6)	30.3	21.2	16.6	13.6	10.6	7.6		
Non	26.4	25.5	17.9	12.26	12.26	5.66		
Homologous.	33.3	25.9	14.8	9.9	9.9	6.17		
	30.6	16.3	14.3	14.2	12.2	12.2		
Mean	30.15	22.22	15.9	12.49	11.24	7.91		
Standard Deviation	2.84	4.49	1.66	1.91	1.18	2.98		
A. corni.								
(2n=6)	22.0	22.0	16.1	16.1	11.9	11.9		
Homologous.	25.9	24.7	12.9	12.9	11.8	11.8		
	26.2	23.8	14.3	14.3	11.9	9.5		
Mean.	24.7	23.5	14.4	14.4	11.8	11.1		
Standard Deviation	2.34	1.37	1.6	1.6	0.06	1.36		
A. corni.								
(2n=8)	33.3	25.5	7.8	7.29	7.29	7.29	6.25	5.21
Homologous	28.1	26.6	9.38	7.8	7.8	7.8	6.25	6.25
	31.5	27.0	9.0	7.9	6.7	6.7	5.6	5.6
	31.9	30.0	7.1	7.1	7.1	6.19	5.7	4.8
	31.6	26.6	7.59	7.59	7.59	6.34	6.34	6.34
	30.9	26.5	8.8	8.8	7.4	5.9	5.9	5.9
	32.5	32.5	6.2	7.7	5.7	5.7	5.2	4.6
	27.0	25.4	11.1	7.94	7.94	7.94	6.35	6.35
	26.8	26.8	10.1	8.0	7.25	7.25	7.2	6.5
Mean.	30.4	27.4	8.56	7.79	7.27	6.79	6.09	5.73
Standard Deviation.	2.44	2.32	1.54	0.48	0.70	0.82	0.57	0.71

Table 1.Each specimen is represented by one row. Columns represent ranked chromosomes, number 1 being the longest.

CHROMOSOME LENGTHS, given in percentages.

Specimens collected from Dogwood.

A. corni.	1.	2.	3.	4.	5.	6.	7.	8.
(2n=6)	23.1	22.6	16.6	14.6	12.1	11.1		
Homologous.	23.7	23.7	15.1	13.8	12.1	11.6		
Mean	23.4	23.2	15.9	14.2	12.1	11.35		
Standard Deviation.	0.42	0.78	1.1	0.57	0	0.35		
A. corni.	30.5	27.7	9.7	7.5	7.5	6.3	6.0	5.0
(2n=8)	29.4	27.8	8.1	7.7	7.7	6.9	6.5	6.0
Homologous.	39.4	10.6	10.1	8.7	8.2	7.7	7.7	7.7
	30.7	29.6	8.2	7.7	6.4	6.0	5.6	5.6
	31.9	24.5	9.3	7.8	7.8	7.4	5.9	5.4
Mean	32.4	24.0	9.1	7.9	7.5	6.9	6.34	5.9
Standard Deviation.	4.0	7.7	0.9	0.47	0.68	0.72	0.83	1.0
A. corni. (2n=7) Non Homologous.	30.3	21.2	16.2	11.1	8.1	7.1	6.1	
Ranked mean lengths of the homologous chromosomes of the 2n=8 and 2n=6 forms combined.	28.9	24.1	14.4	11.45	8.18	7.03	5.91	

These correspond well with the observed lengths of chromosomes in the 2n=7 form and suggest that it is a hybrid of 2n=8 and 2n=6 (see page 175).

Table 1. continued. Each specimen is represented by one row. Columns represent ranked chromosomes, number 1 being the longest.

COMPARISON OF THE CHROMOSOMES OF THE 2n=12 FORM OF ANOECIA FURCATA WITH ANOECIA VAGANS. (Table 2.) (Plates 62 & 63)

When the percentage lengths of A.furcata's chromosomes were compared with the percentage lengths of A.vagans' chromosomes it was found that there was a significant difference between numbers 3(at P=0.05), 4(at P=0.1) and 10(at P=0.1) (Table 2).

3(mean 14.1) and 4(mean 11.9) are longer in A.vagans than in A.furcata(means 11.36 and 10.21 respectively) while 10(mean 4.8) is shorter in A.vagans than in A.furcata(mean 5.39). It is possible that chromosome number 10 of A.furcata dissociated and a section fused with either 3 or 4 to give the percentage lengths that are now found in A.vagans or more likely, (as, because of it's life cycle A. furcata seems to be apomorphic) 3 or 4 in A.vagans dissociated and a section fused with 10 to give the percentage lengths now found in A. furcata.

The fact that there is no very clear relationship between the chromosome lengths of A. furcata and A.vagans might be expected as they are distinct species.

COMPARISON OF THE CHROMOSOMES OF THE 2n=13 AND 2n=12 FORMS OF ANOECIA FURCATA. (Table 2 and Fig. 82)(Plates 63 & 64)

Ranking of chromosomes (Table 2) shows that in the 2n=13 form, chromosome 3 is not significantly different(at p=0.1) in length from 4 plus 13. This suggests that 4 and 13 may be the result of dissociation in what had been 3's homologous chromosome. in addition the mean length of chromosomes 3 and 4 of the 2n=12 form is not significantly different(at p=0.1) from the mean length of the summed lengths of 4 plus 13 of the 2n=13 form. This suggests that either the 2n=13 form arose from the 2n=12 form by dissociation of one of the second longest pair of chromosomes(3 or 4) or the 2n=12 form arose from the 2n=13 form by fusion of chromosomes 13 and 4.

As A. furcata probably had a holocyclic ancestral form with homologous chromosomes, it is likely that the 2n=13 form is derived from the 2n=12 form.

A possible mechanism for deriving either the 2n=6 form from the 2n=8 form, or the 2n=8 form from the 2n=6 form.

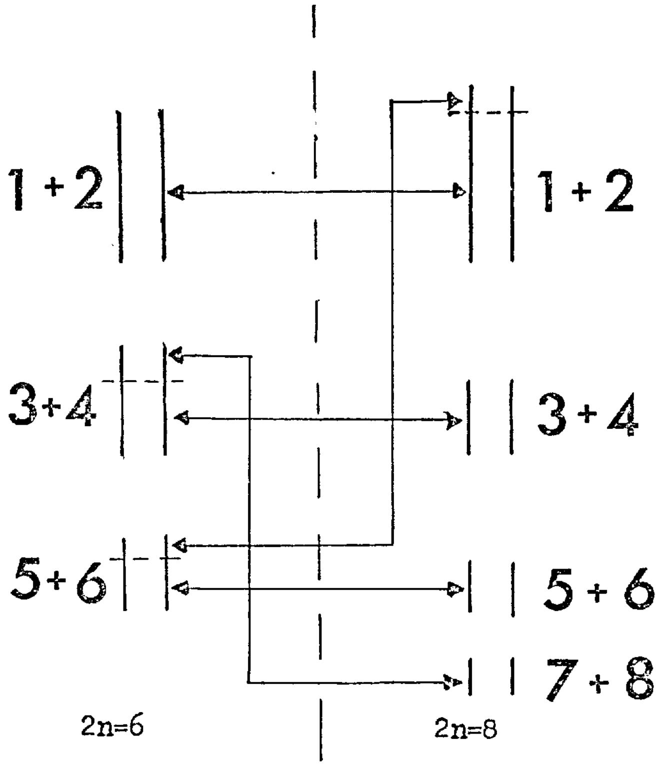


FIG. 81 Anoecia corni.

THE STATUS OF THE 2n=7 AND 2n=8 FORMS OF A.CORNI.

The percentage length measurements for the 2n=7 form of A. corni conform well with the hypothesis that it is a hybrid between the 2n=8 and 2n=6 forms. If the means of the homologous chromosomes of the 2n=8 and 2n=6 forms are ranked to give the seven chromosomes to be expected from a hybrid and compared with the observed chromosome lengths of the 2n=7 form a very good correlation results (see table 1).

The 2n=8 and 2n=6 karyotypes, which are here referred to as forms of A. corni are not easily separated morphologically but may nevertheless be separate species(see page 290).

CHROMOSOME LENGTHS, given in percentages.

Specimens collected from grass roots.

A. furcata.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
(2n=13)	18.0	15.8	14.7	8.7	6.0	5.4	5.4	4.9	4.36	4.36	4.36	4.1	3.8
Non Homologous.	14.4	13.3	11.1	8.9	6.67	6.67	5.6	5.6	5.6	5.6	5.6	5.6	4.4
Mean.	16.2	14.55	12.9	8.8	6.34	6.04	6.04	5.25	4.98	4.98	4.98	4.85	4.1
Standard Deviation	2.5	1.77	2.5	0.14	0.47	0.90	0.90	0.50	0.88	0.88	0.88	1.06	0.42
A. furcata.													
(2n=12)	17.5	15.0	10.0	9.17	8.3	6.7	6.7	5.8	5.8	5.8	5.0	4.17	
Homologous.	18.0	14.0	12.0	12.0	6.0	6.0	6.0	6.0	5.0	5.0	5.0	5.0	
	13.0	13.0	11.7	10.4	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	
	16.0	15.1	14.2	11.3	5.7	5.7	5.7	5.7	5.7	5.7	4.7	4.7	
	17.4	16.3	13.0	12.0	5.4	5.4	5.4	5.4	5.4	5.4	4.35	4.35	
	19.5	15.6	10.4	10.4	6.5	6.5	5.2	5.2	5.2	5.2	5.2	5.2	
	13.6	13.6	8.2	6.2	5.5	5.5	5.5	5.5	4.8	4.1	4.1	2.3	
Mean.	16.43	14.66	11.36	10.21	6.27	6.04	5.86	5.73	5.49	5.39	4.98	4.6	
Standard Deviation.	2.38	1.17	2.00	2.03	0.998	0.53	0.57	0.43	0.57	0.75	0.78	1.27	

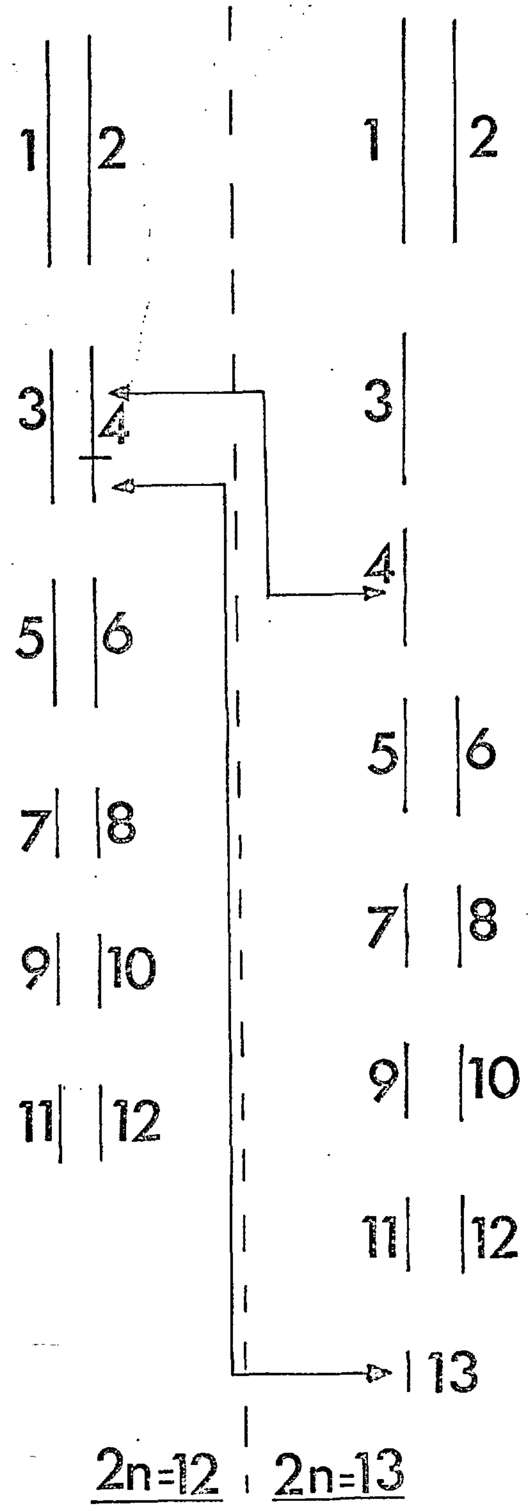
Table 2. Each specimen is represented by one row. Columns represent ranked chromosomes, number 1 being the longest.

CHROMOSOME LENGTHS, given in percentages.

Specimens collected from grass roots.

A. vagans.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
(2n=12)	16.3	15.1	15.1	12.8	5.8	5.8	5.2	5.2	4.7	4.7	4.7	4.7
	16.5	15.6	15.2	12.1	6.7	6.7	5.4	5.4	4.5	4.5	4.0	3.6
	17.2	14.6	13.3	10.6	6.1	6.1	6.1	6.1	5.1	5.1	5.1	4.5
	16.2	14.4	12.6	12.0	6.6	6.6	6.0	6.0	6.0	4.8	4.8	4.2
Mean.	16.55	14.9	14.1	11.9	6.3	6.1	5.7	5.7	5.1	4.8	4.7	4.3
Standard Deviation.	0.45	0.54	1.3	0.22	0.42	0.34	0.44	0.44	0.67	0.25	0.47	0.48

Table 2 Continued. Each specimen is represented byone row. Columns represent ranked chromosomes, number 1 bing the longest.



A possible mechanism for deriving either the 2n=13 form from the 2n=12 form, or the 2n=12 form from the 2n=13 form.

FIG 82 *Anoecia furcata.*

Plate 59. _Anoecia corni_. 2n=6.

Plate 60. _Anoecia corni_. 2n=8.

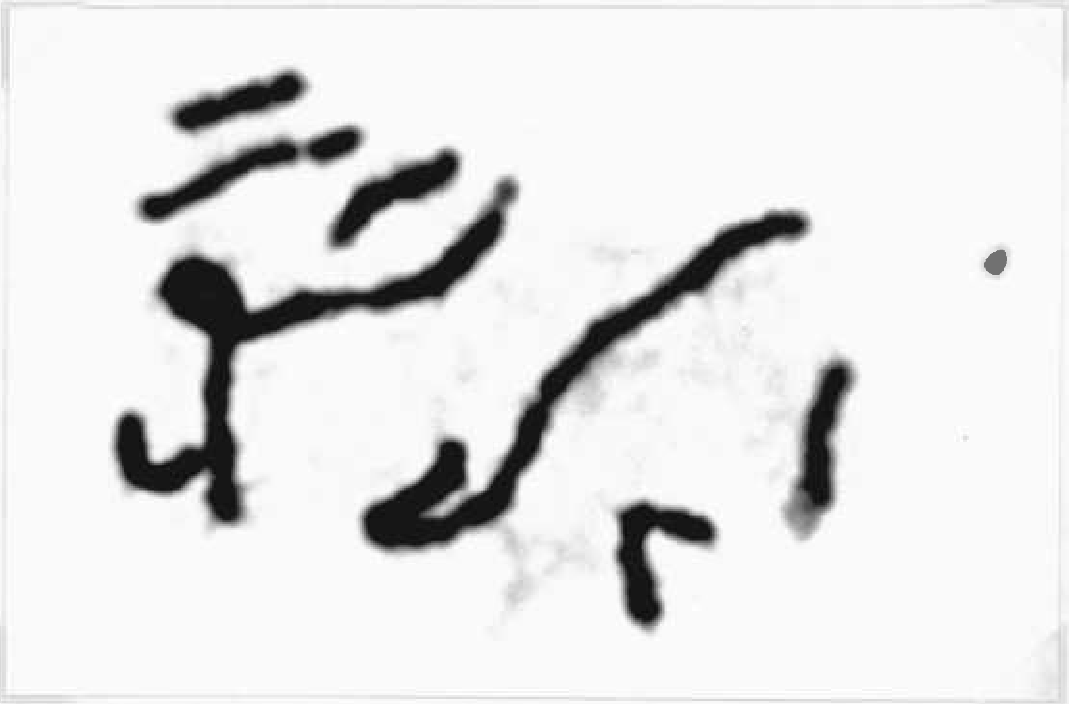


Plate 61. Anoecia corni. 2n=8. (From dogwood)

Plate 62. Anoecia vagans. 2n=12. (From grass roots).

Plate 63. Anoecia furcata 2n=12.

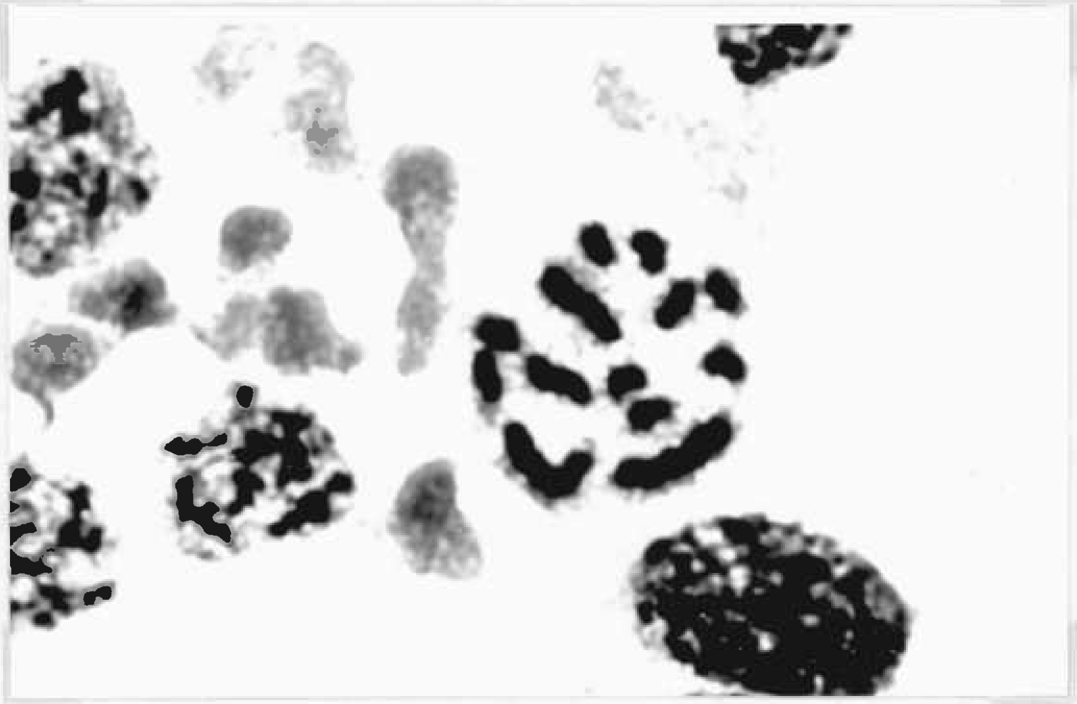


Plate 64. Anoecia furcata. 2n=13.

FUNDATRIX EFFECT IN ANOECIA CORNI.

Measurements of antennae, metathoracic legs and rostra were made for fundatrices, fundatrigeniae, virginoparae and sexuparae in order to examine characteristics of the fundatrices compared with other morphs.

Figs. 83-88 show lengths of antennae, rostra and metathoracic legs, plotted against body length. Figs. 83-85 compare fundatrices, apterous fundatrigeniae and apterous virginoparae. Figs. 86-88 compare alate fundatrigeniae, alate virginoparae, and sexuparae. There is a mean increase in length of the three characters plotted against body length from fundatrix to fundatrigenia to virginopara and from alate fundatrigenia to virginopara to sexupara. The only exception is rostral length in sexuparae. Sexuparae have a relatively shorter rostrum than virginoparae.

Fundatrices are most distinct and show no overlap with apterous fundatrigeniae for any of the three characters. The straight lines on the graphs indicate an approximate percentage (given by the figure at the top of the line) of body length for the character figured.

These results show that it is possible to distinguish between morphs when a large sample is available,for example in a suction trap catch where a large peak is probably largely contributed by one morph or on grass roots where a number of alates may either be alate virginoparae or sexuparae.

The relationship between body length and rostrum length in *Anoecia corni*.

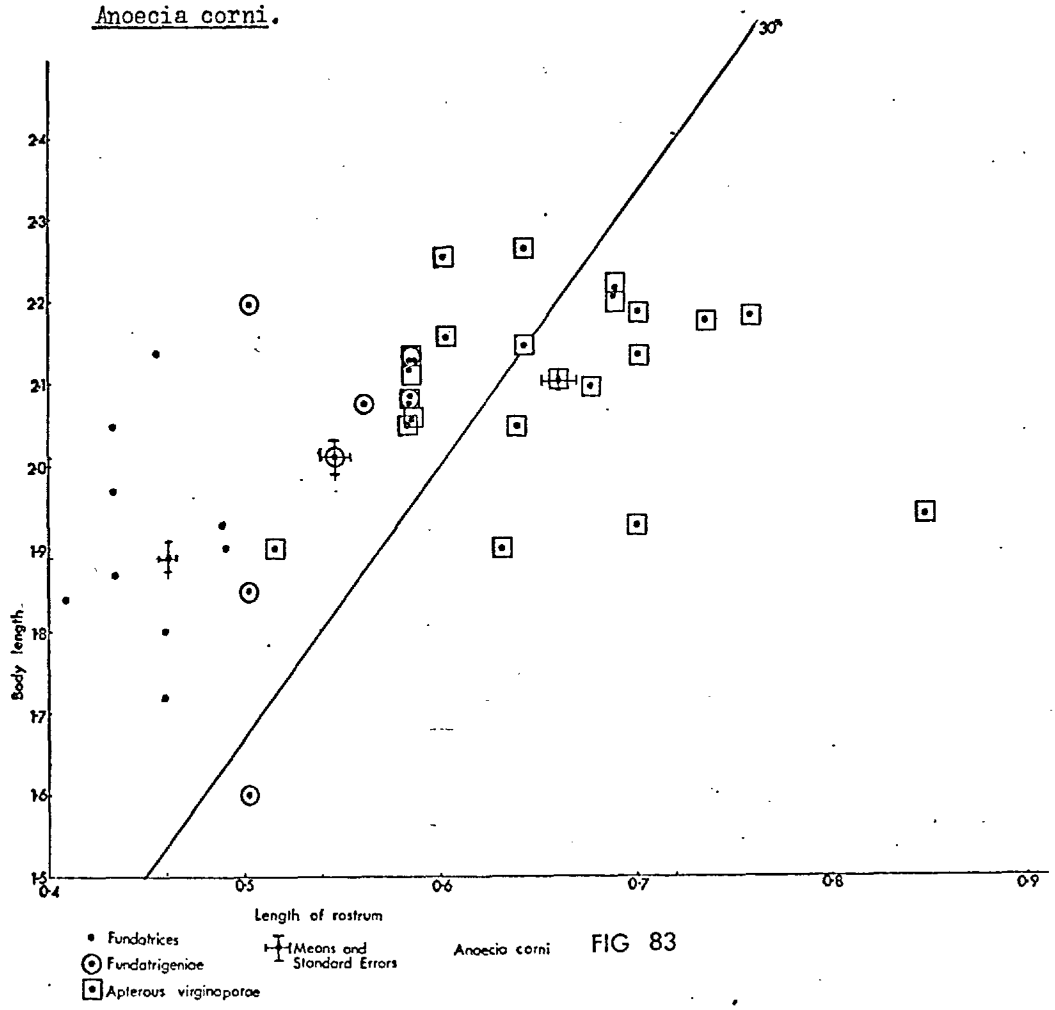
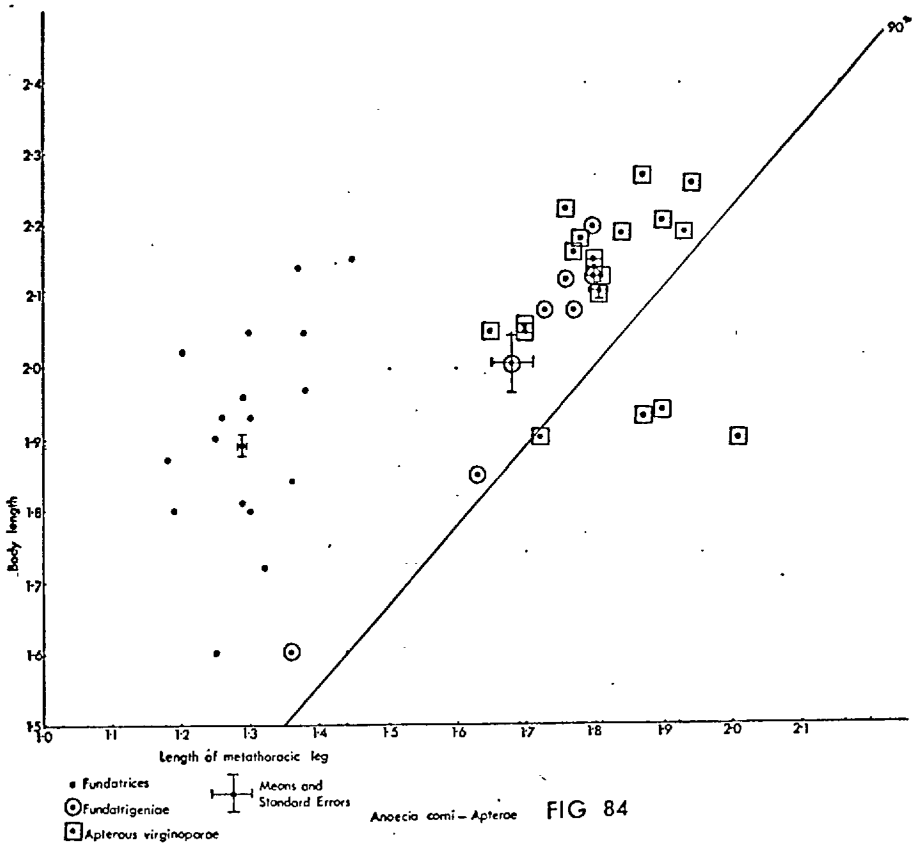


FIG 83

The relationship between body length and length of metathoracic leg in Anoecia corni.



Anoecia corni – Apterae FIG 84

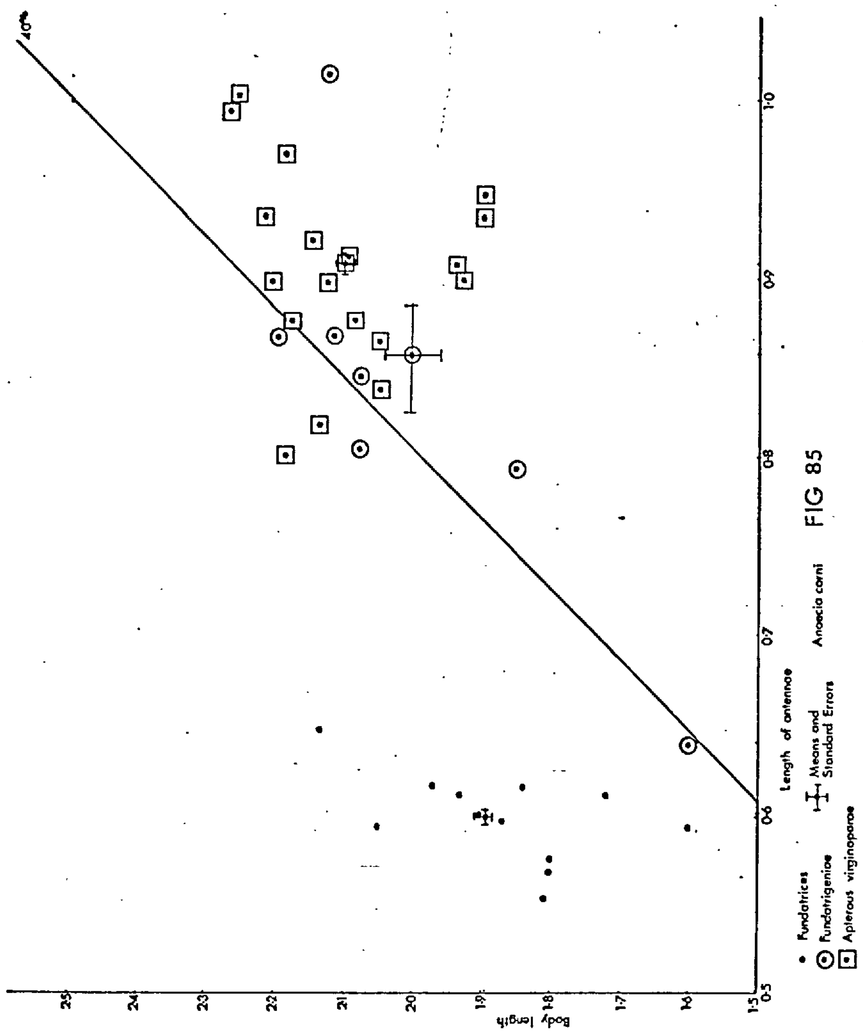


FIG 85

The relationship between body length and antenna length in *Anoecia corni*.

The relationship between body length and rostrum length in *Anoecia corni*.

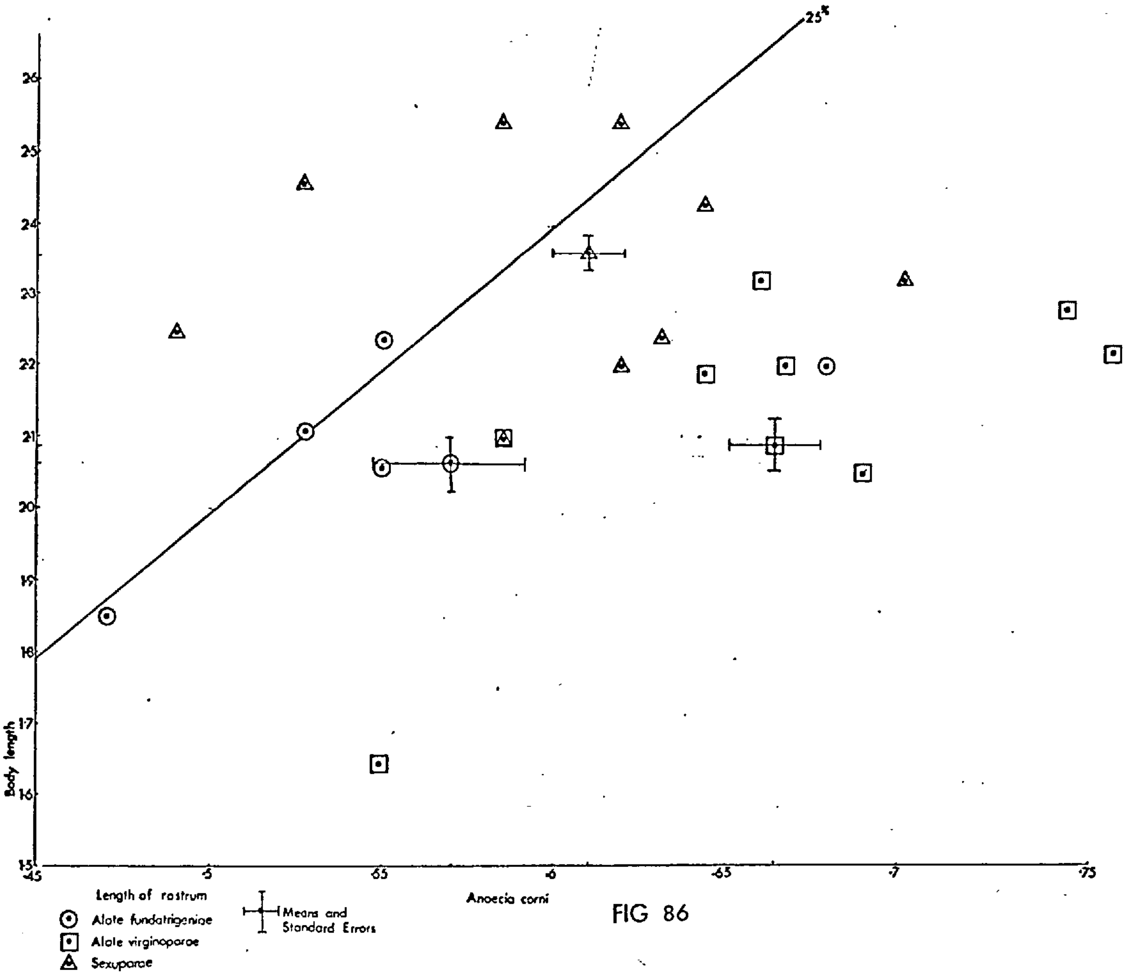
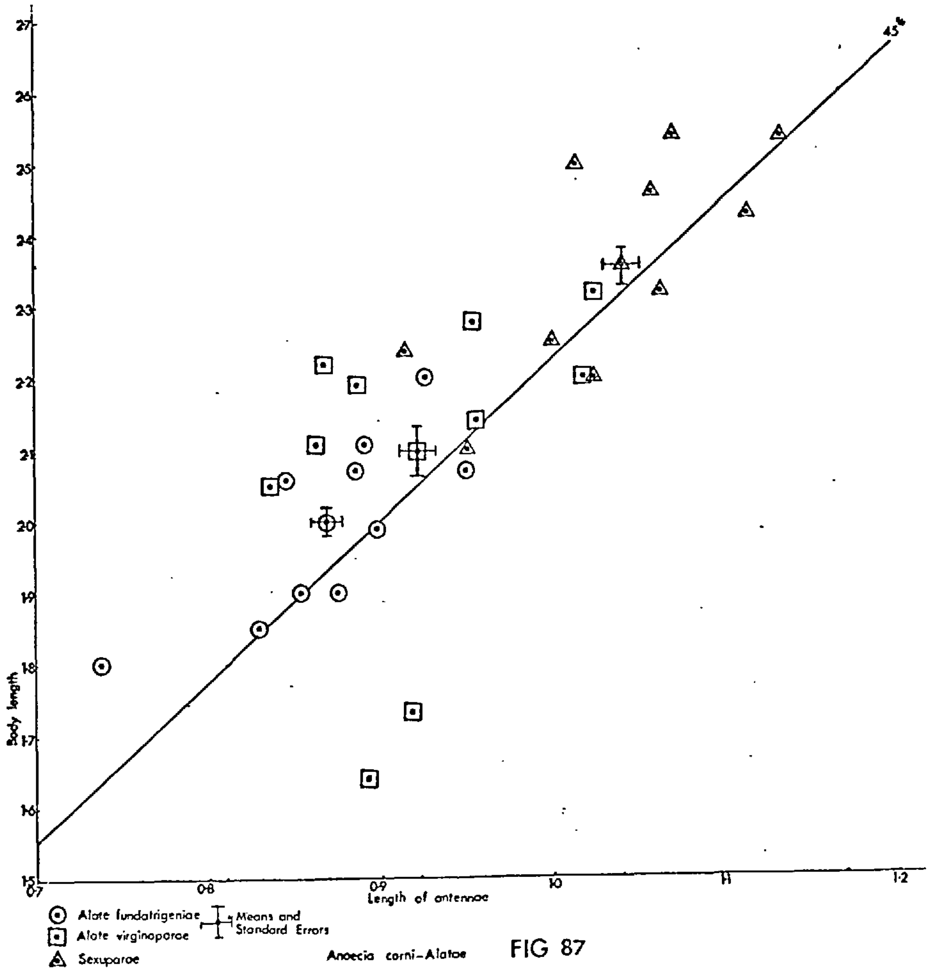


FIG 86

The relationship between body length and antenna length in *Anoecia corni*.



Anoecia corni-Alatae

FIG 87

The relationship between body length and length of metathoracic leg in *Anoecia corni*.

