Wax production by coccinellid larvae (Coleoptera)

R. D. POPE   British Museum (Natural History), London

ABSTRACT. Details of wax and wax-producing structures belonging to twenty species of coccinellid larvae, including members of the Scymnini, Ortaliini, Hyperaspini, Coccidulini, Noviini, Cryptognathini, Azyini and Telsimiini are described and/or illustrated with photographs taken by means of the scanning electron microscope. Published records of wax-production by larvae of Telsimiini and Chilocorini are examined and evaluated. The means by which wax precursors reach the outer surface of the epicuticle is discussed. Some of the physical properties of coccinellid and other waxes, such as their adhesiveness and UV reflectance, are recorded and the ecological significance of these factors is discussed. The contribution made by the present study to current opinion concerning the classification and possible phylogeny of the Coccinellidae is discussed and assessed.

Introduction

The larvae of many predaceous coccinellid species have visible coatings of waxy threads and the gross appearance of these coverings has often been described. On a few occasions (e.g. Böving, 1917; Wille, 1926; Taylor, 1935) attempts have been made to examine certain species for the nature of their wax and the means by which it is formed, but the only comparative morphological study appears to be that by Steinweder (1929). In every case, however, the results were limited by the fact that the fineness of the threads and the smallness of the secretory devices placed their details beyond the reach of the light microscope.

The purpose of the present paper is to convey the results of an investigation into the nature and formation of coccinellid wax using the scanning electron microscope and to discuss the findings in relation to: (1) The problems involved in the transport of wax through insect cuticle and its formation into

regular and repeated shapes without a mould. (2) The ecology and feeding habits of the group. (3) Current opinions concerning the classification and possible phylogeny of the Coccinellidae.

Kamiya (1965: 94, 95) lists the Scymnini, Hyperaspini, Telsimiini, Stethorini and Ortaliini as having wax-covered larvae. Both the existing literature and the present study show his account to be inaccurate and incomplete. Taylor (1935) gives a justifiably convincing description of wax production by the larvae of *Cryptognatha nodiceps* Mshl. (Cryptognathini) and *Azya trinitatis* Mshl. (Azyini) while the larvae of *Stethorus punctillum* Wse. (Stethorini) do not exude visible wax, despite Kamiya's assertion. In addition, the larvae of *Rodolia* Muls. (Noviini) and those of certain Coccidulini (*Rhyzobius ventralis* (Er.) and *Lindorus lophantae* (Blaisd.)) are on record as being wax-bearing and Wille (1926) added Chilocorini to the list of tribes including wax-producing larvae.

The following account includes the twenty species available so far, arranged in the genera and tribes to which they are currently allotted. It is evident that revisionary taxonomic

Correspondence: Mr R. D. Pope, Department of Entomology, British Museum (Natural History), London SW7 5BD.

work is needed, at generic level and above, particularly in respect of the Australian fauna, but a formal treatment of this nature is outside the scope of the present work.

Scymnini

The Scymnini are the largest tribe in the family, including over 600 described species with representatives in all parts of the world. More than eighteen genera have been assigned to the tribe, but a large majority of the species, over 570, belong either to *Scymnus* Kugelann, *Diomus* Mulsant or *Nephus* Mulsant. The food range of the tribe comprises many species of Sternorrhyncha, but the records are rather confused. Hodek (1973: 108) summarizes the published lists of Balduf (1935: 150–152) and Sasaji (1971: 29) as 62% coccids, 23% aphids and some (presumably 15%) aleyrodids.

In most of the species for which the life history is known, or recorded, it is clear that the larvae are bulk producers of filamentous wax in all instars except the first. The present study has discovered that the means by which this wax is moulded and distributed are remarkably consistent throughout the three major genera of the tribe. As a result, the European species *Scymnus* (*Pullus*) *auritus* Thunberg, chosen for detailed study because of its relatively ready availability as a living larva, may be taken as illustrative not only of the large genus *Scymnus* but of *Diomus* and *Nephus* as well.

Scymnus (*P.*) *auritus*. Although a full-grown larva is no more than about 5 mm long, its white waxy covering is clearly visible to the naked eye (Fig. 1). It is present to a limited extent on first instar larvae, but absent from newly-moulted individuals. Full development of the wax covering appears to take about 24 h. It is of delicate construction and easily removed or damaged by abrasion, but a larva can restore lost areas of wax at any time throughout its life. Low magnification (< 50×) shows the 0.25 mm thick waxy covering to be a tangle of fine threads, regularly arranged in discrete blocks or areas on the upper and lateral surfaces of the thoracic and abdominal segments. On the mesonotum, metanotum and first eight abdominal segments, these blocks correspond to the dorsal,

dorsolateral and lateral setiferous or otherwise ornamented areas in non-wax-bearing coccinellid larvae. The pronotum has a characteristic pattern of ten marginal tufts and a central, wax covered area. The head has no wax covering.

SEM examination of a de-waxed specimen showed that the abdominal cuticle between wax-bearing areas has a stellate-pleated surface configuration (Wigglesworth, 1933), an arrangement permitting great expansion between moults, clearly an advantage to a species achieving large, but irregularly-timed meals. Under the wax tufts, the cuticle bears a regular system of erect, socketed setae of varying lengths, surrounded by two types of secretory structure (Fig. 5). Immediately around the setae, often on a shallowly prominent area, is an irregular ring or rings of pores, each about 2.0 μm in diameter, which can be seen (Fig. 6) to have an internal arrangement of struts around an even smaller (0.6 μm diameter) central orifice. The second type of secretory structure looks like a perforated disc (Fig. 7) of from 4.5 to 6.0 μm diameter and occurs over the rest of the wax-bearing areas between and around the setae and the 2.0 μm multilocular pores. Each disc appears to have a varying number of minute (0.1 – 0.4 μm diameter) pores arranged around a central, imperforate area. In vertical section, the discs can be seen to be supported on a short stalk and are clearly much thicker than the surrounding cuticle.

Figs. 8–11 are all from a freeze-dried specimen, killed about 20 min after some of the wax covering had been removed by means of a fine needle. Several points are immediately apparent. Firstly, as might have been expected, the two types of secretory structure produce quite different results. The secretion from the discs comes not from the apparent pores, but from the embossed framework surrounding them (Fig. 8). A hollow tube is produced, the walls of which are also hollow, mirroring in cross section the lace-like tracery on the surface of the disc (Fig. 7). This maximizes the bulk and stiffness obtainable from a given amount of secretion and represents a most efficient use of materials. However, the tubes would appear to have very little tensile strength, for many short lengths can be seen (Fig. 9), perhaps broken off by pressing
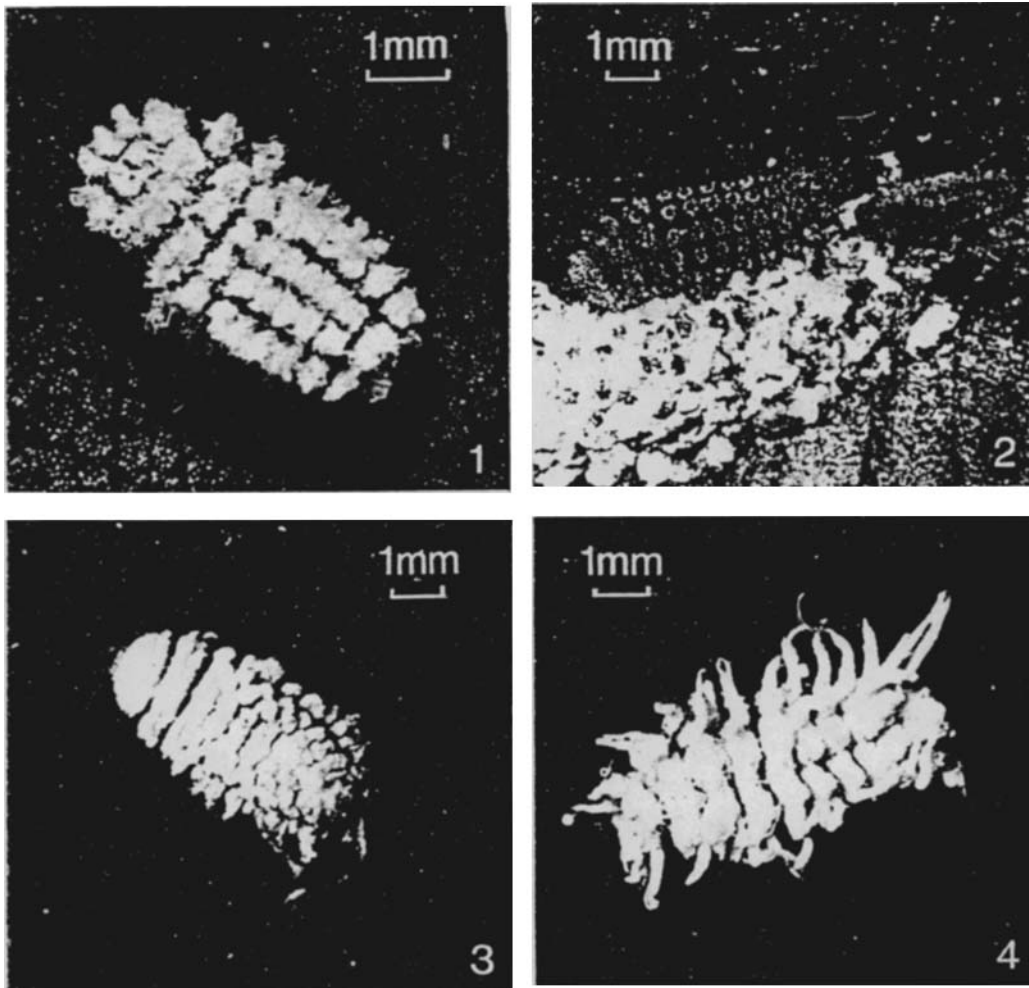
FIGS. 1—4. Photographs of fourth instar larvae. 1. *Scymnus* (*Pullus*) *auritus* Thunb. (X10). 2. *Rhyzobius ventralis* (Er.) (X6). 3. *Hyperaspis onerata* (Muls.) (X6). 4. *Cryptolaemus montrouzieri* Muls. (X6).

against one another as the cuticle flexes with the movements of the insect. The fine, solid threads (Fig. 10) emerging from the multi-locular pores immediately surrounding the erect setae are clearly extruded from the central, inner opening. They evidently have greater strength than their hollow counterparts, often achieving a length in excess of 60 µm, more than 100 times their diameter. Entangling with one another and with the hollow tubes secreted by the discs (Fig. 11), they form the cottonwool-like tufts seen in Fig. 1.

The fine threads seem to receive support from the erect setae (Figs. 9 and 11), often adhering to them as well as to one another. In addition, sections of hollow tube secretion can be seen attached to finer threads. It would seem that the threads are in some way sticky, perhaps from their intrinsic chemical nature, or possibly from a separate coating applied via the gaps between the struts as the thread is forced out from the central opening of the multilocular pores.

SEM examination of seven species belonging to *Scymnus* (*Pullus*), *Scymnus* (s.s.), *Nephus*, *Nephus* (*Scymnobius*) and *Diomus* showed that, as in *S.* (*P.*) *auritus* their wax
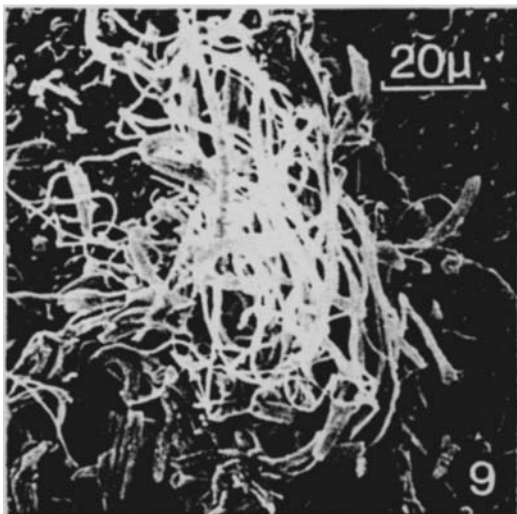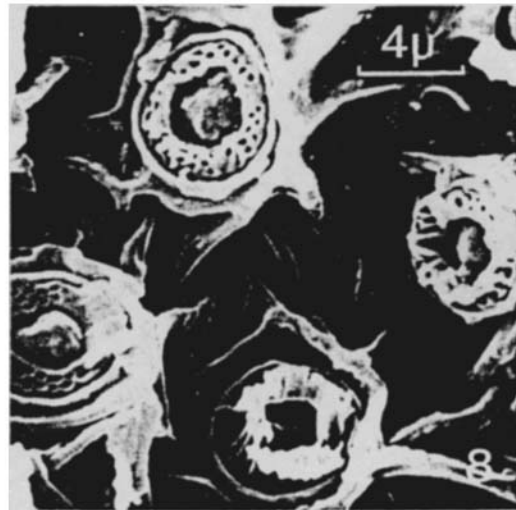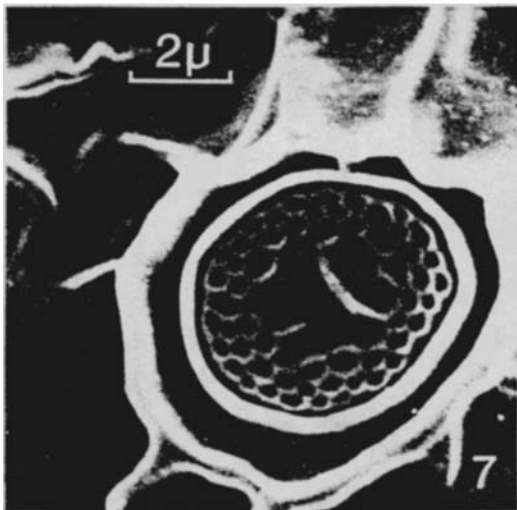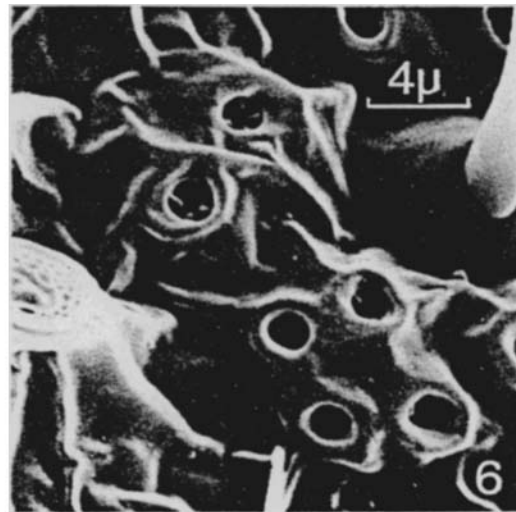
covering contained two distinct components arising from a mixture of tube-secreting discs and thread-producing pores. The size and configuration of the wax-producing pattern on the discs varied from genus to genus and species to species (Figs. 12–17), but the appearance of thread-producing pores immediately surrounding the erect setae was relatively constant, the struts surrounding the central opening merely being less easy to discern in some species than in others.

Pseudoscymnus simmondsi Chapin & Ahmad from India and Pakistan (Figs. 18–21) has wax-producing structures that are simpler than those of other Scymnini so far examined. The first seven abdominal segments are each equipped with four setiferous, pore-bearing tubercles, regularly spaced across the disc. Each tubercle (Fig. 18) has two socketed setae, one larger than the other, obviously intended to support filamentous wax arising from the surrounding pores. The pores on the setiferous tubercles are small, 1.0–$2.0\,\mu m$ in diameter. They have no visible internal struts and appear (Fig. 19) to produce a fine (0.5–$1.0\,\mu m$ diameter), very thin-walled tube of wax. Surrounding each setiferous tubercle is an area of strongly pleated cuticle, and between the pleats, in the position occupied in *Scymnus, Nephus* and *Diomus* by the secretory discs, are shallowly raised rings, 1.2–$3.0\,\mu m$ in diameter (Fig. 20). These evidently produce simple, thin-walled tubes of wax, similar to those produced by the pores of the setiferous tubercles, but somewhat larger in diameter. Elsewhere on the dorsal surface of each abdominal segment, the cuticle is also strongly stellate-pleated and, in addition, has fine-pointed, curving, spicular outgrowths arising from the ridges of the pleats (Fig. 18, top left). The lateral margins of the thoracic and abdominal segments are each furnished with a prominent tubercle (Fig. 21) reminiscent of those found in *Rhyzobius ventralis* (p. 183) and *Rodolia* sp. (p. 181). Each tubercle bears about twelve long, socketed

setae. The setae vary in length, but may be as much as $500\,\mu m$ long. Between and around the setae, numerous fine-pointed spicules arise from the otherwise smooth surface of the cuticle. No likely sources of wax secretion were discovered and it is to be assumed that the very long setae must be either tactile, or simply deterrent.

Also included in the Scymnini, but readily separable from the *Scymnus, Nephus, Diomus* complex, is the Australian genus *Cryptolaemus* Mulsant. Seven species have been described, but only one, *C.montrouzieri* Muls. ('the mealybug destroyer') is well known and has had its early stages described. The larva (Fig. 4) is covered with white, filamentous wax, long tufts protruding from the body in all directions, those along the lateral margins tending to be longer than the others. SEM examination of the larva of *C.montrouzieri* produced results in close agreement with a taxonomic assessment based upon adult characteristics. As with *Scymnus, Cryptolaemus* larvae have more than one type of wax secreting structure and the wax covering includes two main components. In *Cryptolaemus*, both types of secretion take the form of hollow tubes, rather as in *Pseudoscymnus*, but the resemblance to *Scymnus* is greater, for the larger tubes have internal strengthening walls (Fig. 22, inset) and are secreted from a regular embossed pattern (Fig. 22) set in a strongly pleated cuticle over most of the dorsal surface of the thorax and abdomen. In addition, the thorax and abdomen of *Cryptolaemus montrouzieri* bear prominent, setiferous, symmetrically disposed, dome-like tubercles which are evidently associated with the long tufts of wax projecting from the body. The tubercles on the pronotum are shallow and more or less peripheral, those of the meso- and metanotum are more prominent and regularly disposed across each segment; a dorsal pair, one on either side of the midline, two longitudinally disposed dorsolateral pairs, one pair on each side, and a single, prominent

---

FIGS. 5–10. Stereoscan pictures of *Scymnus (Pullus) aurirus* Thunb. Wax-producing structures and wax production. 5. Cuticular surface beneath a single block of abdominal wax filaments (×360). 6. Detail from Fig. 5, showing multilocular pores (×3000). 7. Detail of Fig. 5, showing tracery on secretory disc (×6000). 8. Wax being secreted from tracery on discs (×3000). 9. Short sections of disc-produced wax and longer, solid threads (×600). 10. Solid threads emerging from central orifices of multilocular pores (×3000).
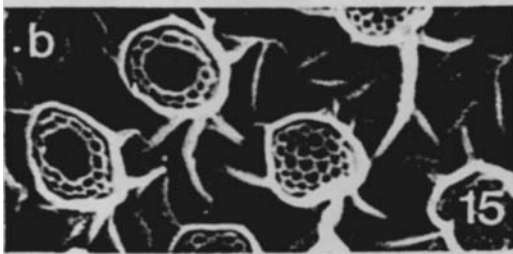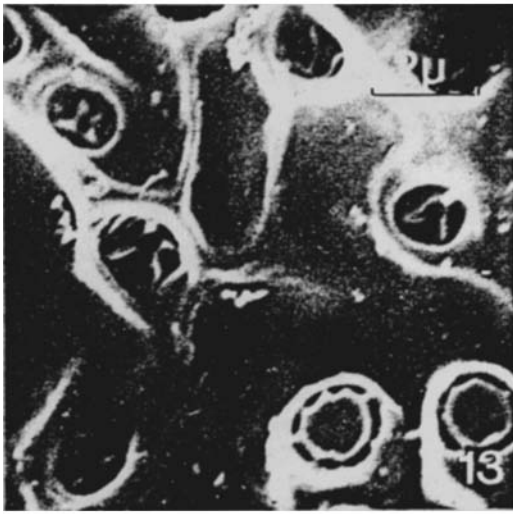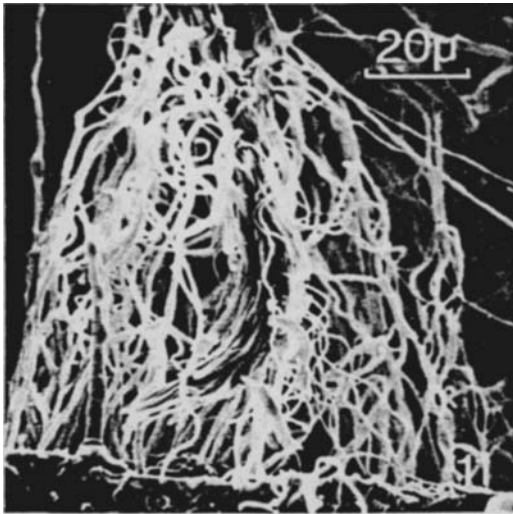
lateral tubercle, one on each side of the segment. The first eight abdominal segments each have a single row of tubercles on their dorsal and lateral surfaces, while segments 3—8 have, in addition, a similar number across their ventral surfaces. The first segment appears to have no tubercles on the underside, the second segment a single median pair and a vestigial structure with a single seta occupying the position of the outermost ventral tubercles of segments 3—8. The tubercles of the underside have smooth surfaces from which arise pointed, socketed setae. On the dorsal and lateral surfaces of the thorax and abdomen, each tubercle (Fig. 23) also bears a number of strong, socketed setae, but, irregularly scattered over the wrinkled surface of each tubercle, between the setae, is a large number of umbilicate, roughly circular depressions about 2.0 μm in diameter. Toward the circumference of each tubercle and over an area of surface immediately surrounding it, the cuticle becomes progressively more strongly rugulose. Here the 2.0 μm depressions are closer (Fig. 23) and arranged in irregularly elliptical groups, very often around an especially prominent cuticular fold. Ultrasonic cleaning, followed by de-waxing, revealed a minute (0.6—1.5 μm diameter) ring-like structure in the base of each depression, sometimes divided by cross members into from two to four cells (Fig. 24) and reminiscent of some of the intermediate structures found in *Nephus* (*Scymnobius*) sp. (Fig. 16). By analogy with the structures found around the abdominal setae in *Pseudoscymnus simmondsi* (Fig. 20), these rings should also secrete tubes of wax. SEM examination of uncleaned specimens of *C.montrouzieri* showed many fine tubes or threads of wax between 0.5 and 1.5 μm in diameter, mostly forming the long tufts associated with the setiferous tubercles of the thorax and abdomen. A curious and, so far, unexplained feature of the long tufts is shown in Fig. 25. The fine threads are trans-

versely crimped and coiled, giving the impression that either their rate of production varies in a rhythmical manner or that the threads are deformed at regular intervals by some movement of the insect's body, perhaps of the associated setiferous tubercles, either by muscular contraction or by variation in body fluid pressure.

Ortaliini

The Ortaliini include over 130 species divided into fourteen or fifteen genera. Species assigned to the group come from all continents except Europe. A majority are found in the Americas, although the largest genus, *Ortalia* Mulsant, including forty-six described species, is confined to Africa, Madagascar and tropical Asia. As with so many coccinellids, hardly anything seems to have been recorded of their life histories and early stages. The larva of *Amida tricolor* (Harold) was described by Kamiya (1965 and (as Sasaji) 1968: 30) and a remarkable account of the life history of *Ortalia pallens* Muls. was published by Harris (1921). No other references have been discovered that do more than give, at the most, a passing comment on food preferences.

The only available larval material for the present study consisted of some final instar exuvia of *Ortalia pallens*. In part dry-preserved specimens, they showed the larva to have been covered by a very thick, strikingly white mass of flocculent wax, including long lateral and caudal tufts after the manner of *Azya* (p.187) or *Cryptognatha* (p.187). SEM examination of a cleaned exuvium revealed areas of wax-secreting structures (Fig. 26) remarkably similar to those of *Cryptolaemus montrouzieri* (Fig. 22), set in a generally stellate-pleated cuticle. No other secretory structures were found, but this may well have been due to the limited possibilities of inspection, using only crumpled, cast skin material. The