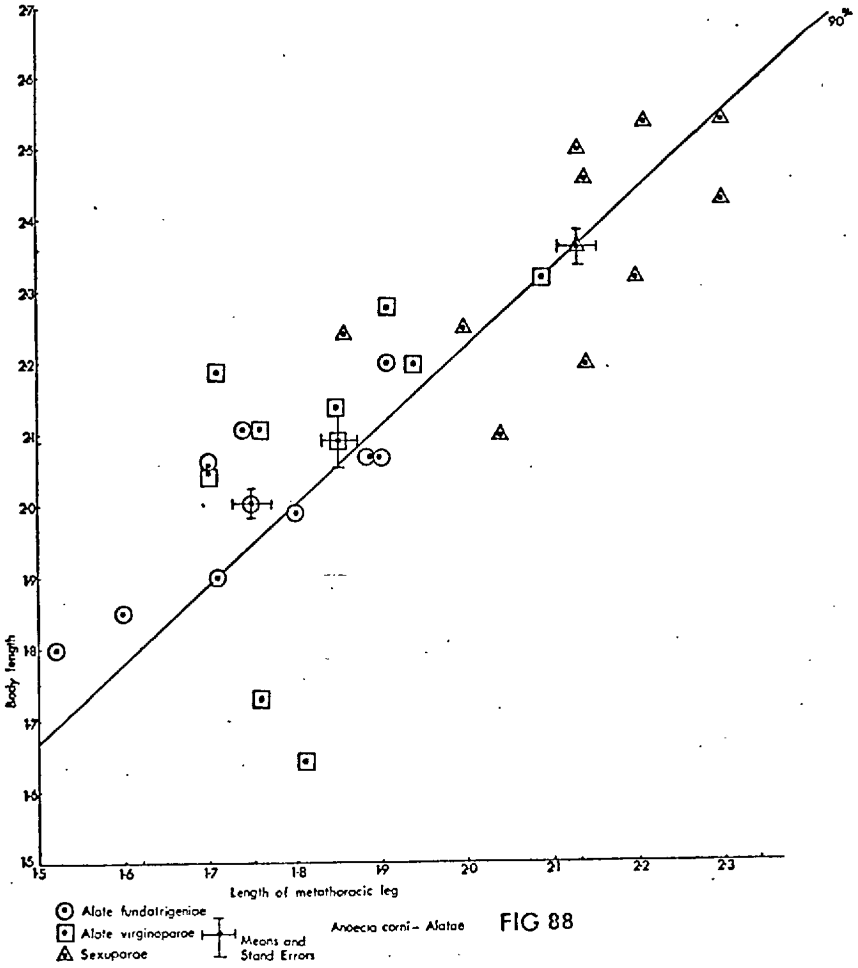


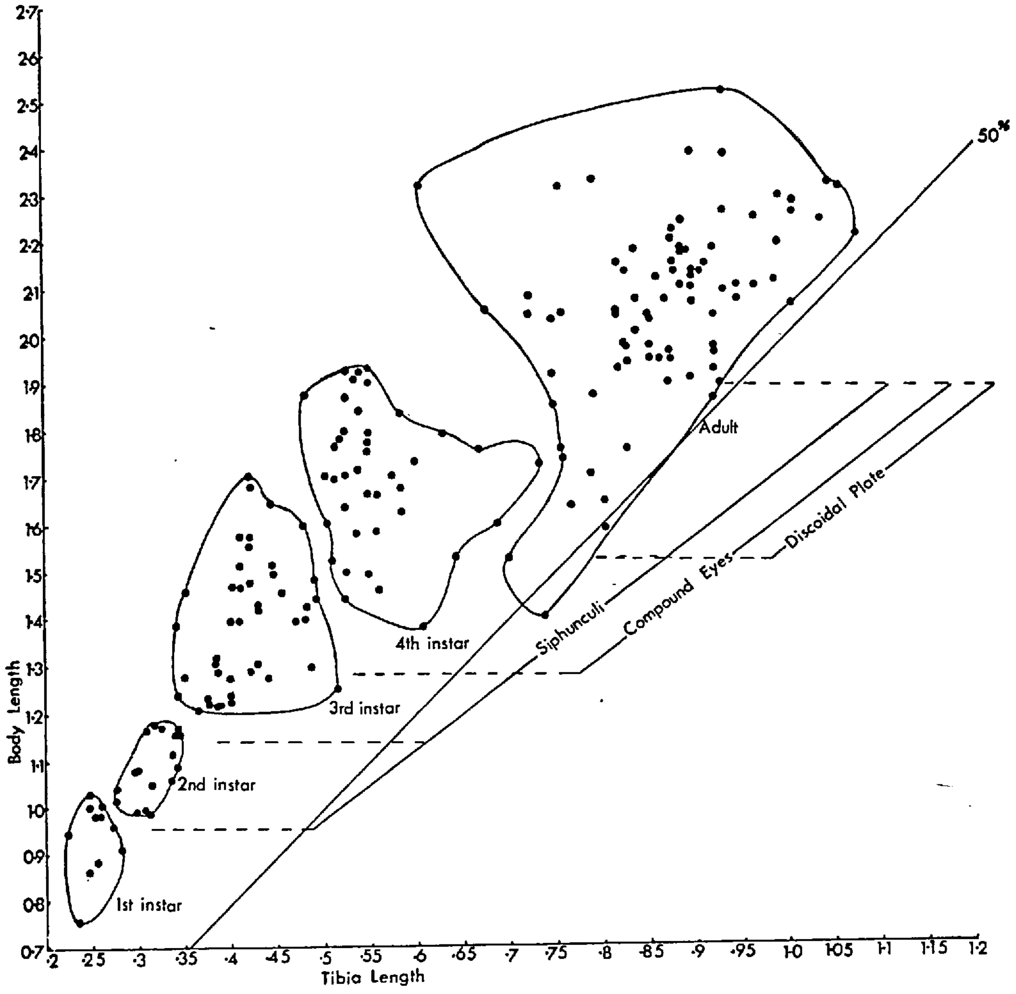
FIG 88

SEPARATION OF INSTARS IN APTEROUS VIRGINOPARAE OF ANOECIA CORNI

A key to the instars of apterous virginoparae of *Anoecia corni* has been prepared. Fig. 89 which can be used in conjunction with the key to separate instars plots body length against tibia length and shows that there is allometric growth of the tibia; higher instars have a relatively longer tibia. The 50% line is the line of isometric growth.

Key to instars of apterous virginoparae in *Anoecia corni*:

(1) Without siphunculi and with 5-segmented antennae. 1st. Instar.
With siphunculi and with 5 or 6-segmented antennae. (2)
(2) Body length less than 1.19 2nd. Instar.
Body length more than 1.2 (3)
(3) Without compound eyes. 3rd. Instar.
With compound eyes. (4)
(4) Without discoidal plate. 4th. Instar.
With discoidal plate. Adult.



Separation of instars in *Anoecia corni* (Apterous virginoparae) FIG 89

HOST PLANT LIST.

A survey of the British hosts of the subterranean stages of myrmecophilous root-feeding aphids was made using field and museum records. The order adopted is that given in Kloet and Hinks (I964). The number of records are represented by x,followed by a number.

LACHNINAE.

Maculolachnus submacula: Rosaceae; *Rosa* sp.x2I.

Stomaphis quercus: Fagaceae; *Quercus* sp.xI, *Q. pedunculatus* xI, *Q. robur* xI.

TRAMINAE

Protrama flavescens:Compositae; *Artemisia vulgaris* x2I, *Centaurea* sp.xI, *Chrysanthemum* sp.xI, Eastop(I953) also gives *Artemisia annua*.

Protrama radicis: Compositae; *Arctium lappa* xI, *Cirsium arvense* x8, *Cynara* sp. xI, *C. scolymus* x2, Eastop (I953) also gives *Carduus marianus*, *Centaurea scabiosa*.

Protrama ranunculi: Ranunculaceae; *Ranunculus* sp. x3, *R. acris* xI, *R. repens* x3, *R. tuber* xI.

Neotrama caudata: Compositae; *Helmintia echioides* xI, *Hieracium* sp. xI, *Hypochoeris radicata* xI, *Lapsana communis* xI, *Sonchus* sp.x6, *S. oleracius* xI, *Taraxacum officinale* xI, Eastop(I953) also gives *Cichorium endiva*, *Picris echioides*, *Sonchus asper*.

Trama rara: Compositae; *Sonchus* sp.?xI, *Taraxacum officinale* x5.
Gramineae;*Dactylis glomerata*? xI.

Trama troglodytes:Compositae; *Achillea millefolium* x4, *Arnica sakhaliensis* xI, *Aster novi-belgii* xI, *Carduus nutans* x4, *Centaurea* sp. xI, *Chrysanthemum leucanthemum* xI, *Cirsium maximum* xI. *C. arvense* xI, *Crepis capillaris* xI, *Cynara cardunculus* xI, *C. scolymus* xI, *Helenium* sp.xI, *Helianthus* sp. x2, *H. deapetalus* xI, *H. multiflonis* xI, *Hemerocallis* sp. xI, *Hypochoeris* sp.xI, *Inula conyza* xI, *Picris echioides* xI, *Sonchus* sp.x4, *S. arvense* xI, *S. asper* xI, *Taraxacum officinale* x3, Eastop(I953) also gives *Artemisia vulgaris*, *Arctium lappa*, *Centaurea nigra*, *Cichorium endina*, *Cirsium lanceolata*, *Doronicium* sp., *Hypochoeris radicata*, *Lapsana communis*, *Leontodon hastilis*, *Sonchus oleraceus*.
Gramineae;Grass roots x3, *Poa annua* xI.

APHIDINAE.

Rhopalosiphum insertum: Gramineae;*Agrostis alba* xI, *Festuca ovina* xI, *Poa annua* x3.

Aphis etiolata: Polygonaceae; *Rumex acetosella* x2.

Aphis sambuci: Caryphyllaceae; *Dianthus* sp. xIO, *Lychnus alba* xI, *Melandrium laciniatum* xI, *Sagina ciliata* x4, *Saponaria* sp.xI, *Silene schafta* xI.

Gramineae;Roots of Gramineae x2,*Bromus* sp. xI.

Onagraceae; *Oenothera* sp. xI.

Plantaginaceae; *Plantago stauries* xI.

Polemoniaceae; *Polemonium* sp. xI.

Polygonaceae; *Lychnis alba* xI, *Rumex* sp. x4, *R. crispus* xI, *R. obtusifolia* xI.

Saxifragaceae; *Saxifraga* sp. xI.

Umbelliferae; *Aciphylla squarrosa* xI, *Aegopodium* sp. xI, *Apium graveolens* xI.

Aphis acetosae: Polygonaceae; *Rumex* sp. xI, *R. acetosa* x3, *R. acetosella* xI,

Aphis(Cerosipha)hypochoeridis: Compositae; *Hypochoeris* sp. x2, *H. glabra* xI, *H. radicata* x6.

Aphis thomasi: No data available.

Aphis verbasci: Scrophulariaceae; *Verbascum phlomoides* x3.

Aphis cliftonensis: Cistaceae; *Helianthemum chaemcistus* xI.

Aphis(Tuberculaphis)crepidis: Compositae; *Crepis* sp. xI, *C.biennis* xI.

Aphis(Tuberculaphis) lambersi: Gramineae;Roots of Gramineae xl

Umbelliferae; *Daucus* sp. x3, *D. carota* x6.

Aphis longirostrata: Plantaginaceae; *Plantago maritima* xI.

Aphis(Tuberculaphis)parietariella: Urticaceae; *Parietaria officinalis* xI, *P. ramiflora* xI.

Aphis(Tuberculaphis)plantaginis: Plantaginaceae; *Plantago major* xI, *P. media* x3.

Aphis(Tuberculaphis)taraxacicola: Compositae; *Taraxacum officinale* xI9.

Aphis(Toxopterina)vandergooti: Compositae; *Achillea millefolium* xI5.

Aphis(Tuberculaphis)violae: Violaceae; *Viola cornuta* x2.

Anuraphis catonii: Umbelliferae; *Carum carvi* xI, *Pimpinella saxifraga* x3.

Anuraphis farfarae: Compositae; *Tussilago farfara* x6.

Anuraphis subterranea: Umbelliferae; *Angelica archangelica* xI, *Heracleum sphondylium* xIO, *Pastinaca* sp. x8,*P. sativa* x5.

Brachycaudus cardui:Boraginaceae; *Borago* sp. x3, *Myastotis* sp. x2.
Compositae; *Achillea millefolium* xI, *Anaphalis yedoensis* xI, *Arctium lappa* x3, *Arcototis* sp.xI, *Aster* sp. xI, *Berkheya adlami* xI, *Chrysanthemum* sp. x4, *C. leucanthemum* xI, *Cirsium* sp. x3, *C. arvense* x2, *C. palustre* xI, *C. vulgare* x5, *Cynara scolymus* xI, *Matricaria inodora* xI, *M. chamomilla* xI, *Senecio* sp.xI, *S. cineraria* xI, *S. jacobeae* x6, *S. vulgaris* x8, *Venidium factuosum* xI.
Cruciferae; *Capsella* sp. xI, *C. bursa-pastoris* xI.
Malvaceae; *Althaea* sp.xI.

Brachycaudus linariae: Scrophulariaciae; *Linaria vulgaris* xI.

Brachycaudus lucifugus: Plantaginaceae; *Plantago lanceolata* xI.

Brachycaudus jacobi: Boraginaceae; *Myosotis* sp. x2, *M. arvensis* xI.

Brachycaudus malvae: Malvaceae; *Malva* sp. xI.

Jacksonia papillata: Gramineae;*Dactylis glomerata* xI, *Festuca ovina* xI, *Poa annua* xI.

Rhopalomyzus poae: Gramineae;Roots of Gramineae xl,*Festuca pratensis* xI, *F. varia* xI, *Koeleria alpicola* xI,*Lonicera alpigena* x3, *Poa pratensis* xI.

ANOECIINAE.

See section on taxonomy of *Anoecia*.

ERIOSOMATINAE.

Tetraneura ulmi:Gramineae;Roots of Gramineae x34,*Agropyron repens* x2, *Agrostis* sp. xI, *A. stolonifera* xI, *Brachypodium pinnatum* xI, *Briza media* xI, *Bromus* sp.xI, *B. carinatus* xI, *Dactylis* sp. xI, *Festuca* sp. x2, *F. pratensis* xI, *F. rubra* xI, *Holcus lanatus* xI, *Hordeum* sp.xI, *Lolium perenne* x2, *Poa* sp. xI,*P. annua* x7, *P. pratensis* xI, *Psamma arenaria* xI, *Triticum aestivum* xI.

PEMPHIGINAE.

Pemphigus bursarius: Compositae; *Lactuca* sp. x2, *Lapsana communis* xI, *Matricaria inodora* xI, *Sonchus* spxIO, *S. arvensis* x2, *S. asper* xI, *S. oleraceus* xI, *Taraxacum* sp. x3.
Cruciferae; *Arabis* sp. xI, *A. blepharophylla* xI.

Prociphilus(Rhizomaria)piceae: Piceaceae; *Picea* sp. x2, *P.abies* x2, *P.excelsa* x3, *P. sitchensis* xI.

FORDINAE.

Paracletus cimiciformis: Gramineae;Roots of Gramineae xl, Festuca ovina xI, F. rubra x2, Setaria viridis xI.

Smynthurodes betae: Boraginaceae; Coreopsis sp. xI, Heliotropia peruvianum xI, Myosotis sp. xI.
Compositae; Achillea millifolium x3, Artemisia vulgaris xI.
Cruciferae; Aethionema oppositifolia xI, Coronopus sp. x2.
Crassulaceae: Sedum maximum xI.
Dipsaceae; Scabiosa sp. xI.
Gentianaceae; Gentiana septemfida xI.
Gramineae;Roots of Gramineae x5,Festuca pratensis xI.
Onagraceae; Epilobium sp. xI.
Solanaceae; Solanum tuberosum xI.

Forda formicaria: Gramineae;Roots of Gramineae x55,Agropyron sp. xI, Agrostis sp. x2, Arrhenatherium elatius xI, Brachypodium pinnatum x2, Briza media x2, Bromus carinatus xI, Carex sp. xI,Dactylis glomerata xI, Festuca sp. xIO, F. ovina x3, F. rubra x7, Glyceria maritima xI, G. maxima xI, Holcus lanatus xI, Lolium perenne x4, Molinia caerulea xI, Poa annua x8, Triticium aestivum xI.

Forda marginata: Gramineae;Roots of Gramineae x10,Agropyron repens xI, Agrostis sp. x2, Bromus sterilis xI, Festuca ovina x2, Heliotrichum pratense xI, Poa annua x1, Psamma arenaria xI.

Aploneura lentisci: Gramineae;Roots of Gramineae x23,Bromus sterilis xI, Dactylis sp. xI, D. glomerata x2, Festuca sp. xI, F. pratensis xI, Glyceria maxima xI, Poa annua x5, P. pratensis xI, P. trivialis x2, Triticium aestivum xI.
Scrophulariaceae; Veronica raoulli? x1.

Baizongia pistaciae: Gramineae;Roots of Gramineae x12,Agrostis sp. x5, Briza media x2, Festuca sp. x3, F.ovina xI, Poa annua xI.

Geoica eragrostidis: Gramineae;Roots of Gramineae x24,Agrostis sp. xI, Briza media x2, Deschampsia sp. xI, Festuca sp. x8, F. ovina xI, F. pratensis xI, F. rubra x5,Triticium aestivum xI.

Geoica setulosa: Gramineae;Roots of Gramineae x8,Briza media xI, Festuca sp. x5, F. ovina xI, F. pratensis xI,Triticium aestivum xI.

Aleophagus myseri: Liliaciae; Aloe sp. xI, A. aristata xI.

RELATIONSHIPS WITH ANTS.

The types of relationship which exist between aphids and ants have been classified by Stammer and Greim (Greim 1952) and this classification was slightly altered by Zwölfer (1958) to suit the situation that is found in the relationship between ants and root aphids. The three groups named by Stammer and Greim are:- Myrmecobiont, myrmecophilous and myrmecoxenous. Zwölfer (1958) defines these terms as follows:-

Myrmecobiont is the term for a species of aphid which is completely dependent on ants and is fed by them.

(Tullgren (1925), Greim (1952), Zwölfer (1958) and Blackman (1974) either state or imply that Paracletus cimiciformis is fed by the ant, Tetramorium caespitum. These statements are based on observations reported in a paper by Adlerz (1913). Translation of the relevant section of the paper however shows that Adlerz did not observe P. cimiciformis being fed by Tetramorium caespitum. He simply kept a number of P. cimiciformis from the middle of June until the first week of September without food in a nest of Tetramorium caespitum and as they survived he concluded that they had been fed by the ants.) Myrmecobiont is used exclusively for P. cimiciformis by Zwölfer (1958) and in view of the absence of evidence for it being fed by ants the term is dropped from the present classification.

Myrmecophilous is defined by Zwölfer (1958) as applying to species which are regularly visited by ants and which hibernate entirely or partly in ant's nests but which are shown by breeding experiments not to be completely dependent on ants.

Myrmecoxenous species are not, or only exceptionally, visited by ants. They appear only occasionally in ants' nests and then only as tolerated guests.

The same terms are used in this study but the field work which has been done and examination of the literature require some redefinition of the existing terms, and the introduction of one new one. The term myrmecobiont, for the reasons given above, has been dropped.

1. Obligate Myrmecophilous species spend the entire year in the company of ants underground. They may be anholocyclic and over-winter parthenogenetically or they may be holocyclic and lay over-wintering eggs which are cared for by ants. In both cases they have abandoned the primary host and are benefiting from ant-attendance throughout the year.

Facultative Myrmecophilous species have two populations, one is holocyclic and returns to the primary host where the eggs are laid and are not cared for by ants; the other is anholocyclic and overwinters parthenogenetically in the soil in company with ants. Myrmecoaestivous species have no relationship with ants in the winter but are readily attended by ants during the summer. Myrmecoxenous species are not, or only exceptionally, visited by ants.

Advantages of ant attendance to root aphids.

The advantages of ant attendance to root aphids are the same as the advantages to all aphids but with some additions resulting from the specialized environment in which they live.

Way (1963) gives the following advantages to be derived from ant attendance:-

(1) Protection from natural enemies.
(2) Benefits derived within the ants' nests and shelters.
(3) Transport.

Nixon (1951) also includes improved hygiene through removal of honeydew.

(1) Protection from natural enemies.

In the case of root aphids protection is not great. Fewer predators and parasites are able to attack root aphids than aerial aphids but those that do are not deterred by ants. Stary(1961) and Zwölfer (1958) state that the degree of parasitism of root aphids attended by ants is high. In the present study more than 50 Anoecia corni which had been parasitized by Aclitus obscuripennis Forst. were found in a colony feeding on Dactylis glomerata and attended by Lasius niger at Denham in Bucks. on 30/7/76. More than 30 Tetraneura ulmi which had been parasitized by Paralipsis enervis (Nees) were found in a colony feeding on Agrostis stolonifera and attended by Lasius flavus at Denham in Bucks. on 2/9/75. Lasius flavus did not attack P.enervis in the laboratory. Larvae of Aphidoletes aphidimyza (Rondani) (Cecidomyiidae) were found preying on Anuraphis subterranea in the leaf bases of Heracleum sp. at Denham in Bucks. on 16/8/75. The aphids were attended by Lasius niger. A. aphidimyza has been recorded as a predator of root aphids (Harris 1973) but Anuraphis subterranea is not given in Harris's (1973) list of prey species.

(2) Benefits derived within ants' nests and shelters.

Zwölfer (1958) states that the microclimate within ants's nests is favourable to root aphids. He states that it provides protection from excessive moisture, and attack by fungi although not complete protection from frost. The suntrapping properties of Lasius flavus mounds (Waloff and Blackith, 1962) means that they provide a higher temperature than the surrounding soil and they are also well drained.

Aphid eggs kept within ants' nests also benefit from the microclimate and in addition they are licked by ants which prevents shrivelling and fungal attack (Pontin 1960). Subterranean aphids benefit from the space created within the soil by burrowing ants. Galleries expose roots for aphids to feed upon, give space for new individuals and allow aphids to walk from root to root. In addition, sloping or vertical galleries may assist aphids in escaping from predators because they can fall or roll when feigning death. Where ants have covered aphids in a'tent'of soil they may derive protection from aerial predators and parasites and have a more favourable microclimate.

(3) Transport of attended aphids.

Ants will pick up aphids and carry them. Lasius flavus, L. niger, Formica aquilonia, F. lemani and Myrmica rubra were observed to carry aphids. It has also been observed by other authors eg. Pontin (1960) and Zwölfer (1958). Zwölfer (1958), Webster (1907) and Eidmann (1927) report that aphids were carried to their host plants. Nixon (1951) and Pontin (1960) however conclude that there is comparatively little evidence for trahsport to the host plant. In the present study Lasius flavus failed to transport Trama rara from one empty chamber to another containing roots of Taraxacum officinalis. Pontin (1960) considers that it is unlikely that ants recognize both aphid species and the species of their host plants and correctly associate the two. However even if they do not deliberately transport aphids to their host plants it is possible that random carrying of aphids may assist them in finding their own food plants. In the case of grass root feeders which are less specific the chances of being transported to grass roots are very high.

Transport into the nest takes place when ants are disturbed while attending aphids and this takes aphids into favourable microclimates as well as into cavernous areas where roots are likely to be exposed.

(4) Hygiene through removal of honeydew.

Removal of honeydew is very important for root aphids unless they possess wax glands and can coat their honeydew droplets with wax. Zwölfer (1958) found that although the following aphids were closely associated with ants they were able to survive without ants in breeding experiments:- *Paranoecia pskovica*, *Anoecia zirnitzi*, *A. corni*, *A. furcata*, *A. vagans*, *Baizongia pistaciae*, *Geoica eragrostidis*, *G. setulosa*, *Forda formicaria*, *Forda marginata* and *Smynthurodes betae*.

In the present study *Trama rara*, *Protrama radicis*, *P. flavescens* and *Trama troglodytes* did not survive without ants as they became coated in honeydew and were attacked by fungus. The Commonwealth Mycological Institute at Kew gave the following identifications for fungi growing on *Anoecia corni* which died on being contaminated with honeydew:- *Mucor circinelloides* van Teigham, *Entomophora* sp., *Verticillum* sp, *Cladosporium* sp., *Fusarium* sp. and *Erysiphe tortilis* Wallr. ex Fr. It is thought that most of these fungi were saprophytic, feeding either on dead aphids or the honeydew. *Entomophora* sp., at least may have been responsible for death.

Observations of *Anoecia corni* in the field and in the laboratory show that virginoparae are not capable of ejecting their honeydew but sexuparae, sexuales and fundatrices can squirt the honeydew some distance from the anus. In the field the following species were always found with ants:- *Anoecia zirnitzi*, *A. corni*, *A. vagans*, *A. furcata*. *Tetraneura ulmi*, *Protrama flavescens*, *P. radicis*, *P. ranunculi*, *Trama rara*, *T. troglodytes*, *Geoica eragrostidis*, *G. setulosa*, *Forda formicaria*, *F. marginata*, *Baizongia pistaciae* and *Smynthurodes betae*. It was found very difficult to rear the grass-roots feeding species successfully in the laboratory, and it was therefore not possible to determine if they could survive for long periods without ants. However if they can it would seem to be an artificial situation as they are invariably ant-attended in the field. Even those species which do not rely on ants to care for their overwintering eggs may be dependent on shelter for the overwintering viviparae, as well as requiring the removal of their honeydew by ants. Honeydew proved lethal to species of the Traminae which could be satisfactorarily reared in the laboratory in the presence of ants (see above).

Obligate Myrmeciphilous Species

The following British root aphids can be described as obligate myrmecophiles:- *Paranoecia pskovica*, *Anoecia zirnitzi*, *A. furcata*, *Trama rara*. *T. troglodytes*, *Protrama flavescens*, *P. ranunculi*, *P. radicis*, *Neotrama caudata*, *Geoica eragrostidis*, *G. setulosa*, *Forda formicaria*, *F. marginata*, *Aphis etiolata*, and probably *Aphis hypochoeridis*, *A. taraxacicola*, *A. plantaginis*, *A. violae*, *A. cliftonensis*, and *A. acetosae*.

Facultative Myrmecophilous Species.

Tetraneura ulmi and *Pemphigus bursarius* are facultative myrmecophilous species because they both have two populations, one overwinters in the soil with ants and the other returns to the primary host, in the case of *T. ulmi* this is *Ulmus* spp. and in the case of *P. bursarius* it is *Populus* spp. of the *nigra* group.

Anoecia corni also has two populations, one of which overwinters on grass roots and the other returns to the primary host, dogwood. *A. corni* is exceptional in that it is often attended on the primary host and has been shown to lay its eggs in the soil. Here they may be collected by ants.

Myrmecoaestivous Species.

There are many species which live in subterranean semi-subterranean habitats with ants during the summer months and return to the primary host in the autumn. These species have a less close relationship with ants and tend to be less subterranean than myrmecophilous species, often feeding on the root collar where they can only be classified as subterranean by virtue of the fact that they are covered by a 'tent' of soil by ants. The following are examples:- Some *Dysaphis* spp., *Anuraphis subterranea*, *A. farfarae*, *A. catonii*, *Brachycaudus cardui*, *Aphis sambuci* and *Anoecia vagans*.

Myrmecoxenous Species.

The only species that produces copious wax and which was observed with ants, was *Aploneura lentisci*. This was only on one occasion ,early in spring when,perhaps the ant, *Lasius flavus* was more in need of a source of honeydew than it is at other times of the year. *Aploneura lentisci* is often found in the vicinity of ants' nests as would be expected for such a widespread species which is found almost everywhere. Normally, when found in the area of an ants' nest it is not within the galleries but is found feeding on very fine roots in quite tight packed soil which has not been penetrated by ants. Thecabius affinis, Kaltenbachiella pallida, Rhopalosiphoninus staphyleae and Colopha compressus are other examples of myrmecoxenous species.

Strategies open to root aphids.

Ants are such a universal phenomenon for root aphids that they exert a selective pressure in the same way as other environmental factors such as climate. Generally speaking, in the subterranean part of their life cycle root aphids have two courses open to them, they can either exploit the benefits to be derived from ants and accept a certain amount of predation (Pontin, 1960) or they can attempt to isolate themselves from ants.

Factors affecting ant attendance.

(1) Unacceptable honeydew.

It has been suggested (Weber 1935; Cottier 1953; Klöft 1960) that when sap is taken from some location other than the sieve tubes of the phloem the excretion is poor in sugars and does not attract ants. The observation of Lasius flavus attending Aploneura lentisci demonstrates that in this case the honeydew was acceptable to ants, although A. lentisci is not usually attended.

(2) Avoidance of contact.

Aploneura lentisci is often physically separated from ants which are close by because it lives in tight packed soil feeding on very fine roots. It is capable of living in soils which are too dry for other root aphids and this may also discourage ants. It is possible that A. lentisci will move away from ants if they happen to open galleries in the area in which it is feeding. There are aerial aphids eg. Megoura viciae which are not attended because they feign death and drop from plants when disturbed. However root aphids which feign death are ant-attended and probably have adapted this behaviour to allow ants to carry them more easily.

(3) Remaining motionless and expelling honeydew to a distance.

Amongst aerial aphids Myzus persicae is ignored by Lasius flavus and Formica aquilonia because it remains motionless and is not contaminated with honeydew because this is expelled to some distance. Trama rara exudes drops of honeydew slowly and allows them to be supported by the perianal hairs until an ant removes them. If they are not removed they may drop off but inevitably some honeydew remains and eventually the anus is sealed by dried honeydew which becomes subject to fungal attack. Often the birth of nymphs is prevented or the adults' long hind legs become entangled. This seems to be the case with all root aphids which do not produce wax and this method of avoiding ants does not apply to root aphids.

The perianal hairs or trophobiotic organ may be important in determining ant attendance. The variations in shape of the trophobiotic organ are discussed by Schmidt (1952 b) and Zwölfer (1958). Zwölfer found that of the myrmecophilous root aphids which he examined the only one to lack a trophobiotic organ was Paracletus cimiciformis.. This aphid is assumed by Schmidt (1952) to provide exudates , secreted from the cuticle (Plate 56) for ants and only rarely produces honeydew (Zwölfer 1958). In holding drops of honeydew, perianal hairs become contaminated and the smell/taste of honeydew may assist in arresting passing ants.

In Trama rara and other other Lachnids (Eastop 1972; Hille Ris Lambers, 1969) the perianal hairs (and many of the body hairs) are strongly recurved. In the present study Trama rara was examined using the scanning electon microscope and was found to have recurved hairs. Unless the recurving of the hairs is an artefact of prepartion for viewing with both the light and scanning electon microscopes it is possible that in the living specimen it could serve to retain small drops of honeydew to attract ants.

(4) Host alternation.

Host alternation prevents continuous association with ants. In myrmecophilous aphids, those species which have the closest association with ants have no host alternation. In the Anoeciinae, Paranoecia pskovica, Anoecia zirnitzi and A. krizusi no longer return to the primary host. A. furcata has almost if not entirely, eliminated the primary host. Anoecia corni has a population which has eliminated the primary host and A. vagans has complete host alternation. Evolution of monoecy is most complete in those species which are secondarily holocyclic (Mordvilko 1928) eg. A. zirnitzi, A. krizusi and Paranoecia pskovica. In the Fordinae all British forms are monoecious and anholocyclic which is probably due to the loss of Pistacia from Britain during glaciation (Mordvilko 1928). Anholocyclic forms may have evolved at the time that Pistacia died out in Britain or may have spread more recently from the Mediterranean area where Pistacia still occurs. Perhaps as a result of this, British Fordinae except for Aploneura lentisci are closely associated with ants. Tetraneura ulmi and Pemphigus bursarius have one monoecious anholocyclic population and one dioecious holocyclic population. In the Traminae all species are normally anholocyclic and monoecious.

(5) Wax production.

In dealing with honeydew, subterranean aphids either produce large quantities of wax to envelope it or they allow ants to remove it. There is no real intermediate position because when enough wax is produced to envelope honeydew it is obscured from ants and they are not motivated to remove it. It is perhaps possible that aphids such as Baizongia pistaciae can increase wax production if not ant attended but they were not found without ants.

The closeness of the ant-aphid relationship.

The closer the relationship an aphid has with one species of ant the less likely it is to be attended by a wide range of ants. Myrmecoaestivous aphids may be attended by many ant species which are active in the summer months and which by chance, or because of biotope preferences, come across them. The dioecious populations of facultatively myrmecophilous root aphids have the same choice as myrmecoaestivous aphids but the monoecious populations are more likely to be attended by ants which will provide a suitable overwintering environment. Formica rufa attends a wide range of aphids in the summer including root aphids (Zwölfer 1958) and has been shown to attend Protrama flavescens and Trama rara in the present work, although it does not keep aphids in its nest over winter. Any monoecious summer population which is attended by Formica rufa will not survive the winter and thus there is a selective pressure for monoecious root aphids which are ant attended to evolve a relationship with ants that will provide suitable winter conditions. Facultative myrmecophily represents a watershed in ant-aphid relations between a loose wide ranging relationship and a close relationship between the aphid and a small number of ant species. This is demonstrated in the genus Anoecia where A. furcata (obligately myrmecophilous) is usually attended by Lasius flavus which is a subterranean ant. A. corni (facultatively myrmecophilous) is attended by a wide range of ants including L. flavus, L.niger and Myrmeca rubra (Tab.4)

Obligate myrmecophilous species such as Geoica eragrostidis ,G. setulosa, Anoecia furcata, Forda marginata, Baizongia pistaciae were almost always found with Lasius flavus. Forda formicaria (obligate myrmecophilous) is found with a wider range of ants possibly because it produces more alates than these species, allowing summer colonizations. Holocyclic obligate myrmecophilous species were found exclusively with Lasius flavus, eg. Paranoecia pskovica and Anoecia zirnitzi. Paracletus cimiciformis (obligate myrmecophilous) is usually found with Tetramorium caespitum, very occasionally with Lasius flavus.

Numbers of aphid species available to subterranean ants.

Lasius flavus and Tetramorium caespitum are the most subterranean of the British aphidicolous ants. Neither of these ants seems so restricted in its choice of aphids as obligate myrmecophilous aphids are in their choice of ants (Tabs.3&4).Although Lasius flavus shows adaptions to subterranean life, for example small eyes and relatively little pigment,its behaviour is sufficiently versatile to allow it to attend a wide range of aphids. It will attend any aphids upto and including root collar level. These latter are covered with a 'tent' of soil. It does not however attend aerial aphids which are available to Lasius niger. Lasius niger also attends subterranean aphids but Lasius flavus seems more successful perhaps because of its egg tending behaviour and because it is more active than Lasius niger in the winter months.

Disadvantages of myrmecophily to aphids.

The disadvantages of myrmecophily are those which accompany overspecialization in any field. The survival of myrmecophilous aphids depends on the survival of their attendant ants. Their distribution is restricted to, at maximum, the distribution of their attendant ants.

The two closely related species, Aploneura lentisci and Baizongia pistaciae illustrate this point. A. lentisci (myrmecoxenous) is found on the roots of grass in almost any situation or habitat and has a wide distribution. B. pistaciae (obligate myrmecophilous) was found only in habitats suitable for Lasius flavus. Paracletus cimiciformis (obligate myrmecophilous) is even more restricted because its host ant *Tetramorium caespitum* has a smaller range than *L. flavus* (Bolton and Collingwood).

The relationship between British ants and root aphids.

	Stomaphis quercus	Maculolachnus submacula	Protrama flavescens	" radicis	" ranunculi	Neotrama caudata	Trama rara	" troglodytes	Rhopalosiphum insertum	Aphis etiolata	" sambuci	" hypochaeridis	" thomasi	" verbasci	" cliftonensis	" crepidis	" insularis	" parietariella	" plantaginis	" taraxacicola	" vandergooti	" violae	Acaudinum scabinosae	Dysaphis brancoi	" anthrisci	" radicola	" chaerophylli	" hirsutissima	" newskyi	" angelicae	" lauberti	" crataegi	" ranunculi	" tulipae	" crithmi	" bonomii	" lappae	" pyri	" maritima
Ponera coarctata	Does not attend aphids																																						
Hypoponera punctatissima	Does not attend aphids																																						
Myrmica lobicornis																										⊠s		⊠s	⊠s	⊠s	⊠s	⊠s	⊠s			⊠s			
" rubra												■																											
" ruginodis									■																														
" sabuleti																																							
" scabrinodis																																							
" schencki																																							
" specioides																																							
" sulcinodis																																							
Sifolinia karavajevi	Permanent social parasites of Myrmica species																																						
Formicoxenus nitidulus																																							
Leptothorax acervorum																																							
" interuptus																																							
" nylanderi																																							
" tuberum																																							
Anergates atratulus	Permanent social parasite of Tetramorium caespitum																																						
Strongylognathus testaceus	Obligate slave-making ant																																						
Tetramorium caespitum																																							
Solenopsis fugax																																							
Myrmecina graminicola																																							
Stenamma westwoodi																																							
Tapinoma erraticum																																							
Formica aquilonia																																							
" cunicularia																																							
" exsecta																																							
" fusca																																							
" lemani																														s										
" lugubris																																							
" pratensis																																							
" rufa																																							
" rufibarbis																																							
" sanguinia																																							
" transkaucasica																																							
Lasius alienus																										⊠s				⊠s	⊠s	⊠s	⊠s			⊠s			
" brunneus																																							
" flavus			■	■		■	■	■		●																										ⓟ			
" fuliginosus	■																																						
" mixtus																																							
" niger			■	■	■		■	■			■	■								■	■		s			m		s	s				■		s				h▽
" umbratus																												s											
Species unspecified																								s	s		s							s			s	s	

Solid symbols represent records from the presnt study.
Open symbols with letters in,represent records from the literature.
Squares indicate species which were found in association.
Circles indicate that aphid eggs were found in the ant's nest.
Squares with diagonals indicate that the genus of ant was recorded but the species was not given.

Key to authors:- b=Brian,M.V.;d=Donisthorpe,H.St.J.K.;
m=Mordvilko,A.K.;ma=Martin,J.H.;p=Pontin,A.J.
r=Richards,O.W.;s=Stroyan,H.L.G.;t=Theobald,F.V.
z=Zwölfer,H.

Table 3.

The relationship between British ants and root aphids.

	Anuraphis catonii	" farfarae	" subterranea	Brachycaudus cardui	" jacobi	" linariae	" lucifugus	" persicae	Jacksonia papillata	Rhopalomyzus poae	Anoecia furcata	" disculigera	" corni	" vagans	" major	Neanoecia zirnitzi	Paranoecia pskovica	Colopha compressa	Tetraneura ulmi	Prociphilus bumelliae	" fraxini	" pini	" xylostei	Rhizomaria piceae	Thecabius affinis	Pemphigus bursarius	Paracletus cimiciformis	Smynthurodes betae	Forda formicaria	" marginata	" skorkini	Aploneura lentisci	Baizongia pistaciae	Geoica setulosa	" eragrostidis	Aloephagus myseri	Truncaphis newsteadi
Ponera coarctata																																					
Hypoponera punctatissima																																					
Myrmica lobicornis																																					
" rubra	■	■									■		■	■					■										■								
" ruginodis											■		t	z																							
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" interuptus																																					
" nylanderi																																					
" tuberum																																					
Anergates atratulus																																					
Strongylognathus testaceus																																					
Tetramorium caespitum											z		t						z								z	b			z		z				
Solenopsis fugax																			z														z				
Myrmecina graminicola																																					
Stenamma westwoodi																																					
Tapinoma erraticum																																					
Formica aquilonia																																					
" cunicularia																																					
" exsecta																																					
" fusca													t						z																		
" lemani																																					
" lugubris																																					
" pratensis											z																										
" rufa													p						z																		
" rufibarbis																																					
" sanguinia																																					
" transkaucasica																																					
Lasius alienus													p						p									r	■								
" brunneus																																					
" flavus											■		■	■		ⓟ	●	z	■								□	■	■	■	z	■	■	■	■		
" fuliginosus													d																								
" mixtus											z								z																		
" niger			■								■		■	■			z		■							■			■	d			z		■		
" umbratus																			■																		
Species unspecified																																					

Solid symbols represent records from the present study.
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z=Zwölfer,H.

Table 4.

List of British Myrmecophilous Root Aphids.

APHIDINAE.	Relationship with ants.
Rhopalosiphum insertum.	Myrmecoaestivous
Aphis etiolata	Obligate myrmecophilous
" sambuci	Myrmecoaestivous
" acetosae	Obligate myrmecophilous ?
" hypochoeridis	Obligate myrmecophilous
" thomasi	?
" verbasci	?
" cliftonensis	?
" crepidis	Obligate myrmecophilous
" insularis	?
" lambersi	Obligate myrmecophilous ?
" parietariella	?
" plantaginis	Obligate myrmecophilous ?
" taraxacicola	Obligate myrmecophilous
" vandergooti	Obligate myrmecophilous
" violae	?
Acaudinum scabinosae	Obligate myrmecophilous ?
Dysaphis brancoi	Myrmecoaestivous
" anthrisci	Myrmecoaestivous
" radicola	Obligate myrmecophilous
" chaerophylli	Myrmecoaestivous
" hirsutissima	Obligate myrmecophilous
" newskyi	Obligate myrmecophilous
" angelicae	Myrmecoaestivous
" lauberti	Myrmecoaestivous
" crataegi	Myrmecoaestivous
" ranunculi	Myrmecoaestivous
" tulipae	Facultative myrmecophilous
" crithmi	Obligate myrmecophilous ?
" bonomii	Obligate myrmecophilous
" lappae	Obligate myrmecophilous
" pyri	
" maritima	
Anuraphis catonii	Myrmecoaestivous
" farfarae	Myrmecoaestivous
" subterranea	Myrmecoaestivous

List of British Myrmecophilous Root Aphids. Continued.