FIGS. 11—16. Stereoscan pictures of wax production and wax-producing structures in *Scymnus* and allied genera. 11. Entangled threads and tubes of wax on dorsum of *Scymnus* (*Pullus*) *auritus* Thunb (X600). 12. *Scymnus* sp. (Zaira, Africa). Socketed seta, multilocular pores and secretory discs (X3000). 13. *Scymnus nigrinus* Kug. (Europe). Multilocular pores and secretory discs (X6000). 14. *Nephus* sp. (Pakistan). Multilocular pores, secretory discs and rings (X2000). 15. *Diomus* sp. (U.S.A.). Multilocular pores (a) and secretory discs (b) (X3000). 16. *Nephus* (*Scymnobius*) sp. (U.S.A.). Multilocular pores, secretory discs and intermediate structures (X2500).
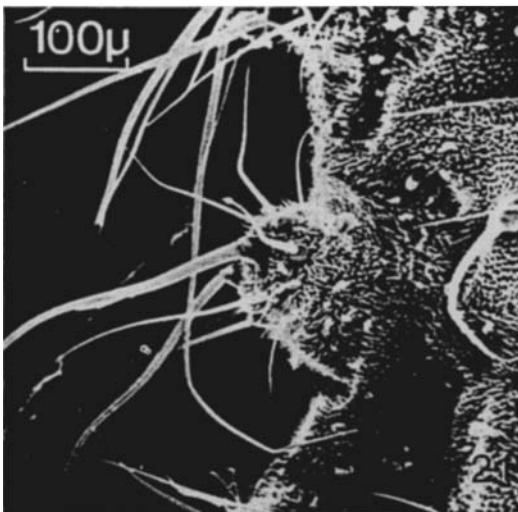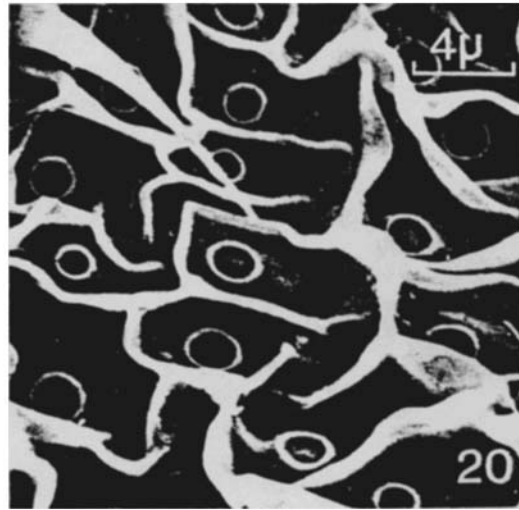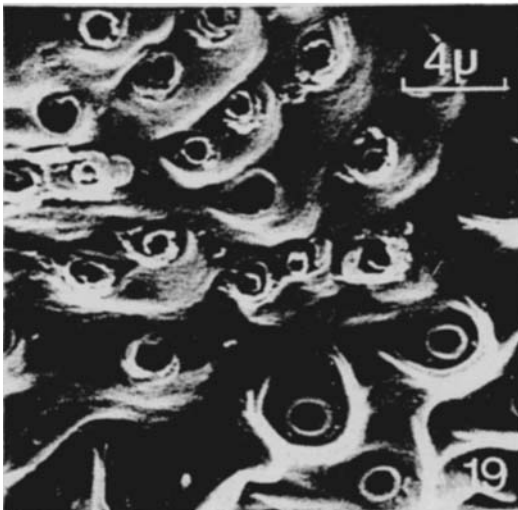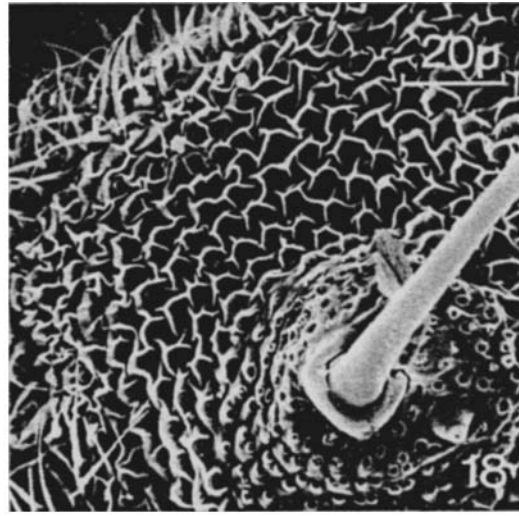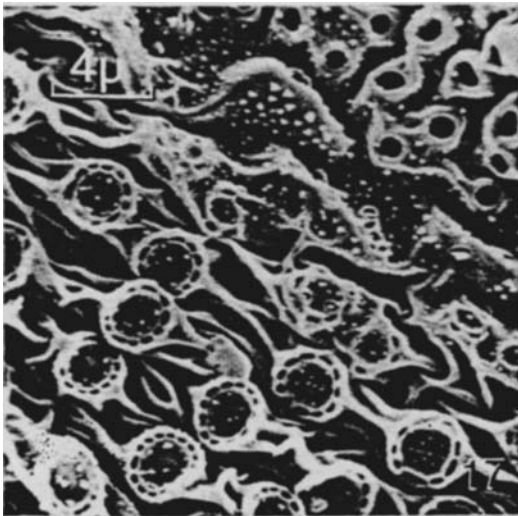
wax-secreting structures in Fig. 26 vary in diameter from about 2.2 to 2.8 μm. Examination of associated wax threads showed a majority of them to be about 2.0 μm across, but a few were much thinner, averaging 0.6 μm in diameter. These could be the product of some undiscovered secretory formation, but it is also possible that they were broken threads, being the output of a single 'cell' from one of the cogwheel-like structures in Fig. 26, for the diameter of these units varies from about 0.5 to 1.2 μm.

Hyperaspini

The Hyperaspini are a relatively homogeneous tribe of some 500 species divided into fourteen genera. Most of them (more than 400) belong to *Hyperaspis* Dejean or to *Brachyacantha* Dejean, two closely related genera whose centres of distribution are the Americas, although species of *Hyperaspis* occur in Europe, Asia and Africa. Available information indicates that the food range of the tribe is about 75% scale insects and mealybugs. The group is therefore important, actually or potentially as a source of biological control agents, several species being currently considered by the West Indian station of the Commonwealth Institute of Biological Control for introduction into other tropical countries against infestations of mealybugs on Cassava.

Most authors describing *Hyperaspis* larvae (e.g. Howard, 1900: 18; Simanton, 1916: 65; Böving, 1917: 622; Silvestri, 1919: 86; McKenzie, 1932: 12–13) or those of *Brachyacantha* (e.g. Wheeler, 1911: 169–174) refer to the obvious coating of waxy threads on every instar except the first. Hafez & El-Ziady (1952: 211), however, state that the larvae of *H.vinciguerrae* Capra are entirely devoid of wax until just prior to pupation. El-Ali (unpublished thesis, 1972) reviewed

five hyperaspine genera (fifteen species of *Hyperaspis* and one each of *Hyperaspidius* Crotch, *Thalassa* Muls., *Brachyacantha* Dejean and a new genus, erected by him to accommodate the myrmecophilous *Hyperaspis acanthicola* Chapin). In his experience, larvae of *Hyperaspidius* and of the new genus do not secrete visible wax, while those of *Brachyacantha* species do and those of *Hyperaspis* vary in that while some species produce wax filaments, many others do not.

The present study is based on two species of *Hyperaspis*, *H.jucunda* (Muls.) and what is believed to be *H.onerata* (Muls.) together with some exuvia of *Brachyacantha quadripunctata* (Melsh.). A fourth instar larva of *H.onerata* (Fig. 3) is clearly covered by a thick layer of flocculent wax arranged in broken bands across the thoracic and abdominal segments and in tufts arising from their lateral margins. At relatively low magnification, SEM examination of cleaned and de-waxed specimens of *H.jucunda* (Fig. 29) shows two types of cuticular outgrowth arising from between the folds of roughly reticulate surface pleating. These are in addition to normal and extremely long (up to 150 μm) socketed setae. Basal 'collars' belonging to broken-off examples of some of these very long setae are visible in Fig. 29. Often surrounding the collars, but sometimes in a transverse strip across a segment, are small (0.75–1.0 μm diameter) papilliform spicules (Fig. 30), usually set singly, but occasionally occurring in pairs within a pleat enclosure. Elsewhere over the dorsal and lateral surfaces of the thoracic and abdominal segments, many pleat enclosures contain a short, cylindrical outgrowth with a serrate apical rim about 2.0–2.5 μm in diameter (Fig. 31). Most of the cylinders are complete, but some were seen (*H.onerata*, Fig. 34) to be open-sided.

SEM examination of uncleaned examples of both available species of *Hyperaspis* and an exuvium of *Brachyacantha quadripunctata*

FIGS. 17–22. Stereoscan pictures of wax-producing structures in *Scymnini*. 17. *Scymnus* (*Pullus*) *coccivora* Ayyar (Pakistan). Multilocular pores and secretory discs (X3000). 18–21. *Pseudoscymnus simmondsi* Chapin & Ahmad. 18. Socketed setae and tubercle on dorsal abdominal surface (cuticular spicules top left) (X620). 19. Tube-producing pores on tubercle (remains of wax tubes within pores) (X3000). 20. Secretory rings on pleated cuticle (X3000). 21. Lateral tubercle on abdominal segment; socketed setae and spicules (X125). 22. *Cryptolaemus montrouzieri* Muls. Abdominal secretory discs and wax secretion (inset) (X3000).
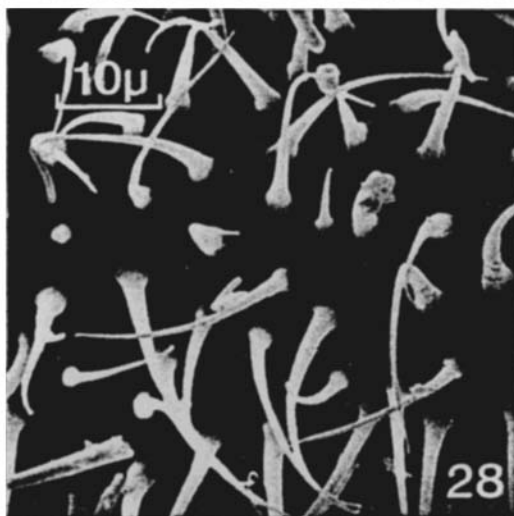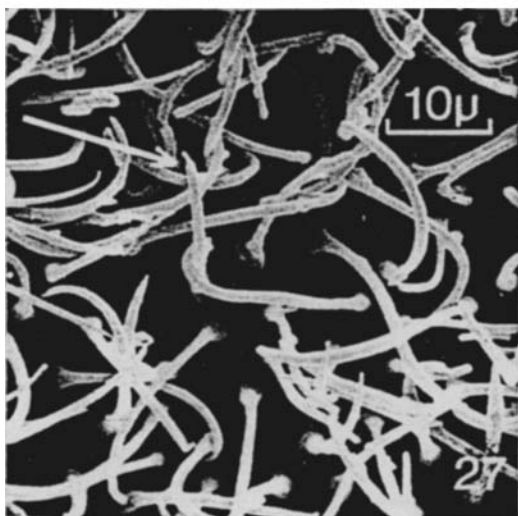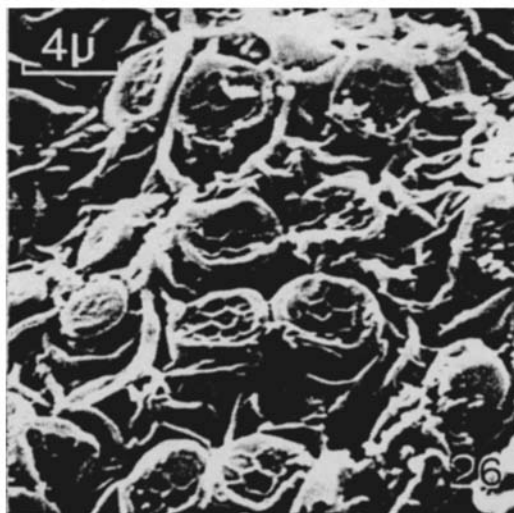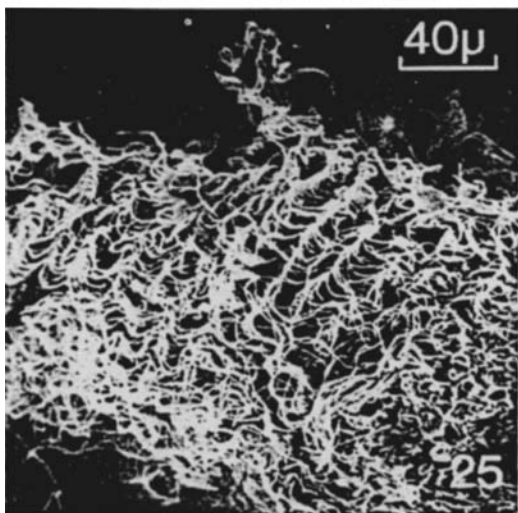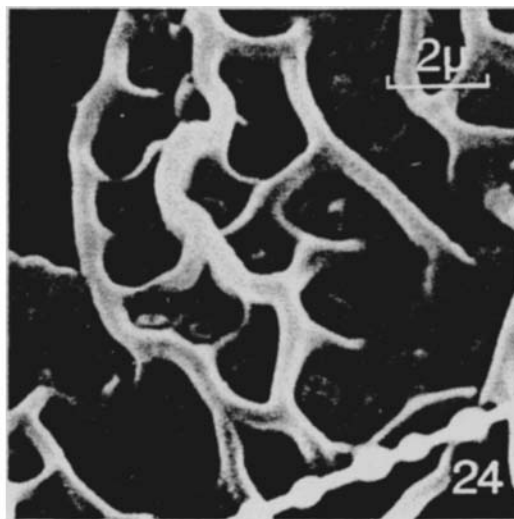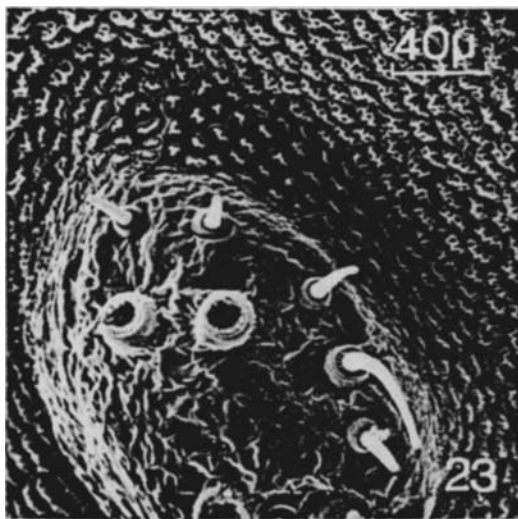
revealed the physical appearance of the wax covering and the way in which it is formed. Fig. 32 shows an assemblage of wax 'threads' on the surface of *H.jucunda*. The larger 'threads' are clearly ribbed tubes varying from about 2.3 to 2.7 μm in diameter and the smaller ones are solid rods of from 0.7 to 0.9 μm in diameter. The tubes are easier to explain than the rods, as Figs. 33 and 34 quite obviously demonstrate. In Fig. 33 a short length of tube has plainly been formed by secretion from and subsequent solidification on the serrated apex of a cylindrical cuticular outgrowth and in Fig. 34 the mass of wax consists of open-sided tubes which are without doubt the product of the incomplete cuticular cylinders visible in the left-hand half of the picture.