Brachycaudus cardui.	Myrmecoaestivous
" *jacobi*	Myrmecoaestivous
" *linariae*	?
" *lucifugus*	?
" *persicae*	Obligate myrmecophilous
Jacksonia papillata	Myrmecoxenous
Rhopalomyzus poae	Myrmecoxenous

ANOECIINAE.

Anoecia furcata	Obligate myrmecophilous
" *disculigera*	Myrmecoaestivous
" *corni*	Facultative myrmecophilous
" *vagans*	Myrmecoaestivous
" *major*	Myrmecoaestivous
" *zirnitzi*	Obligate myrmecophilous
" *krizusi*	Obligate myrmecophilous
Paranoecia pskovica	Obligate myrmecophilous

ERIOSOMATINAE.

Tetraneura ulmi.	Facultative myrmecophilous
Colopha compressa	Myrmecoxenous
Kaltenbachiella pallida	Myrmecoxenous

PEMPHIGINAE.

Prociphilus bumelliae	?
" *fraxini*	?
" *pini*	?
" xylostei	?
Rhizomaria piceae	?
Thecabius affinis	Myrmecoxenous
Pemphigus bursarius	Facultative myrmecophilous

FORDINAE

Paracletus cimiciformis	Obligate myrmecophilous
Smynthurodes betae	Obligate myrmecophilous
Forda formicaria	Obligate myrmecophilous
" *marginata*	Obligate myrmecophilous
" *skorkini*	Obligate myrmecophilous ?

List of British Myrmecophilous Root aphids. Continued.

Aploneura lentisci	Myrmecoxenous
Baizongia pistaciae	Obligate myrmecophilous
Geoica eragrostidis	Obligate myrmecophilous
" *setulosa*	Obligate mymecophilous
Aloephagus myseri	?
Truncaphis newsteadi	?

LACHNINAE

Stomaphis quercus	Obligate myrmecophilous ?
Maculolachnus submacula	Myrmecoaestivous ?

TRAMINAE.

Protrama flavescens	Obligate myrmecophilous
" *radicis*	Obligate myrmecophilous
" *ranunculi*	Obligate myrmecophilous
Neotrama caudata	Obligate myrmecophilous
Trama rara	Obligate myrmecophilous
" *troglodytes*	Obligate myrmecophilous

ADAPTATIONS TO SUBTERRANEAN LIFE.

Introduction.

British myrmecophilous root aphids from six different subfamilies show convergence in adaptations to a subterranean mode of life. The subfamilies are:- Aphidinae, Anoeciinae, Eriosomatinae, Pemphiginae, Traminae and Fordinae. *Aphis fabae* was taken as a typical aerial aphid for comparison with root aphids. The characters which are considered to be adaptations to subterranean life are not all unique to this habitat but amongst root aphids there seems to be a trend towards their development. For example wax glands are also important to aphids inhabiting galls , spatulate hairs are also present in *Iziphа* spp. and *Saltusaphis* spp. which are aerial aphids and monoecy is common amongst aerial aphids but, in the context of root aphids the characters listed below seem to be of adaptive significance. (Unless otherwise stated adaptations refer to subterranean apterous virginoparae).

(1) Shortening of legs.
(2) Shortening of antennae
(3) Reduction or loss of compound eyes
(4) Reduction in the number of secondary rhinaria
(5) Increased body rotundity.
(6) Reduction of alate production
(7) Trend towards monoecy,either with holocycly or anholocycly.
(8) Behavioural adaptations to the presence of ants which are frequent in a subterranean environment.
    a. Carriage by ants.
    b. Hind leg vibration.
(9) Presence of wax glands.
(10) Loss of pigment.
(11) Reduction or loss of siphunculi.
(12) Presence of spatulate hairs.

Fig. 90 summarizes the extent to which the above adaptations are believed to have occurred.

Aphidinae.

Aphis etiolata shows reduction of antennae and eyes and increased body rotundity. Alates are unknown and a holocyclic monoecious life cycle has developed on the roots of Rumex acetosella. Death feigning, associated with carriage by ants is present. A. etiolata is pale green which may represent a reduction in pigmentation.

Anoeciinae.

Paranoecia pskovica, Anoecia krizusi and A. zirnitzi show slight reduction in leg and antenna length and complete loss of compound eyes and secondary rhinaria. Alates are unknown from these three species. They are monoecious and holocyclic. The apterae of Anoecia corni, A. vagans and A. furcata which are all to some extent dioecious retain compound eyes, and secondary rhinaria(ie. are alatiform) and show less reduction of antennae and legs. Of these species, A. furcata, which has not been found on the primary host although sexuparae have been taken in suction traps, has the smallest eyes and fewest secondary rhinaria. All the Anoeciinae were invariably found with ants in the subterranean part of their life cycles and A. corni, A. vagans and A. furcata feigned death. Immature stages lack pigment and are white or cream in colour. Spatulate hairs are present in A. corni, A. zirnitzi, A. vagans and A. furcata. Siphunculi are reduced (in comparison to Aphis fabae)to simple low cones but are still functional.

Eriosomatinae.

Legs and antennae are reduced in Tetraneura ulmi. Compound eyes and secondary rhinaria are lacking and there is a monoecious anholocyclic population on the roots of grasses. The The body is rotund and the siphunculi may be lacking, or if present, are only simple ring structures. Rosette-shaped wax glands are present and death is feigned. Normally specimens are purple or reddish-purple in colour but Zwölfer (1958) records isolated populations with a strong whitish-yellow colour.

Pemphiginae.

Pemphigus bursarius shows reduction in leg and antennal length and compound eyes and secondary rhinaria are not present. Wax glands are present and there is a monoecious anholocyclic population.

Traminae.

True apterae of Trama troglodytes have no compound eyes. The Tramina have 0-5 secondary rhinaria on the third antennal segment. Alatae of Protrama radicis are rare. The Traminae are all monoecious, almost exclusively on Compositae. They are normally anholocyclic (Eastop 1952) but there are records of sexuales (Del Guercio 1899; Morvilko 1935; Verma and Mathur 1966).

Both apterae and alatae of the Traminae vibrate their elongate hind tarsi rapidly when disturbed and will also do so when contacted by an ant. The Traminae also feign death. Eastop (1952) states that true apterae have no pigmentation and are white or whitish but most specimens are to some extent alatiform and have some of the pigmentation of the alatae.

Fordinae.

All of the British myrmecophilous Fordinae show adaptations to subterranean life, but the most extremely adapted is Aploneura lentisci which, however, does not rely on ants to remove its honeydew. A. lentisci shows great reduction in leg and antenna length and has no compound eyes. In contrast to most root aphids it does not show increased rotundity but has a spindle shaped body which it is able to shorten and lengthen in a maggot-like fashion and this may enable it to move through packed soil that has not been opened up by ants. A. lentisci readily produces alates but Baizongia pistaciae and Forda marginata produce very few. Monoecy and anholocycly are the rule in British myrmecophilous Fordinae. Mordvilko (1935) suggests that in northern Europe the Fordinae became anholocyclic when the primary host, Pistacia spp. were eliminated by glaciation. This nevertheless represents an adaptation to subterranean life. All British species show death feigning behaviour. In the British forms only Aploneura lentisci and Baizongia pistaciae have wax glands although Geoica eragrostidis and G. setulosa produce a wax dust generally over the cuticle. Only Forda spp. show any distinct pigmentation and in apterae of Forda formicaria this varies with the degree of alatiformity. The most apterous forms are white while more alatiform apterae are greenish. Alates are produced when populations become crowded. Specimens spread up from the roots to the lower grass stems where the green alatiform apterae may be well camouflaged.

Discussion of adaptations to subterranean life.

Shortening of antennae and legs probably allows greater ease of movement in confined areas where speed, which is given by long legs, is unnecessary. This trend is seen at its most extreme in Aploneura lentisci which lives in the most confined habitats (Fig. 43). It is a fine root feeder, is not usually associated with ants and does not benefit from their galleries. Underground in dark conditions with stagnant air, compound eyes and secondary rhinaria are liable to loss or reduction. Although some aerial aphids may also lack secondary rhinaria, it is true that the apterae of those species which have the most subterranean life cycles have the least number of secondary rhinaria. For example, Paranoecia pskovica and Anoecia zirnitzi are monoecious and holocyclic and do not, or very rarely, have secondary rhinaria. A. furcata which is monoecious and anholocyclic has fewer secondary rhinaria than A. corni or A. vagans which are partially or completely dioecious.

In many root aphids increased rotundity may be a consequence of reduced mobility; they become feeding and reproducing machines to an even greater extent than aerial aphids. It may also be of benefit to myrmecophilous aphids living and feeding in sloping or vertical ant galleries (see page 197).

Reduction of alate production, monoecy and anholocycly or holocycly on the secondary host are inter-related phenomena. Monoecy may result from the contraction of the primary host's range (Mordvilko 1935) or perhaps because of a selective advantage in omitting the hazardous migrations to and from the primary host, as may have happened with Paranoecia pskovica, Anoecia zirnitzi, A. krizusi and A. furcata. Monoecy may also result from the advantages of ant attendance. Aphids feed on the secondary host at a time when ants are most active, making it more likely that attendance will take place on the secondary host than the primary host. Anoecia corni was always found with ants on the secondary host but only about 30% of the time on the primary host. A selective advantage may be gained from extending attendance from summer into spring, autumn and winter by remaining on the secondary host throughout the year. Holocycly on the secondary host suggests a highly evolved situation in which the sexual stages of the life cycle have also been transferred to the secondary host as for example in Paranoecia pskovica and Anoecia zirnitzi.

Myrmecophilous root aphids have become behaviourally adapted to accept ant attendance in the following ways:-

(a) They do not try to escape from ants.

(b) They adopt a motionless 'death feigning' position when being carried by ants.

(c) The Traminae vibrate their elongate hind tarsi at ants. The hind legs may be directed over the head or at the side of the aphid so that the tarsi vibrate in the direction of an attending ant. This behaviour may be a modification of a defense behaviour in which the hind legs are vibrated to repel parasites or predators (Way 1963). In the Traminae it seems to be used to communicate with ants and may be mistaken by ants for the antennal movements of another ant. It may also serve to communicate between aphids.

In some cases relationships with ants are so close that ants will look after aphid eggs through the winter (Pontin 1960; and observations made in the present study). This is especially true for Paranoecia pskovica and Anoecia zirnitzi. Eggs of P.pskovica were found in March in Lasius flavus mounds and fundatrices were reared. Oviparae of A. zirnitzi were found in November in L. flavus mounds. Pontin (1960) reared both species from eggs found on L.flavus mounds though, some of the specimens were misidentified (see systematic section). It was found that A. corni descends from dogwood to lay its eggs in the soil and there, the eggs may be collected by ants.

Subterranean aphids adopt one of two strategies for disposing of honeydew. They either rely on ants or they produce wax from wax glands to coat the honeydew and render it less dangerous.

Thecabius affinis is not attended by ants and is always covered in large quantities of white wax. Some of the myrmecophilous root aphids have wax glands and in general the quantity of wax produced bears an inverse relationship to the degree of myrmecophily. Aploneura lentisci is very infrequently attended and produces large quantities of wax from extensive glands on the head thorax and abdomen (Fig 44B) . Pemphigus bursarius produces much wax and can be described as myrmecoxenous (see page196). Baizongia pistaciae produces infrequent wax strands from glands on the head, thorax and abdomen. In Britain it is always found with Lasius flavus but Zwölfer (1958) did not always find it with ants. Tetraneura ulmi has wax glands but does not produce significant quantities of wax in the subterranean part of its life cycle. It was always found with ants.

In subterranean conditions cuticular pigment can no longer serve its normal functions of protection from ultraviolet rays, colouring for camouflage, mimicry or any other purpose. Those root aphids which are most subterranean usually show the greatest loss of pigment. Geoica eragrostidis, G. setulosa, Aploneura lentisci, Baizongia pistaciae and immature Anoecia spp. are all white or cream. Forda formicaria and species of the subfamily Traminae show incresed pigmentation with increased alatiformity. Tetraneura ulmi and Forda marginata are pigmented orange and green respectively and are exceptions to the rule as they both have populations which remain subterranean throughout the year.

Reduction of siphunculi in root aphids may be the result of two selective pressures. Myrmecophilous aphids, whether aerial or subterranean often have short siphunculi eg. Tuberolachnus salignus or Thelaxes dryophila. It is suggested that under the protection of ants aphids have less need to defend themselves with their siphunculi. In the case of root aphids, as well as enjoying the protection of ants, the confines of a subterranean life may benefit aphids with short siphunculi.

The adaptive significance of spatulate hairs is an enigma. Spatulate hairs occur in aerial aphids eg.Iziphа spp. but are most pronounced in subterranean forms such as Geoica spp. (Fig. 54. Plate 49) and Anoecia spp. (Fig. 25 Plate 17.) and occasionally in Baizongia pistaciae. There are however many subterranean aphids which do not have spatulate hairs eg. Forda spp., Aploneura lentisci, Smynthurodes betae, Tetraneura ulmi and others.

Spatulate hairs in both Geoica eragrostidis and Anoecia furcata show a seasonal variation in frequency (Figs.79&94) They are more frequent in the summer months, which suggested that they may be produced in response to increasing temperature. However Anoecia furcata reared at 7°C did not show any decrease in numbers of spatulate hairs. Alates of Geoica eragrostidis and Anoecia furcata have reduced numbers of spatulate hairs compared with apterae, which supports the suggestion that they are of benefit to subterranean aphids.

Possible benefits of spatulate hairs to subterranean aphids are:-

(a) As a protection against abrasion by the soil. They normally are directed posterior~~al~~ly, especially in Geoica spp. and would permit forward movement in a confined area but are quite stiff hairs, capable of keeping the body surface from contact with the soil.

(b) In the case of Geoica eragrostidis they may serve to prevent excessive water loss. It has been observed that a drop of moisture often forms under the hair blade and is held between it and the body surface. In dry conditions this may be helpful in preventing des~~s~~iccation which might explain the increased frequency of spatulate hairs in summer forms.

Adaptations to a subterranean environment in myrmecophilous root aphids.

	Aphidinae	Anoecinae	Eriosomatinae	Pemphiginae	Traminae	Fordinae
Reduction of legs		◆	◆◆	◆		◆◆◆
Reduction of antennae	◆	◆	◆◆	◆		◆◆◆
Reduction of eyes	◆	◆◆◆	◆◆◆	◆◆◆	◆◆	◆◆◆
Reduction of secondary rhinaria		◆◆◆	◆◆◆	◆◆	◆◆	◆◆◆
Increased body rotundity	◆	◆	◆◆◆	◆◆		◆◆◆
Reduction of alate production	◆◆◆	◆◆◆			◆◆◆	◆
Monoecy and Anholocycly		◆◆◆	◆◆	◆◆	◆◆◆	◆◆◆
Monoecy and Holocycly	◆◆◆	◆◆◆				
Behavioural adaptations	◆◆	◆◆	◆◆		◆◆◆	◆◆
Presence of wax glands			◆◆	◆◆◆		◆◆
Loss of pigment		◆			◆	◆◆
Reduction or loss of siphunculi		◆◆	◆◆◆		◆	◆◆◆
Presence of spatulate hairs		◆◆				◆◆

◆	Adaptation weakly represented by at least one species within the subfamily
◆◆	Adaptation moderately represented by at least one species within the subfamily
◆◆◆	Adaptation strongly represented by at least one species within the subfamily

FIG. 90.

<u>Relationship between body length and length of metathoracic leg in 14 species of root aphid.</u> (See Table 10 for data)

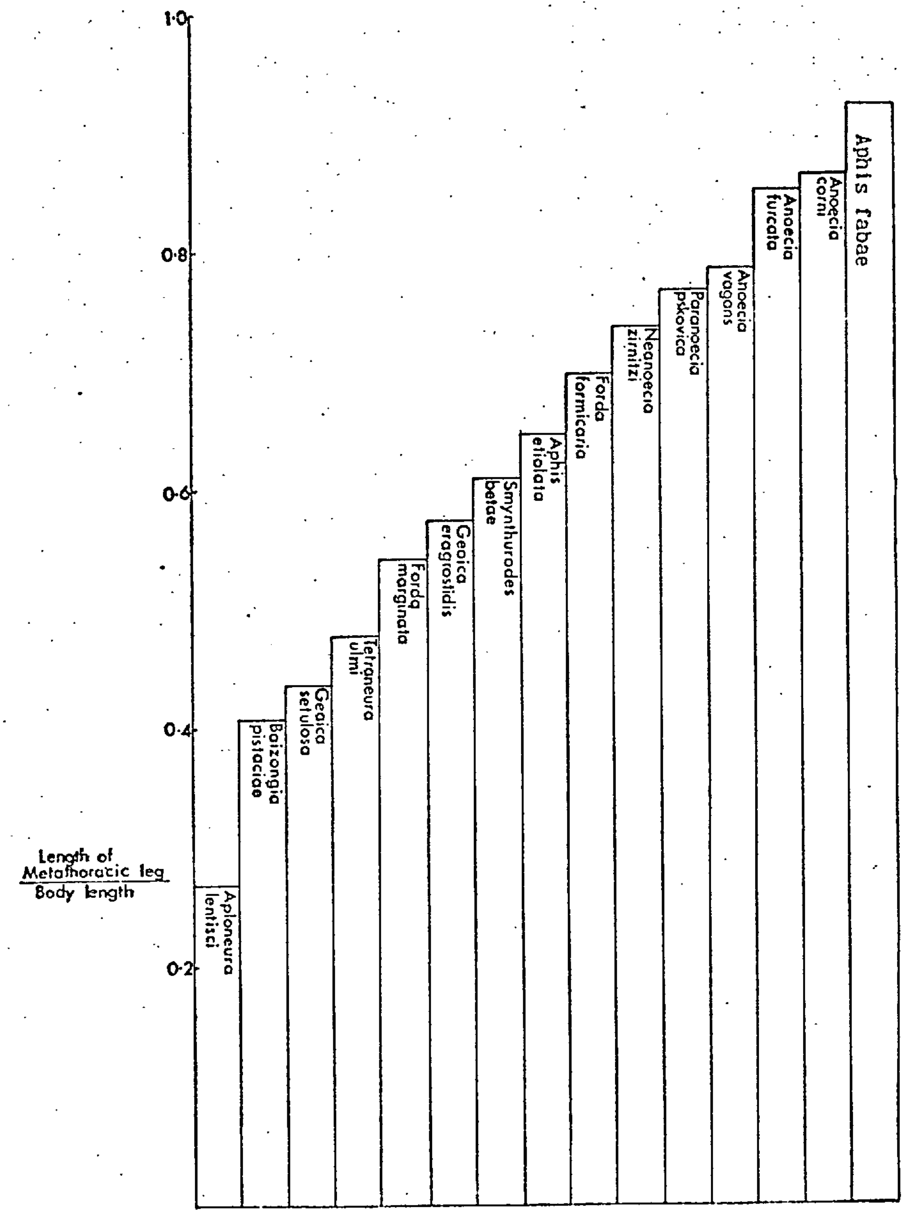


FIG 91

Relationship between body length and rostrum length in 14 species of root aphid. (See Table 10 for data)

FIG 92

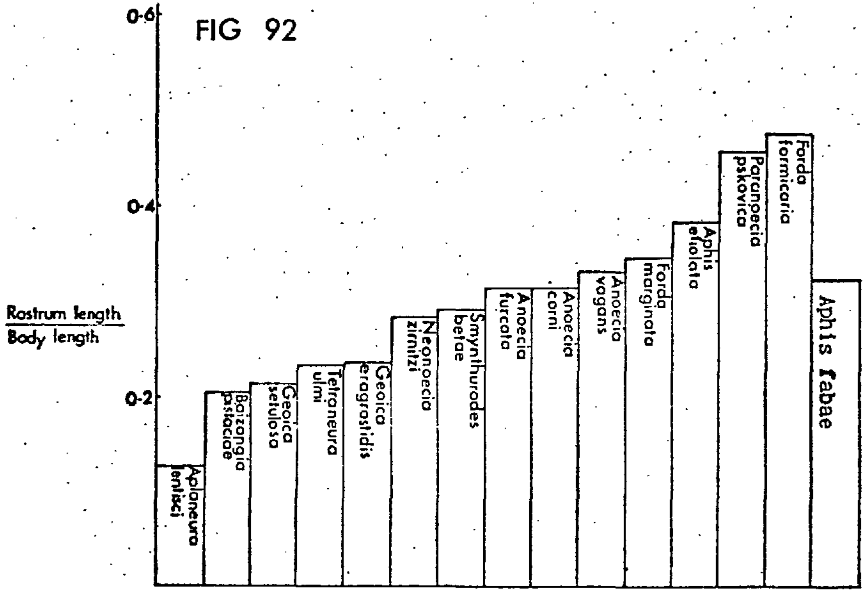
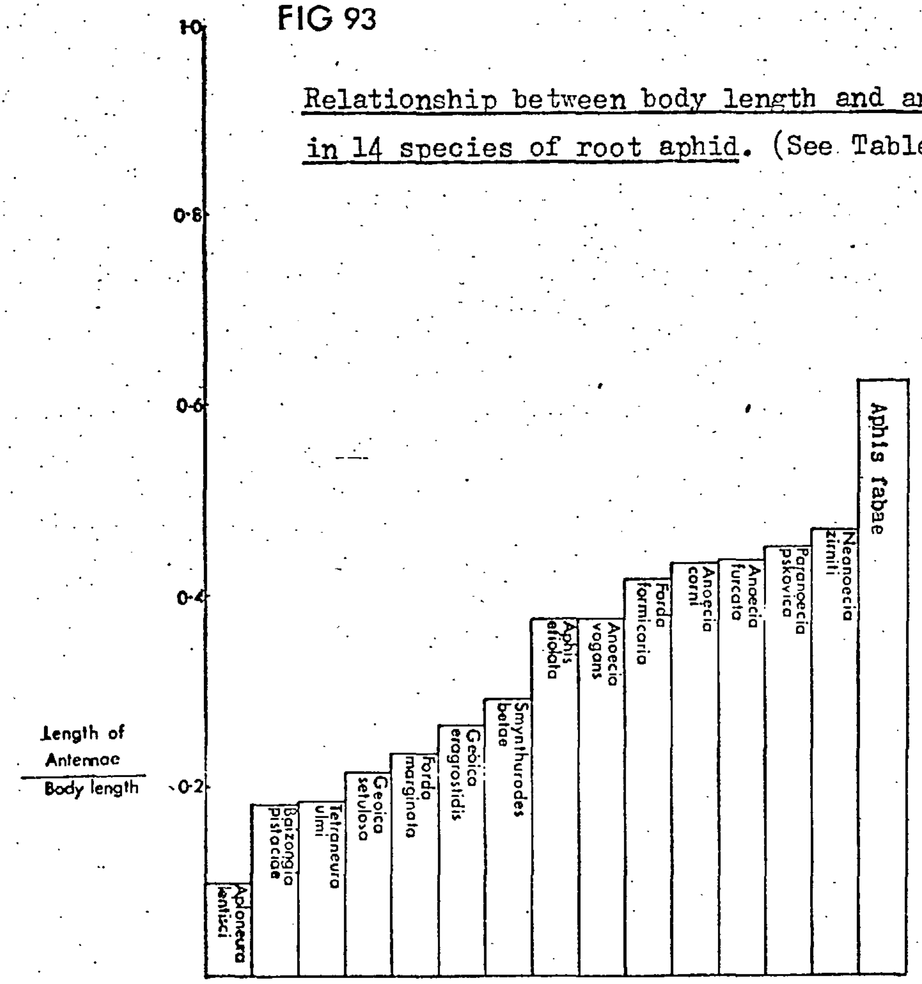


FIG 93

Relationship between body length and antenna length in 14 species of root aphid. (See Table 10 for data)



Seasonal variation of hair type in Geoica eragrostidis.

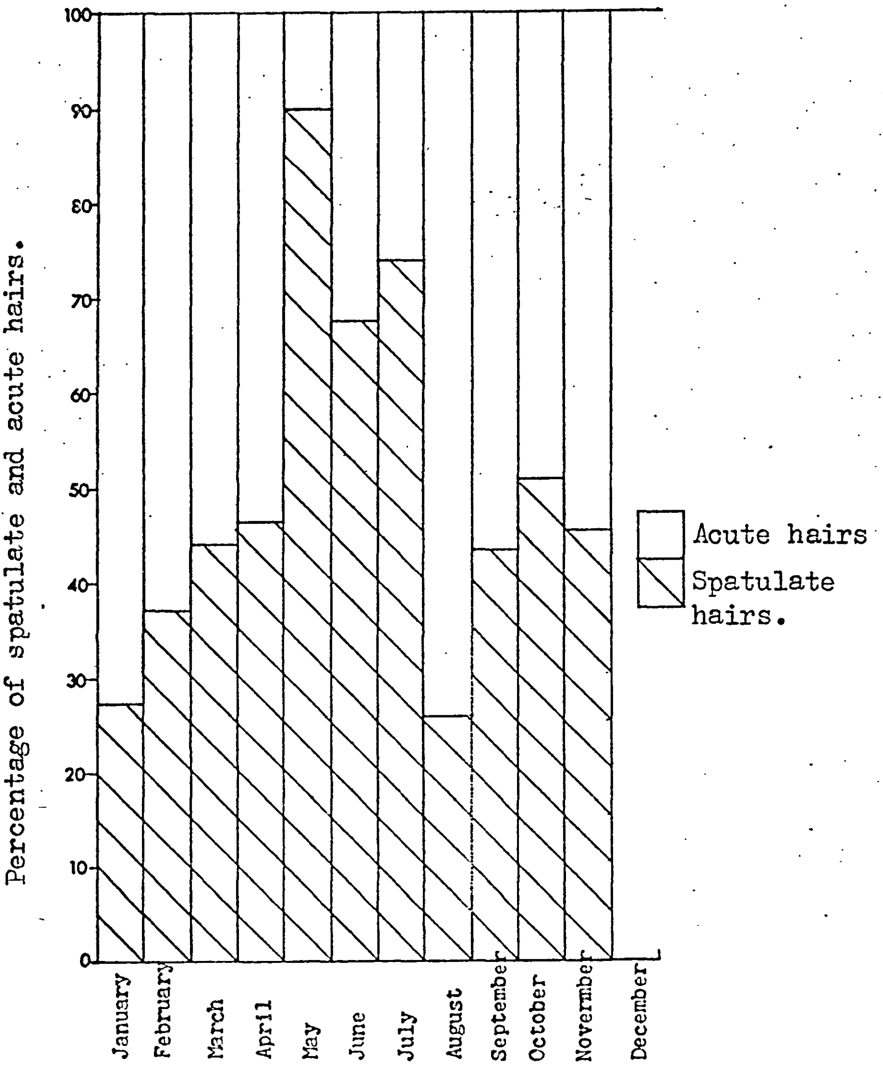


FIG 94

SUCTION TRAP CATCHES.

Introduction.

A system of 21 suction traps is co-ordinated from Rothamsted Experimental Station . I have been permitted to examine root aphid catches from 1968 to 1976. Figures for the following myrmecophilous root aphids have been recorded for these traps in this period:- Anoecia corni, A.furcata, A. vagans, Forda marginata, F. formicaria, Geoica eragrostidis, G. setulosa, Aploneura lentisci, Baizongia pistaciae, Smynthurodes betae, Tetraneura ulmi, Trama rara, T. troglodytes, Protrama flavescens, and P. ranunculi. The suction trap catches have been represented as histograms to show seasonal flight patterns. (Figs. 103-116). Specimens of the genus Anoecia had all been recorded as Anoecia corni but the taxonomic study in this work showed that there were three species present in the catches:- Anoecia corni, A. furcata, and A. vagans. The entire catches of Anoecia for the years 1975 and 1976 were mounted on slides so that they could be identified and the relative numbers of the three species entering traps could be established.

The following suction traps recorded the species listed above:-

1968: Rothamstead Tower, Rothamstead Farm, Wye College, Brooms Barn, High Mowthorpe, Cockle Park, Dundee, Silwood Park.

1969: Brooms Barn, High Mowthorpe, Newcastle, Dundee, Silwood Park, Rosewarne, Aberystwyth, East Craigs, Rothamstead Tower, Rothamstead Farm, Wye College, Cockle Park.

1970: Rothamstead Tower, Rothamstead Farm, Wye College, Brooms Barn, High Mowthorpe, Newcastle, Dundee, Silwood Park, Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Garston, Elgin.

1971: Rothamsted Tower, Rothamsted Farm, Wye College, Brooms Barn, High Mowthorpe, Newcastle, Dundee, Silwood Park, Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Garston, Elgin, Hereford, Rothamsted Farm II.

1972: Rothamsted Tower, Rothamsted Farm, Wye College, Brooms Barn, High Mowthorpe, Newcastle, Dundee,Silwood Park, 1972 cont. Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Garston, Elgin, Hereford, Shardlow Hall, Rothamsted Farm II, Rothamsted Tower (4ft.).

1973: Rothamsted Tower, Rothamsted Farm I, Wye College, Brooms Barn, High Mowthorpe, Newcastle, Dundee, Silwood, Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Garston, Elgin, Rosewarne, Shardlow, Rothamsted Farm II, Rainham, Rothamsted 4ft. Tower.

1974: Rothamsted Tower, Wye College, Brooms Barn, High Mowthorpe, Newcastle, Dundee, Silwood Park, Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Elgin, Hereford, Shardlow Hall, Rainham, Preston, Rothamsted 4ft. Tower.

1975: Rothamsted Tower, Wye College, Brooms Barn, High Mowthorpe, Newcasle, Dundee, Silwood Park, Rosewarne, Aberystwyth, East Craigs, Starcross, Long Ashton, Garston, Elgin, Hereford, Shardlow, Rainham, Preston, Ayr, Writtle.

1976: Rothamstead Tower, Rothamsted 4ft Tower, Wye College, High Mowthorpe, Silwood Park, Rosewarne, Starcross, Long Ashton, Elgin, Hereford, Copenhagen, Shardlow, Rainham, Preston, Ayr, Writtle, Aberystwyth, Brooms Barn, Newcastle, Dundee, East Craigs.

The use of week numbers instead of dates.*

The analysis of annual records eg. suction trap catches is simplified if the numbered 'weeks' contain the same dates in successive years. This is achieved by dropping the dates February 29th and December 31st from the calendar. The weeks then become, by number, as follows:-

Week number	Dates	Week number	Dates
1	Jan. 1- Jan. 7	27	July 2- July 8
2	Jan. 8- Jan. 14	28	July 9- July 15
3	Jan. 15- Jan. 21	29	July 16- July 22
4	Jan. 22- Jan. 28	30	July 23- July 29
5	Jan. 29- Feb. 4	31	July 30- Aug. 5
6	Feb. 5- Feb. 11	32	Aug. 6- Aug. 12
7	Feb. 12- Feb. 18	33	Aug. 13- Aug. 19
8	Feb. 19- Feb. 25	34	Aug. 20- Aug. 26
9	Feb. 26- Mar. 4	35	Aug. 27- Sept. 2
10	Mar. 5- Mar. 11	36	Sept. 3- Sept. 9
11	Mar. 12- Mar. 18	37	Sept. 10- Sept. 16
12	Mar. 19- Mar. 25	38	Sept. 17- Sept. 23
13	Mar. 26- Apr. 1	39	Sept. 24- Sept. 30
14	Apr. 2- Apr. 8	40	Oct. 1- Oct. 7
15	Apr. 9- Apr. 15	41	Oct. 8- Oct. 14
16	Apr. 16- Apr. 22	42	Oct. 15- Oct. 21
17	Apr. 23- Apr. 29	43	Oct. 22- Oct.28
18	Apr. 30- May 6	44	Oct. 29- Nov. 4
19	May 7- May 13	45	Nov. 5- Nov. 11
20	May 14- May 20	46	Nov. 12- Nov. 18
21	May 21- 27	47	Nov. 19- Nov. 25
22	May 28- June 3	48	Nov. 26- Dec. 2
23	June 4- June 10	49	Dec. 3- Dec. 9
24	June 11- June 17	50	Dec. 10- Dec. 16
25	June 18- June 24	51	Dec. 17- Dec. 23
26	June 25- July 1	52	Dec. 24- Dec. 30

Table 5.

*As recommended by research workers at Rothamsted Experimental Station.

Suction trap catches of Anoecia species.

Figs.103-114 show the seasonal flight pattern of the three species, A. corni, A. vagans, and A. furcata showing that flight within the genus does not start before the last week in April and on average reaches a peak in the second week in September which represents the peak of the return flight from grass roots to Cornus spp. The small peak in the spring confirms field observations that many fewer alates migrate from Cornus spp. to grass roots than take part in the return migration. This suggests high egg mortality as many sexuales are produced but comparatively few fundatrices appear in spring. The middle of July to the middle of August is a period in which the majority of alates are virginoparae, flying from grass roots to grass roots. The greatest catches occur between weeks 27 and 31, ie. from July 2nd to August 5th. All the histograms show a clear peak representing the large return migration from grass roots to Cornus spp. The maximum peak of migration varies between the weeks 36 to 41, ie. September 3rd to October 14th.

Seasonal flight patterns for Anoecia corni, A. vagans and A. furcata 1975 and 1976.

The histograms of Anoecia flight patterns for 1975 and 1976 have a background graph of the mean weekly maximum temperature (calculated from daily maxima) for 18 meteorological station offices, chosen to cover the area of the suction traps for a comparison of the temperature with trap catches.

Fig.103 shows the flight pattern for Anoecia corni for 1975. Migration from Cornus spp. began in week 24 (June 11-June17) when the mean weekly maximum temperature was 19.4°C. The peak of the return migration was in week 35(August 27- Sept2) (MWMT*=21.0°C). Migration was effectively over by week 44(Oct 29-Nov.4)(MWMT=13.4°C) except for one anomolous specimen in week 51 (Dec.17-Dec.23). Alate numbers followed temperature trends for 15 out of 21 weeks.

Fig.104 shows the flight pattern for A. vagans. Migration from Cornus spp. began in week 30(July 23-July29) (MWMT=20°C). Numbers show peaks in weeks 35, 40 and 43 and these correspond with peaks in A. corni numbers, suggesting that both species

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* Mean weekly maximum temperature

were responding to the same climatic conditions. As in A. corni, migration finished in week 44(Oct.29-Nov.4)(MWMT=13.4). Alate numbers followed temperature trends for 11 out of 15 weeks.

Fig. 104 shows the flight pattern for Anoecia furcata for 1975. Alates began flying from grass roots in week 23 (June 4-June 10) (MWMT= 19.2°C). A peak occurred in week 31 (July 30-Aug. 5) (MWMT= 25.0°C). Except for a small peak in week 43 (Oct. 22-Oct. 28)(MWMT=13.5°C) there was no equivalent of the autumn return migration which occurs in A. corni and A. vagans. Alate numbers followed temperature trends in 16 out of 22 weeks.

Fig. 106 shows the flight pattern for Anoecia corni for 1976. Migration began in week 23 (June 4-June10)(MWMT=20.5°C). The peak for the return migration occurred in week 39 (Sept. 24-Sept.30)(MWMT=17°C). Migration ceased in week 45 (Nov. 5-Nov. 11)(MWMT=10°C). Alate numbers followed temperature trends in 16 out of 21 weeks.

Table of first appearances for Anoecia corni 1976.

Suction trap	Date	MWMT for nearest met. station.	Latitude.
Elgin	25/7	19°C	N 862°5'
Ayr	28/7	18°C	N 623°3'
High Mowthorpe	16/9	10°C	N 468°6'
Preston	16/7	23°C	N 440°1'
Shardlow	19/8	24°C	N 330°4'
Hereford	6/7	19°C	N 247°6'
Rothamsted Tower	26/7	24°C	N 213°4'
Writtle	9/7	29°C	N
Rainham	5/6	18°C	N 184°2'
Long Ashton	6/6	19°C	N 170°0'
Silwood	10/6	31°C	N 168°7'
Wye	15/6	19°C	N 147°0'
Starcross	26/7	21°C	N 082°1'
Rosewarne	14/6	18°C	N 041°1'

Mean MWMT for all traps = 21°C SE ± 1.39

Table 6.

Fig.105 shows the flight pattern for A. vagans for 1976. Migration from Cornus spp. began in week 26 (June 25-July 1) (MWMT=26°C). A peak of alates occurred in week 39 (Sept 24-Sept30) (MWMT=17°C). Migration ceased in week 43 (MWMT= 12.5°C). The peak occurrence of alates coincides with a rise in temperature. Alate numbers moved in the same direction as temperature trends in 12 out of 18 weeks.

Table of first appearances for Anoecia vagans 1976. Table 7.

Suction trap	Date	MWMT for nearest met. station	Latitude.
Ayr	10/8	22°C	N 623 3'
High Mowthorpe	26/9	18°C	N 468 6'
Preston	5/9	19°C	N 440 1'
Shardlow	8/9	23°C	N 330 4'
Hereford	17,18/9	17°C	N 247 6'
Rothamsted Tower	26/6	32°C	N 213 4'
Writtle	7/8	22°C	
Long Ashton	17/7	23°C	N 170 0'
Silwood Park	6/7	33°C	N 168 7'
Wye College	2/8	20°C	N 147 0'
Starcross	7/8	22°C	N 082 1'
Rosewarne	12/8	22°C	N 041 1'

Mean MWMT for all traps = 22.75 SE± 1.43.

Fig. 105 shows the flight pattern for A. furcata for 1976. Alates began flying in week 23 (June 4- June 10) (MWMT= 20.5°C) Peaks occurred in weeks 32 (Aug. 6- Aug.12)(MWMT =21.4°C) and 41 (Oct. 8- Oct. 14)(MWMT= 41.8°C). The latter may represent production of sexuparae. The occurrence of alates coincided either with or immediately followed a rise in temperature. Alate numbers move in the same direction as temperature trends in 10 out of the 20 weeks for which temperature trends are available.