The fine, solid threads in Fig. 32 have approximately the same diameter as the cuticular papillae illustrated in Fig. 30. No positive physical connection between a thread and a papilla was found, but neither did it prove possible to discover another source through which the threads might have been extruded. Some papillae appeared to have secretion attached to their apices, but never in so clearly defined a shape as to provide evidence as was found for the relationship between the cylinders and the tubes.

SEM examination of the *Brachyacantha* exuvium produced less good results, but sufficient evidence was obtained to show that the sources of wax secretion are much the same as those in *Hyperaspis*. Fig. 35 is of the cuticular outgrowths on the dorsum of an abdominal segment. They are much smaller than those of *Hyperaspis jucunda*, 0.9–1.4 μm in diameter, and appear to arise from the surface pleats rather than from the enclosures between them. Many of the outgrowths can be seen to be incomplete cylinders and would produce curling, open-sided tubes of wax like those in Fig. 34.

Noviini

Following Gordon's revision of the tribe (1972), the Noviini appears to be an homo-geneous group of four genera, *Novius* Mulsant, *Rodolia* Mulsant, *Anovia* Casey and *Eurodolia* Weise. It currently includes some seventy-three species, more than two-thirds of which are Afro-Asian, twelve are Australian and one is European. Published feeding records indicate an almost exclusive diet of various scale insects for the entire tribe. Some of the species, such as *Rodolia cardinalis* (Muls.) and *R.koebelei* (Coquillet), were among the first (1889) successful biological control agents to be used against scale insect infestations on citrus crops. The life history of the former species has been described and illustrated many times since then and, if they refer to it at all, authors agree that the larva is covered with a thin coating of powdery or granular wax.

Material available for SEM examination included *Rodolia cardinalis*, one unnamed species of *Rodolia* from Australia and one from India. Some evidence for a granular surface deposit was seen but its nature is unknown. The wax secretion of *Rodolia* species is predominantly a mass of fine, solid threads between 0.6 and 1.0 μm in diameter (Fig. 27). The threads vary greatly in length. Longer ones often lie free on the surface of the larva and are frequently coiled, or tangled together. Most short threads appear to arise from small protuberances on the cuticle. Usually, the protuberance is more or less circular in plan and the thread is of uniform diameter, but sometimes a thread is widened and flattened near its union with the cuticle, the actual junction being elongate and more or less 'c' shaped in plan view. Where threads are numerous, no cuticular outgrowths are visible, apart from the small protuberances to which the threads are attached. By contrast, on de-waxed specimens, or on those parts of others where there appears to be no wax formation, the surface of the cuticle is closely set with hollow, pointed, spicular outgrowths of varying sizes (Fig. 28). Most spicules are circular in section and have a distinct, slightly bulbous base, but some are flattened, with bases that

FIGS. 23–28. Stereoscan pictures of wax-producing structures and wax of *Scymnini*, *Ortaliini* and *Noviini*. 23–25. *Cryptolaemus montrouzieri* Muls. 23. Dorsal abdominal tubercle (X300). 24. Secretory rings in folded cuticle near base of tubercle (X6000). 25. Crimped wax threads from wax 'pencil' (X300). 26. *Ortalia pallens* Muls. wax-secreting discs on dorsal surface of abdomen (X3000). 27–28. *Rodolia* sp. 27. 'Wax threads' on surface of abdomen (emergent spicule arrowed) (X1250). 28. Spicules on abdomen of de-waxed specimen (X1250).
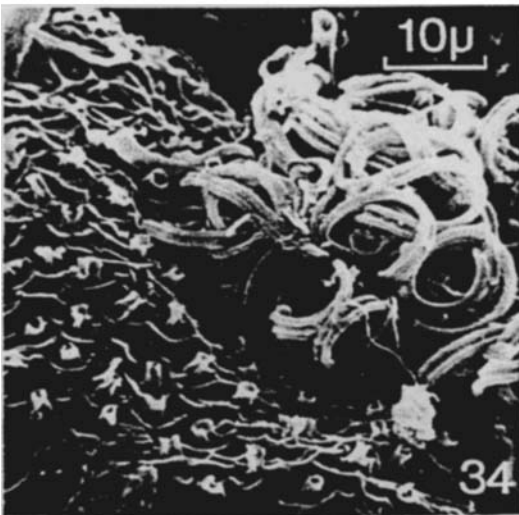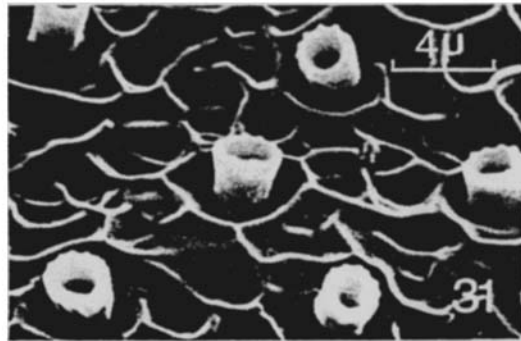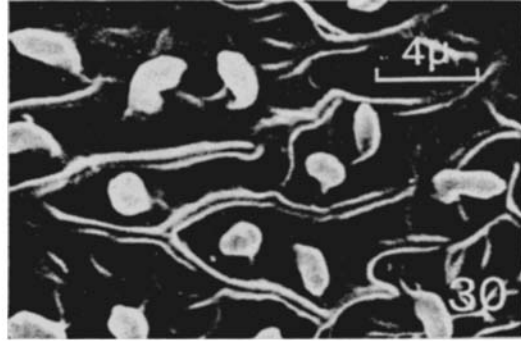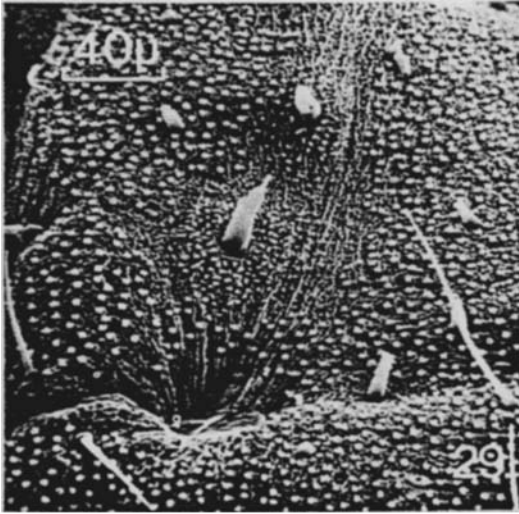
are concave on one side. The shapes and sizes of these bases, together with the absence of visible spicules in wax-bearing areas, suggests strongly that the wax threads are actually formed around them. If this were to be the case, then it would be most likely that the wax is exuded from the base of a spicule, the thread so formed growing upward, using the spicule as a support at first, but often breaking off and curling when beyond the cuticular core. Evidence in favour of this assumption comes from the discovery of a few short threads with what seems clearly to be the tip of a spicule emerging from their apices (Fig. 27, arrowed).

The larval stages of *Novius cruentatus* (Muls.), the sole European representative of the tribe, have been described on several occasions, e.g. by Perris (1862: 226), Weise (1887: 183) and Klausnitzer & Schulze (1975: 359—361) and are obviously closely related to those of *Rodolia*. No wax secretion is recorded and no material has been available for study, but it is considered highly probable that *Novius* produces threads of wax from its spicules, as does *Rodolia*. The description and illustrations of the larva of *Anovia virginalis* (Wickham) (Rees, 1947: 118) also indicate a close affinity with *Rodolia*. Again, though unrecorded, a wax coating is to be expected. The larva of the only described species of *Eurodolia*, *E.severini* (Wse.) from Tasmania, is unknown.

Coccidulini

The Coccidulini are a relatively diverse tribe from the standpoint of both adult and larval morphology. About 170 species are assigned to some twenty-eight genera. Examples occur in all five continents, but a majority, almost 100 species, are Australasian. Such feeding records as are available indicate that many species, especially those of *Rhyzobius*, eat scale insects, but some, such as the European

Rhyzobius litura (F.) (Schilder & Schilder, 1928: 247) and members of the Australian genus *Scymnodes* Blackburn (Swezey, 1915: 451; A. M. Richards, personal communication) feed exclusively on aphids. Very little information is available concerning the life histories and larval appearances of most Coccidulini except where a species is of economic interest, or has been used in biological control (e.g. *Rhyzobius ventralis* (Er.) and *Lindorus lophantae* (Blaisd.)). Even in these two instances, conflicting evidence is offered. Flanders (1930: 808) says that the larvae of *Rhyzobius ventralis* have a thin, powdery coating of wax until the prepupal stage when further secretion causes the insect to be 'completely covered with a mass of cottony wax'. Of *Lindorus lophantae* the same author states that the dorsum of the larva is 'covered with tufts of wax, but not completely hidden'. Grandi (1911: 332) is in reasonable agreement with Flanders about *Lindorus*, but D. J. Greathead (personal communication) considers its larva to be devoid of wax. No *Lindorus* larvae have been available for SEM examination, but a series of photographs of fourth instar larvae of *Rhyzobius ventralis*, one of which is reproduced in Fig. 2, demonstrate that its wax production is limited, in gross appearance, to a series of small, whitish dots on the pronotum and a band of rings of dots across the mesonotum, metanotum and first eight abdominal segments. Each of these rings surrounds one of the six setiferous tubercles ornamenting each segment. In the prepupal stage, a thin covering of fine, translucent, xylol-soluble threads is produced, becoming more obvious as the larval skin is shrugged backwards during pupation.

SEM examination of a fourth instar larva and of prepupal exuvia showed that whereas a majority of the dorsal surfaces consist of stellate-pleated cuticle the wax-encircled tubercles are relatively smooth and bear large, socketed setae set among spicules of various

---

FIGS. 29—35. Stereoscan pictures of wax and wax-producing structures in *Hyperaspini*. 29—33. *Hyperaspis jucunda* (Muls.). 29. View across abdominal segment of de-waxed specimen (X300). 30. Secretory papillae near socketed seta on abdomen (X3000). 31. Secretory cylinders on abdominal segment (X3000). 32. Wax tubes and threads (X1250). 33. Wax tube arising from cuticular cylinder (X3000). 34. *Hyperaspis onerata* (Muls.). Open-sided cuticular cylinders and their secretion (X1250). 35. *Brachyacantha quadripunctata* (Melsh.). Surface of abdominal segment with socketed seta and cuticular cylinders (X1250).
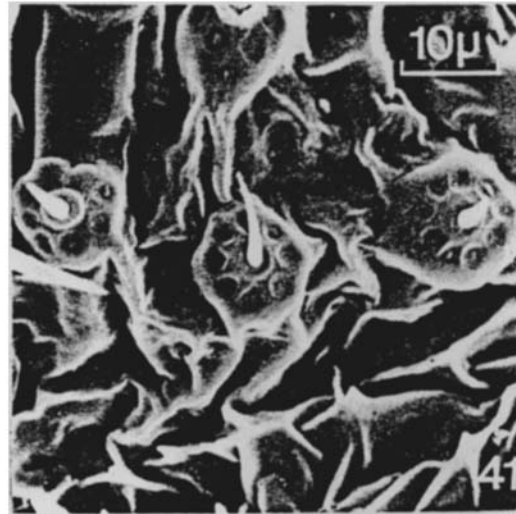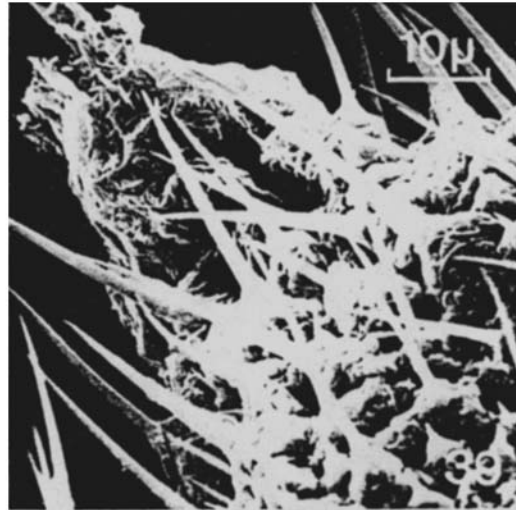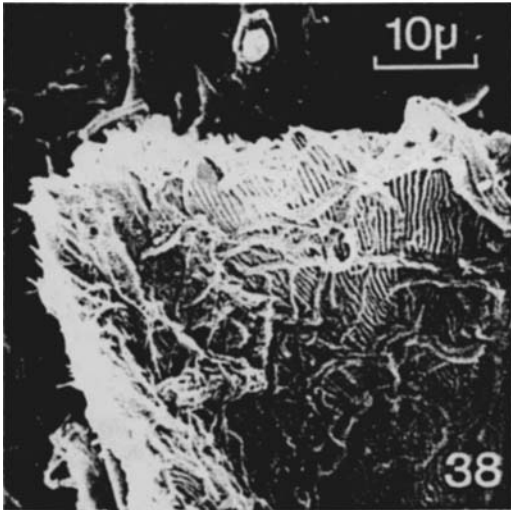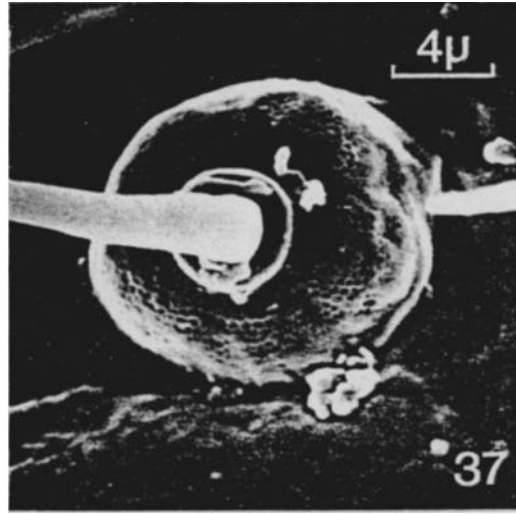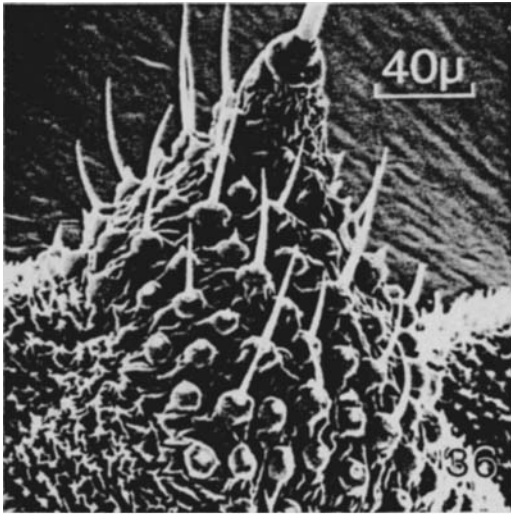
sizes, similar to those found in *Rodolia* (Fig. 28). Some spicules seemed to have an exudate adhering to them and a few solid rods, or threads, of about 1.3 μm diameter were seen lying on the surface of the tubercles. The rods could well be sections of the fine threads visible in the living prepupa, but no originating secretory structures could be found with certainty. It would also appear that at least some of the cuticular spicules may be secretory, but the evidence is not nearly so convincing as was the case with *Rodolia* (p.181).