Table of first appearances for Anoecia furcata 1976 Table 8.

Suction trap	Date	MWMT for nearest Met. Station	Latitude.
Elgin	18/8	15°C	N 862 5'
Ayr	11/8	26°C	N 623 3'
Preston	24/8	18°C	N 440 1'
Shardlow	22/9	21°C	N 330 4'
Rothamstead Tower	8/8	24°C	N 213 4'
Writtle	5/6	18°C	
Rainham	4/6	14°C	N 184 2'
Long Ashton	25/7	22°C	N 170 0'
Silwood	2/7	31°C	N 168 7'
Wye	2/8	20°C	N 147 0'
Starcross	27/7	20°C	N 082 1'
Rosewarne	10/6	16°C	N 041 1'

Mean MWMT for all traps = 19.6°C

Summary of Anoecia suction trap catches for 1975 and 1976.

Anoecia corni produced the highest catches with a total of 950 in 1975 and 638 in 1976, A. vagans produced 222 in 1975 and 287 in 1976 and A. furcata produced 126 in 1975 and 73 in 1976.

A. corni has a population which overwinters on grass roots and another which overwinters as the egg either on, or in the soil at the base of Cornus spp. The records show that alates are produced earlier in A. corni than A. vagans. This may be accounted for by the fact that grass root populations have a food source which is available earlier in the year and can reproduce to population levels where alate virginoparae are produced before A. vagans has produced alate fundatrigeniae. A. vagans is stated by Börner (1950) to have only one fundatrigenia generation while A. corni has been observed during this study to have two. A. vagans may have elected (evolutionarily speaking) to leave Cornus spp. as soon as possible because it does not have an overwintering population already occupying niches on grass roots or it may require an initial higher temperature in the spring before it can start development and therefore does not have time for two fundatrigenia generations on Cornus spp. The mean weekly maximum temperature for first alate production (1976) in A. vagans is higher than A. corni; 22.8°C and 21°C respectively, which together with the relative distribution of the two species in Britain (Figs. 97,98,101 & 102)which suggests that Anoecia vagans is adapted to higher temperatures than A.corni.

Anoecia furcata was not found on Cornus spp. but was found overwintering on grass roots. The presence of a large population on grass roots in the spring would allow A. furcata to produce alates as soon as climatic conditions allow. A. furcata alates appeared in the traps slightly before A. corni and much earlier than A. vagans.

In 1975 the numbers of alates produced by the three Anoecia species does not follow the MWMT closely but in 1976 there does seem to be a relationship. The peak production of alates for all three species occurs when temperature peaks also occur. Possibly the basal rhythm of the life cycle can be modified by extreme temperatures such as occurred in 1976.

Approximate relative densities of Anoecia species in Britain.

In inferring the approximate relative densities of Anoecia species from suction trap catches the following assumptions must be made:-

(1) Traps have equal opportunities for catching the different species.

(2) Traps in different localities have roughly equal oppotunities for catching Anoecia of any species.

(3) That the number of alates caught bears at least some relation to the density of the species as a whole.

The distributions suggested by suction trap catches of A. corni, A. vagans and A. furcata during 1975 and 1976 show a concentration of alate production in a central southern belt of England between the Bristol Channel and Essex. This belt of greatest concentration corresponds roughly with chalk downland which is a very suitable habitat for both Cornus sanguinea and Lasius flavus. The east coast of England and the whole of Scotland produced the lowest catches. A. corni gave the greatest total numbers (950 in 1975 and 638 in 1976) In both years specimens were taken from as far north as Elgin. A. vagans produced totals of 222 for 1975 and 287 for 1976. In neither year were any taken from north of Edinburgh. A. furcata produced the smallest number of alates, 126 in 1975 and 73 in 1976. In both years specimens were taken at Elgin. The catches suggest that *A. vagans* may be limited by temperature as none were taken in areas where the mean daily temperature for the years 1941-1970 was less than 9°C. In 1976 when the highest MWMT was 26.9°C (compared with 25.0 in 1975) and high temperatures were maintainted for a longer period(Fig.105-106) *A. vagans* seems to have been favoured as it produced 28.76% of the total number of alates compared with 17.1 in 1975. Apart from temperature a possible explanation for the absence of *A. vagans* north of Edinburgh is the scarcity of the primary host, dogwood. The distribution map of *Cornus sanguinea* (Fig. 96) shows only some introductions present in northern Scotland. In Britain, *A.vagans* has been found to have only a holocyclic dioecious population and its distribution would be limited by the availability of *Cornus* spp. *A. corni* has a monoecious anholocyclic population on grass roots and *A. furcata* is almost if not entirely monoecious and anholocyclic on grass roots and therefore their distribution may be partially independent of *Cornus* spp.

Suction trap catches of other root aphids. (Tables 9 & 10)

The first alates of *Forda formicaria* appear in the 3rd week of May(week 20). Most alates are produced in early June (week 23) at which time many of them are sexuparae, recognizable by the fact that their embryos do not have stylets. No alates have been caught after August 19th. The sexuparae probably represent a remnant of the return migration to *Pistacia*.

Tetraneura ulmi alates first appear in early June, a peak is reached in the 4th week of September and the autumn return migration to *Ulmus* spp. ceases in the 1st week of November.

Species of *Protrama* and *Trama* were not differentiated for suction trap records. Most *Protrama* were caught between the beginning of August and the 3rd week of September. *Trama* alates are rare(see Table 9).

Catches of *Baizongia pistaciae*, *Smynthurodes betae*, *Forda marginata*, *Geoica eragrostidis*, and *G. setulosa* all produce alates,only infrequently (see Table 10).

Location of 18 weather stations from which temperature records were taken.

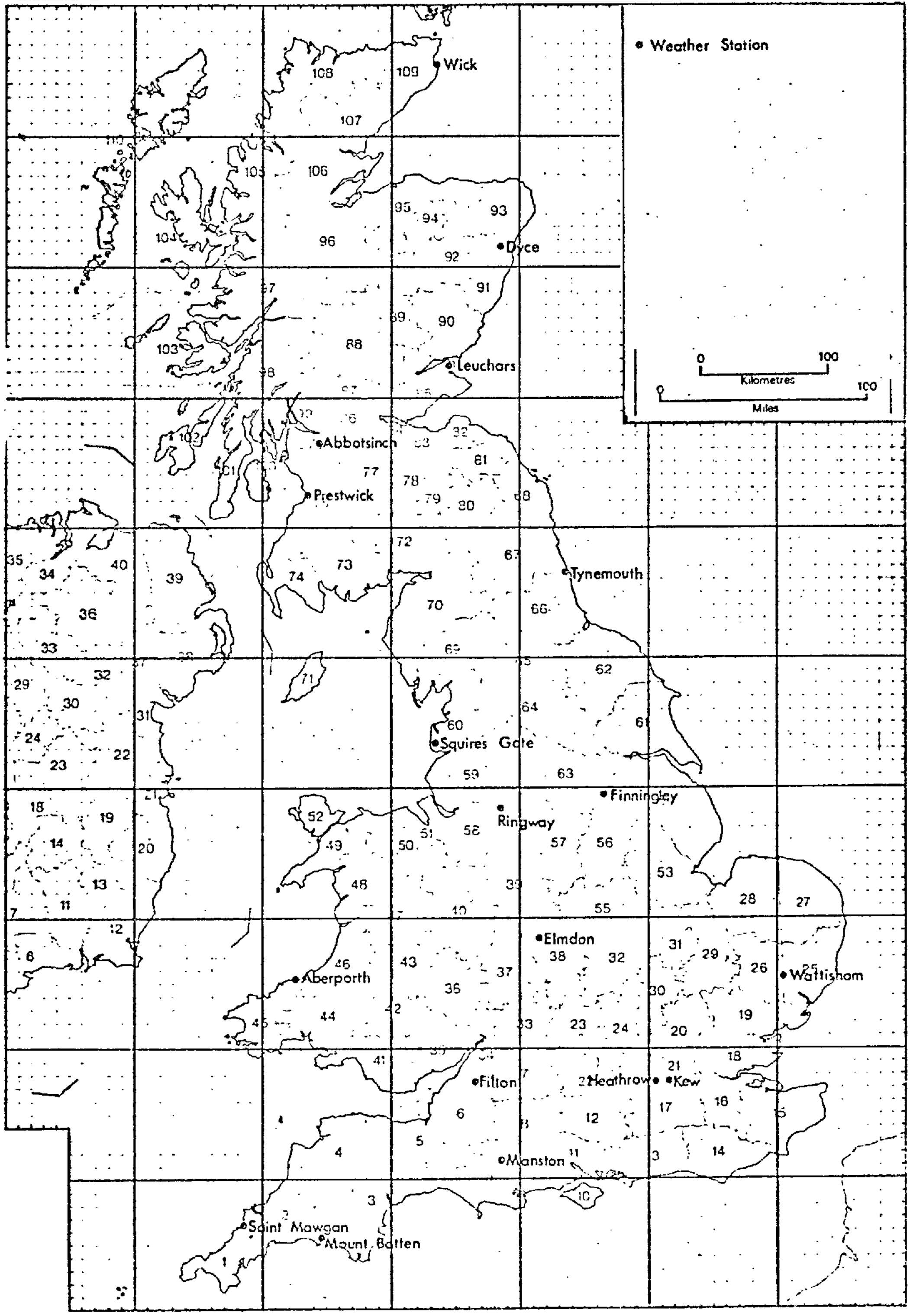


FIG 95

Map of the distribution of Cornus sanguinea in Britain.

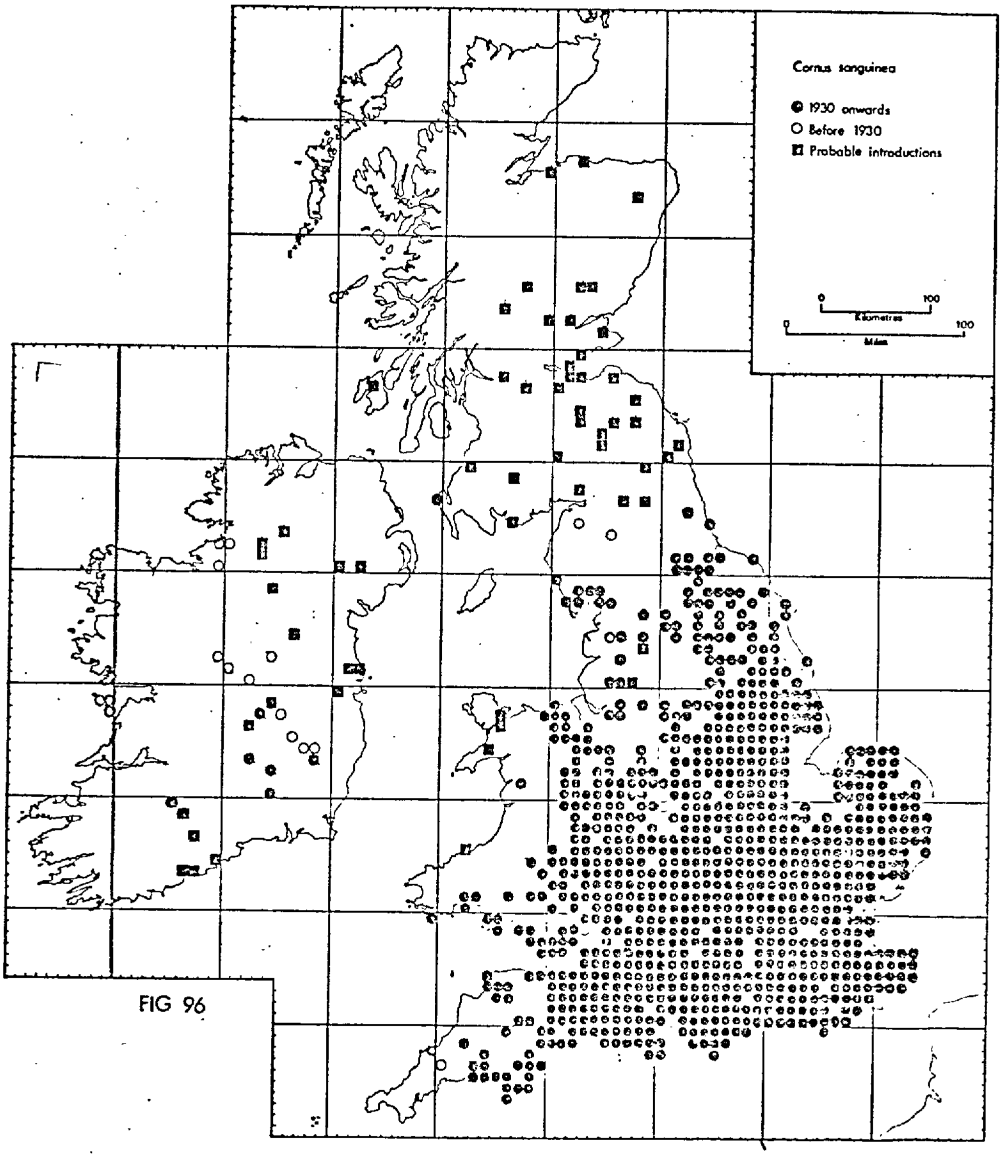


FIG 96

Taken from the Atlas of British Flora.
(Perring and Walters 1962).

Approximate relative density map for Anoecia vagans, based on suction trap catches for 1975.

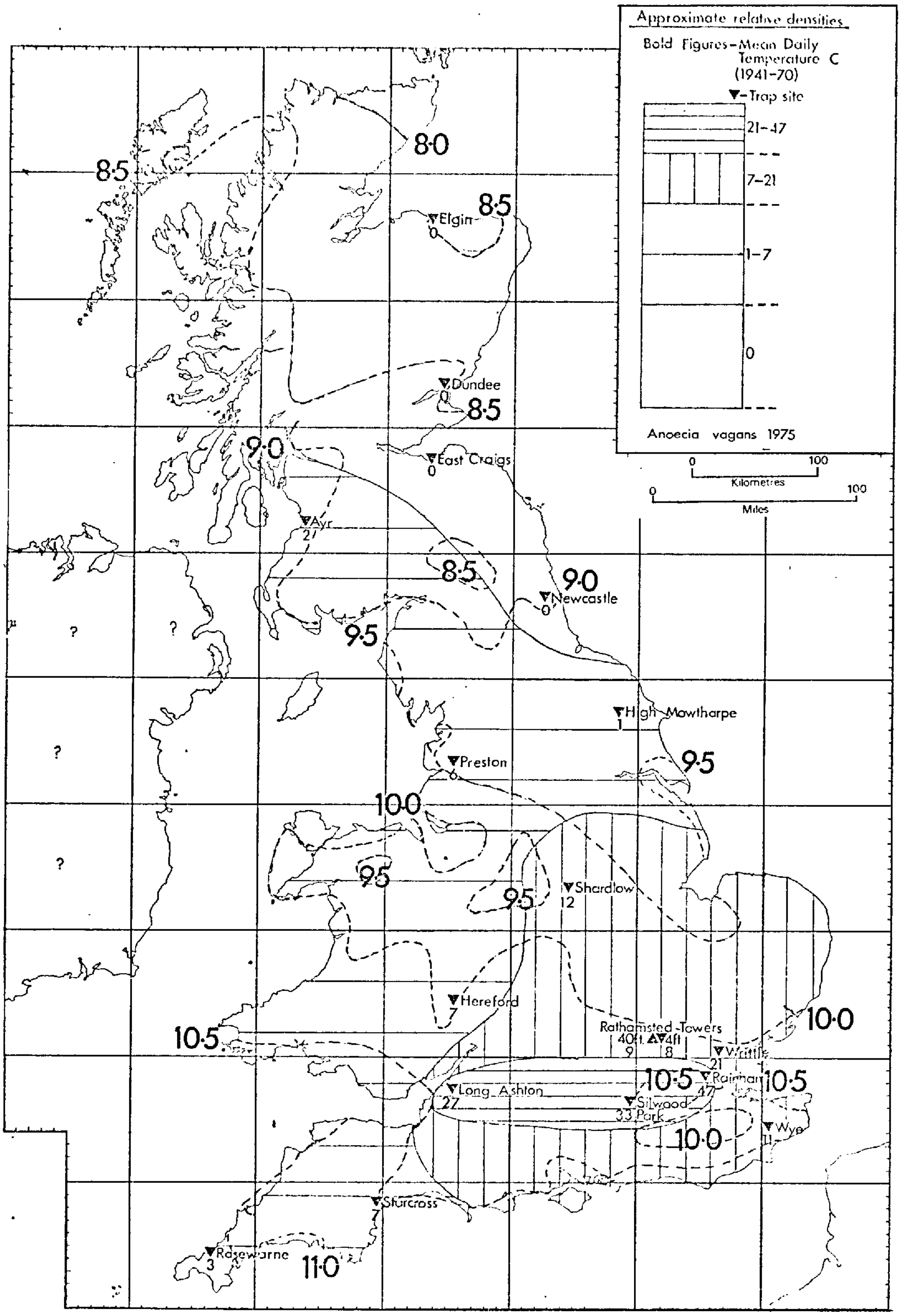


FIG 97

Approximate relative density map for Anoecia corni, based on suction trap catches for 1975.

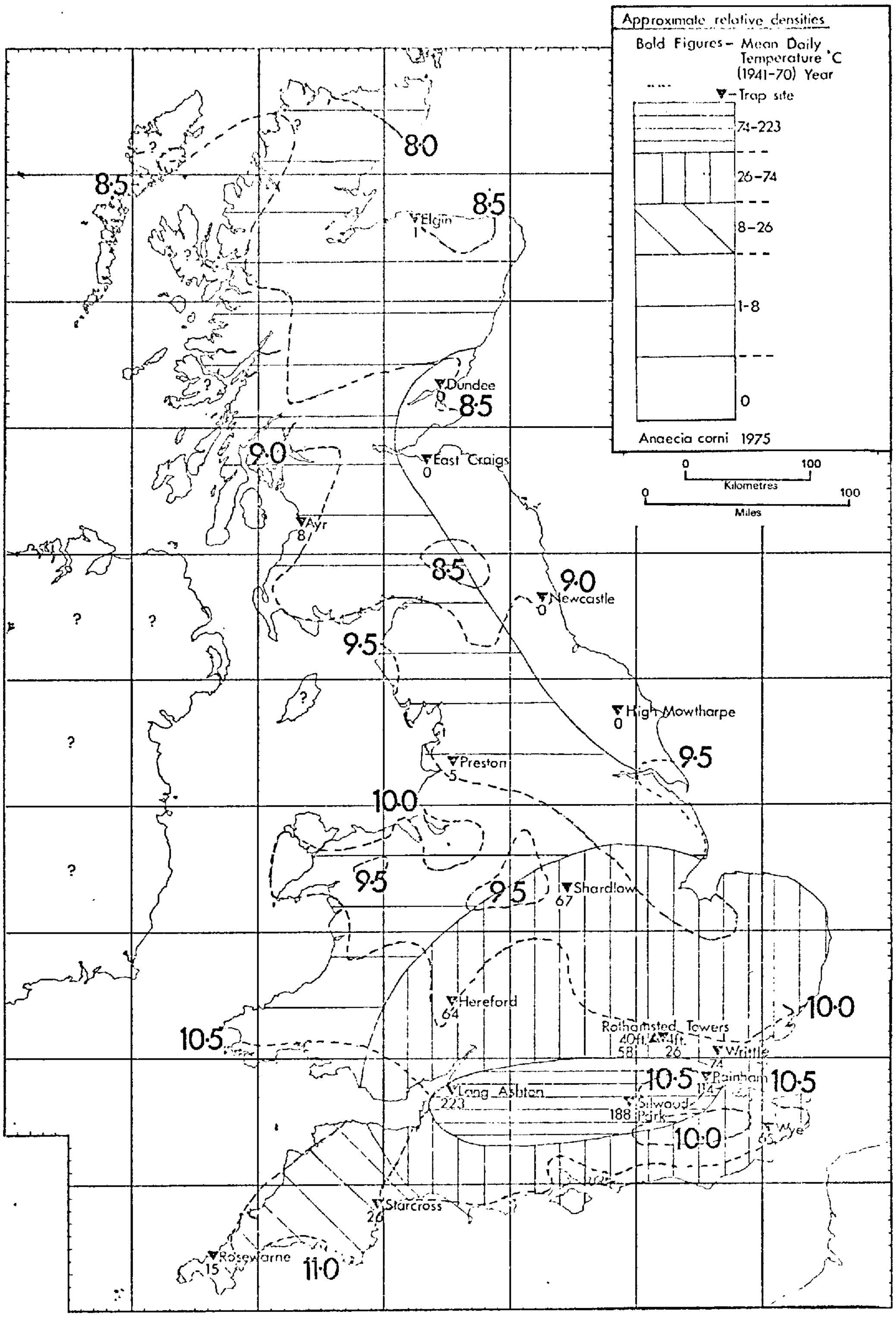


FIG 98

Approximate relative density map for *Anoecia furcata*, based on suction trap catches for 1975.

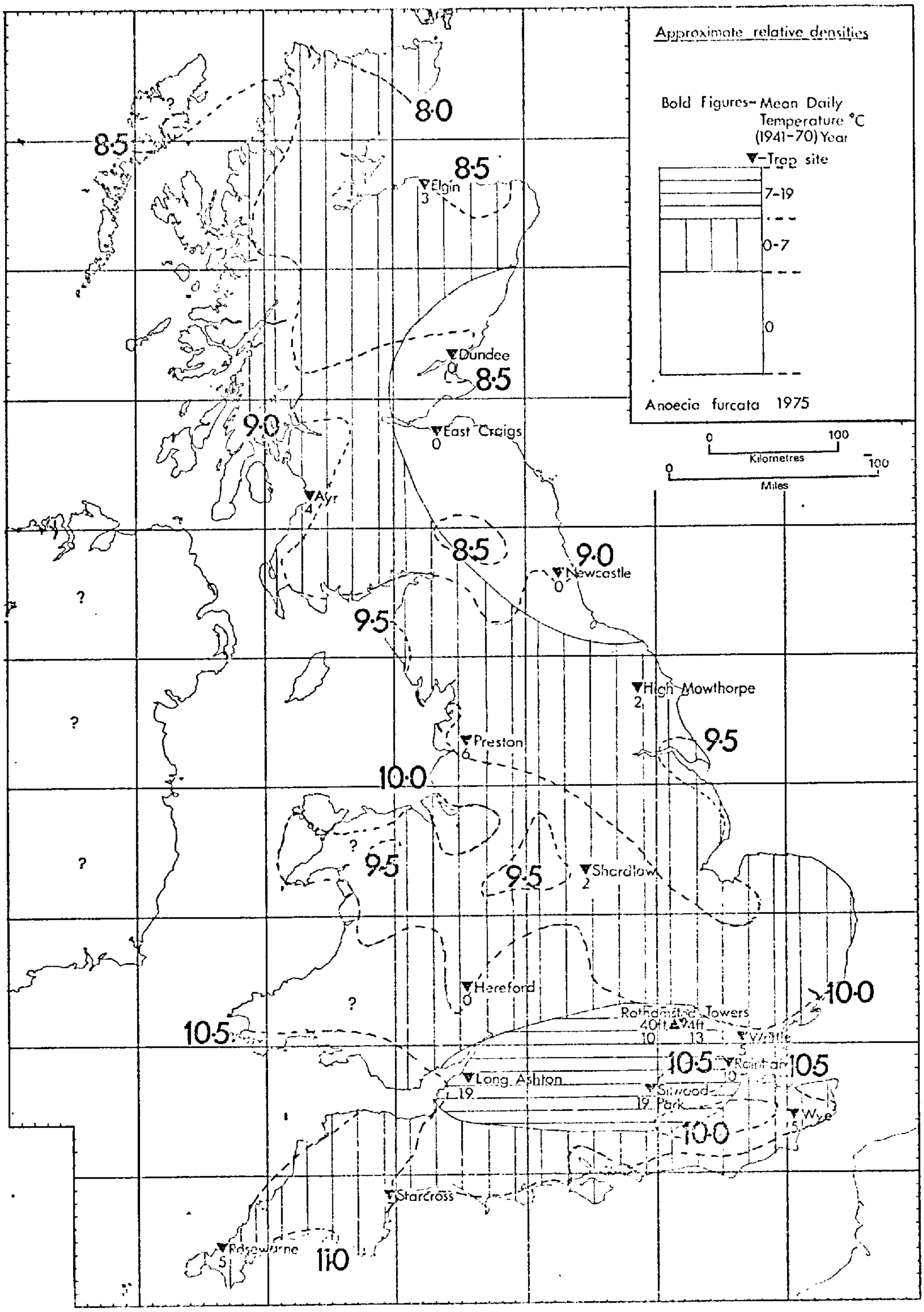


FIG 99

Approximate relative density map for Anoecia furcata, based on suction trap catches for 1976.

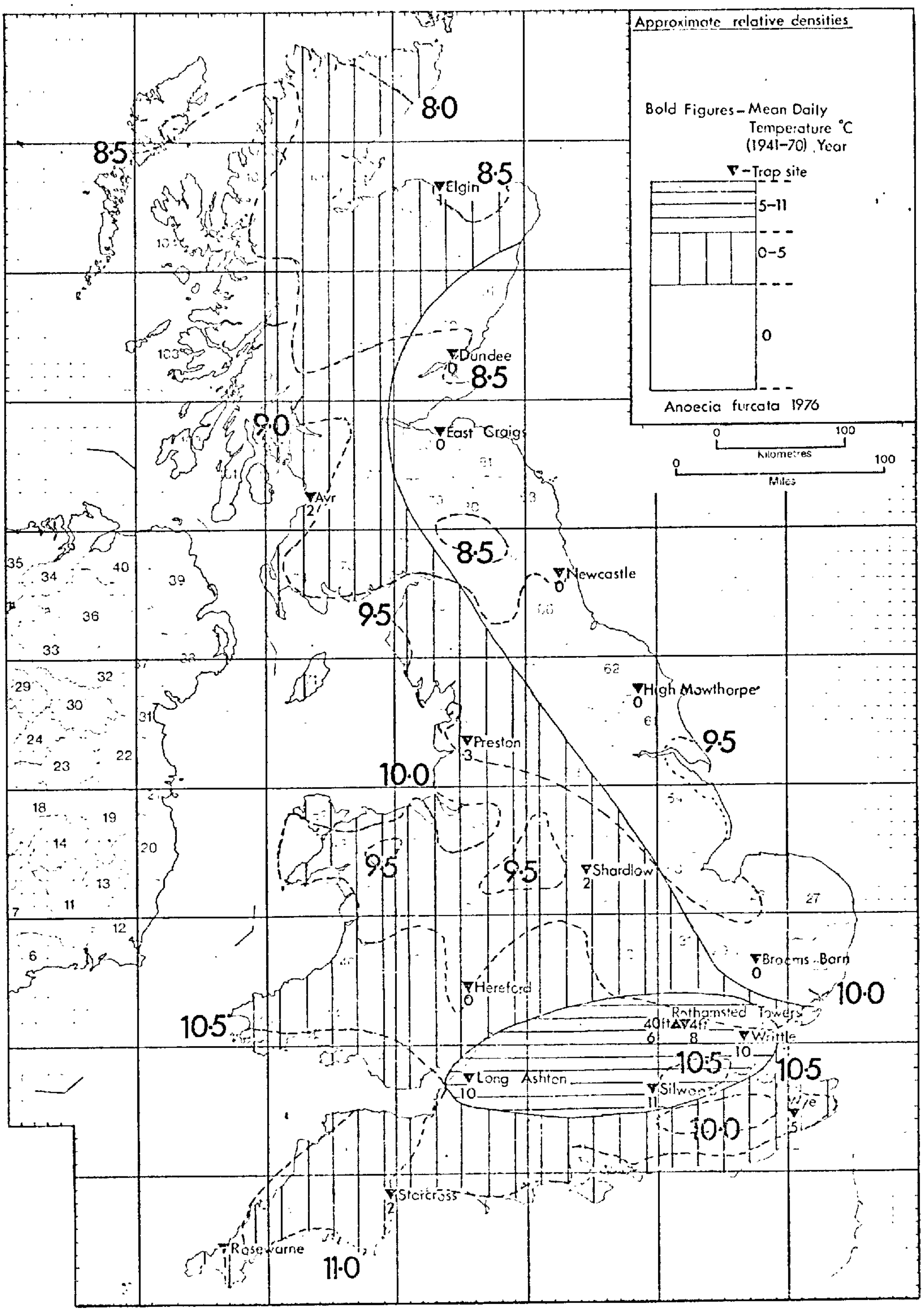


FIG 100

Approximate relative density map for Anoecia corni, based on suction trap catches for 1976.

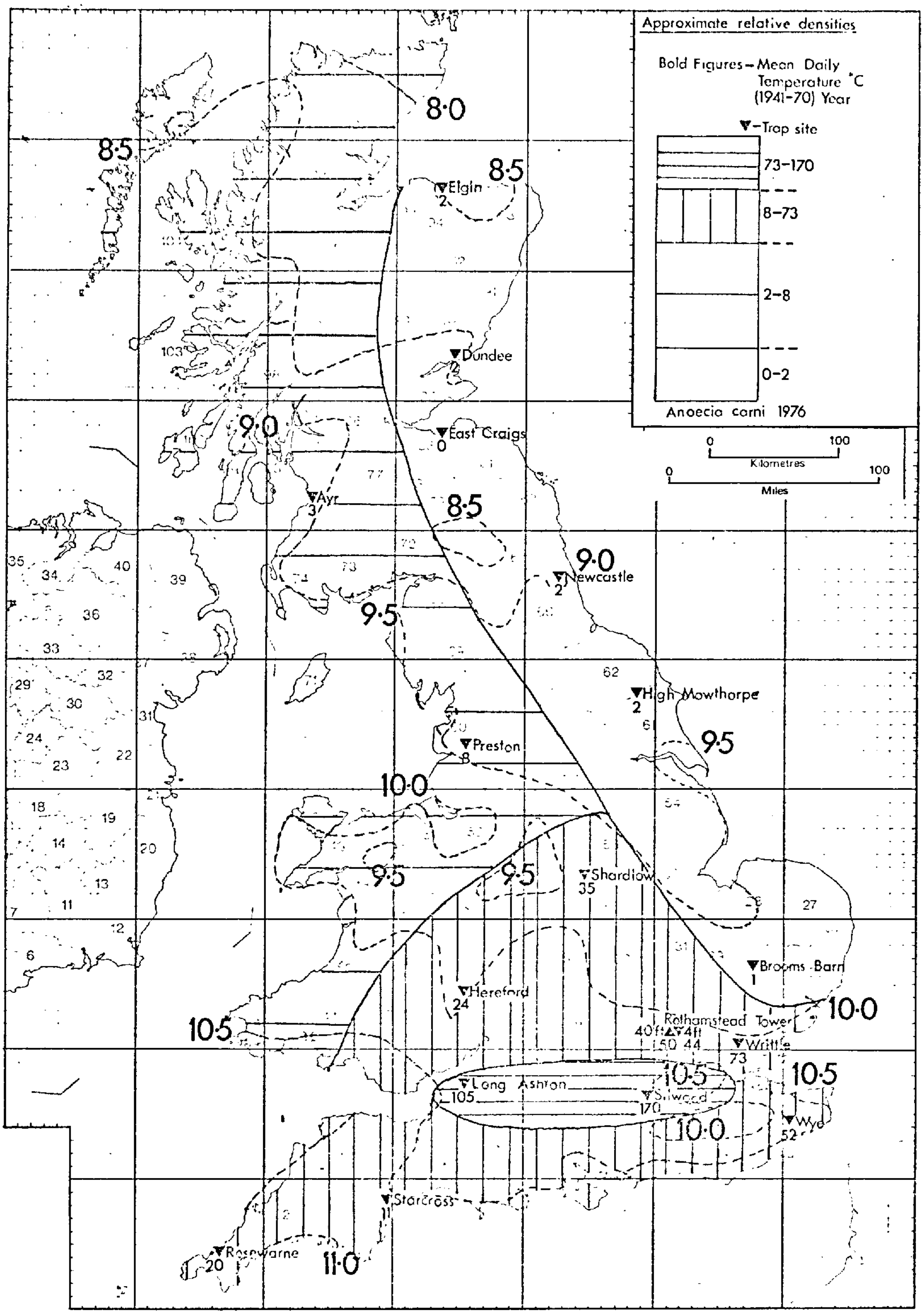


FIG 101

Approximate relative density map for *Anoecia vagans*, based on suction trap catches for 1976.

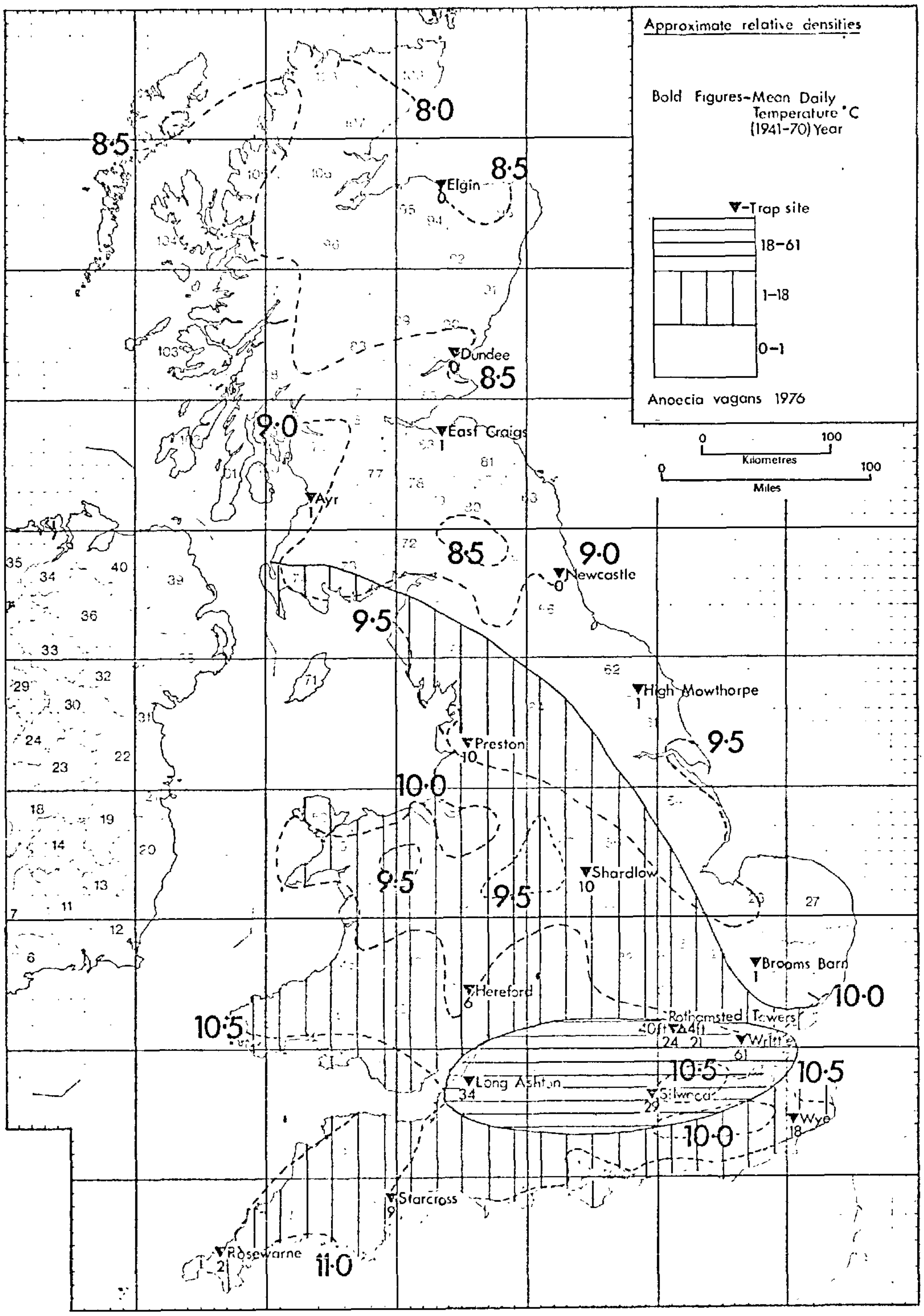
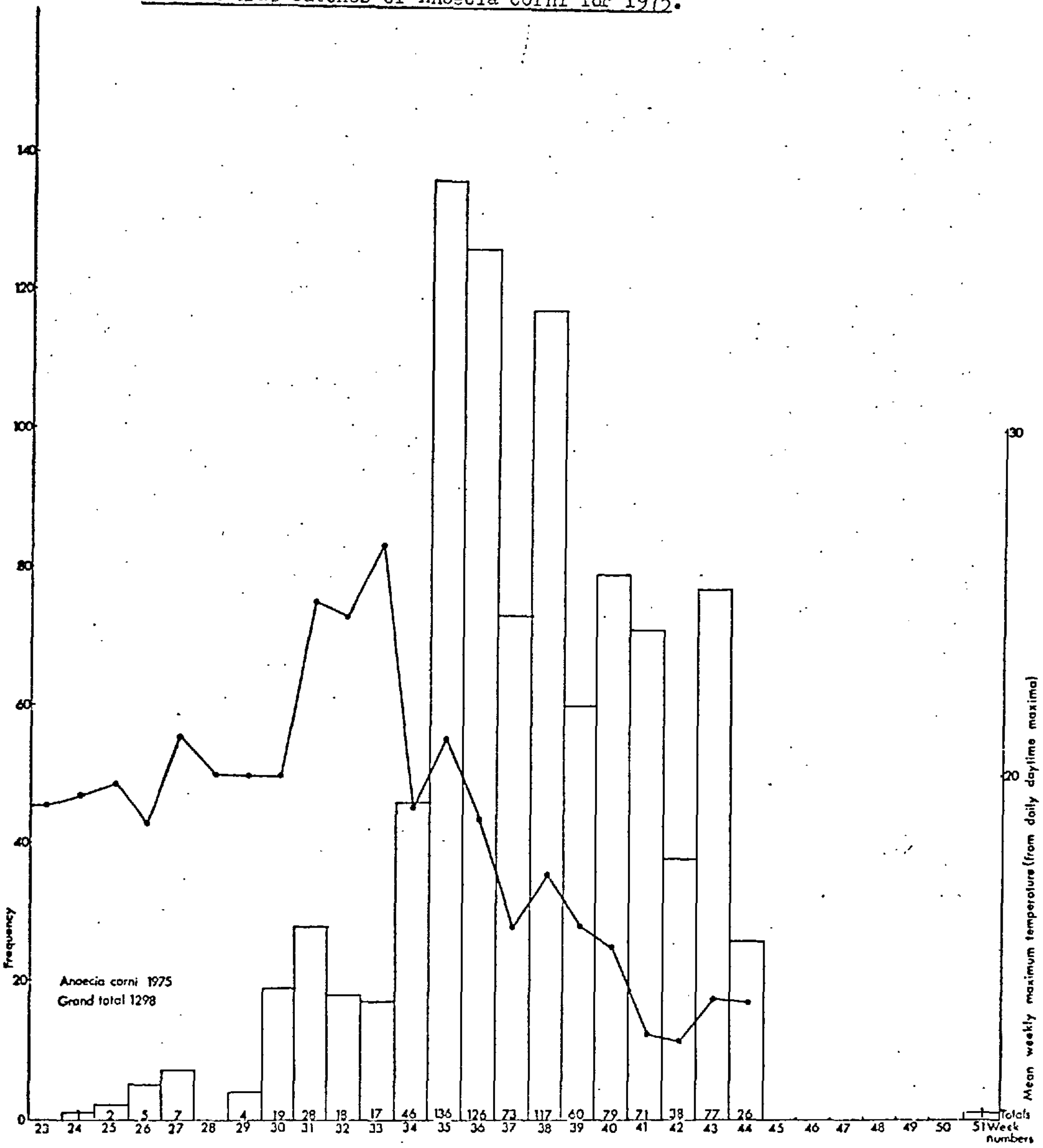


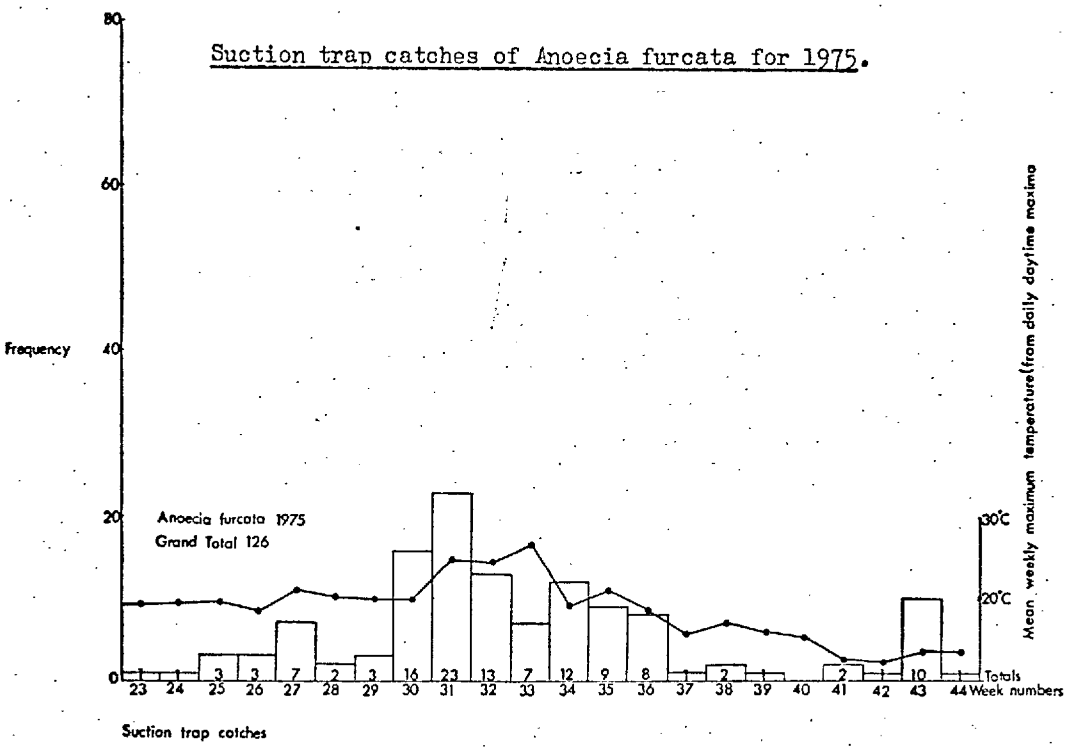
FIG 102

Suction trap catches of Anoecia corni for 1975.