Scymnodes Blackburn, an Australasian genus of nineteen nominal species, is currently included in the Coccidulini, but differs from most other genera in the group in having finely facetted eyes and relatively short antennae, not much longer than the width of the head between the eyes. In both these characters, *Scymnodes* is more like a scymnine. However, the larva of *Scymnodes lividigaster* (Muls.), the type species of the genus and, so far, the only one examined, is far from being characteristically scymnine. The thoracic and first eight abdominal segments each have a pair of very long, horn-like, setiferous proturbances (*senti* in Gage's (1920) terminology) arising from their dorsolateral areas. The pronotum has an additional pair on the anterior margin while the meso- and metathorax also have an additional *sentus* on each side in the lateral position and the abdominal segments a much shorter one arising from each lateral sclerite.

Dorsal wax production by the larva of *Scymnodes lividigaster* is minimal — a double row of very small, silvery patches, two on each abdominal segment near the large, dorsolateral *senti*, a pair of somewhat larger, transverse, sometimes confluent patches on the meso- and metanota, a transverse, anteromedian patch on the fourth abdominal segment and a smaller, similarly positioned patch on segments 5, 6 and 7. SEM examination of a de-waxed larva showed the cuticle beneath the wax patches to be different from the stellate-

pleated construction found elsewhere. Between two pits (Fig. 45), arranged on transverse folds, is a large number of irregularly formed, shallowly raised cylinders, varying from 2.0 to 3.0 μm across their largest dimension. The anteromedian patch on the fourth abdominal segment has similar cylindrical outgrowths, but here they seem to be arranged in more or less distinct groups (Fig. 46). No such organized structures were found on the meso- and metanota. The likeness of the cylinders to those of *Hyperaspis* (Fig. 31) is very striking, and that their mode of action is clearly the same was demonstrated by the discovery of a mass of wax tubes, 2.0—3.0 μm in diameter, sprouting from the dorsal cylindrical outgrowths of a dead, but dry larva. Even more remarkable is the similarity of the cuticular cylinders on *Scymnodes* to the wax-producing 'craters' on the larval cuticle of *Calpodes ethlius* Stoll (Lepidoptera: Hesperiidae), described and illustrated by Locke (1960) and Filshie (1970). The only difference appears to be one of size (*Calpodes* 'craters' vary in diameter between 0.4 and 1.2 μm) for they produce tubes of wax in exactly the same manner as do the cylinders of *Scymnodes*.

In contrast to the upper surfaces of *S. lividigaster*, the undersides of the thorax and abdomen produce a great deal of visible wax, especially during the last larval instar and prepupal stages. SEM examination of this wax shows it to consist of rather irregularly-formed rods, usually 'T'- or 'Y'-shaped in cross section (Fig. 47) and about 0.8—1.0 μm across their widest measurement. The rods are closely packed and frequently appear to be arranged in groups of from six to ten or more. Cleaning a specimen revealed that, beneath the underside wax, the cuticle bears closely-set, papilliform outgrowths (Fig. 48) approximating in size and outline to the 'T'- and 'Y'-section wax rods of the untreated example. There is no doubt that the wax is extruded from the apices of the papillae, much as it is in *Hyperaspis* (Figs. 30 and 32).

FIGS. 36—41. Stereoscan pictures of wax and wax-producing structures in *Cryptognathini.* 36—39. *Cryptognatha nodiceps* Mrshl. 36. Lateral setiferous tubercle on abdomen (X300). 37. Seta from tubercle showing secretory depressions on socket (X3000). 38. Remains of wax 'pencil' from tubercle, viewed from inside (X1250). 39. Setiferous tubercle with adherent wax threads (X1250). 40—41. *Pentilia castanea* Muls. 40. Setiferous tubercle from lateral margin of abdominal segment (X300). 41. Detail of setae and sockets from Fig. 40 (X1250).
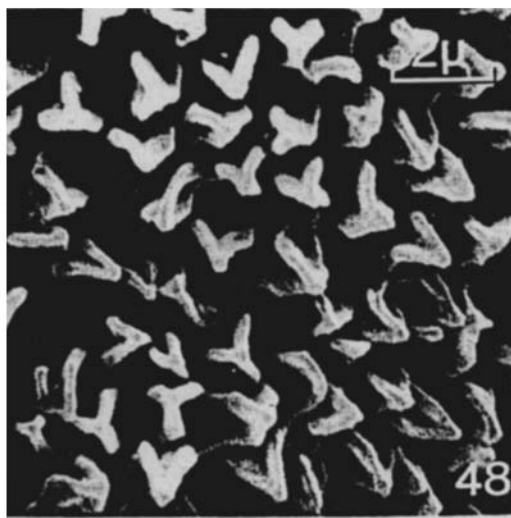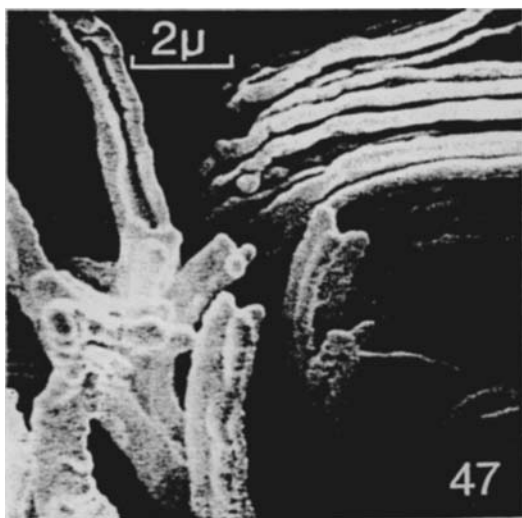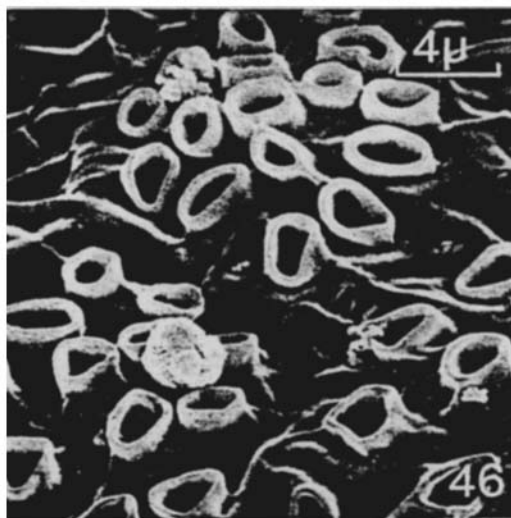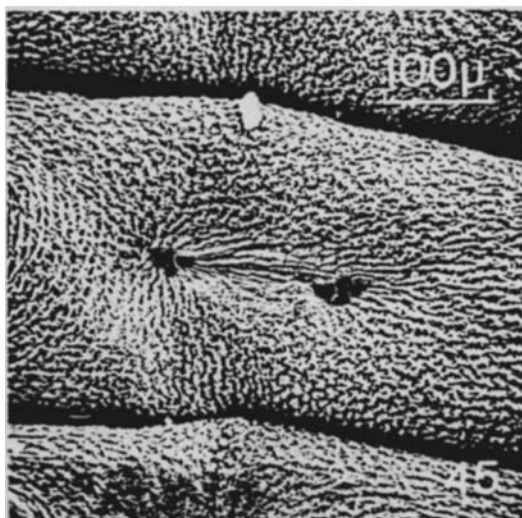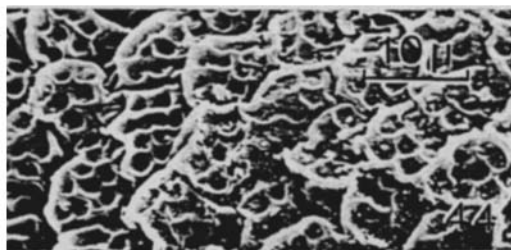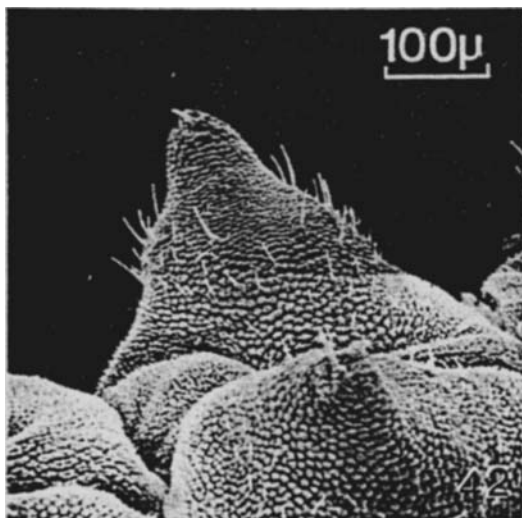
Cryptognathini

This tribe was erected by Gordon (1971: 181–196) to include four genera, *Cryptognatha* Muls., *Pentilia* Muls., *Delphastopsis* Casey and *Curticornis* Gordon. The distribution of the genera is restricted to the Americas and, so far, about fifty species have been described. Their food range, as far as is known, is limited to scale insects and mealybugs. The early stages of *Curticornis* and *Delphastopsis* species appear to be undescribed, but certain species of *Cryptognatha* and *Pentilia*, for example *C.nodiceps* Mshl. and *P.castanea* Muls., had their life histories recorded in considerable detail by Taylor (1935) in a report on the campaign against *Aspidiotus destructor* Sign. (Homoptera: Coccidae) in Fiji.

The larva of *C.nodiceps* is of very striking appearance. Long 'pencils' of white wax (longer than those of *Cryptolaemus montrouzieri* (Fig. 4)) sprout from large, setiferous tubercles (Fig. 36) on the margins of the thoracic and abdominal segments. The 'pencils' are very like those of certain mealybugs, such as *Icerya* species, but their gross similarity is not repeated in the detailed structure, neither are they originated from the same type of orifice. SEM examination of dewaxed specimens of *C.nodiceps* showed the prominent thoracic and abdominal tubercles to be covered with bulbous-socketed setae and equipped at their apices with a single socketed seta much longer than all the rest (Fig. 36). Further cleaning with wax solvents in an ultrasonic vibrator disclosed minute depressions, some 0.2–0.4 μm in diameter (Fig. 37), often arranged in groups over the surface of each bulbous seta socket. Uncleaned, but alcohol-stored examples of *C.nodiceps* were found under SEM examination to have retained considerable amounts of their original wax covering (Figs. 38 and 39). Fig. 38 shows the inner surface of part of a wax 'pencil', somewhat matted together, while Fig. 39 shows how intimately the threads of wax are associated with the socketed setae of the tubercles. Study of the wax threads under greater magnification showed their diameter to be relatively constant at around 0.2–0.3 μm and that, if they tended to occur in bundles, then the diameter of these bundles averaged 1.0–1.3 μm. These measurements are comparable to the diameters of the depressions and the groups of depressions on the seta bases and it is clear that they are the source of the 'pencil'-forming threads of wax.

The larvae of *Pentilia castanea* differ in detail from those of *C.nodiceps*, but there is considerable overall similarity between the two (Taylor, 1935: 76). As in *Cryptognatha*, the lateral margins of the thoracic and abdominal segments bear prominent, setiferous tubercles (Fig. 40), but on the dorsal surfaces of the segments the socketed setae are either scattered singly or arranged in twos and threes across a segment. The seta sockets, both on the lateral tubercles and on the dorsal surfaces of the segments, each have a single ring of from about five to twelve more or less circular indentations (Fig. 41), about 2.0–2.4 μm in diameter, surrounding the seta. By analogy with *Cryptognatha*, each indentation must be the source of a single filament of wax. Similarly, the filaments produced by the sum of the indentations on the seta sockets of an entire tubercle must make up one of the long 'pencils' of wax normally found decorating the lateral margins of a living larva. Lack of suitable material has precluded direct confirmation of this for *P.castanea*, but wax threads from a larval exuvium attached to a pupa of *Pentilia insidiosa* Muls. were measured and found to vary from 1.70 to 2.25 μm in diameter.

Azyini

The Azyini are a very small tribe including only the seven described species of *Azya*

FIGS. 42–48. Stereoscan pictures of wax and wax-producing structures in *Azyini* and *Coccidulini*. 42–44. *Azya* sp. 42. Tubercle on lateral margin of abdomen (×125). 43. Detail from tubercle in Fig. 42 (×600). 44. Detail of secretory structures on general surface of abdomen (×1250). 45–48. *Scymnodes lividigaster* (Muls.). 45. Abdominal segment, left-hand side, dorsal, showing pits joined by transverse folds (×125). 46. Anteromedian dorsal area of fourth abdominal segment showing wax-producing cylinders (×3000). 47. Wax filaments from underside of abdomen (×6000). 48. Wax-producing papillae on underside of abdomen (×6000).

Mulsant together with 'Ladoria' discomaculata Crotch. All eight species are from tropical America, one of them, A.trinitatis Mshl., having been introduced into Fiji during the campaign to control Aspidiotus destructor on coconut. This appears to be the sole species for which there is any detailed account of the life history and early stages. Taylor (1935: 71–74) described and illustrated the full-grown larva, commenting on its similarity to a mealybug, especially when the covering of waxy tufts has become somewhat matted together. His figures and description of the larva minus its wax covering show that Azya appears to have many features in common with both Cryptognatha and Pentilia. SEM examination of a de-waxed Azya larva confirmed some of the similarities, but made clear a number of characteristics by which the genus is quite distinct from the other two. The lateral and dorsolateral regions of the meso- and metathorax and the first eight abdominal segments bear prominent setiferous tubercles (Fig. 42) as in the other two genera, but their detailed makeup is substantially different and it is evident that, in this case, wax is secreted by special centres away from the socketed setae. Fig. 43 shows some of these secretory centres, set on pleated cuticle between the socketed setae on the side of an abdominal tubercle. Each centre has a variable number of shallow, circular depressions on its surface (Fig. 43) which are similar to those on the seta sockets of Pentilia castanea and vary from about 1.0 to 2.0 μm in diameter. On the dorsal surface of the abdomen and between and around the setiferous tubercles of the dorsolateral and lateral areas on each segment are similar secretory structures (Fig. 44), often with more numerous, deeper indentations. No living Azya larva has been available and no direct connection between any of these depressions and a wax thread has been observed, but optical examination of a dried pupal stage of Azya trinitatis showed the wax secretion to consist of a mass of threads about 1.0 μm in diameter, or slightly more. As with Pentilia (p.187), the conclusion seems inescapable that the depressions are the centres of secretion, producing the threads that make up the abundant coating of wax typical of Azya larvae.

Telsimiini

Kamiya (1965: 94) was the first to record Telsimiini as having wax-bearing larvae, citing T.nigra (Wse.) from Japan as the example. The tribe includes only two genera, the monotypic Hypocyrema Blackburn from Australia and Telsimia Casey with fourteen described species ranging in distribution from Africa to China and Japan and then southward through the Pacific to Australia. Few records of the food preferences of Telsimiini appear to exist, but a majority seem to be predaceous on scale insects or mealybugs; only Telsimia nigra being recorded additionally as an aphid feeder.

No material belonging to T.nigra has been available, but the illustration and description given by Kamiya make it clear that the larva possesses lateral setiferous tubercles on the thorax and abdomen which appear very similar to those of Cryptognatha nodiceps (Fig. 36) and Pentilia castanea (Fig. 40), especially the latter. Kamiya does not describe the appearance of the wax coating borne by T.nigra, but it would seem reasonable to suppose that it is quite obvious, covers all the upper parts of the thorax and abdomen and is in no way remarkably different from that seen on larvae of other tribes recorded as wax-bearing by the same author. If this is so, then any caudal or lateral 'pencils' should be less extreme than in either Cryptognatha or Pentilia and the general body covering more abundant, much as in Hyperaspis (Fig. 3) or Scymnus (Fig. 1).

By contrast, larvae of Telsimia (formerly Notolipernes) subviridis (Blackb.), recently discovered associated with eriococcids, margarodids and pseudococcids on Casuarina and presented to the writer by Dr A. M. Richards, have very little wax on the dorsal surfaces, but extremely long, seta-supported, movable 'pencils' of wax sprout from the lateral margins of the thoracic and abdominal segments. The general appearance is very similar to that of Pentilia castanea (p.187). SEM examination of a de-waxed specimen showed that each wax 'pencil' originates from a large, setiferous tubercle (Fig. 49). Each thoracic tubercle has four or five very long (up to 250 μm) setae set in flask-shaped sockets arranged around the apex of an extra,
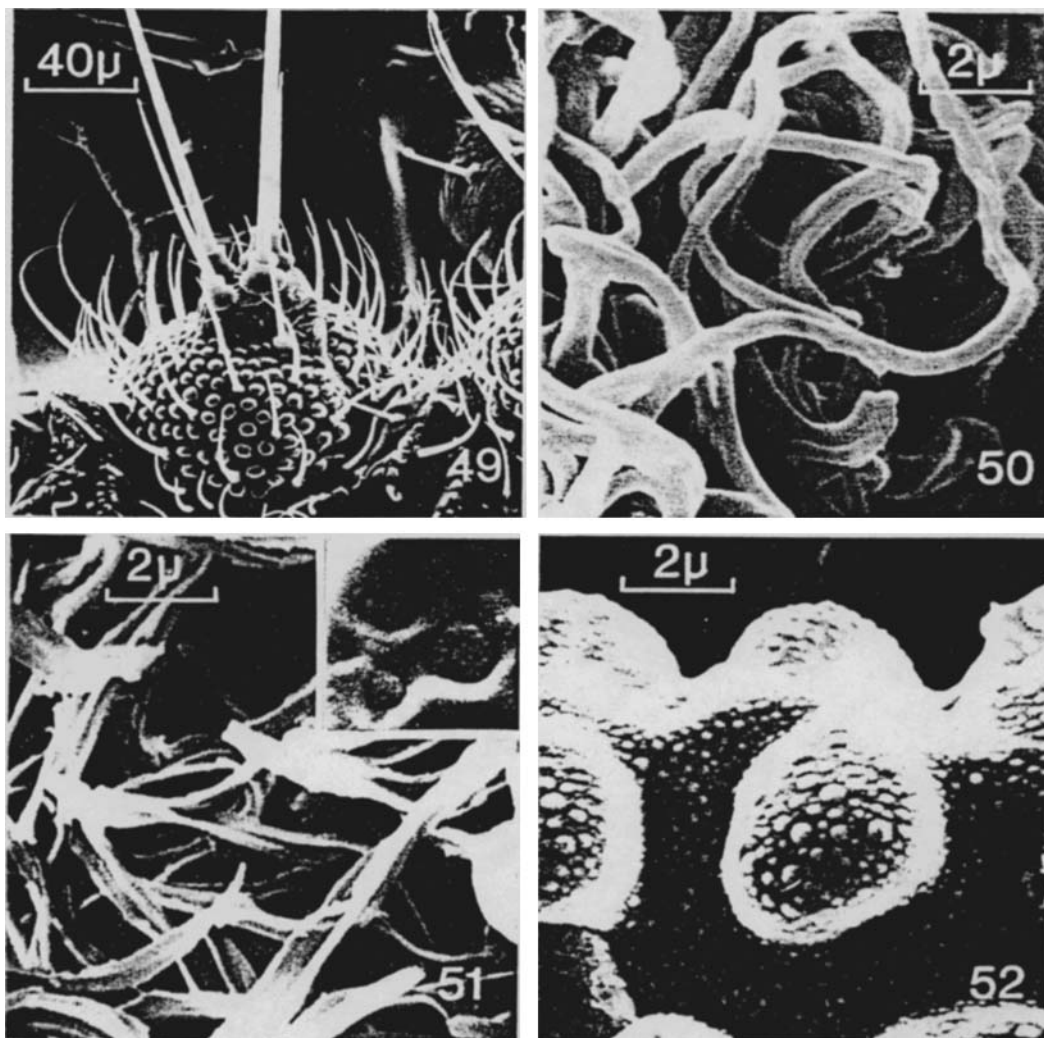
FIGS. 49—52. Stereoscan pictures of wax and wax-producing structures in *Telsimia subviridis* (Blackb.).
49. Setiferous tubercle on lateral margin of mesothorax (X320). 50. Solid threads from wax 'pencil'
(X6600). 51. Hemicylindrical wax extrusions from 'pencil'. Inset, detail showing umbilicate depressions
on median prominence of setiferous tubercle (X6600). 52. Pustuliform outgrowths on lateral tubercle
of de-waxed exuvium (X6600).

median prominence (Fig. 49). The abdominal
tubercles are similar, but the median promi-
nence is somewhat smaller and bears two
socketed setae at its apex, one about twice as
long as the other. The main body of the
tubercle bears much shorter, incurved,
socketed setae arising from among small,
closely set, pustuliform outgrowths about
2.5—3.5 μm in diameter.

The wax 'pencils' of *T.subviridis* are made
up of two types of thread; solid, apparently

cylindrical rods varying from about 0.25 to
0.33 μm in diameter (Fig. 50) and more or less
hemicylindrical extrusions varying in cross
sectional diameter from about 0.3 to 0.6 μm
(Fig. 51). It was not possible to judge which
type was the commoner or whether either pre-
dominated in a particular part of the 'pencil',
but the quantity of both shapes would seem
to require a very large number of secretory
centres on each tubercle. Observation of a
newly moulted or recently cleaned living

specimen would be necessary to prove beyond doubt where the wax-producing sites are and how they function, but it is considered that one type, the structure producing hemicylinders, can be seen on a de-waxed specimen, and that the origin of the solid rods can be deduced from evidence obtained by examining the cast skin of a fourth instar larva. The median prominence of each setiferous tubercle (Fig. 49) has a large number of umbilicate depressions on its surface, their central domes varying in diameter from 0.3 to about 0.8 µm (Fig. 51, inset). They are very similar to the structures found on the setiferous tubercles associated with the production of wax 'tails' in *Cryptolaemus* (p.177 and Fig. 23) and it seems highly probable that wax extruded from around the central domes gives rise to the hemicylinders of Fig. 51. The pustuliform outgrowths on the tubercles of a de-waxed specimen appear smooth-surfaced and without any trace of secretory structures, but it is believed that they are, none the less, the sites at which the solid rods of wax are produced. Fig. 52 shows a few of these outgrowths from a tubercle on the de-waxed cast skin of a fourth instar larva. The droplets on the surface must be dried, insoluble material associated with the moulting process which has passed through the old cuticle via minute canals (p.190). The smaller droplets, similar to those on the general surface of the cuticle between the outgrowths, most probably travelled through the canals involved with the production of the epicuticular cement layer. The larger droplets, apparently restricted to the domes of the pustuliform outgrowths, approximate in size to the diameters of the wax rods (Fig. 50). It is suggested that they indicate the sites of dense concentrations of wax canal openings, similar to those which must occur in the depressions on the seta sockets of *Cryptognatha nodiceps* (p.187 and Fig. 37), but flush with the surface of the cuticle and so invisible under SEM examination.

Chilocorini

This tribe, including over 200 species in eighteen genera, has representatives in all parts of the world. Although most species appear to feed principally or exclusively on scale insects or mealybugs, only one species, *Harpasus* (formerly *Curinus*) *zonatus* Muls., is credited with having wax-bearing larvae (Wille, 1926). Although Wille's illustration of the adult beetle is appropriate for *H.zonatus*, his descriptions and figures of the larva and pupa are very unlike those of the other genera in the tribe. The mature larva is shown to have an obvious coating of wax over the dorsum and long 'pencils' of wax extend from the lateral margins of the thoracic and abdominal segments. The drawing of a de-waxed larva makes it clear that the 'pencils' of wax arise from setiferous tubercles and an enlarged representation of a tubercle shows what are evidently large, socketed setae, the sockets being divided into five or six cells by radial septa. All these features are quite untypical of the Chilocorini, but very characteristic of the Cryptognathini, especially *Pentilia* (p.187). It seems certain that Wille must have misidentified the species with which he worked and that the Chilocorini do not have wax-bearing larvae.

Discussion

The formation and secretion of wax

The problems associated with the transport of wax through insect cuticle have been investigated by several workers, but notably by Locke (1960, 1961, 1965). In 1960 he was able to demonstrate the presence of minute canals, 60–130 Å in diameter, running between secretory epidermal cells and the outer surface of the epicuticle in the wax-bearing larvae of *Calpodes ethlius* Stoll (Lepidoptera: Hesperiidae). Since then, similar structures have been found in the cuticle of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae), *Galleria mellonella* (L.) (Lepidoptera: Galleriidae) and *Apis mellifera* L. (Hymenoptera: Apidae) (Locke, 1961) and in *Ceroplastes pseudoceriferus* Green (Homoptera: Coccidae) (Tamaski *et al.*, 1969).