Suction trap catches

FIG 103


Suction trap catches of Anoecia furcata for 1975.
80
60
Frequency 40
20
0
Anoecia furcata 1975
Grand Total 126
1
1
3
3
7
2
3
16
23
13
7
12
9
8
1
2
1
2
1
10
1
Totals
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44 Week numbers
Suction trap catches
30°C
20°C
Mean weekly maximum temperature(from daily daytime maxima

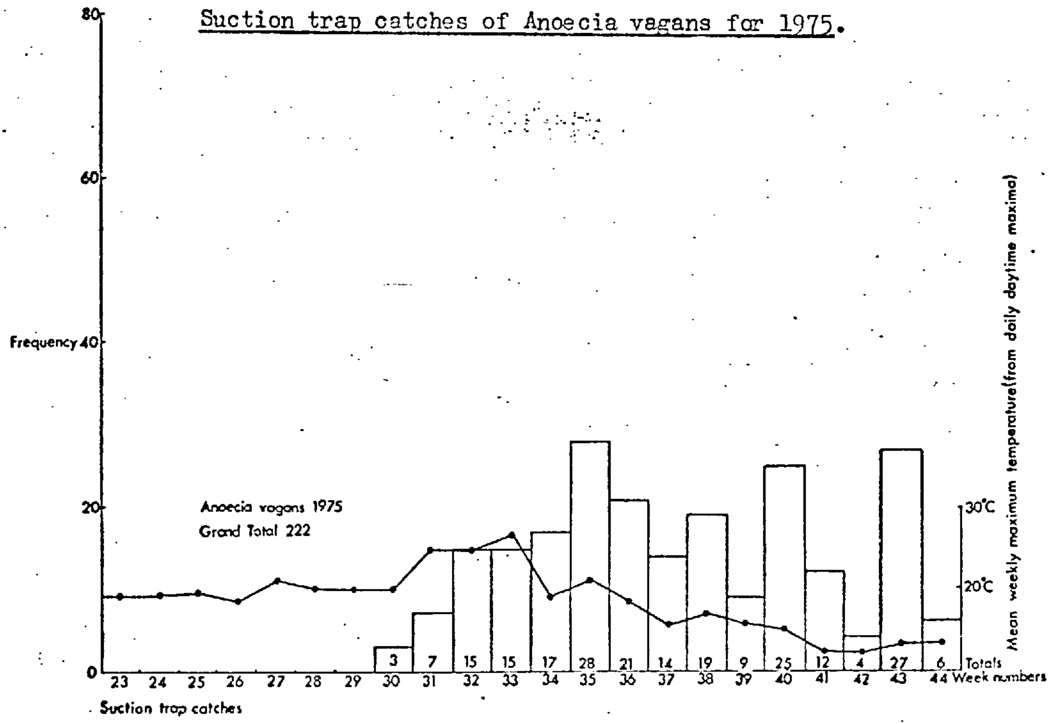
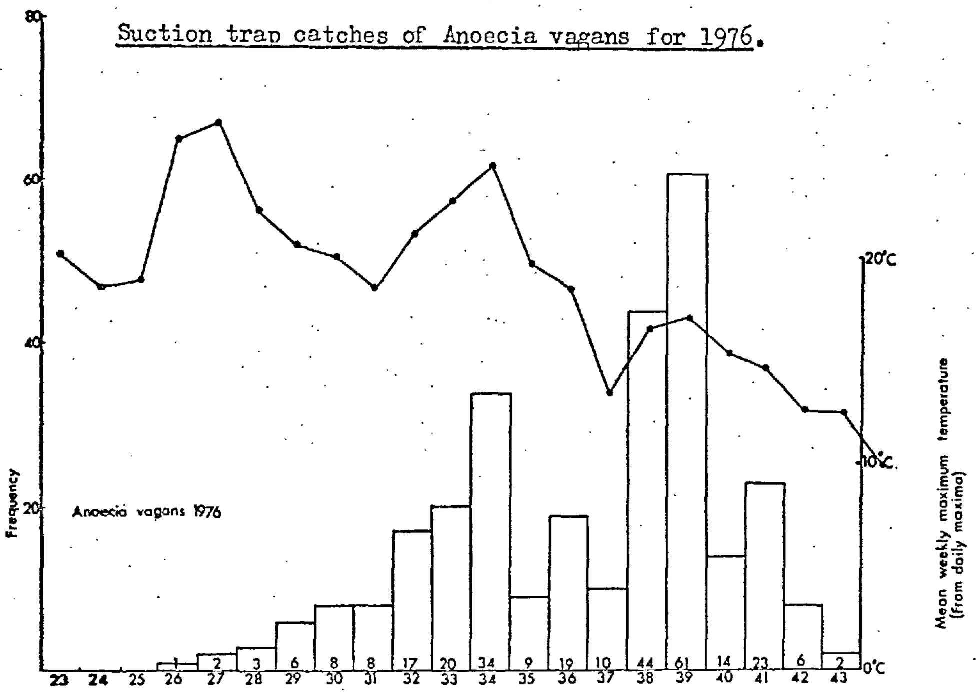

Suction trap catches of Anoecia vagans for 1975.
80
60
Frequency 40
20
0
Anoecia vagans 1975
Grand Total 222
3
7
15
15
17
28
21
14
19
9
25
12
4
27
6
Totals
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44 Week numbers
Suction trap catches
30°C
20°C
Mean weekly maximum temperature(from daily daytime maxima)

FIG 104

Suction trap catches of Anoecia vagans for 1976.



Suction trap catches of Anoecia furcata for 1976.

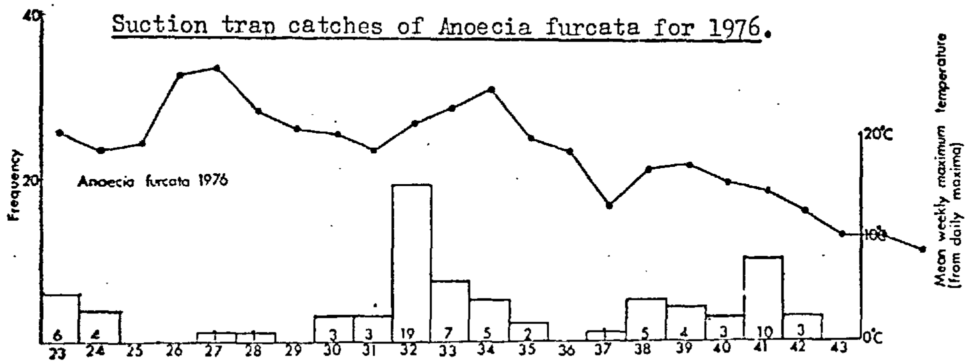


FIG 105

Suction trap catches of Anoecia corni for 1976.

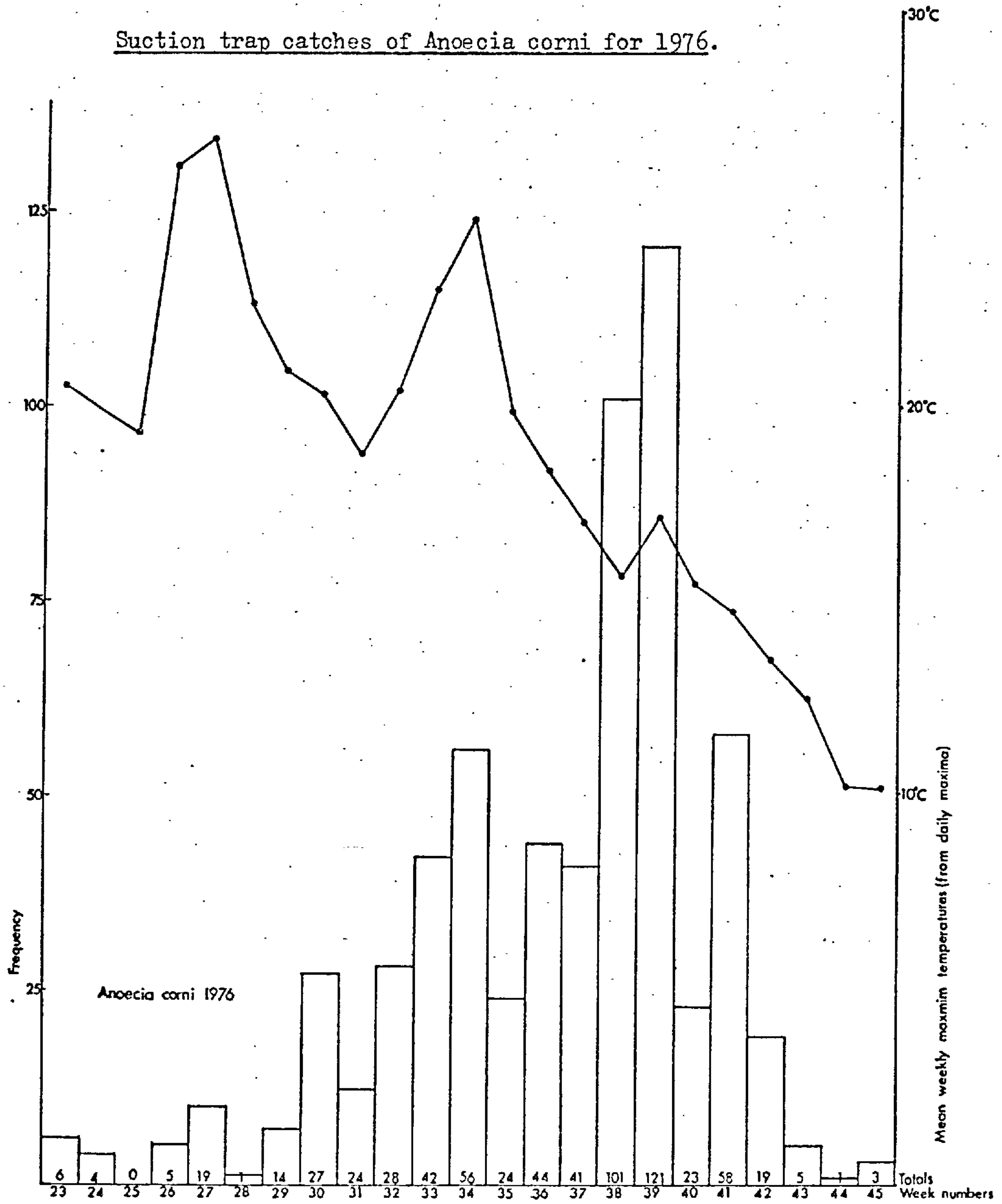


FIG 106

Suction trap catches for Anoecia spp. for 1968.

(Figures for 3 species combined)

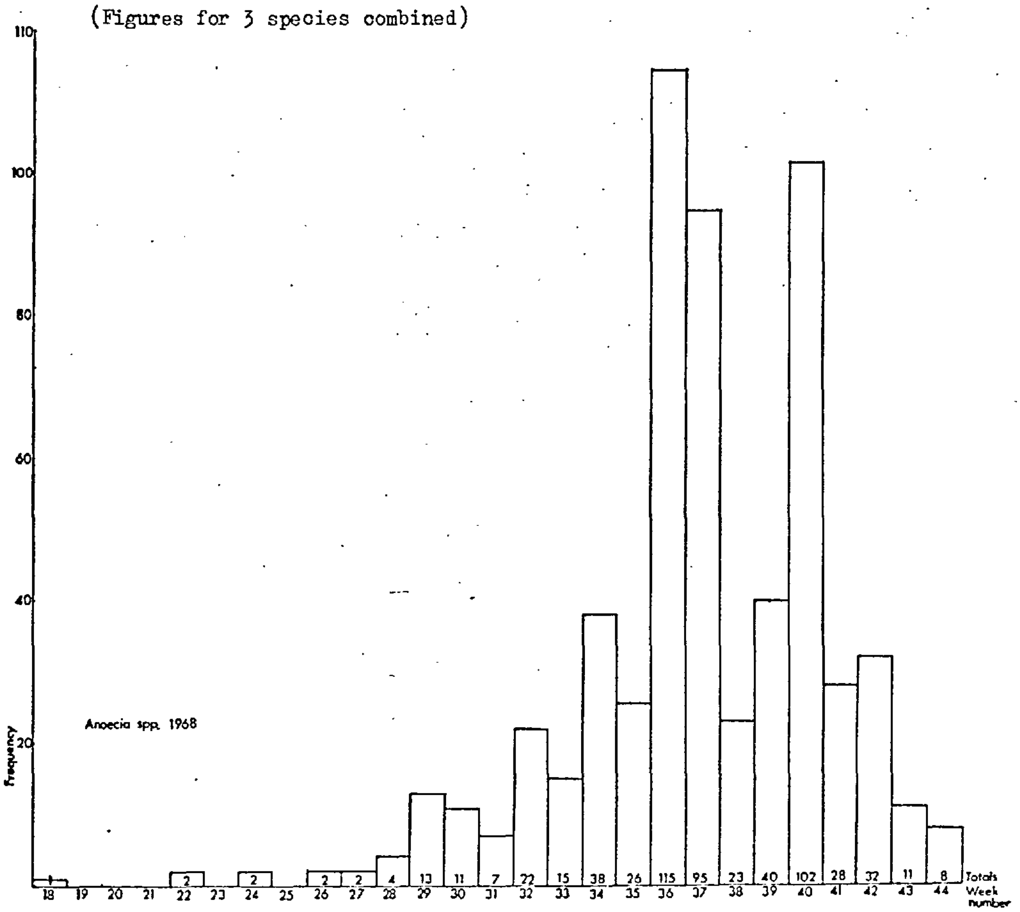


FIG 107

Suction trap catches for Anoecia spp. for 1969.
(Figures for 3 species combined)

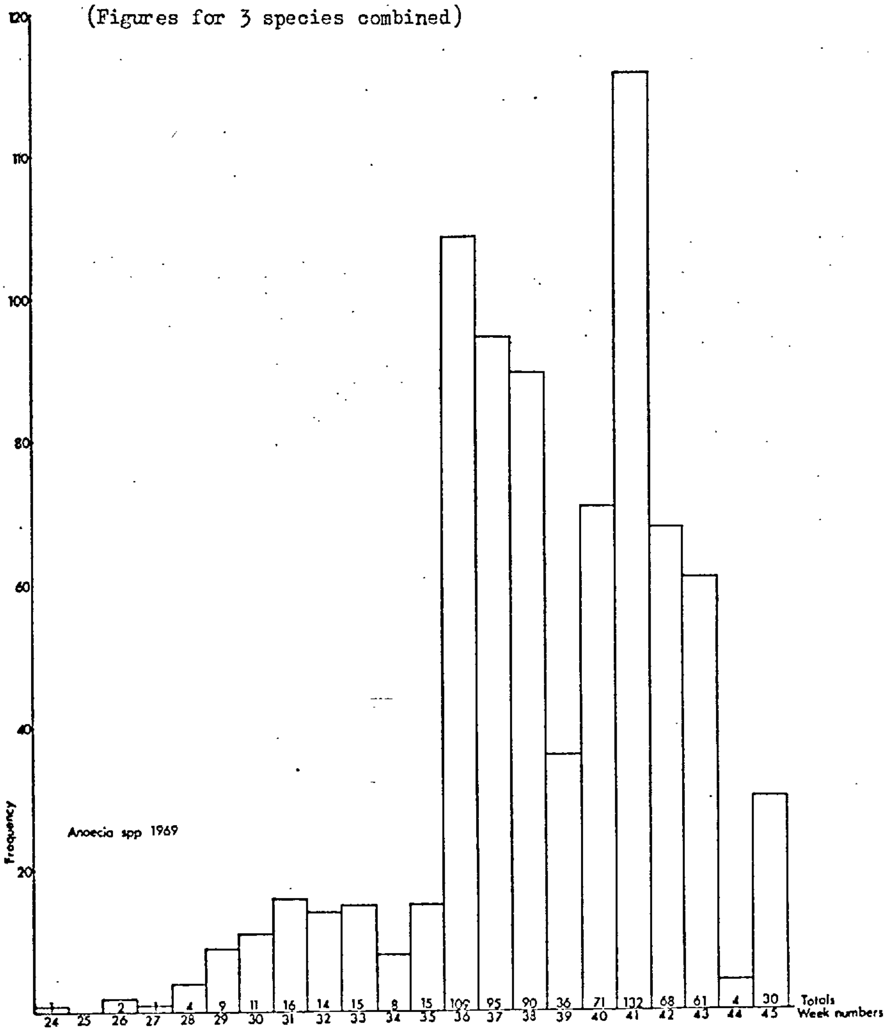
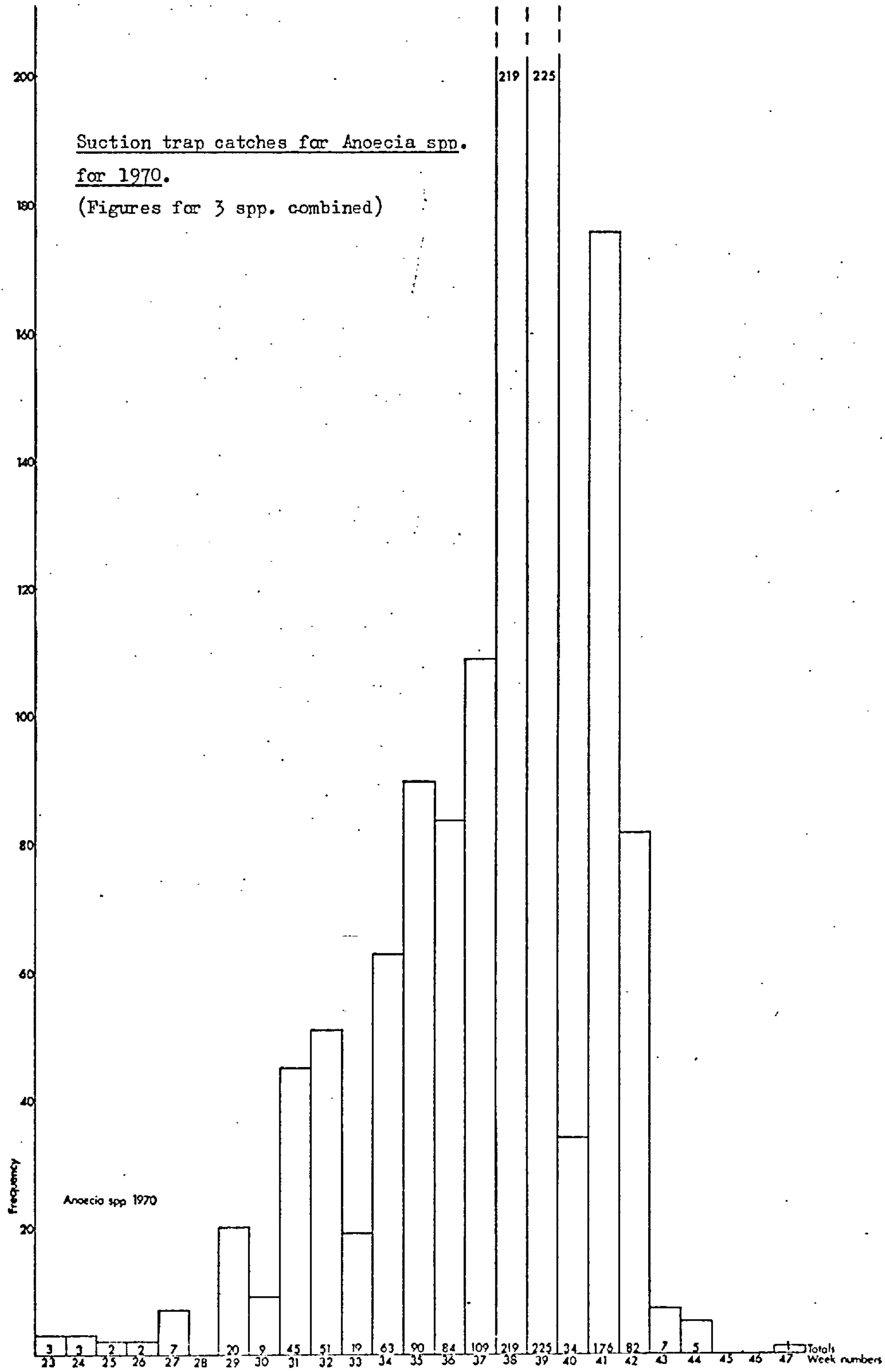
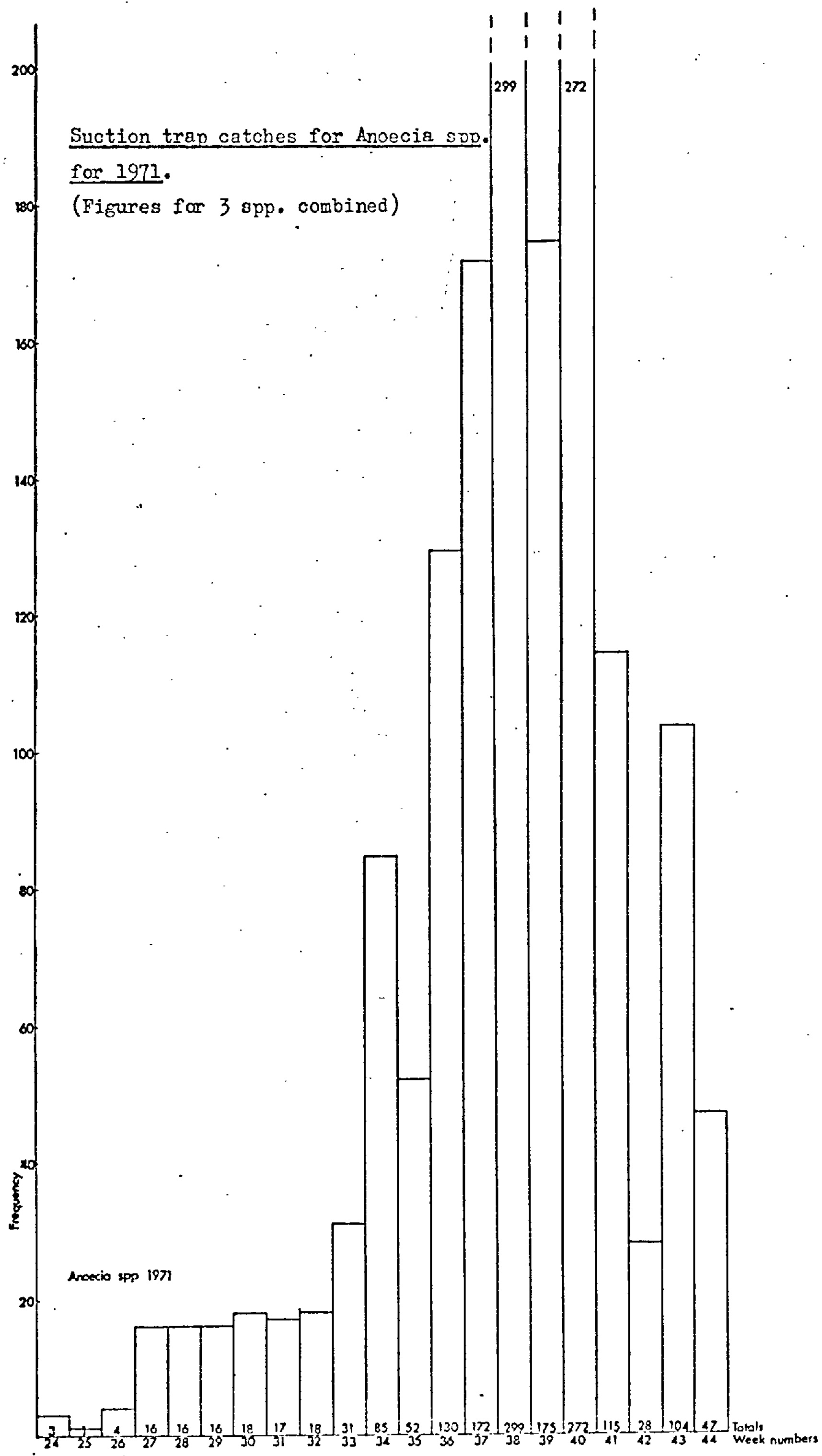


FIG 108



Suction trap catches for Anoecia spp. for 1970.
(Figures for 3 spp. combined)

FIG 109



Suction trap catches for Anoecia spp. for 1971.

(Figures for 3 spp. combined)

FIG 110

Suction trap catches for Anoecia spp. for 1972.

(Figures for 3 species combined)

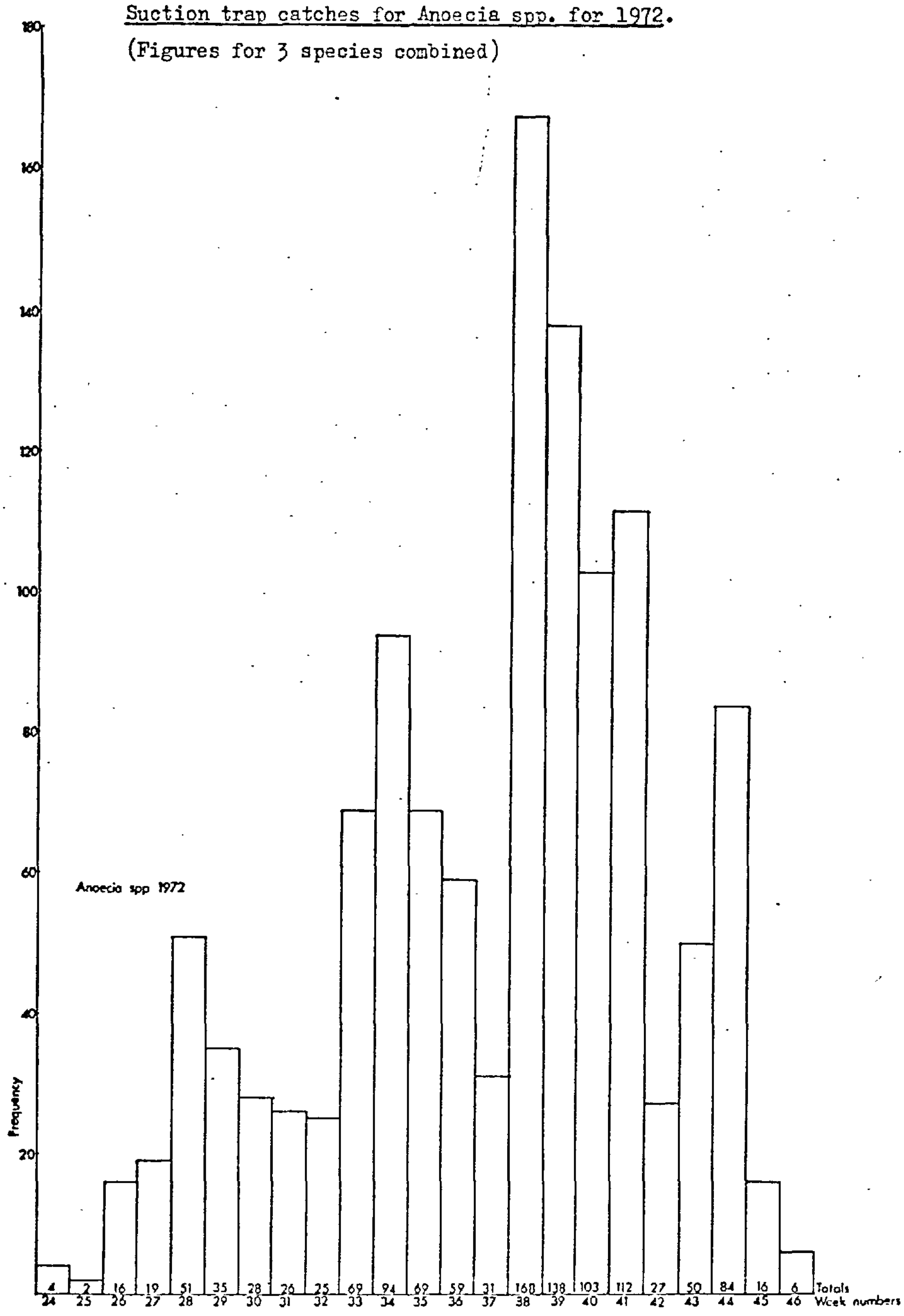
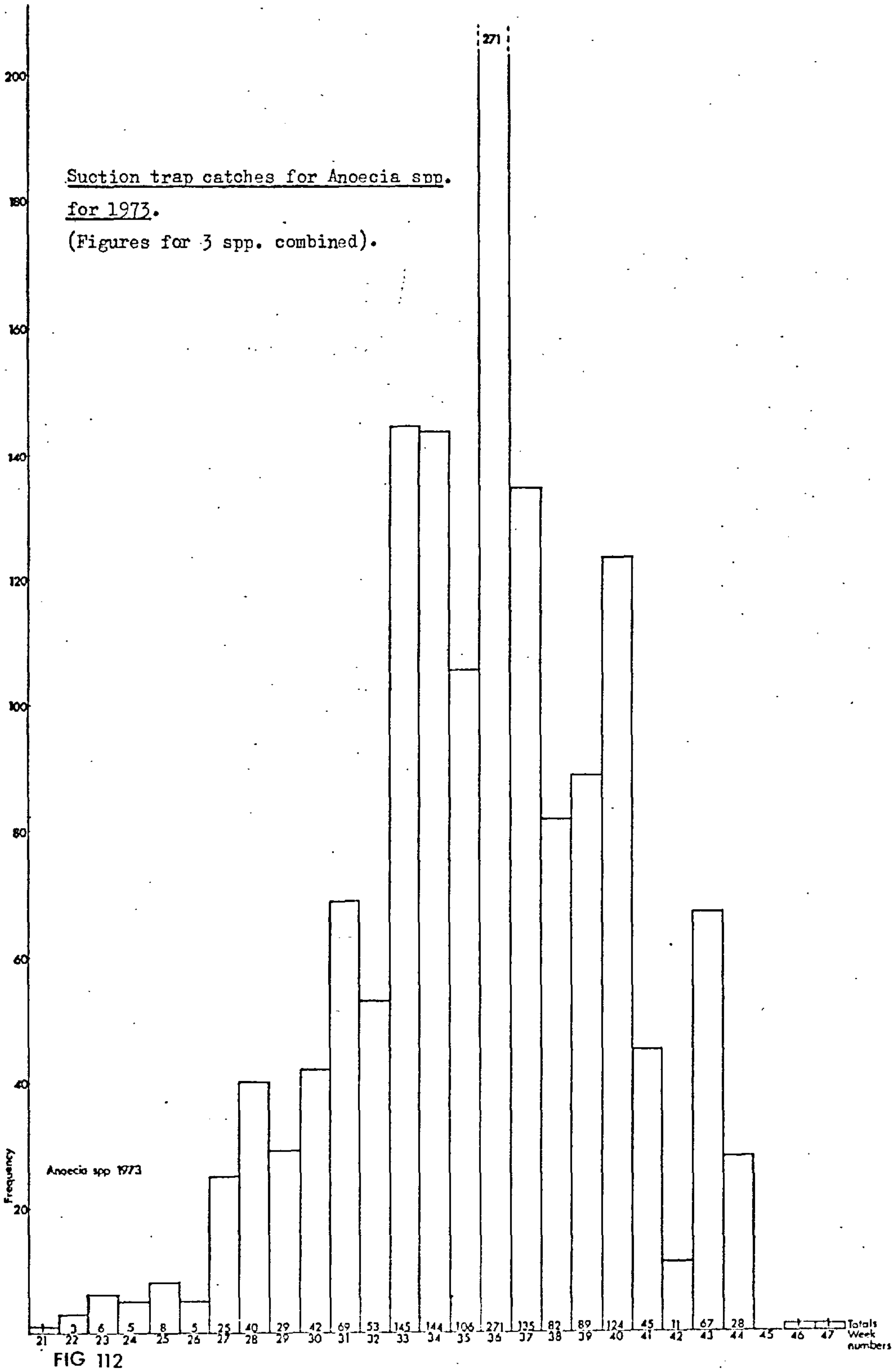


FIG 111



Suction trap catches for Anoecia spp. for 1973.
(Figures for 3 spp. combined).

FIG 112

Suction trap catches for Anoecia species for 1974.
(Figures for 3 spp. combined.)

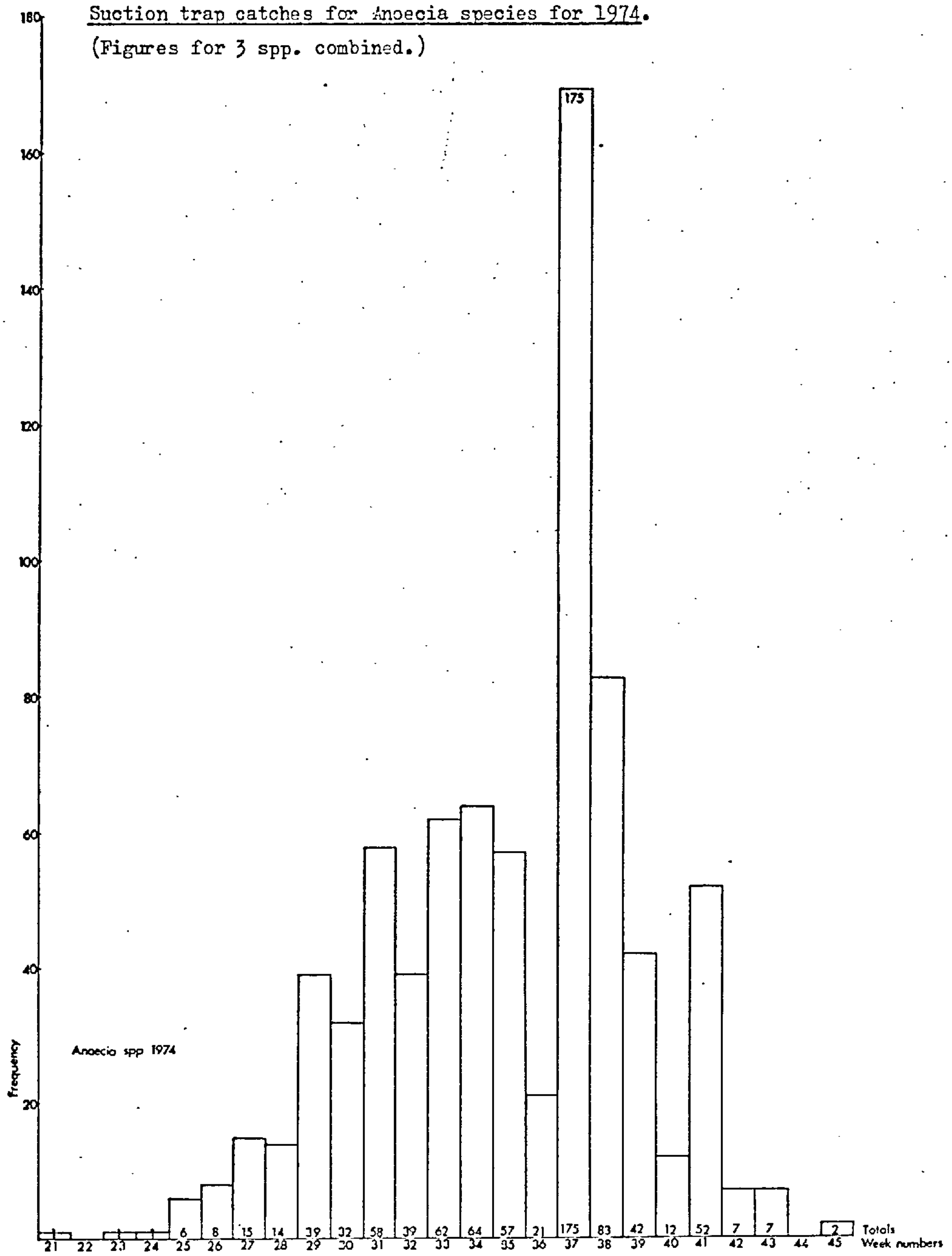
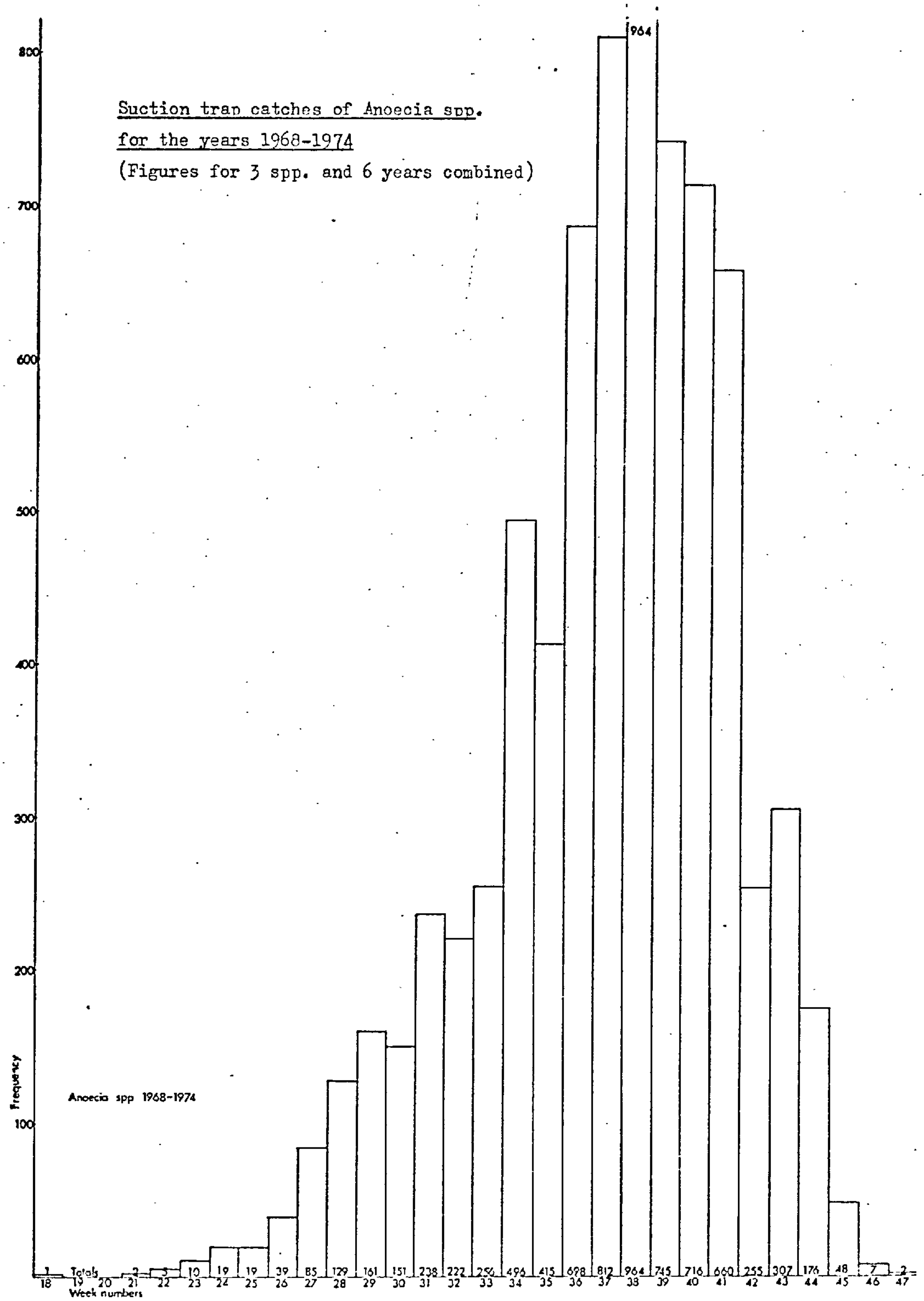


FIG 113



Suction trap catches of Anoecia spp. for the years 1968-1974

(Figures for 3 spp. and 6 years combined)

FIG 114

Suction trap catches of Aploneura lentisci for 1968-1975.

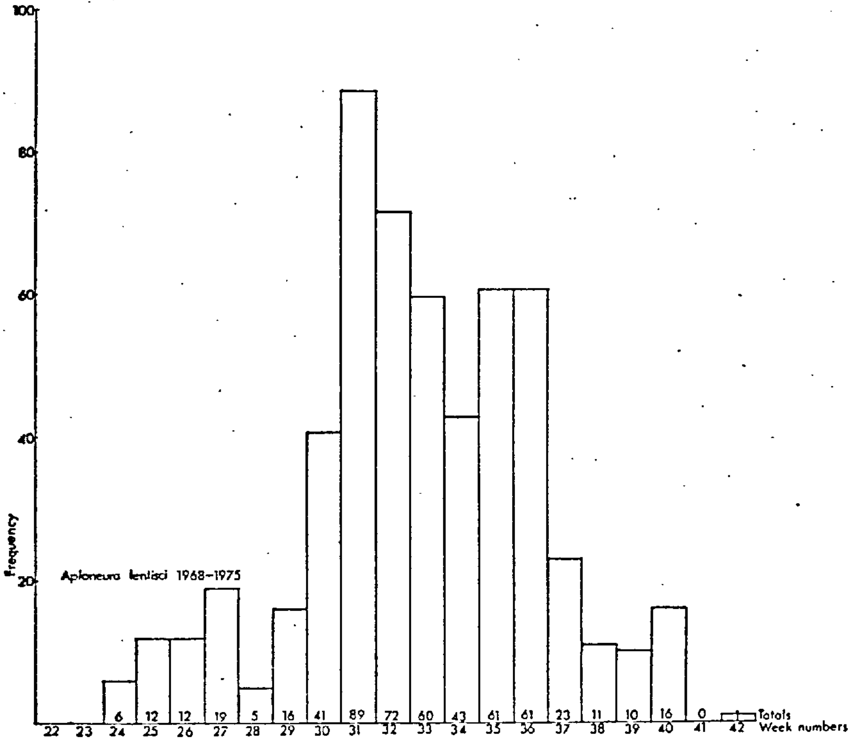
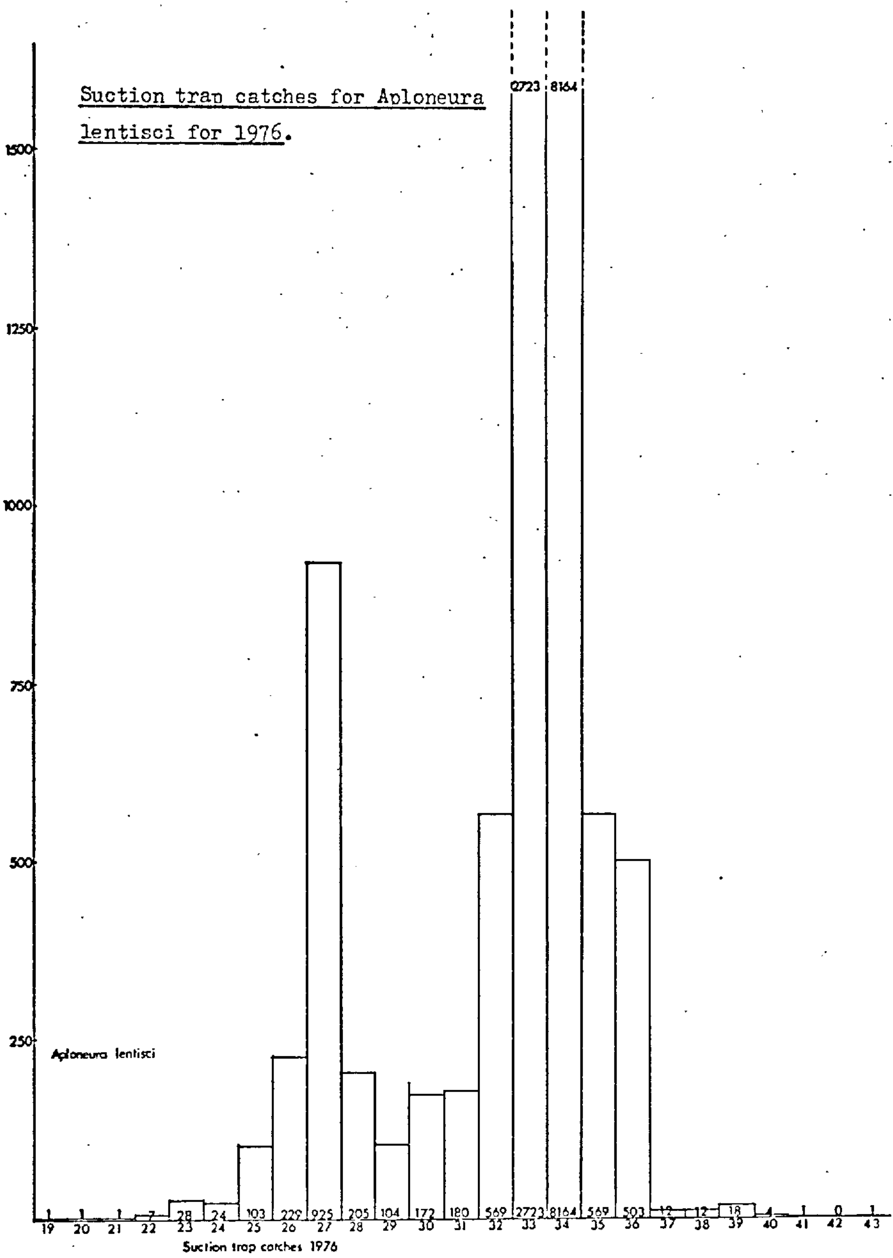


FIG 115



Suction trap catches for Aploneura lentisci for 1976.

FIG 116

Week numbers.	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Forda formicaria.	1	8	15	31	25	14	4	21	1	3	8	2	0	1	0	0	0	0	0	0	0	0	0	0	0
Tetraneura ulmi.	0	0	0	1	2	15	36	46	21	22	23	38	22	23	25	27	22	42	79	105	62	36	6	22	15
Protrama spp.	0	0	5	6	4	4	2	3	4	0	2	5	5	12	18	10	20	12	9	3	5	6	3	3	1
Trama spp.	0	0	0	2	4	3	5	6	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0

Suction trap catches for F.formicaria, T.ulmi, Protrama spp., Trama spp. from 1968-1975.

(See Figs. 97-102 for sites of traps).

Table 9.

Week numbers.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Baizongia pistaciae	0	0	0	0	0	0	2	5	1	3	8	3	3	0	2	2
Smynthurodes betae	0	1	0	0	0	0	1	4	0	0	1	1	1	0	0	0
Forda marginata	0	0	2	3	6	2	1	4	0	0	0	0	0	0	0	0
Geoica eragrostidis	0	0	0	0	2	0	3	0	0	1	0	2	0	0	0	0
Geoica setulosa	0	0	0	0	0	2	4	0	0	0	0	1	1	2	0	0
Geoica spp.	1	0	0	0	1	0	3	0	0	1	2	0	0	0	0	0

Suction trap catches for B.pistaciae, S.betae, F.marginata, G.eragrostidis, G.setulosa and Geoica spp. from 1968-1975.

(See Figs. 97-102 for sites of traps).

Table 10.

DISTRIBUTION MAPS OF BRITISH MYRMECOPHILOUS ROOT APHIDS.

Distribution maps have been prepared for the myrmecophilous Anoeciinae, Fordinae and Traminae. They are 10 kilometre square maps as used by the biological records centre at Monks Wood. Each dot on the map represents at lest one record from the 10 kilometre square in question.

Data are derived from my own collecting, from the British Museum (Natural History) collections and from data provided Dr. A.J. Pontin and Dr. H.L.G. Stroyan. Most records are concentrated in the South East of England where most collecting has been done but information from suction traps and collecting trips to other parts of Britain gives some information about range. The true density of distribution will only be clear when much more collecting has been done.