No attempt was made during the current investigation to establish the existence of such canals beneath the secretory structures of coccinellid larvae, but it is extremely unlikely that a single family would have developed

some entirely different means of wax trans-
port. It is reasonable to assume that the discs
and depressions, the cylinders, papillae and
spicules are all fed from below by close-set,
minute canals, much as are the crater rims in
Calpodes ethlius (Locke, 1960) (p.190).

Most of the wax produced by various
Homoptera, including aphids, flattids and
cixids, appears to originate from distinct pits
or depressions in the cuticle. The wax thread
or group of threads so produced seems to be
of the same diameter as the pit or depression
and so it is easy to assume that their physical
form may be dictated by mechanical
constraint. The situation with the solid
threads arising from the central orifices of the
multilocular pores in the *Scymnus* complex is
strictly comparable and their shape could
well be imposed by the same means. The
secretions from the seta sockets in *Crypto-
gnatha*, *Pentilia* and *Azya* also begin in
hollows, though much shallower ones, but the
regularity of the rods and tubes produced by
the *Hyperaspini* and *Scymnodes*, as well as
those secreted by the discs and rings in the
Scymnini, must be controlled by some other
process. Wax flows from one epicuticular pore
to the next within the secretory area, but
never spreads outside. The simplest explana-
tion would be a short period of time between
emergence from a pore and solidification,
sufficient for the coalescence of the outputs
from adjacent pores, but not much more. In
this way a kind of crust would be formed and
be raised from the surface of the epicuticle by
the continuing secretion of lipids from
beneath.

The function of the wax

There can be no doubt that the visible
coatings of waxy threads protect their wearers
in various ways. Many wax-covered species
feed on scale insects and mealybugs which
also produce a thick coating of wax, and it
would appear likely that the coccinellid larvae
are more or less immune from molestation by
the ants attending the coccids and mealybugs
for the honeydew they exude.

The resemblance of some species, such as
Cryptolaemus montrouzieri and certain
Hyperaspis, to mealybugs is quite remarkable,
but it is doubtful whether the perfection of

the disguise would, by itself, ensure its
owner's safety. In a number of the species
examined, including those of *Scymnus*,
Cryptolaemus and *Hyperaspis*, the wax threads
were found to be markedly sticky, adhering
both to each other and to needles or bristles
used to tease the coating away from the
larva. Bearing in mind the sizes involved, an
ant investigating a *Scymnus* or *Cryptolaemus*
larva would be faced with, in human terms, a
4- or 5-inch thick mass of strongly adhesive,
spaghetti-sized rods, very difficult to bite into
and very likely both to entangle limbs and
block up delicate sense organs. According to
Harris (1921), the larva of *Ortalia pallens*
Muls., with an even thicker coating of wax
than either *Scymnus* or *Cryptolaemus*, makes
more than a passive, defensive use of its dis-
guise. The larvae tend to congregate near the
entrance of an ant burrow. Their white waxy
tufts appear to excite the curiosity of the ants
which, if they approach too closely to the
head end of a larva, are siezed by 'the power-
ful mandibles, and their bodily juices rapidly
sucked out, after the manner of an ant lion'.

In addition to protection against predators,
the waxy coating of some species is held
(El-Ali, unpublished thesis) to reduce the
incidence of parasitism. However, according
to Essig (1911) the wax of *Hyperaspis lateralis*
Muls. appears not to provide an effective
shield against attack by *Homalotylus* species
(Hymenoptera: Encyrtidae).

One further property of coccinellid wax,
doubtless having a bearing on its function, was
noted during the course of the investigation.
Its whiteness is an 'insect white'; that is to say
that it scatter-reflects light in the ultraviolet
region as well as throughout the entire visible
spectrum. Photographs taken using a light
source rich in UV and with a narrow-band UV
filter between the subject and the camera
(Pope & Hinton, 1977) clearly demonstrated
the wax to be highly UV reflective. Similar
experiments carried out with certain scale
insects (*Icerya purchasi* Mask., *I.aegyptiaca*
(Dougl.)), mealybugs (*Phenacoccus gossypii*
Towns. & Ckll) and woolly aphids (*Phyllaphis
fagi* (L.), *Eriosoma lanigerum* (Hausm.) and a
species of *Pineus*) showed that the wax of
these too is strongly UV reflective. Therefore,
from the point of view of a predaceous insect,
there would be no difference in colour

between the wax of a coccinellid larva and that of a coccid, mealybug or aphid.

All these comments are valid in respect of the Scymnini, Hyperaspini, Ortaliini, Cryptognathini, Azyini and Telsimiini, but cannot apply equally well to the Noviini and Coccidulini and it is apparent that *Scymnodes lividigaster* represents a very special case. The fine threads formed round the cuticular spicules in *Rodolia* are by no means so conspicuous as the fluffy disguises of *Scymnus* or *Hyperaspis* species, but they may still be sufficient to deter an insect predator. The waxy rings of *Rhyzobius ventralis* (Fig. 2) cannot be in the same category and there is no readily recognizable explanation of their function, unless they form, in conjunction with the purplish-grey colour of the cuticle, a warning pattern suggesting distastefulness.

The larva of *Scymnodes lividigaster* is remarkable in a number of ways. As there is so little of it, the upper surface wax, like that of *Rhyzobius*, must act as a positive signalling device, rather than a protective cover. On the other hand, the wax produced by the papillae of the underside is used in a way, so far as is known at present, unique among Coccinellidae. Dr A. M. Richards (personal communication) reports that, just prior to

pupation, the larva anchors the apex of its abdomen to the upper surface of a leaf, and then rotates about this pivotal point, smearing the leaf with wax from its papillae as it goes. It then becomes still and pupates, the pupa producing quite large amounts of wax over most, but not all, of its upper surfaces so that it comes to resemble a bird-dropping. Although the smear of wax is very thin, it is plainly visible to the naked eye. It must serve a preventive function, but field observation and experiment will be necessary to the discovery of the details.

Wax production and classification

As Kamiya (1965) remarked 'The occurrence of wax-like exudation ... is rather important from the phylogenetic viewpoint'. The present study has revealed many hitherto unknown details and allows a number of pertinent observations to be made.

In general terms the findings complement or reinforce our understanding of coccinellid phylogeny as set out by Sasaji (formerly Kamiya) in 1968 and 1971 and by Kovář in Hodek (1973) (Fig. 53). They sometimes emphasize the closeness of certain relationships, but also permit the acceptance of some of the modifications to current opinion sug-
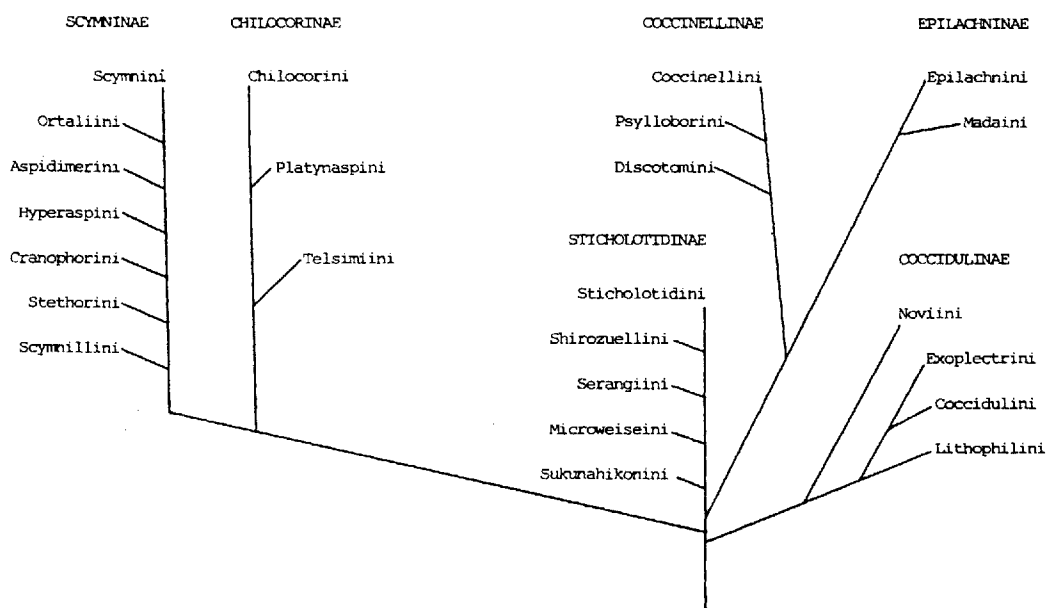

FIG. 53. Dendrogram depicting coccinellid phylogeny, redrawn from Sasaji (1971), with additions from Gordon (1975, 1977).

gested by Kapur (1970). In detail, a few anomalies, such as '*Diomus*' *notescens* (p.193), have already come to light, but further study will undoubtedly disclose many more. It is also possible to place certain groups (Cryptognathini and Azyini) overlooked, or ignored for lack of material by both Sasaji and Kovář, and to predict with some confidence that certain Australian genera, *Scymnodes* and its allies, will necessitate the erection of a new tribe in the course of a full taxonomic revision of the fauna.

Basically, the wax-secreting structures so far found in coccinellid larvae may be segregated into four distinct groups: the scymnine/hyperaspine, the cryptognathine/azyine, the telsimiine and the noviine/cocciduline. The relatively small amounts of secretion and the spicular originating structures of the noviine/cocciduline group are the simplest form of cuticular specialization for wax-production in present-day Coccinellidae, while the much more efficient, duplex system developed in the scymnine/hyperaspine group, seen at its most sophisticated in *Scymnus* and its close allies, is the most complex.

In the closely related genera *Scymnus*, *Nephus* and *Diomus*, all species examined have multilocular pores with a central, wax-extruding orifice and patterned secretory discs of varying complexity. It is likely that all species correctly assigned to any of these three genera will prove to have this typical, duplex system, or something very similar. As a result, it becomes obvious that the Australian *Diomus notescens* (Blackburn), whose larva has no visible wax secretion at all, properly belongs to some quite different genus, perhaps to one as yet undescribed. *Cryptolaemus* and *Pseudoscymnus* are both clearly related to the *Scymnus* complex, but, in their different ways, are easily distinguished from it. *Pseudoscymnus* Chapin was described by its author as being closer to *Cryptogonus* Mulsant, a genus usually placed in the Aspidimerini, than to *Scymnus* proper. Larvae of *Pseudoscymnus simmondsi* demonstrate very plainly the links with *Scymnus* and its allies. The reduction of the patterned secretory discs to a simple ring is close to the situation seen in a species of *Nephus* from Pakistan (Fig. 14) and here too it seems possible that the pores immediately surrounding the socketed setae resemble those

of *Pseudoscymnus* rather than *Scymnus*. On the other hand, the strongly setose and spicule-bearing lateral tubercles of the thorax and abdomen in *Pseudoscymnus* are quite unlike anything so far found in the *Scymnus* complex. They may well prove to indicate a relationship with the Aspidimerini, but the only larva of that tribe so far described, that of *Cryptogonus horishanus* (Ohta) (Sasaji, 1968: 36), is said to be 'elliptical, extremely flattened without any setose tubercles'.

In *Cryptolaemus* the cogwheel-like secretory discs are essentially similar to the discs of the *Scymnus* complex and occupy the same relative positions, but the smaller secretory structures on and around the setiferous tubercles represent a different developmental line; they seem to be no more than reduced, partially embedded versions of the larger, disc-like structures, quite different from the multilocular pores of *Scymnus*.

Ortalia Mulsant, exemplified by *O.pallens* Muls., is obviously closely related to the Japanese *Amida* Lewis. Kamiya (1965: 97) regarded the affinities of *Amida* as very uncertain, but by 1968 (as Sasaji, 1968: 24–25) had decided to include it in the Ortaliini and to consider that tribe as the most advanced unit within the subfamily Scymninae. The septate secretory discs found in the larva of *O.pallens* (Fig. 26) are remarkably similar to the structures borne by *Cryptolaemus* (Fig. 22). This, together with adult characters accepted as apomorphic for the subfamily, such as truly trimerous tarsi, five visible abdominal segments in both sexes and eyes deeply emarginate around the antennal insertions, strongly support Sasaji's contention. The very limited amount of ecological information available (p.191) also indicates a very specialized way of life for *Ortalia*. Unfortunately, even less seems to be known about the life histories and early stages of the Ortaliini than about most coccinellid tribes. A brief survey of the adults revealed a disparate group of genera and further study will almost certainly result in the tribe being segregated into two or more units. There is no doubt that a revision should include examination of the larval stages, for the presence or absence of wax-secreting structures will have an important bearing on the disposition of the genera.