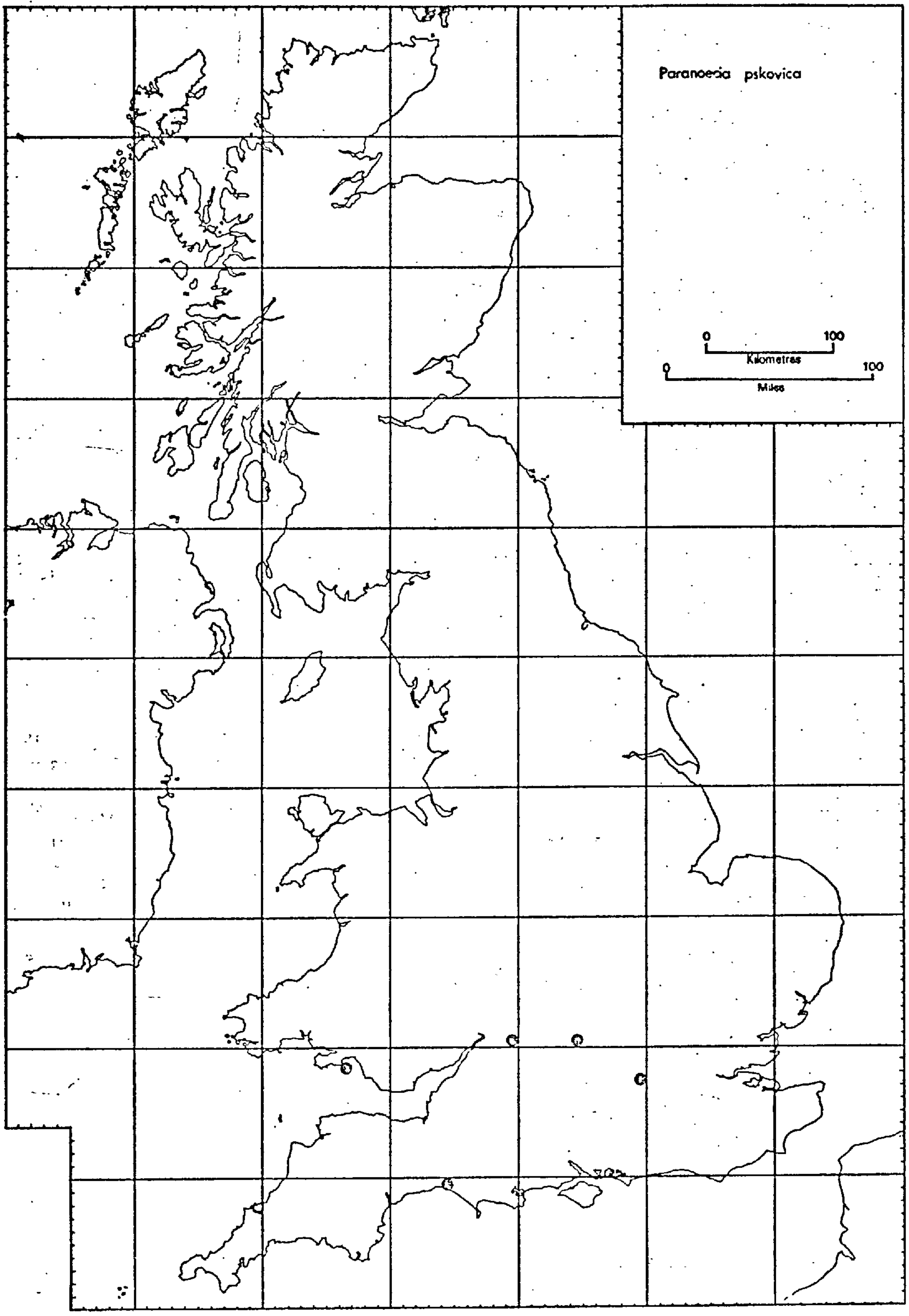


FIG 117

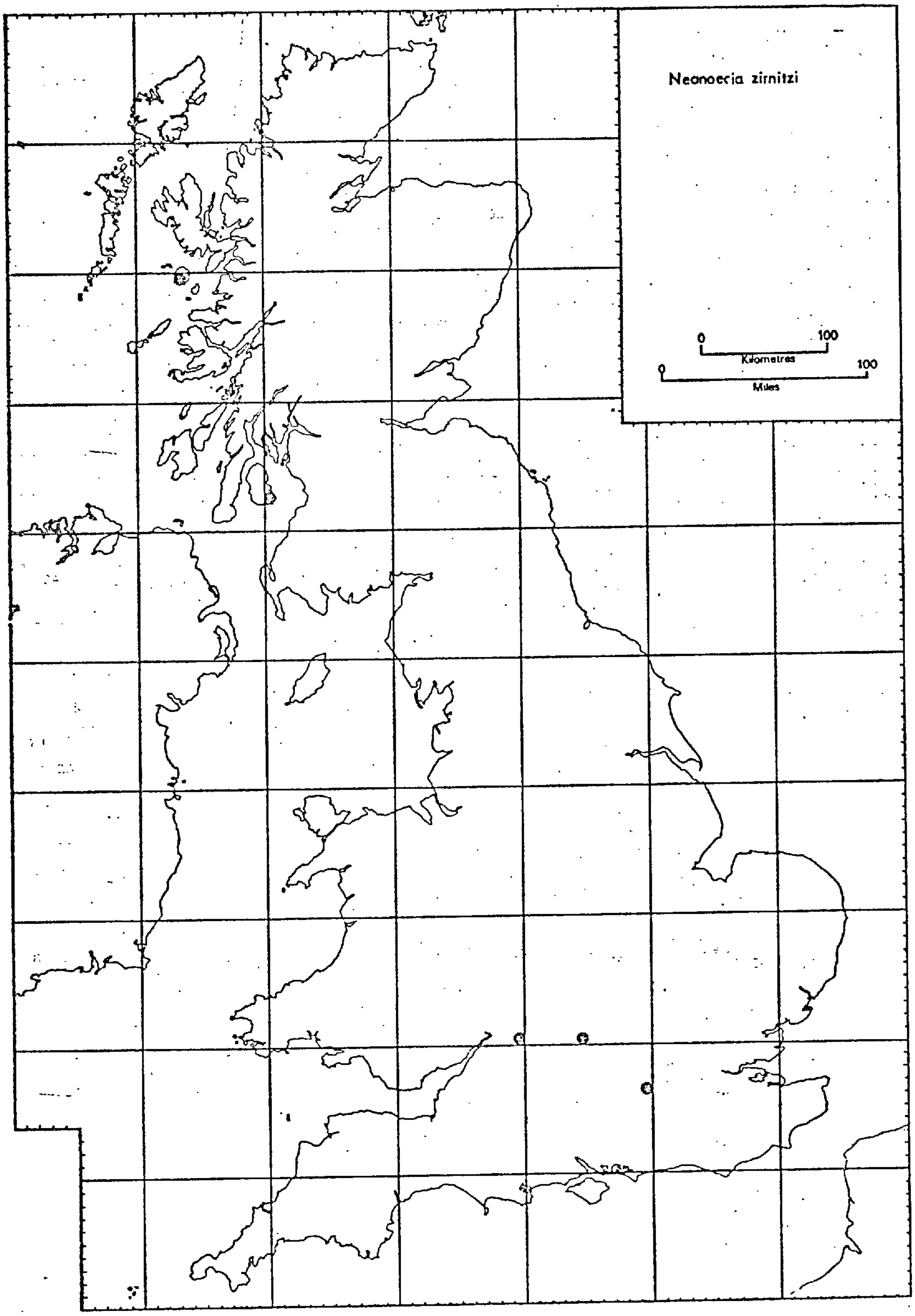


FIG 118

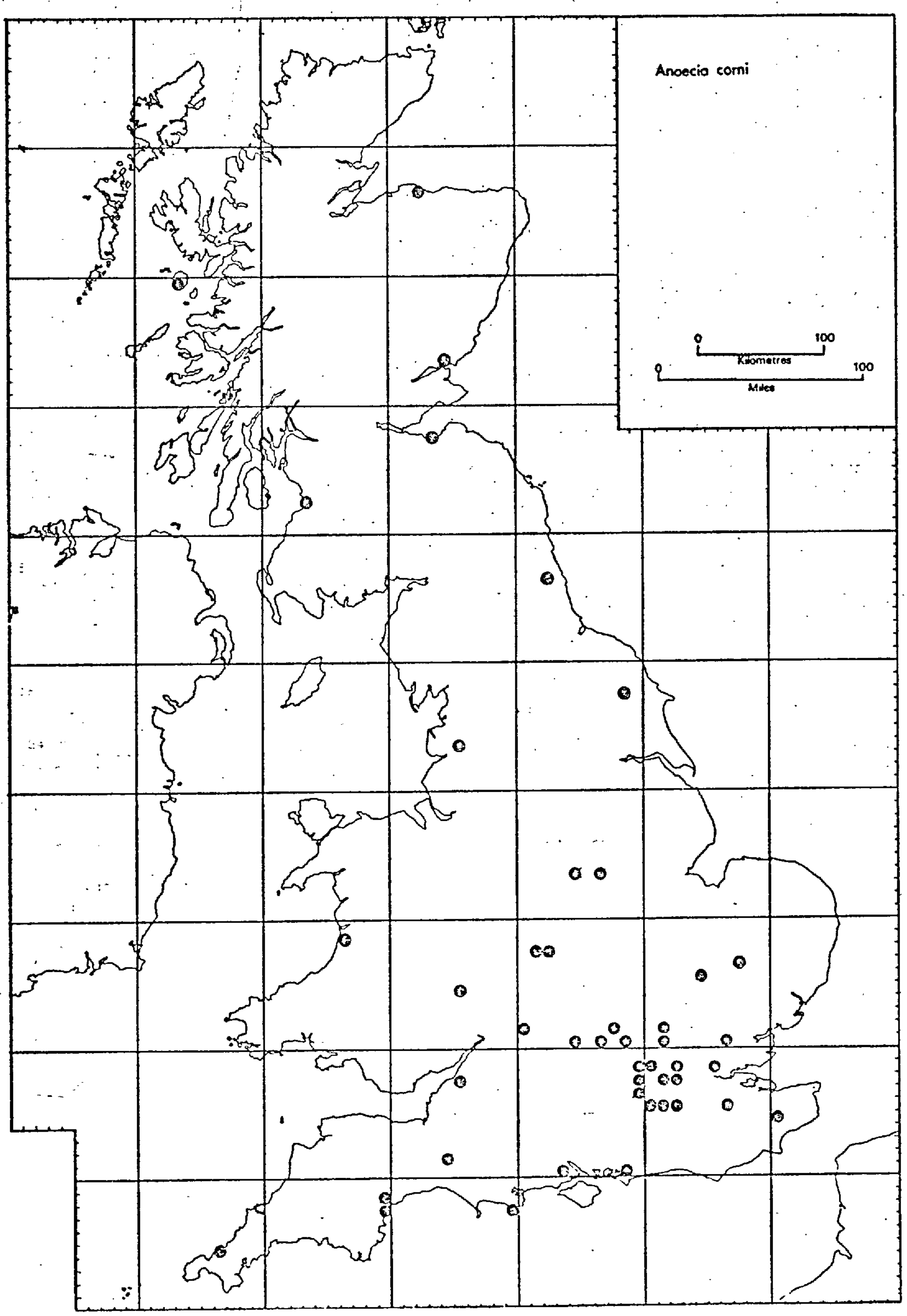


FIG 119

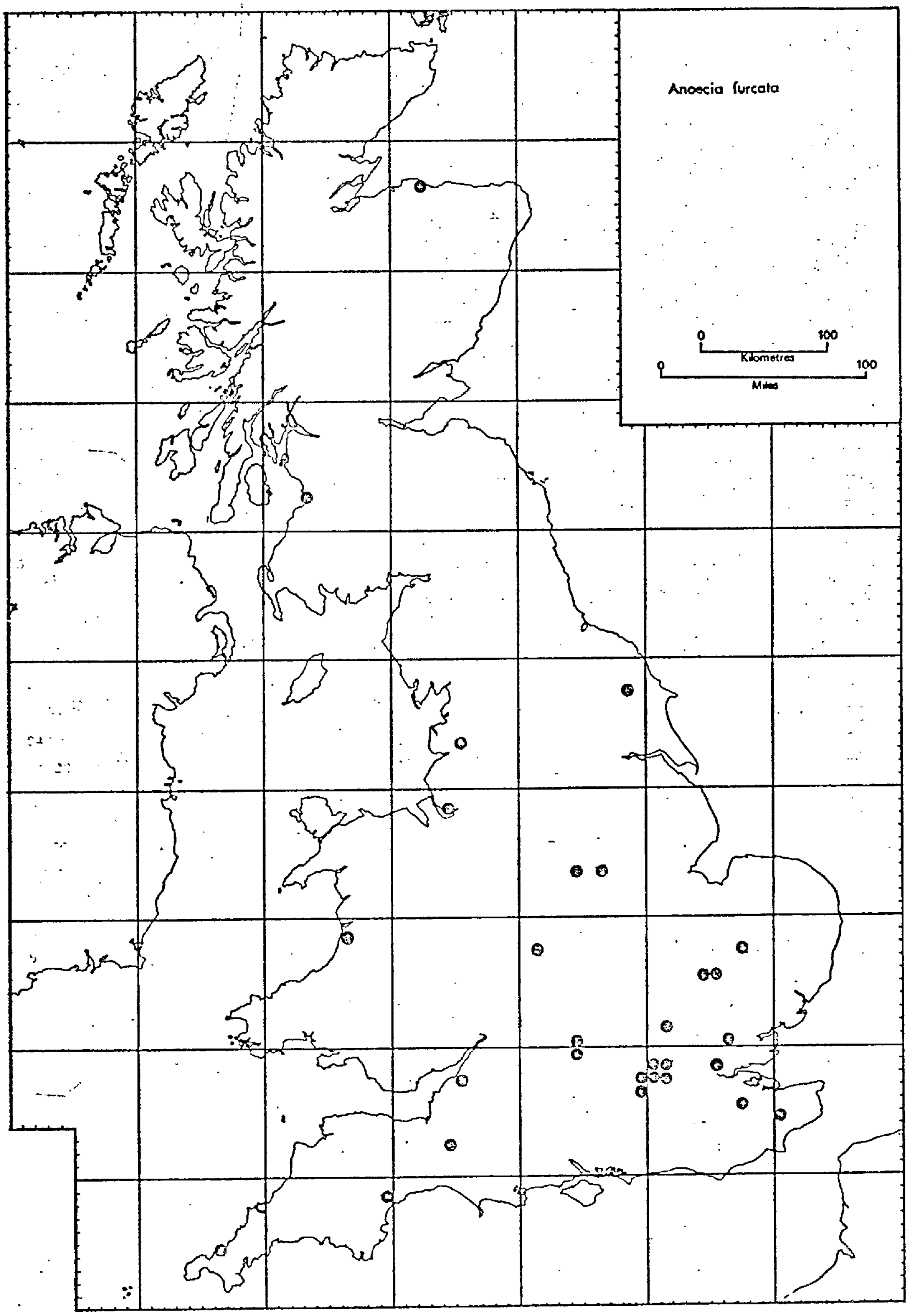


FIG 120

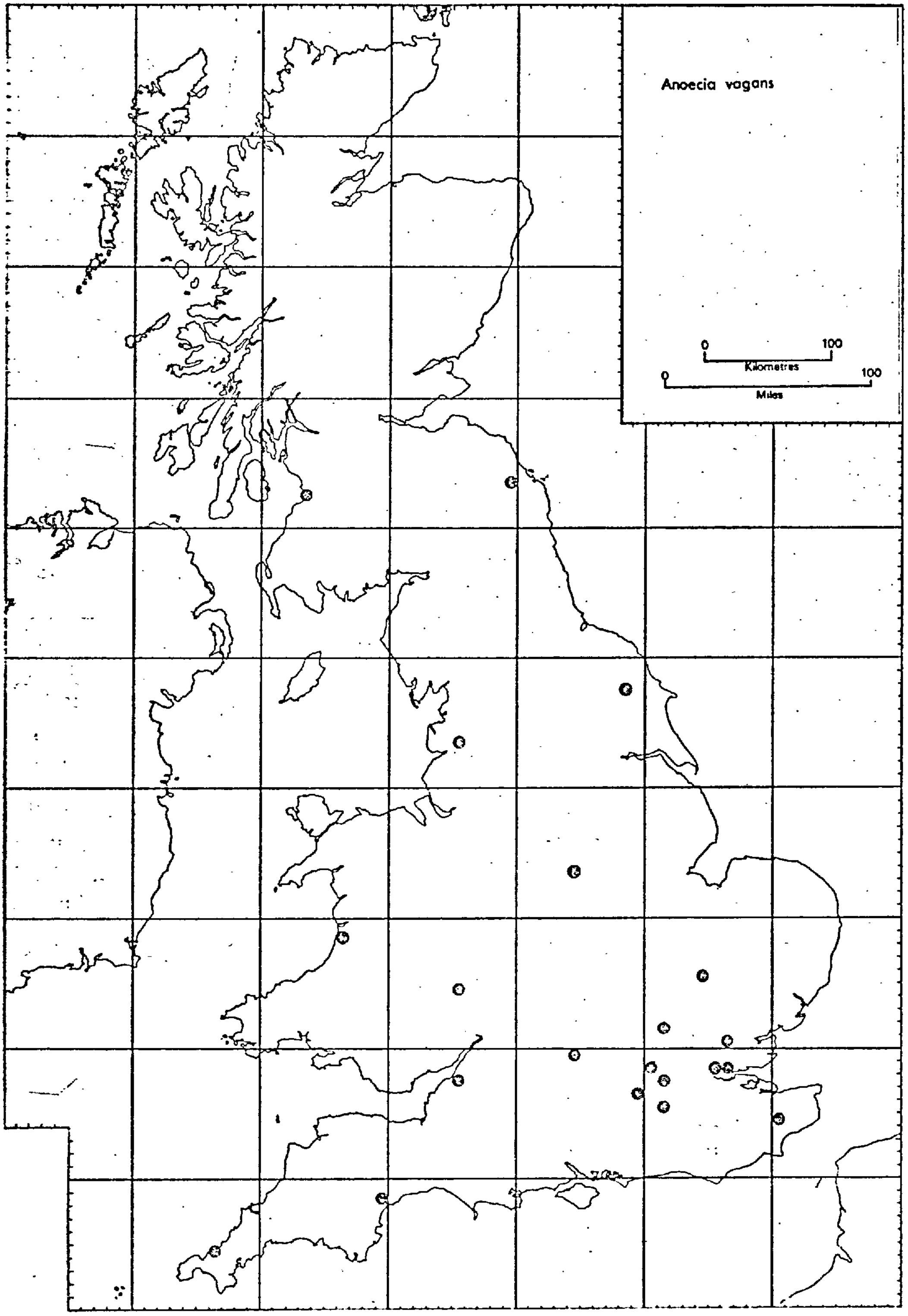


FIG 121

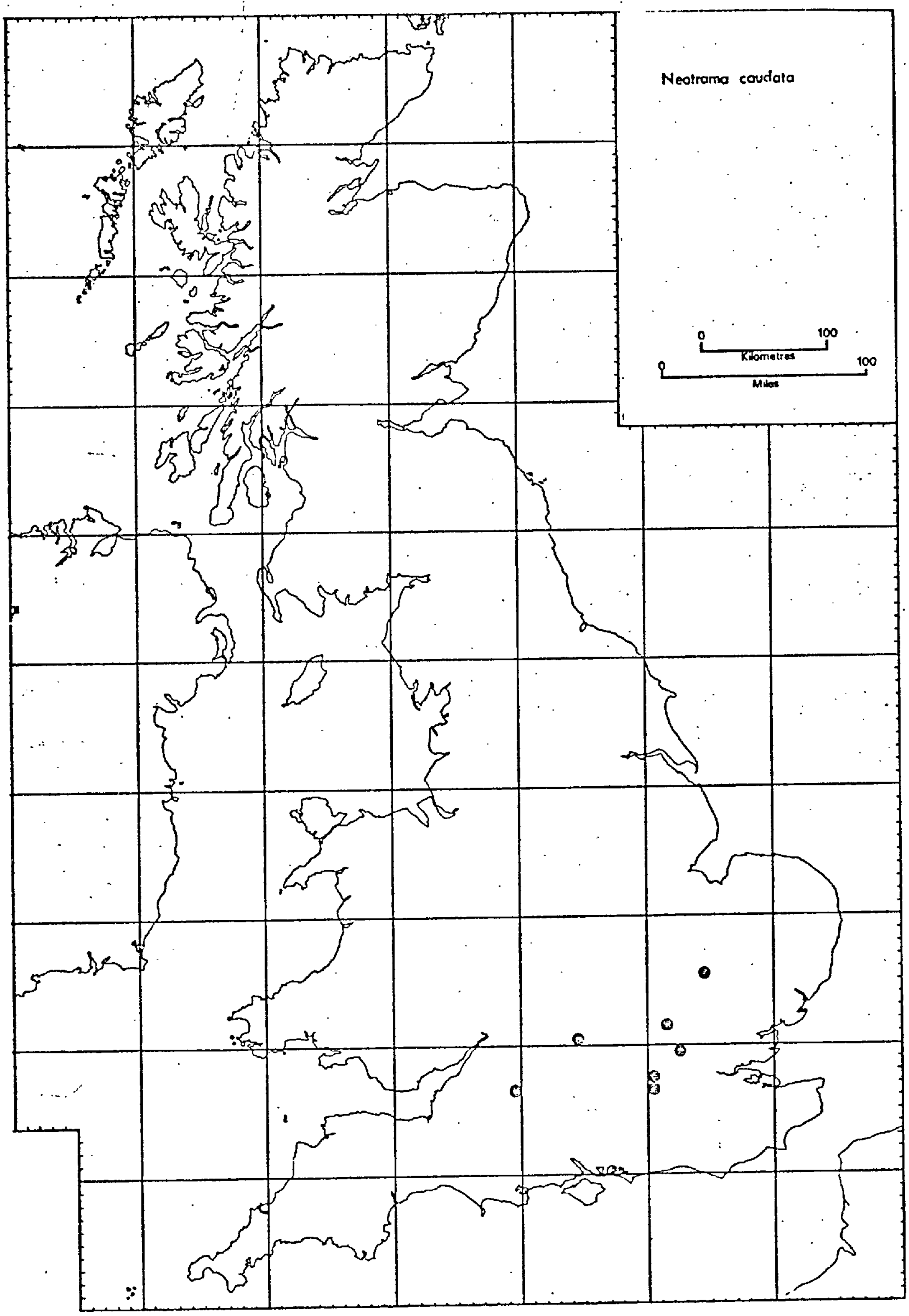


FIG 122

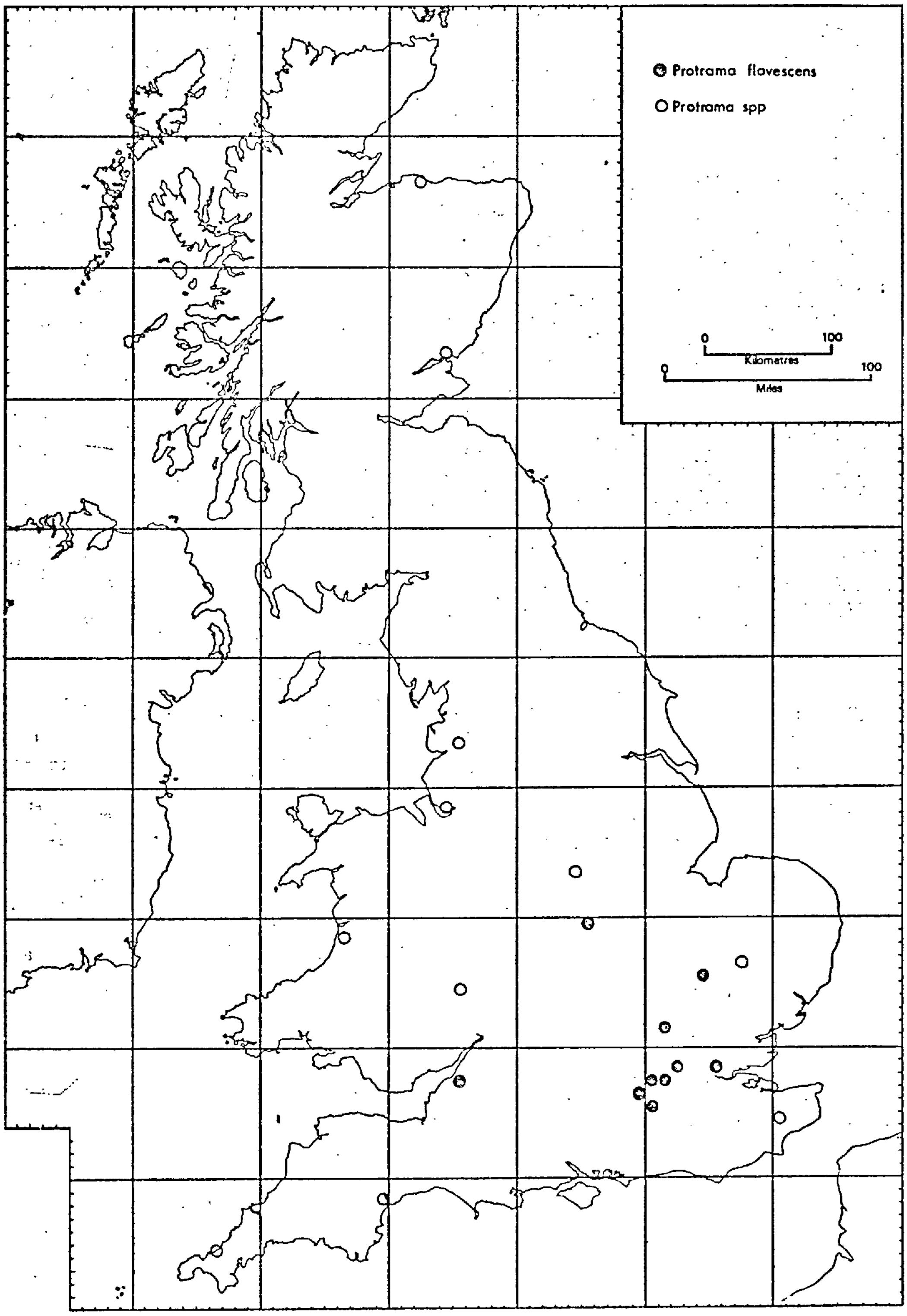

Protrama flavescens
Protrama spp
0
100
Kilometres
0
100
Miles

FIG 123

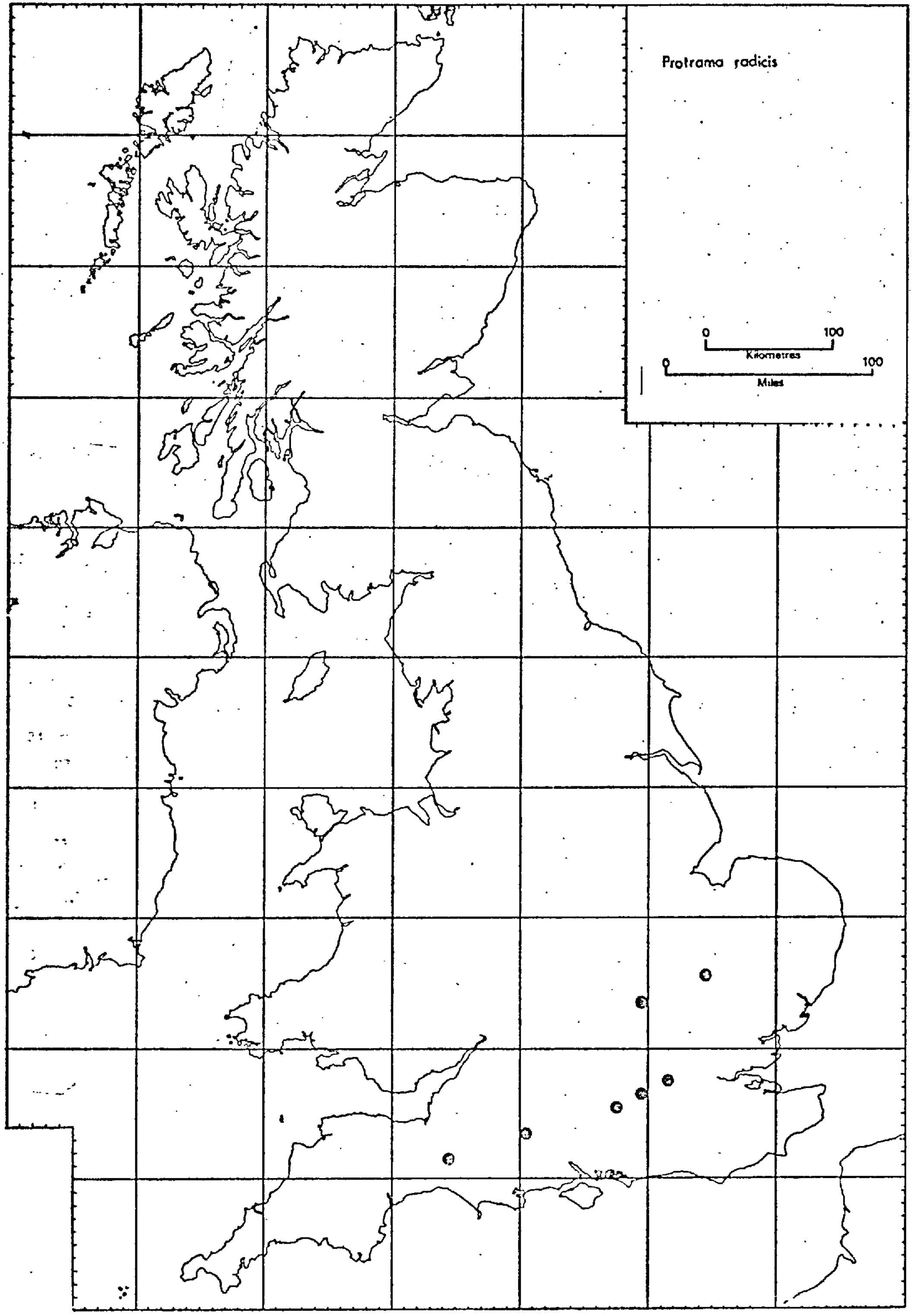


FIG 124

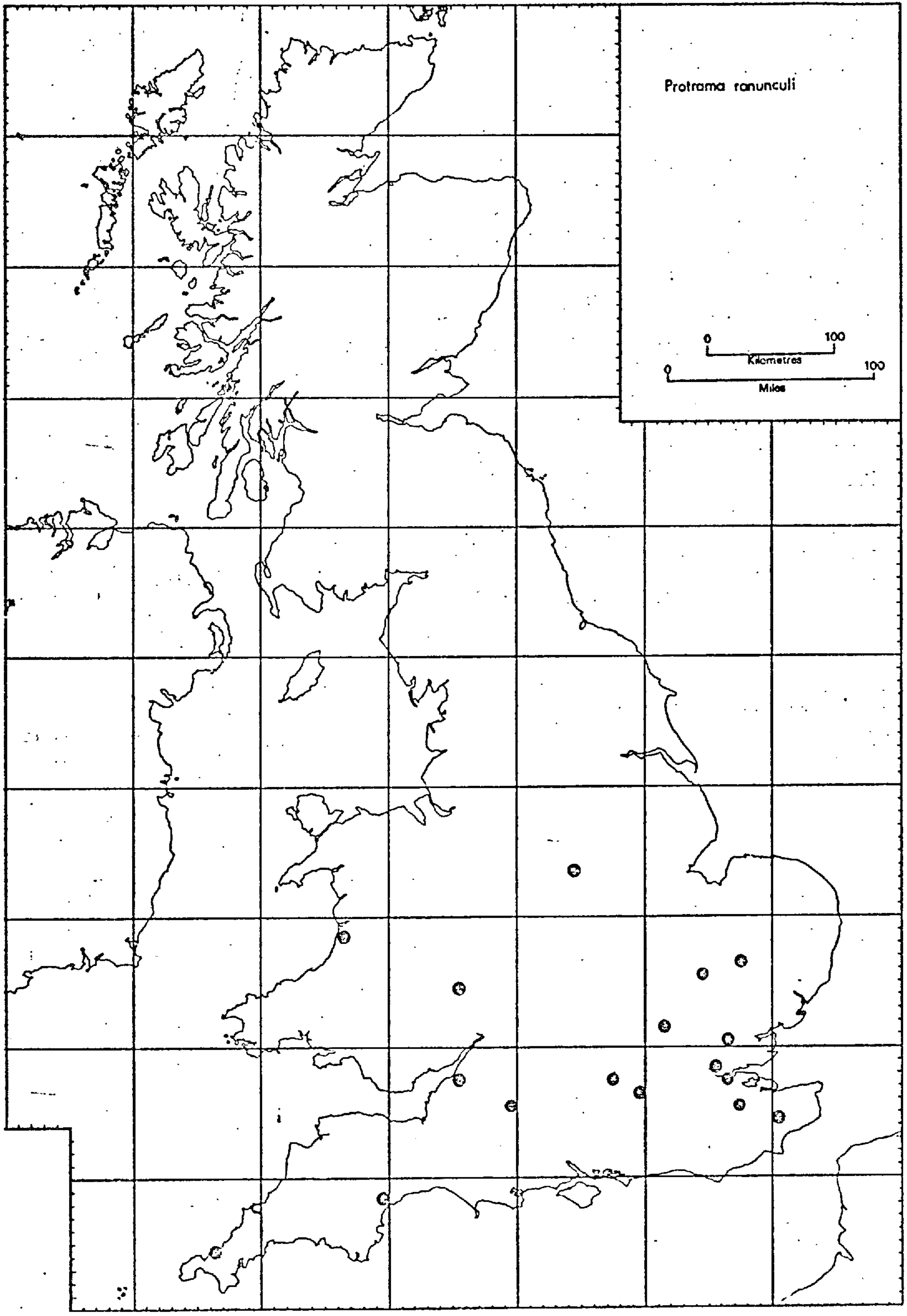


FIG 125

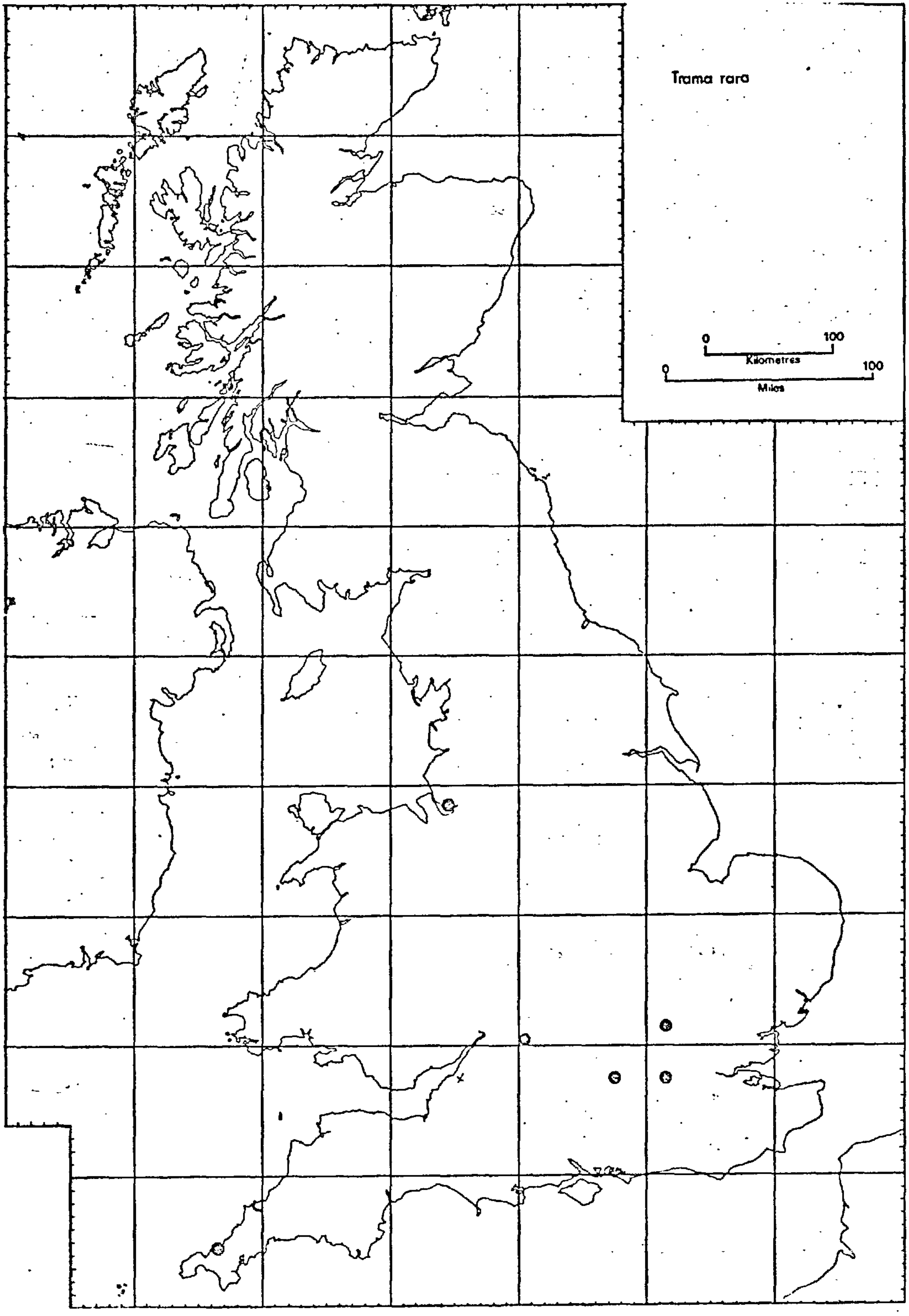


FIG 126

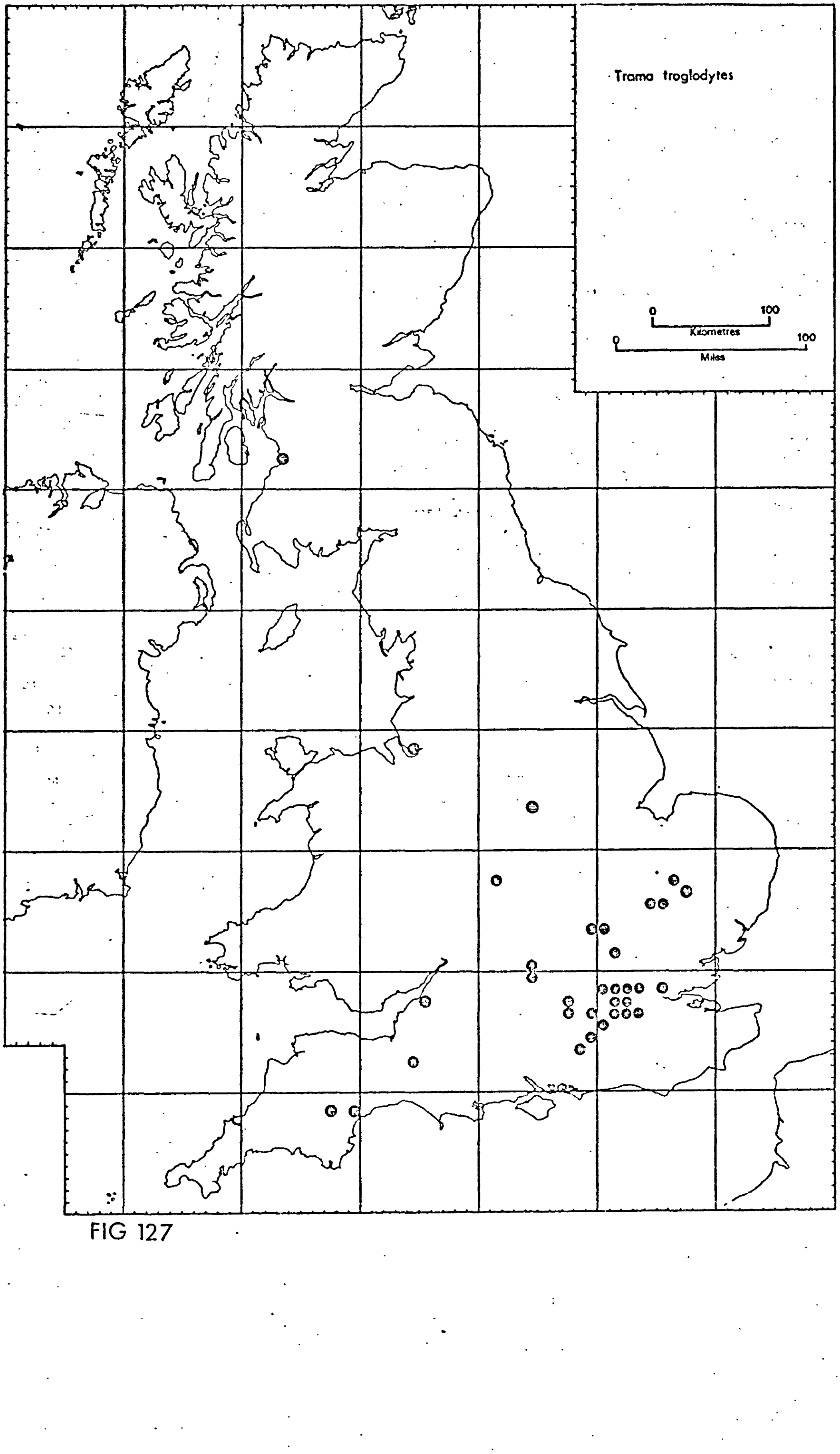


FIG 127

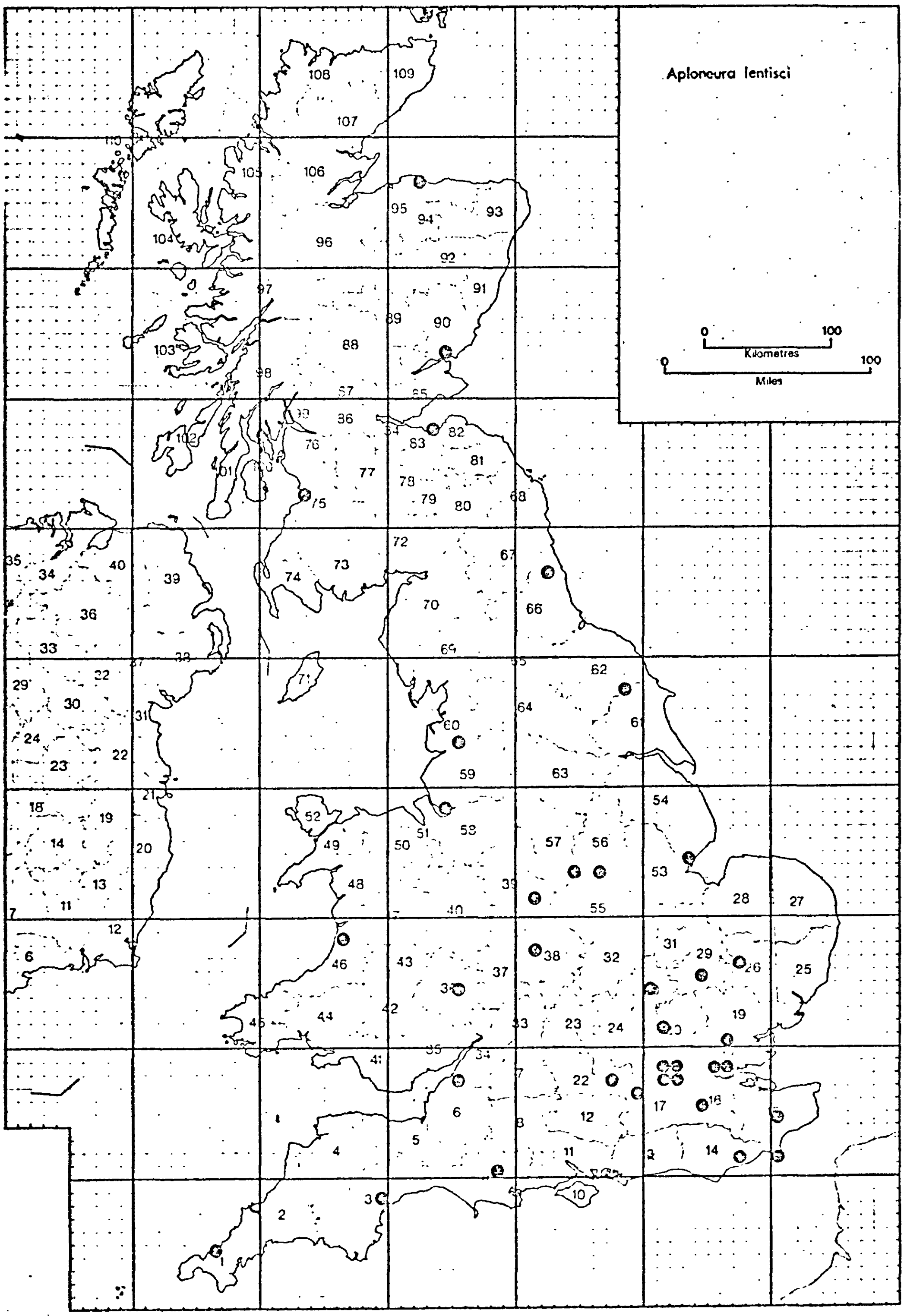

Aploneura lentisci
0
100
Kilometres
0
100
Miles
108
109
107
106
96
95
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FIG 128