13*

Sasaji (1968: 23) also included the Hyperaspini among the Scymninae, but indicated that, although the adults show many advanced charactersitics, such as glabrous upper surfaces, angulate tibiae, foveolate elytral epipleura and an asymmetrical aedeagus, the larvae appear very primitive, being without sclerotized body segments and having relatively simple mandibles and unspecialized antennae. Like the Scymnini, the Hyperaspini possess two types of wax-producing structure (Figs. 30 and 31), one of them usually being closely associated with long, socketed setae. The wax-producing cylinders (Fig. 31) may easily be derived by simplifying a typical scymnine disc to the ring-structure seen in Pseudoscymnus (Fig. 20) and drawing it upward from the surface of the cuticle. The relationship between the papillae of Hyperaspis (Fig. 30) and the multilocular pores of Scymnus species (Fig. 6) is obviously much less close, but the solid threads of wax they both produce are clearly comparable. Probably the most interesting feature of hyperaspine wax production is its apparent absence from the larval stages of certain species (Hafez & El-Ziady, 1952; El-Ali, unpublished thesis). Hyperaspis, for all its size, is a genus of closely similar species, but of those recorded by El-Ali as non-wax-producing, almost all, according to him, showed a reduction in the number of antennal segments from eleven to ten.

The Australian genus Scymnodes Blackburn, currently placed in the Coccidulini, is, as was mentioned earlier, atypical of the group and the adults have several characters in common with the Scymnini. However, the wax-producing structures on the upper surfaces of Scymnodes are highly individual. Although in some ways resembling the cuticular cylinders of Hyperaspis, their very limited distribution, apparently not conforming to the 'dorsal, dorsolateral, lateral' sequence seen in the Scymnini and most other groups, sets the genus well apart from the existing tribes in the Scymninae. In addition, the underside papillae, with their special-purpose secretion, though perhaps reminiscent of the papillae in Hyperaspis, reinforce the suggestion that Scymnodes requires the establishment of a new tribe. Certain other genera, also from Australia, and possibly a few species currently assigned to Rhyzobius, appear, as adults, to be quite closely related to Scymnodes. It is probable that, when the larvae of these are discovered, they will be found to exude wax from similar structures and so should be included in the same tribe.

The wax-producing structures found in the Cryptognathini/Azyini and in the Noviini/Coccidulini are so different from each other and from those occurring in the Scymninae that there can be little doubt that the three groups represent long-separated lines of development. The Noviini were placed by Sasaji (1968) in the Coccidulinae, along with the Exoplectrini, Lithophilini and Coccidulini, and the subfamily held to derive from a very early dividing point in Coccinellid evolution. The general similarities between noviine and cocciduline larvae were first commented on by Böving (1917: 633) who, however, was not in a position to see the minute cuticular spicules occurring on the surface of both. The presence of these spicules, together with their being the source of wax in Rodolia and possibly in some species of Rhyzobius, emphasizes the closeness of the two groups. The larva of Lithophilus connatus (Panzer) is evidently without visible wax secretion, but the situation in the Exoplectrini is uncertain as no larvae of this group have either been described or been available for examination. An examination of adult Exoplectrini shows a wide range of general form and detailed structure, so much so that the tribe appears composite. In addition, the material used by Sasaji to form a judgement on the tribe's taxonomic position appears from the key to tribes (Sasaji, 1968: 30; 1971: 44) to have been misidentified. In the circumstances, nothing can justifiably be predicted concerning possible wax-production by the larvae.

The Cryptognathini and Azyini, clearly associated by their wax-producing structures, are not treated together by any modern author except, perhaps, Kapur (1970: 11), who placed them fairly close to one another in his linear arrangement of the coccinellid tribes. Gordon's (1971) revision of the Cryptognathini at first suggests that the tribe belongs in the Scymninae, as defined by Sasaji (1968), but ends by preferring an intermediate position, somewhere between the Sticholotinae and the Scymninae. Using the

wax-producing structures as a principal guide, the Cryptognathini and Azyini must have had a common origin, quite distinct from all the subsidiary branches in Sasaji's 1968 dendrogram except, possibly, that leading to the Chilocorinae (see Fig. 53).

Sasaji (1968: 20) included the Telsimiini among the Chilocorinae, regarding the tribe as the most primitive living exponents of the subfamily, citing male genitalia with a very simple sipho, slightly narrowing apical segments of the maxillary palpi and a short metendosternite as plesiomorphic for the subfamily. The wax-forming structures, insofar as they are exemplified by those of *Telsimia subviridis*, show definite links with *Cryptolaemus* in the Scymninae on the one hand and *Cryptognatha* of the Cryptognathini on the other. In other characters, such as the antennae and mouthparts, the larva of *Telsimia nigra* (Wse.) seems closer to the Chilocorinae than to the Scymninae, but it appears better for the moment to regard the Telsimiini as a relatively isolated group, separated long ago from an ancestral stock which gave rise to both the present day Scymninae and the Chilocorinae. Thus, Kamiya's somewhat tentative suggestion is strongly supported. In any attempt to understand the phylogeny of the Coccinellidae, it is not only necessary to know whether or not the larvae produce visible wax, but to take into account the cuticular structures by means of which the exudate is moulded. Some groups, such as the Exoplectrini and Ortaliini, are already clearly composite and a study of their larvae will aid an understanding of their construction and relationships. As well as a knowledge of its shape and originating structures, a study of the chemistry of Coccinellid wax and such physical properties as its melting point, will also have a bearing on ecological and taxonomic work. The chemical composition of scale insect wax shows considerable interspecific variation, but is apparently constant for a given species, and it has been shown that the waxes of hive bees (*Apis mellifera*), bumblebees and various scale insects all have quite different, habitat-correlated, melting points.

Acknowledgments

I am happy to express my gratitude to the following who helped in various ways during

the course of the investigation: Dr A. M. Richards (Australia) for specimens, first-hand information on the biology of Australian species and for permission to reproduce Fig. 2; Drs G. A. Samuelson (Hawaii), F. D. Bennett (Trinidad), M. A. Ghani (Pakistan), T. Sankaran (India), D. J. Greathead (U.K.), R. D. Gordon (U.S.A.) and Mr K. Houston (Australia) for the loan or gift of specimens; Mr D. Claugher and the staff of the Electron Microscope Unit (BM(NH)) for their ready help at all times with specimen preparation and photographic processing; Mr D. Cooper for the preparation of serial sections; Messrs R. T. Thompson and P. M. Hammond for reading the manuscript and offering constructive suggestions for its improvement.

References

Balduf, W.V. (1935) *The Bionomics of Entomophagous Coleoptera*. John C. Swift, New York.

Böving, A. (1917) A synopsis of the coccinellid larvae in the United States National Museum, with a description of the larva of Hyperaspis binotata Say. *Proceedings of the United States National Museum*, 51, 621–650.

Chapin, E.A. (1962) Pseudoscymnus, a new genus of Asiatic Scymnini (Coleoptera: Coccinellidae). *Psyche*, 69, 50–51.

El-Ali, A.A. (undated) A biosystematic study of hyperaspini of California with emphasis on the immature stages. Unpublished thesis, University of California, Berkeley.

Essig, E.O. (1911) The natural enemies of the citrus mealybug. *Pomona College Journal of Entomology*, 3, 518–522.

Filshie, B.K. (1970) The resistance of epicuticular components of an insect to extraction with lipid solvents. *Tissue and Cell*, 2, 181–190.

Flanders, S.E. (1930) Wax secretion in the Rhizobiini. *Annals of the Entomological Society of America*, 23, 808–809.

Gage, J.H. (1920) The Larvae of the Coccinellidae. *Illinois Biological Monographs*, 4, 23–294.

Gordon, R.D. (1971) A generic review of the Cryptognathini, new tribe, with a description of a new genus (Coleoptera: Coccinellidae). *Acta Zoologica Lilloana*, 26, 179–196.

Gordon, R.D. (1972) The Tribe Noviini in the New World (Coleoptera: Coccinellidae). *Journal of the Washington Academy of Sciences*, 62, 23–31.

Gordon, R.D. (1975) A revision of the Epilachninae of the western hemisphere (Coleoptera: Coccinellidae). *Technical Bulletin: U.S. Department of Agriculture*, Washington, 1493.

Gordon, R.D. (1977) Classification and phylogeny of the New World Sticholotidinae (Coleoptera: Coccinellidae). *Coleopterists Bulletin*, 31, 185–228.

Grandi, G. (1911) *Dispense di Entomologia Agraria.* Premiato Stab. Tipografico Vesuviano, Portici.

Hafez, M. & El-Ziady, S. (1952) Studies on the biology of *Hyperaspis vinciguerrae* Capra, with a full description of the anatomy of the fourth stage larva (Coleoptera: Coccinellidae). *Bulletin de la Société Fouad 1er d'Entomologie,* 36, 211−246.

Harris, R.H.T.P. (1921) A note on Ortalia pallens Muls. *South African Journal of Science,* 17, 170−171.

Hodek, I. (1973) *Biology of Coccinellidae.* Dr W. Junk, Holland.

Howard, L.O. (1900) The beneficial work of Hyperaspis signata. *Bulletin, United States Department of Agriculture, Bureau (Division) of Entomology* (n.s.), 26, 17−18.

Kamiya, H. (1965) Comparative morphology of the Japanese Coccinellidae, with Special Reference to the Tribal Phylogeny of the Family (Coleoptera). *Memoirs of the Faculty of Liberal Arts, Fukui University Ser. II, Natural Science,* 14, 83−100.

Kapur, A.P. (1970) Phylogeny of Ladybeetles. In: Fifty-seventh Indian Science Congress Kharagpur, 1970, Section of Zoology and Entomology. Presidential address, 1−14. Indian Science Congress Association, Calcutta.

Klausnitzer, B. & Schulze, J. (1975) Die Larve von Novius cruentatus (Mulsant) (Col., Coccinellidae). *Deutsche Entomologische Zeitschrift* (N.F.), 22, 359−361.

Korschefsky, R. (1931−32) Coccinellidae. In: *Coleopterorum Catalogus,* partes 118 + 120. W. Junk, Berlin.

Locke, M. (1960) The cuticle and wax secretion in *Calpodes ethlius* (Lepidoptera: Hesperidae). *Quarterly Journal of Microscopical Science,* 101, 333−338.

Locke, M. (1961) Pore canals and related structures in insect cuticle. *Journal of Biophysical and Biochemical Cytology,* 10, 589−618.

Locke, M. (1965) Permeability of insect cuticle to water and lipids. *Science, New York,* 147, 295−298.

MacKenzie, H.L. (1932) The biology and feeding habits of *Hyperaspis lateralis* Mulsant (Coleoptera—Coccinellidae). *University of California Publications in Entomology,* 6, 9−20.

Perris, E. (1862) Histoire des Insectes du Pin maritime. Supplément aux Coléoptères et Rectifications. *Annales de la Societé Entomologique de France,* (4), 2, 173−243.

Pope, R.D. & Hinton, H.E. (1977) A preliminary survey of ultraviolet reflectance in beetles. *Biological Journal of the Linnean Society,* 9, 331−348.

Rees, B.E. (1947) Taxonomy of the larvae of some north American Noviini (Coleoptera, Coccinellidae). *Pan-Pacific Entomologist,* 23, 113−119.

Sasaji, H. (1968) Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia,* 35, 1−38.

Sasaji, H. (1971) Coccinellidae. In: *Fauna Japonica.* Academic Press, Japan.

Schilder, F.A. & Schilder, M. (1928) Die Nahrung der Coccinelliden und ihre Beziehung zur Verwandtschaft der Arten. *Arbeiten aus der Biologischen Reichsanstalt für Land- und Forstwirtschaft,* 16, 213−282.

Silvestri, F. (1919) Contribuzioni alla conoscenza degli insetti dannosi e lei loro simbionti. VI (1) La Cocciniglia del Prugno (*Sphaerolecanium prunastri* Fonsc.). *Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricoltura. Portici,* 13, 70-192.

Simanton, F.L. (1916) The Terrapin Scale: an important enemy of peach orchards. *Bulletin, United States Department of Agriculture, Washington,* 351, 1−96.

Steinweder, J.B. (1929) Notes on the origin of the wax secretion of certain coccinellid larvae. *Pan-Pacific Entomologist,* 6, 26−32.

Swezey, O.H. (1915) Some results of the introduction of beneficial insects in the Hawaiian Islands. *Journal of Economic Entomology,* 8, 450−456.

Tamaki, Y., Yushima, T. & Kawai, S. (1969) Wax secretion in a scale insect, *Ceroplastes pseudoceriferus* Green (Homoptera: Coccidae). *Applied Entomology and Zoology,* 4, 126−134.

Taylor, T.H.C. (1935) The campaign against *Aspidiotus destructor* Sign. in Fiji. *Bulletin of Entomological Research,* 26, 1−102.

Weise, J. (1887) Ueber die Lebenweise von *Novius cruentatus* Muls. *Deutsche Entomologische Zeitschrift,* 31, 181−183.

Wheeler, W.M. (1911) An ant nest coccinellid (*Brachyacantha quadripunctata* Muls.). *Journal of the New York Entomological Society,* 19, 169−174.

Wigglesworth, V.B. (1933) The physiology of the cuticle and of ecdysis in *Rhodnius prolixus* (Triatomidae, Hemiptera); with special reference to the function of the oenocytes and the dermal glands. *Quarterly Journal of Microscopical Science,* 76, 269−318.

Wille, J. (1926) Curinus (Orcus) zonatus Muls. (Coccinellidae), ein Feind der Schildläuse an Orangenbäumen. *Zeitschrift für Angewandte Entomologie,* 12, 357−375.