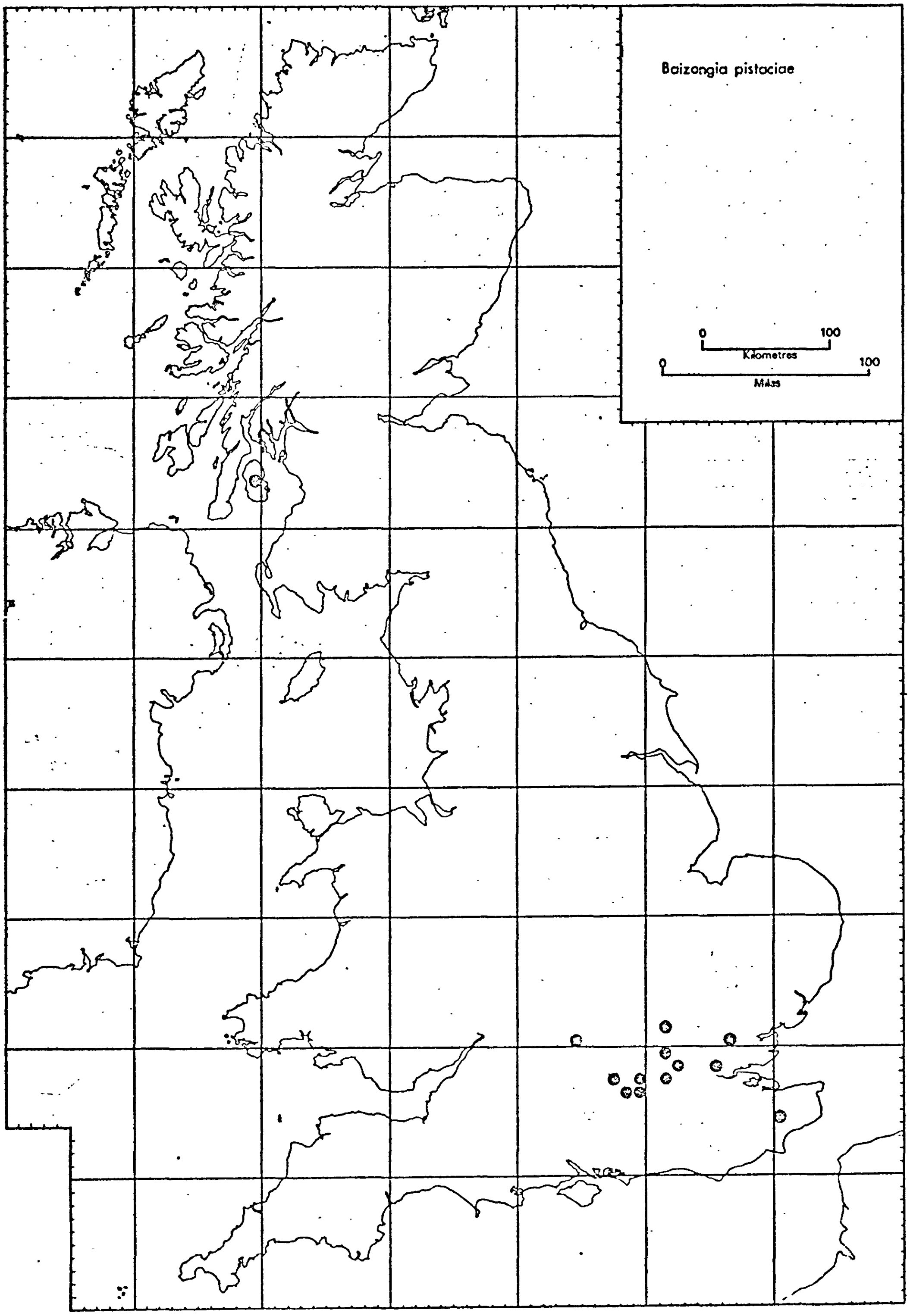

FIG 129

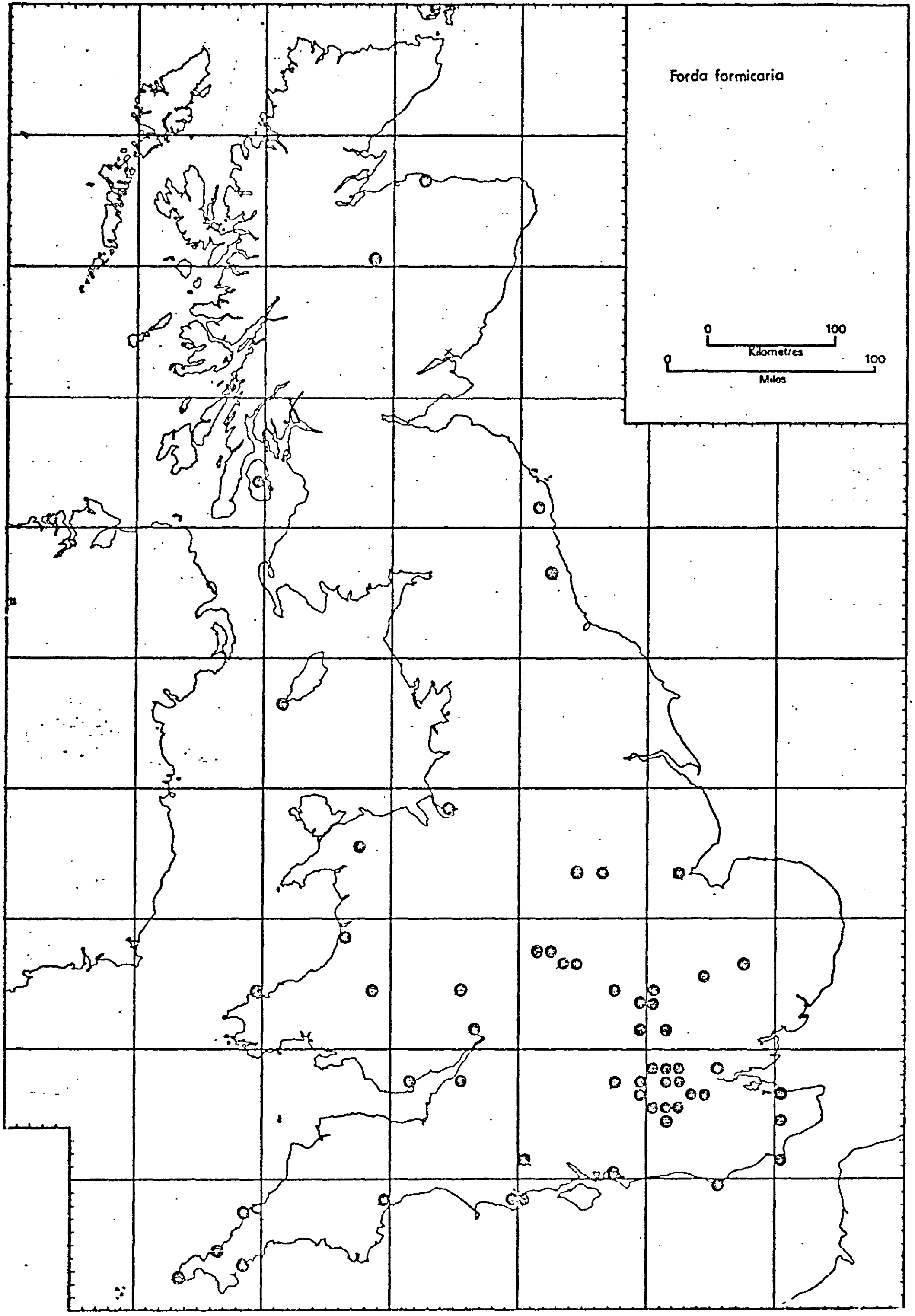

FIG 130

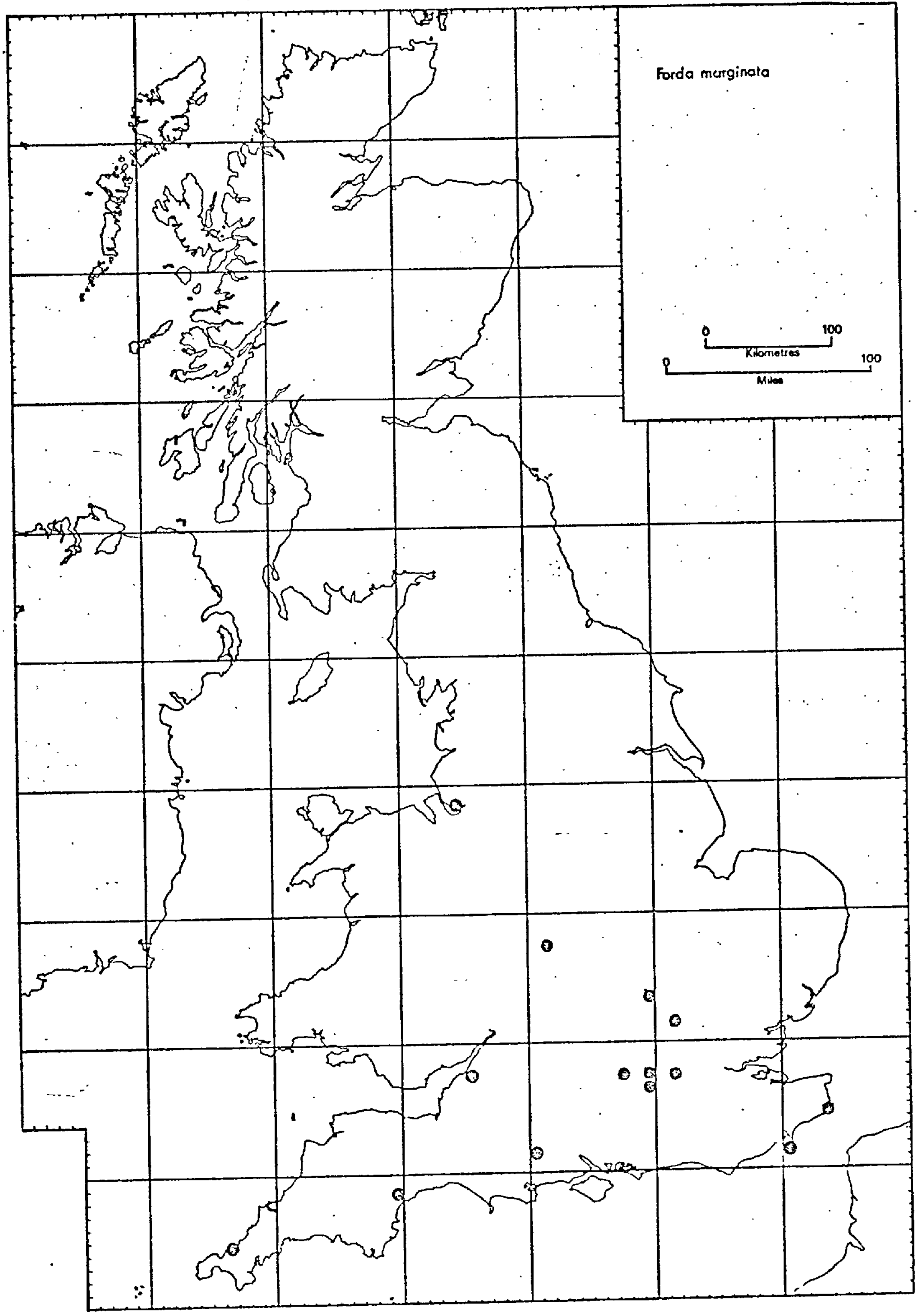

FIG 131

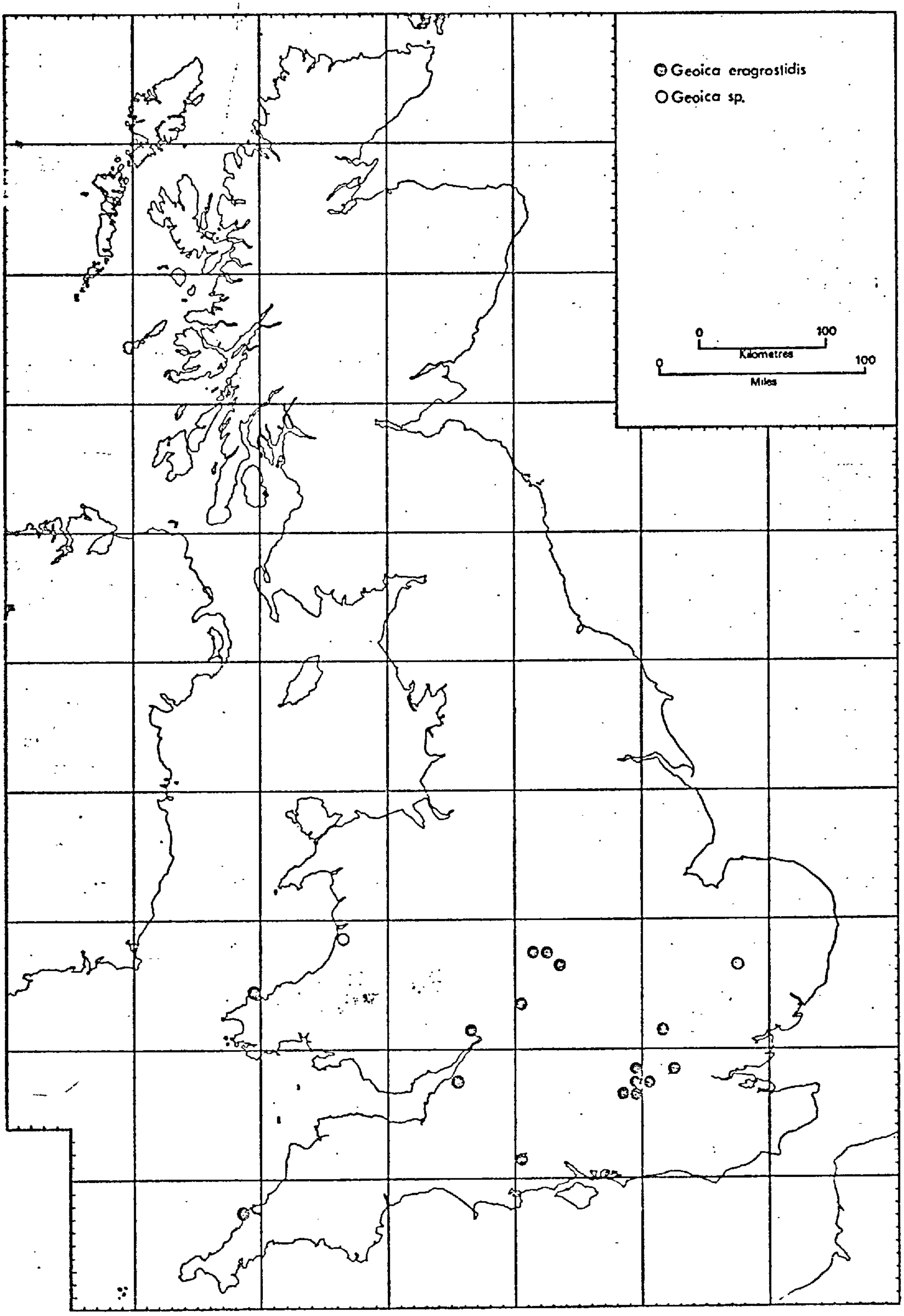

FIG 132

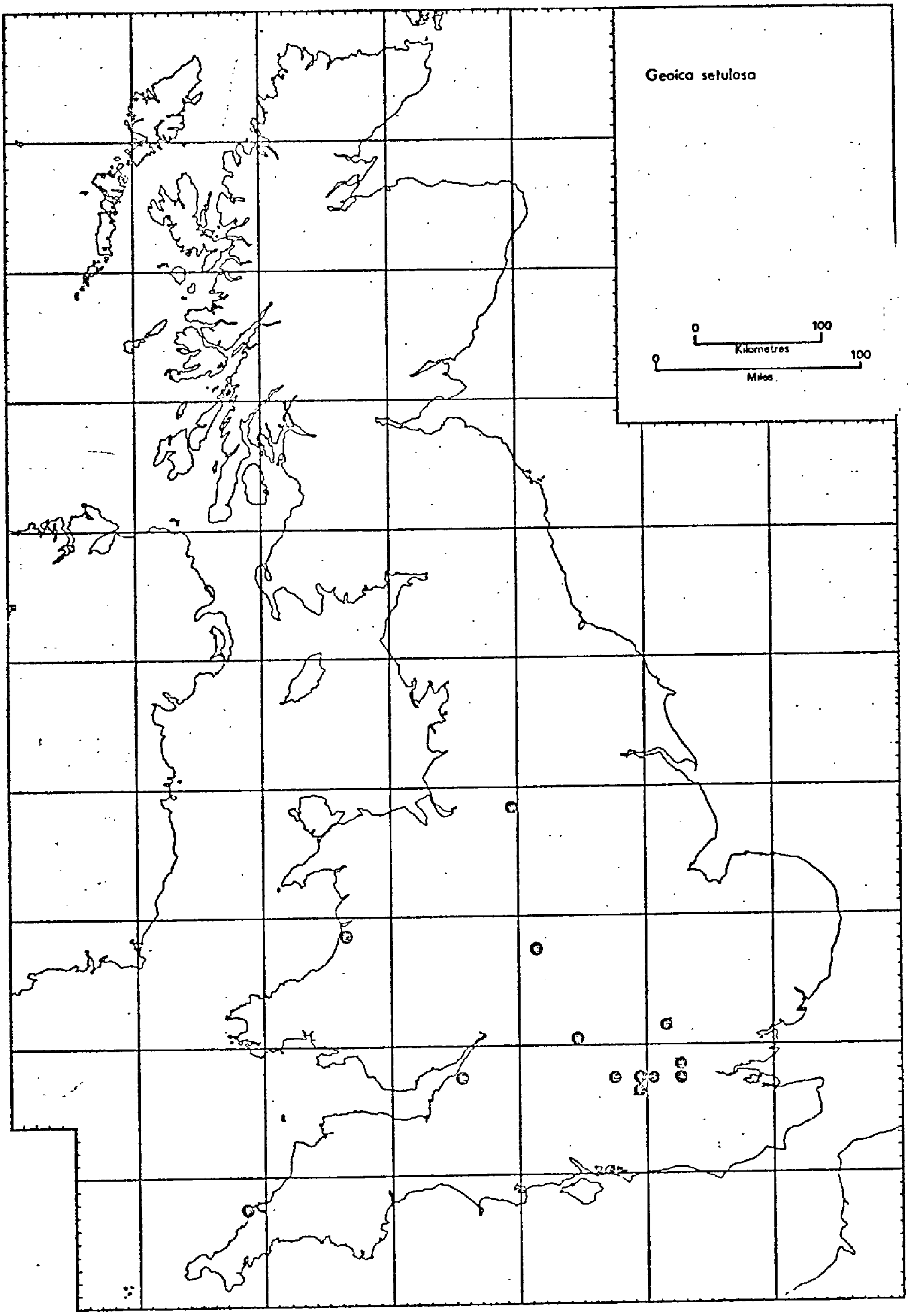

FIG 133

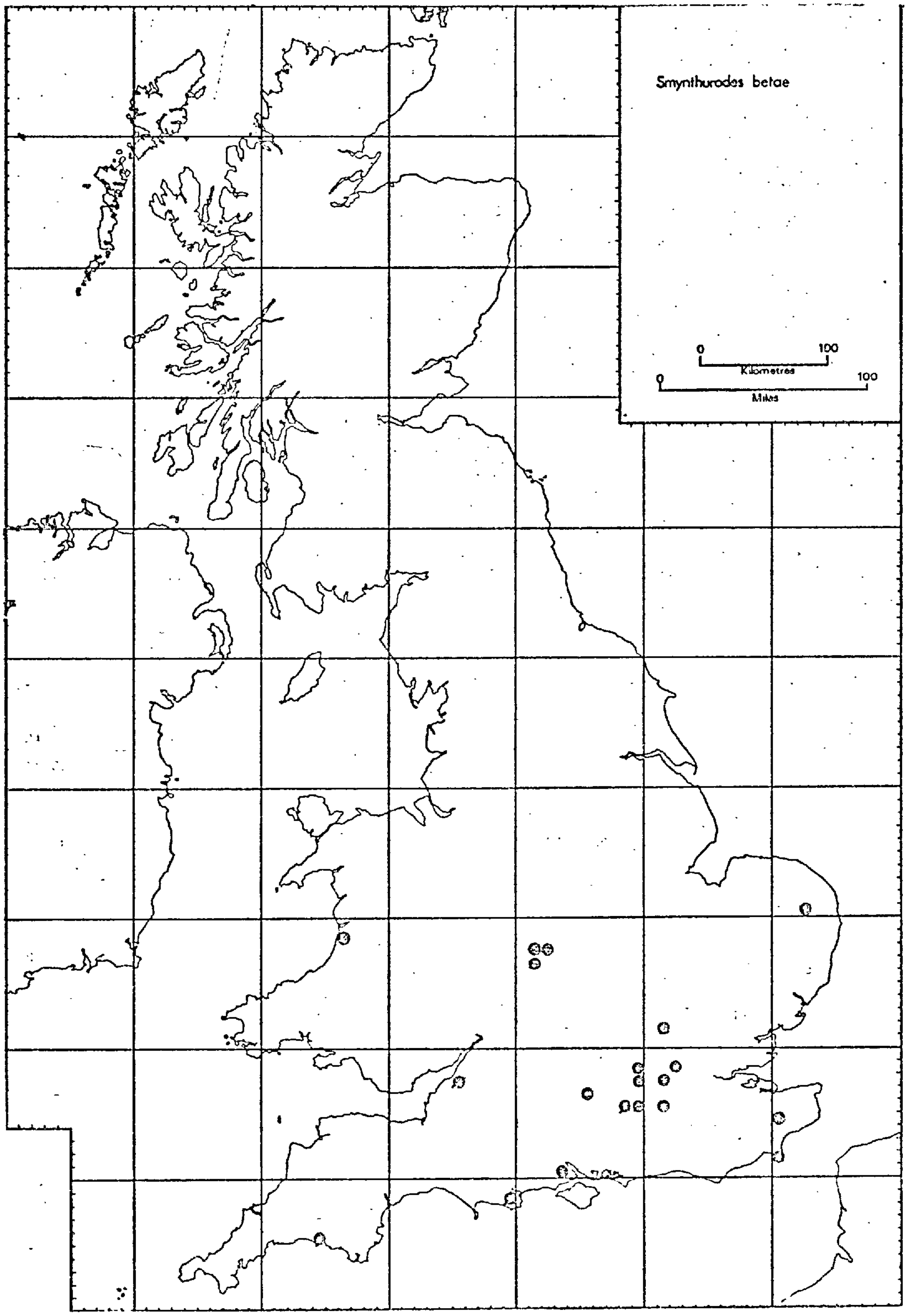

FIG 134

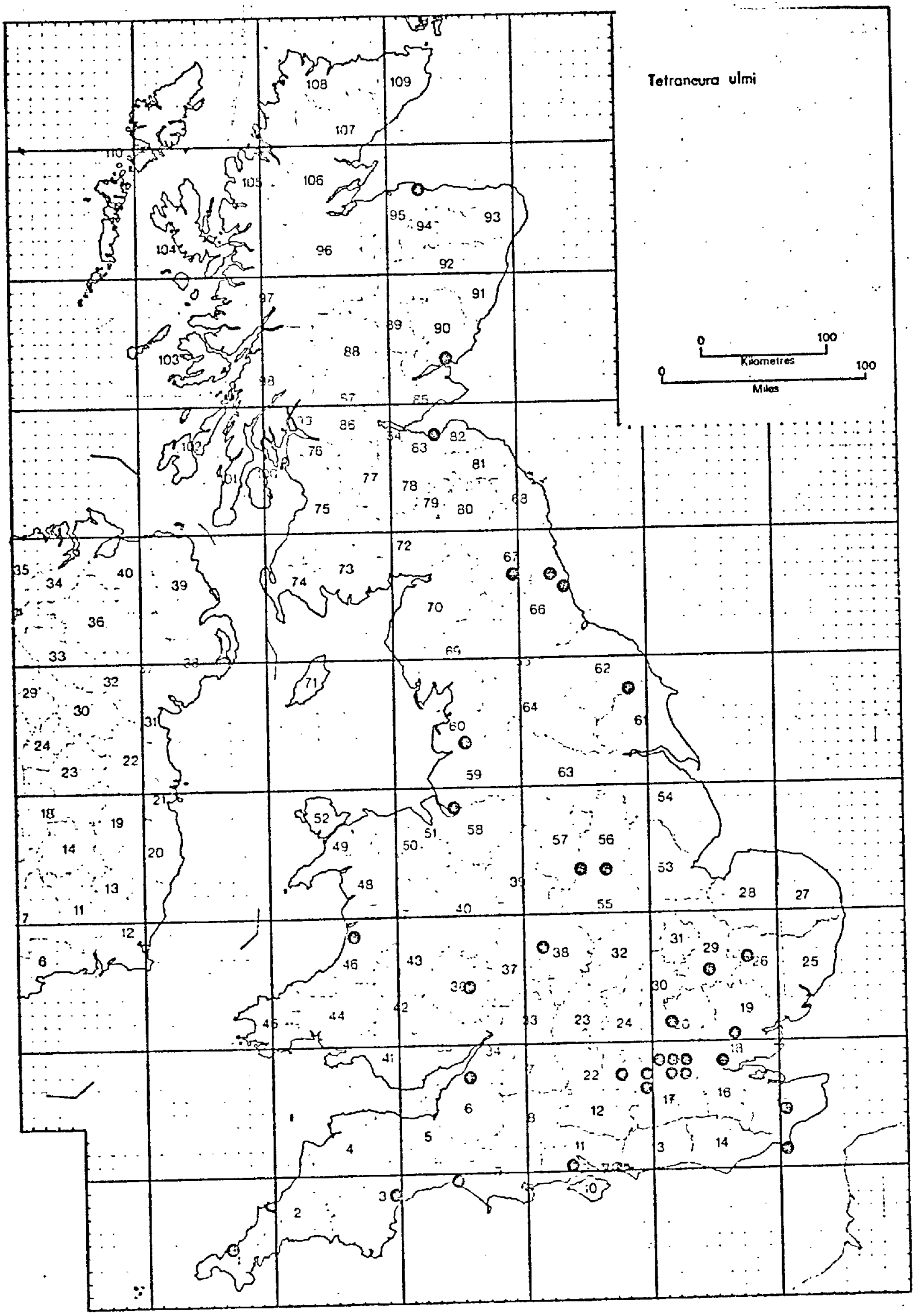
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FIG 135

BIOMETRIC DATA FOR THE ANOECIINAE. Table 11.
(Range is given followed by mean and standard error.).

Species and morph.	Body length.	Body width.	Hind tibia length.
Anoecia corni.			
Fundatrix	1.72-2.14 1.89±.033	1.03-1.31 1.18±.018	0.357-0.632 0.49±.038
Apterous Fundatrigenia	1.6-2.2 2.01±.08	1.0-1.38 1.27±.05	0.57-0.85 0.747±.037
Alate Fundatrigenia	1.8-2.2 2.0±.041	0.83-1.03 0.966±.022	0.88-1.04 0.95±.023
Apterous Virginopara	1.9-2.27 2.11±.026	1.17-1.5 1.35±.02	
Apterous (2n=8)* Virginopara	1.97-2.5 2.29±.025	1.25-1.7 1.49±.022	0.87-1.06 1.39±.332
Apterous (2n=6)* Virginopara	1.76-2.22 1.97±.07	1.17-1.56 1.29±.031	0.76-1.04 0.89±.018
Alate Virginopara	1.64-2.28 2.09±.072	0.95-1.24 1.07±.032	0.80-1.17 0.92±.047
Sexupara	2.1-2.54 2.36±.05	1.05-1.25 1.18±.02	1.05-1.19 1.12±.015
Ovipara	0.834-1.04 0.93±.02	0.396-0.55 0.47±.016	
Males	0.79-0.811 0.80±.009	0.288-0.328 0.31±.02	
Anoecia vagans			
Alate Fundatrigenia	1.84-1.97 1.91±.065	0.89-0.91 0.90±.012	0.78-0.80 0.79±.006
Apterous Virginopara	2.19-2.48 2.28±.031	1.29-1.68 1.45±.046	1.64-2.08 0.83±.032
Alate Virginopara	1.88-2.25 2.1±.05	0.84-1.16 0.98±.04	0.80-0.94 0.88±0.02
Sexupara	1.98-2.53 2.3±.055	1.0-1.36 1.2±.04	1.0-1.06 1.06±.02
Anoecia furcata			
Apterous Virginopara	1.65-1.99 1.96±.04	1.1-1.3 1.2±.02	0.69-0.99 0.8±.03
Alate Virginopara	1.53-2.27 1.86±.06	0.77-1.06 1.0±.024	
Sexupara	2.13-2.57 2.3±.05	1.02-1.31 1.2±.03	0.97-1.03 0.96±.02
Anoecia zirnitzi			
Apterous Virginopara	1.42-1.68 1.55±.04	1.07-1.12 1.1±.01	0.374-0.558 0.5±.03

Species and morph	Body length	Body width.	Hind tibia length.
Aneocia zirnitzi continued.			
Ovipara			
Male (1 specimen)	1.12	0.65	0.339
Paranoecia pskovica			
Apterous Virginopara	2.25-2.4 2.26±.065	1.4-1.6 1.5±.034	
Anoecia major			
Apterous Virginopara	2.46-2.8 2.58±.046	1.57-1.7 1.65±.029	1.15-1.22 1.18±.017
Alate Virginopara	2.21-2.98 2.52±.081	1.11-1.58 1.3±.058	1.09-1.44 1.26±.041
Sexupara	2.34-2.69 2.56±.046	1.19-1.46 1.31±.039	1.25-1.38 1.32±.01

Species and morph.	Prothoracic Leg.	Mesothoracic Leg.	Metathoracic Leg.
<u>Anoecia corni</u>.			
Fundatrix	0.79-0.96 0.881+.015	0.88-1.04 0.973+.012	1.19-1.37 1.29+.016
Apterous Fundatrigenia	0.924-1.27 1.14+.043	0.983-1.37 1.23+.047	1.36-1.8 1.69+.06
Alate Fundatrigenia	1.07-1.29 1.27+.031	1.03-1.36 1.22+.035	1.54-1.9 1.75+.044
Apterous Virginopara			1.65-2.01 1.82+.023
Alate Virginopara	1.17-1.45 1.3+.033	1.21-1.45 1.3+.028	1.7-2.09 1.84+.042
Sexupara	1.4-1.65 1.5+.027	1.3-1.52 1.45+.027	1.86-2.3 2.13+.045
Ovipara	0.443-0.552 0.48+.012	0.472-0.58 0.526+.01	0.58-0.684 0.62+.012
Male	0.518-0.558 0.54+.02	0.523-0.578 0.55+.028	0.61-0.673 0.64+.031
<u>Anoecia vagans</u>			
Alate Fundatrigenia	1.12-1.26 1.2+.07	1.12-1.15 1.14+.02	1.58-1.63 1.6+.03
Apterous Virginopara			1.64-2.08 1.8+.036
Alate Virginopara	1.09-1.33 1.23+.03	1.12-1.32 1.23+.03	1.67-1.93 1.77+.032
Sexupara	1.36-1.57 1.5+.02	1.31-1.45 1.4+.02	1.95-2.12 2.0+.09
<u>Anoecia furcata</u>			
Apterous Virginopara			1.52-1.77 1.7+.04
Alate Virginopara	1.09-1.37 1.23+.023	1.03-1.16 1.2+.021	1.46-1.83 1.7+.03
Sexupara	1.38-1.76 1.48+.057	1.19-1.37 1.31+.024	1.91-1.97 1.96+.02
<u>Anoecia zirnitzi</u>			
Apterous Virginopara			0.877-1.43 1.15+.07
Ovipara			
Male			
<u>Paranoecia pskovica</u>			
Apterous Virginopara.			1.5-1.87 1.74+.043

Species and morph.	Prothoracic Leg.	Mesothoracic Leg.	Metathoracic Leg.
<u>Anoecia major</u>			
Apterous Virginopara			

Species and morph.	Total Antenna length	Antennal segment I	Antennal segment II
<u>Anoecia corni</u>			
Fundatrix	0.552-0.647 0.598±0.0074	0.058-0.075 0.066±.0021	0.058-0.069 0.064±.0011
Apterous Fundatrigenia	0.64-1.17 0.86±.06	0.058-0.075 0.068±.003	0.058-0.075 0.07±.0023
Alate Fundatrigenia	0.737-0.95 0.869±.019	0.058-0.75 0.066±.0021	0.058-0.075 0.07±.0019
Apterous Virginopara	0.82-1.04 0.91±.013	0.058-0.092 0.072±.0012	0.063-0.092 0.076±.008
Apterous (2n=8) Virginopara	0.82-1.05 0.918±.01	0.058-0.092 0.072±.002	0.069-0.092 0.078±.001
Apterous (2n=6) Virginopara	0.811-1.01 0.91±.012	0.063-0.081 0.072±.001	0.063-0.081 0.074±.001
Alate Virginopara	0.836-1.02 0.922±.021	0.052-0.069 0.06±.005	0.063-0.075 0.07±.0017
Sexupara	0.915-1.13 1.04±.022	0.058-0.075 0.07±.002	0.069-0.086 0.078±.002
Ovipara	0.299-0.345 0.332±0.007	0.029-0.04 0.035±.0014	0.035-0.04 0.039±.001
Males	0.40-0.43 0.42±.001	0.035-0.04 0.038±.003	0.04-0.046 0.04±.003
<u>Anoecia vagans</u>			
Alate Fundatrigenia	0.686-0.754 0.72±.034	0.058-0.069 0.064±.006	0.063-0.069 0.066±.003
Apterous Virginopara	0.807-0.971 0.883±.02	0.058-0.081 0.067±.003	0.069-0.081 0.072±.002
Alate Virginopara	0.721-0.863 0.81±.02	0.052-0.069 0.62±.002	0.063-0.075 0.07±.002
Sexupara	0.92-1.04 0.98±.02	0.058-0.081 0.069±.002	0.069-0.075 0.07±.001
<u>Anoecia furcata</u>			
Apterous Virginopara	0.772-0.9 0.82±.04	0.058-0.075 0.066±.002	0.063-0.086 0.07±.003
Alate Virginopara	0.772-0.967 0.89±0.015	0.052-0.063 0.061±.001	0.058-0.075 0.068±.001
Sexupara	0.939-1.0 0.99±.01	0.63-0.081 0.07±.002	0.058-0.081 0.074±.003
<u>Anoecia zirnitzi</u>			
Apterous Virginopara	0.57-0.714 0.651±.02	0.055-0.063 0.058±.002	0.064-0.08 0.08-0.07
Male	0.508	0.058	0.058

Species and morph	Total Antenna length	Antennal segment I	Antennal segment II
Paranoecia pskovica			
Apterous Virginopara	0.913-1.12 1.02±.029	0.081-0.092 0.086±.002	0.098-0.121 0.111±0.0046
Anoecia major.			
Apterous Virginopara	1.15-1.25 1.2±.021	0.086-0.109 0.099±.005	0.081-0.092 0.086±.002
Alate Virginopara	1.07-1.66 1.2±.07	0.069-0.098 0.087±.004	0.075-0.092 0.083±.002
Sexupara	1.15-1.24 1.2±.015	0.069-0.098 0.084±.005	0.058-0.086 0.078±.004

Species and morph	Antennal segmentIII	Antennal segmentIV	Antennal segmentV
Anoecia corni			
Fundatrix	0.23-0.247 0.229±.004	0.086-0.098 0.09±.0013	0.138-0.161 0.149±.0019
Apterous Fundatrigenia	0.21-0.59 0.322±.056	0.069-0.115 0.1±.0078	0.098-0.138 0.123±.0054
Alate Fundatrigenia	0.27-0.368 0.322±.0087	0.086-0.127 0.112±.0041	0.104-0.127 0.122-.0025
Apterous Virginopara	0.27-0.374 0.314±.004	0.109-0.155 0.128±.002	0.121-0.196 0.142±.002
Apterous (2n=8) Virginopara	0.27-0.362 0.311±.0045	0.109-0.155 0.13±.008	0.127-0.196 0.155-0.0027
Apterous (2n=6) Virginopara	0.276-0.374 0.32±.007	0.109-0.144 0.123±.003	0.121-0.155 0.14±.0024
Alate Virginopara	0.311-0.403 0.345±.011	0.104-0.155 0.121±.005	0.121-0.144 0.133±.004
Sexupara	0.345-0.499 0.40±0.01	0.121-0.161 0.14±.005	0.127-0.155 0.15±.004
Ovipara	0.075-0.121 0.098±.005	0.04-0.075 0.05±.002	0.104-0.115 0.109±.001
Male	0.121-0.138 0.13±0.008	0.069-0.075 0.072±.003	0.127-0.138 0.13±.006
Anoecia vagans			
Alate Fundatrigenia	0.247-0.265 0.256±.009	0.058-0.104 0.081±.023	0.092-0.104 0.098±.006
Apterous Virginopara	0.276-0.339 0.31±.009	0.109-0.121 0.118±.002	0.109-0.132 0.122±.003
Alate Virginopara	0.259-0.305 0.29±.07	0.098-0.167 0.115±.009	0.104-0.121 0.11±.002
Sexupara	0.345-0.403 0.37±.006	0.109-0.144 0.13±.003	0.121-0.15 0.14±.003
Anoecia furcata			
Apterous Virginopara	0.253-0.38 0.28±.013	0.092-0.127 0.113±.0054	0.109-0.155 0.125±.004
Alate Virginopara	0.259-0.357 0.325±.007	0.104-0.127 0.012±.003	0.109-.15 0.13±.003
Sexupara	0.339-0.403 0.36±.007	0.132-0.15 0.14±.002	0.127-0.15 0.14±.002
Anoecia zirnitzi			
Apterous Virginopara	0.117-0.167 0.09±.003	0.067-0.98 0.09±.003	0.096-0.115 0.11±.002
Male	0.144	0.098	0.15
Paranoecia pskovica			
Apterous Virginopara	0.357-0.473 0.421±.02	0.149-0.184 0.16±.0065	0.149-0.184 0.169±.006

Species and morph	Antennal segmentIII	Antennal segmentIV	Antennal segmentV
Anoecia major			
Apterous Virginopara	0.4-0.45 0.43±.025	0.144-0.167 0.16±.005	0.167-0.178 0.17±.003
Alate Virginopara	0.408-0.529 0.44±.014	0.138-0.167 0.16±.005	0.161-0.173 0.17±.003
Sexupara	0.46-0.512 0.487±.008	0.155-0.173 0.166±.002	0.167-0.173 0.168±.002

Species and morph	Antennal segmentVI	Rostrum length	Last rostral segment ,length
Anoecia corni			
Fundatrix		0.43-0.49 0.452±.0091	0.098-0.109 0.105±.0012
Apterous Fundatrigenia	0.15-0.196 0.177±.0055	0.23-0.32 0.547±.016	0.503-0.585 0.125±.0024
Alate Fundatrigenia	0.161-0.184 0.176±.0026	0.47-0.679 0.557±.094	0.123-0.143 0.134±.0035
Apterous Virginopara	0.161-0.207 0.183±.002	0.585-0.85 0.659±0.017	0.132-0.161 0.15±.0017
Apterous (2n=8) Virginopara	0.161-0.207 0.182±.0027		0.138-0.167 0.154±.001
Apterous (2n=6) Virginopara	0.173-0.207 0.135±.0028		0.15-0.161 0.153±.01
Alate Virginopara	0.178-0.219 0.194±.005	0.55-0.76 0.66±.026	0.144-0.167 0.152±.003
Sexupara	0.178-0.224 0.21±.004	0.49-0.702 0.61±.021	0.138-0.155 0.15±.002
Ovipara		0.27-0.316 0.286±.005	0.073-0.093 0.083±.029
Males		0.219-0.23 0.23±.006	0.07
Anoecia vagans			
Alate Fundatrigenia	0.15-0.161 0.156±.006	0.512-0.644 0.578±.066	0.12-0.132 0.126±.006
Apterous Virginopara	0.161-0.196 0.18±.004	0.702-0.831 0.77±.02	0.132-0.15 0.14±.008
Alate Virginopara	0.167-0.178 0.17±.001	0.644-0.819 0.71±.03	0.132-0.144 0.14±.002
Sexupara	0.19-0.23 0.203±.004	0.6-0.761 0.7±.05	0.132-0.167 0.15±.005
Anoecia furcata			
Apterous Virginopara	0.155-0.213 0.19±.007	0.468-0.632 0.616±.025	0.121-0.15 0.138±.004
Alate Virginopara	0.167-0.207 0.19±.003	0.527-0.714 0.58±.02	0.127-0.144 0.14±.002
Sexupara	0.19-0.213 0.2±.002	0.573-0.725 0.66±.02	0.127-0.15 0.14±.003
Anoecia zirnitzi			
Apterous Virginopara	0.14-0.167 0.15±.002	0.421-0.49 0.456±.012	0.121-0.138 0.13±.004
Male			
Paranoecia pskovica			
Apterous Virginopara	0.161-0.184 0171±.004	0.913-1.1 1.03±.028	0.178-0.207 0.196±.003

Species and morph	Antennal segmentVI	Rostrum length	Last rostral segment, length
<u>Anoecia major</u>			
Apterous Virginopara	0.219-0.224 0.22±.001	0.761-0.936 0.866±.038	0.19-0.213 0.2±.005
Alate Virginopara	0.201-0.247 0.22±.005	0.772-1.04 0.89±.03	0.184-0.224 0.2±.004
Sexupara	0.207-0.23 0.217±.004	0.734-0.995 0.856±.04	0.173-0.207 0.19±.004

Species and morph	Last rostral segment, width.	Accessory rostral hairs	Secondary rhinaria on antennal segmentIII
<u>Anoecia corni</u>			
Fundatrix	0.063-0.075 0.065±.0016	4-6 4.25±3.99	
Apterous Fundatrigenia	0.058-0.088 0.072±.0037	6-9 7.88±.441	0-2 0.68±.176
Alate Fundatrigenia	0.055-0.082 0.068±.0039	6-9 7.0±.516	8-13 10.53±.345
Apterous Virginopara	0.063-0.075 0.071±.0011	8-13 11.04±.171	0-11 3.8±.317
Apterous (2n=8) Virginopara	0.058-0.073 0.064±.001	9-13 11.21	0-11 3.8±.317
Apterous (2n=6) Virginopara	0.058-0.86 0.069±.02	8-13 10.7±.352	0-6 3.0±.396
Alate Virginopara	0.046-0.063 0.056±.003	8-13 11.13±.639	9-12 9.9±.31
Sexupara	0.063-0.088 0.072±.006	11-15 12.9±.48	9-14 11.6±.407
Ovipara	0.038-0.05 0.046±.002	4-8 5.86±.59	
Male	0.04	3-6 4.5±1.5	
<u>Anoecia vagans</u>			
Alate Fundatrigenia	0.076-0.058 0.067±.009	4 4±0	5-8 6.5±.91
Apterous Virginopara	0.052-0.069 0.06±.002	4-7 5.8±.44	0-4 1.58±.4
Alate Virginopara	0.058-0.079 0.06±.003	6-7 6.14±.14	7-10 7.9±.38
Sexupara	0.052-0.069 0.065±.003	6-7 6.4±.2	11-14 12.8±.27
<u>Anoecia furcata</u>			
Apterous Virginopara	0.046-0.069 0.058±.003	6-8 7.5±.2.7	0-5 0.79±.32
Alate Virginopara	0.046-0.075 0.06±.005	6-8 7.0±.37	6-10 8.5±.15
Sexupara	0.058-0.069 0.061±.002	6-7 6.5±.22	8-12 10.0±.31
<u>Anoecia zirnitzi</u>			
Apterous Virginopara	0.058-0.069 0.07±.004	7-10 8.13±	
Male			

Species and morph	Last rostral segment,width	Accessory rostral hairs	Secondary rhinaria on antennal segmentIII
Paranoecia pskovica			
Apterous Virginopara	0.063-0.081 0.074±.002	13-20 16.8±.65	
Anoecia major			
Apterous Virginopara	0.073-0.081 0.08±.002	13-17 14.8±1.03	1-9 3.86±1.2
Alate Virginopara	0.069-0.081 0.07±.004	12-16 14.0±.46	13-17 15.5±.31
Sexupara	0.058-0.086 0.07±.004	12-15 13.7±.42	17-21 18.9±.44

Species and morph	Secondary rhinaria on antennal segmentIV	Secondary rhinaria on antennal segmentV	Secondary rhinaria on antennal segmentVI
Anoecia corni			
Apterous Fundatrigenia	1-3 1.81±.209	0-3 1.13±.239	0-1 0.438±.128
Alate Fundatrigenia	2-4 2.95±.162	2-3 2.74±.129	1-2 1.32±.11
Apterous Virginopara	1-5 3.08±.09	0-5 2.41±.119	0-2 0.43±.059
Apterous (2n=8) Virginopara	2-5 3.15±.096	0-5 2.67±.114	0-2 .426±.067
Apterous (2n=6) Virginopara	1-4 2.77±.207	0-4 1.56±.26	0-1 0.5±.121
Alate Virginopara	2-4 3.1±.159	1-5 2.17±.271	0-1 0.5±.12
Sexupara	2-4 3.0±.103	1-3 1.9±.143	0-2 0.84±.14
Anoecia vagans			
Alate Fundatrigenia	1-3 2.0±.58	0-1 2.5±.35	0
Apterous Virginopara	0-2 1.17±.167	0-1 0.17±.112	0-1 0.17±.112
Alate Virginopara	1-3 1.8±.207	0-1 0.25±.15	0
Sexupara	2-5 3.5±.17	1-3 2.15±.15	0-2 0.9±.19
Anoecia furcata			
Apterous Virginopara	0-3 1.58±.21	0-3 1.32±.217	0-2 0.79±.123
Alate Virginopara	1-4 2.34±.115	1-3 2.1±.101	0-2 1.0±.053
Sexupara	3-4 3.19±.1	1-2 2.0±.09	1-2 1.2±.1
Anoecia major			
Apterous Virginopara	3-5 4.0±.31	1-4 2.7±.42	0-1 0.86±.14
Alate Virginopara	3-6 4.3±.21	2-4 2.8±.18	0-1 0.93±.07
Sexupara	4-6 5.0±.18	2-4 3.36±.17	0-2 0.86±.14

Species and morph.	Eye size, number of facets.
<u>Anoecia corni</u>	
Fundatrix	0
Apterous Fundatrigenia	24-45 33.6±4.84
Alate Fundatrigenia	75-100 83.8±2.8
Apterous Virginopara	35-81 56.3±3.72
Apterous (2n=8) Virginopara	
Apterous (2n=6) Virginopara	
Alate Virginopara	70-100 83.8±5.3
Sexupara	77-110 103.6±3.61
Ovipara	0
Male	3-8 5.25±1.57
<u>Anoecia vagans</u>	
Alate Fundatrigenia	50-60 55±5.0
Apterous Virginopara	31-58 45±5.12
Alate Virginopara	80-100 84.3±4.29
Sexupara	100-110 102.9±1.84
<u>Anoecia furcata</u>	
Apterous Virginopara	24-70 46.2±4.15
Alate Virginopara	60-80 71.8±2.3
Sexupara	60-90 75.6±3.5
<u>Anoecia zirnitzi</u>	
Apterous Virginopara	0-9 4.7±.94

Species and morph	Eye size, number of facets
Paranoecia pskovica	
Apterous Virginopara	0
Anoecia major	
Apterous Virginopara	70-83 74±3.1
Alate Virginopara	150-200 175±9.45
Sexupara	150-200 164±14.3

BIOMETRIC DATA USED FOR COMPARISON OF ADAPTATIONS TO SUBTERRANEAN LIFE IN 14 SPECIES OF ROOT APHIDS(FIGS. 91-93). *

	Body length.	Rostrum l.	Antenna l.	Metathoracic leg l.
1. *Aploneura lentisci*.	2.34±0.07	0.29±0.01	0.22±0.007	0.63±0.03
2. *Baizongia pistaciae*.	2.05±0.1	0.41±0.014	0.36±0.01	0.83±0.02
3. *Tetraneura ulmi*.	2.02±0.067	0.47±0.02	0.37±0.01	0.97±0.03
4. *Geoica setulosa*.	1.88±0.087	0.39±0.01	1.88±0.09	0.78±0.02
5. *Forda marginata*.	2.4±0.08	0.82±0.03	0.56±0.02	1.3±0.05
6. *Geoica eragrostidis*.	1.87±0.08	0.5±0.05	0.5±0.016	1.09±0.06
7. *Smynthurodes betae*.	1.94±0.08	0.56±0.02	0.61±0.04	1.17±0.02
8. *Aphis etiolata*.	1.68±0.03	0.66±0.03	0.64±0.01	1.1±0.04
9. *Anoecia vagans*.	2.28±0.03	0.77±0.02	0.88±0.02	1.8±0.04
10. *Forda formicaria*.	2.67±0.11	1.26±0.34	1.11±0.032	1.85±0.05
11. *Anoecia corni*.	2.12±0.03	0.66±0.02	0.91±0.01	1.82±0.02
12. *Anoecia furcata*.	1.96±0.04	0.62±0.03	0.82±0.04	1.65±0.04
13. *Paranoecia pskovica*.	2.26±0.07	1.03±0.03	1.02±0.03	1.74±0.04
14. *Anoecia zirnitzi*.	1.55±0.04	0.46±0.01	0.651±0.02	1.15±0.07
Aphis fabae.	2.12±0.078	0.55±0.03	1.29±0.05	1.95±0.065.

The measurements for *Aphis fabae* are given for comparison with root aphids.

*The mean is given followed by the Standard Error.

Table 12.

SEPARATION OF THE 2n=6 AND 2n=8 FORMS OF ANOECIA CORNI.

Linear discriminant function analysis. (Fisher 1936)

A discriminant function analysis was done to see if it was possible to separate the 2n=6 and 2n=8 forms of *Anoecia corni* morphologically.

19 characters were measured from 17 specimens of the 2n=6 form and from 30 specimens of the 2n=8 form. The characters used are given in Table 14 and the discriminant scores are given in Table 13. Figure 136 plots the separation given by the analysis.

The analysis found the two forms to be significantly different at P=0.001, however the analysis was unstable due to an ill-conditioned covariance matrix, which means that the percentage contributions of the characters quoted in table 14 could be radically changed by the introduction of additional data. It is evident nevertheless that the 2n=8 form is larger than the 2n=6 form, and the characters which contribute most to the separation are size related. Separation by size related characters is not very satisfactory because of the effect which the environment may have on size but it is just such characters which separate *A. major* from *A.corni* (see taxonomic section) and therefore the possibility that the specimens referred to in this thesis as the 2n=8 form of *A. corni* are in fact *A. major* cannot be ruled out. This question might be answered by collecting *Anoecia* from *Phalaris arundinacea* and determining a chromosome number for *A. major*.

Discriminant scores in the 2n=6 and 2n=8 forms of *Anoecia corni*.

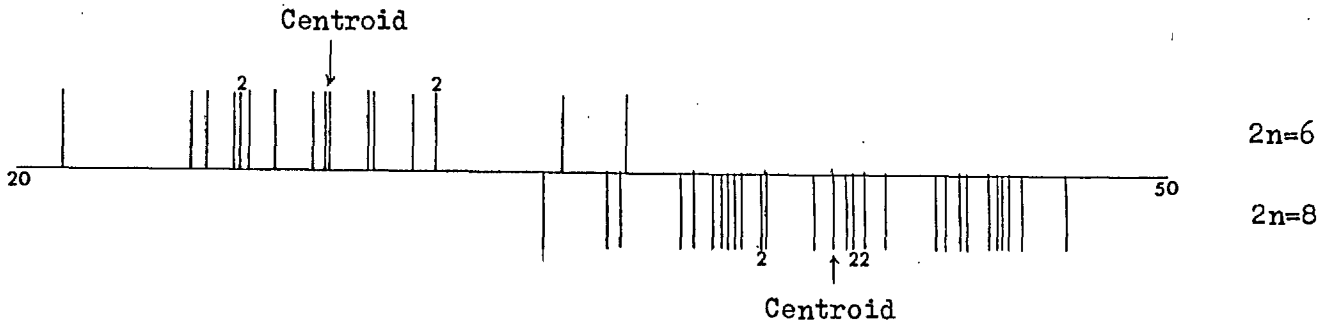
Specimen numbers.	Group 1. (2n=6)	Group 2. (2n=8)
1.	-25.972	-38.363
2.	-24.492	-37.574
3.	-30.870	-43.851
4.	-27.694	-44.709
5.	-26.692	-35.690
6.	-30.870	-45.465
7.	-24.895	-41.993
8.	-29.238	-45.641
9.	-35.873	-47.284
10.	-30.342	-38.756
11.	-25.781	-46.078
12.	-25.569	-41.744
13.	-34.161	-41.513
14.	-25.963	-44.109
15.	-29.289	-41.967
16.	-21.217	-38.147
17.	-28.035	-39.339
18.		-39.256
19.		-38.742
20.		-41.672
21.		-38.450
22.		-37.343
23.		-40.696
24.		-35.263
25.		-33.738
26.		-45.742
27.		-45.305
28.		-44.583
29.		-42.736
30.		-39.464
CENTROID.	-28.056	-41.174

Table 13.

Variables.	Discriminant coefficients.	% contributions of variables.
Body length.	-2.558	5.9
Body width.	-18.570	27.9
Hind tibia l.	-39.840	11.6
Last rostral segment l.	-82.598	0.3
No. of accessory rostral hairs	-0.771	3.3
Last rostral segment,width.	1.913	-0.2
Ant. seg. I, l.	72.104	0.5
" " II, l.	-257.162	8.3
" " III, l.	112.492	7.9
" " IV, l.	18.287	-0.8
" " V, l.	-68.217	5.5
" " VI, l.	236.393	5.9
No. of secondary on ant.III.	-0.357	2.6
No. " " " " IV.	0.385	-1.1
" " " " " V.	-2.070	16.1
" " " " " VI.	4.125	2.2
No. of spatulate hairs on abdominal segment 7.	-1.154	5.5
No.of spatulate hairs on abdominal segment 6.	0.146	-0.6
No. of spatulate hairs on abdominal segment 5.	0.356	-0.9

Table 14. showing the variables used to separate the 2n=6 and 2n=8 forms of *Anoecia corni*.

Separation of the 2n=6 and 2n=8 forms of Anoecia corni.



Linear discriminant function analysis.

Discriminant scores are plotted along the horizontal axis. Lines above the axis represent the 2n=6 form and lines below the axis represent the 2n=8 form.

The numerals at the ends of vertical lines indicate the number of specimens with identical scores.

As can be seen from the plot there is only slight overlap between the two forms but as the matrix for the analysis was unstable the addition of data could change the plot considerably.

FIG. 136.

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DISCUSSION OF FUTURE WORK WITH THE ANOECIINAE.

The following suggestions seem particularly likely yield results.

1. If more Anoecia corni are collected, their chromosome numbers established, and morphological data collected it should be possible to determine with certainty the most significant characters for the separtaion of the 2n=6 and 2n=8 forms.
2. If specimens are collected from Phalaris arundinacea, their chromosome numbers determined and transfers to other grasses attempted it may be possible to decide whether the Anoecia with a chromosome number of 8 is A. major or A. corni.
3. Fundatrigeniae of A. vagans were found but the Fundatrix was not. It remains to be seen if morphological separation of the A. vagans fundatrix from the A. corni fundatrix is possible. Probably the A. vagans fundatrix will be green in colour as is the fundatrigenia. When more specimens are found the sexuales of A. vagans and A. corni may prove to be morphologically separable.
4. A. furcata sexuparae were taken in suction traps but were not found on Dogwood, rearing experiments could decide if a small percentage of A. furcata return to Dogwood.
5. When the chromsomes of A. zirnitzi and Paranoecia pskovica are examined they may shed light on their relationships to other members of the Anoeciinae.

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