

THE BIOLOGY AND ECOLOGY OF ARMORED SCALES^{1,2}

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The armored scales (Family Diaspididae) constitute one of the most successful groups of plant-parasitic arthropods and include some of the most damaging and refractory pests of perennial crops and ornamentals. The Diaspididae is the largest and most specialized of the dozen or so currently recognized families which compose the superfamily Coccoidea. A recent world catalog (19) lists 338 valid genera and approximately 1700 species of armored scales. Although the diaspidids have been more intensively studied than any other group of coccids, probably no more than half of the existing forms have been recognized and named.

Armored scales occur virtually everywhere perennial vascular plants are found, although a few of the most isolated oceanic islands (e.g. the Hawaiian group) apparently have no endemic representatives and are populated entirely by recent adventives. In general, the greatest numbers and diversity of genera and species occur in the tropics, subtropics, and warmer portions of the temperate zones.

With the exclusion of the so-called palm scales (*Phoenicococcus*, *Halimococcus*, and their allies) which most coccid taxonomists now place elsewhere (19, 26, 99), the armored scale insects are a biologically and morphologically distinct and homogenous group. The definition of subfamily and tribal categories within the Diaspididae is a matter of some disagreement among taxonomists, although most recognize at least four major subdivisions: the aspidiotines, diaspidines, parlatorines, and odonaspidines. Borchsenius (19) treated these as subfamilies, whereas earlier workers (8) gave them tribal status within the nominate subfamily of a more inclusive family Diaspididae. Recently Takagi (99) has proposed dividing the Diaspididae into seven tribes (the larger number derived by splitting Balachowsky's Diaspidini and Parlatorini), without designating subfamilies. Takagi's scheme, which is based

¹Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Journal Series No. 1714.

²The survey of literature pertaining to this review was completed in December 1972. The authors express their appreciation to Dr. P. DeBach, University of California, Riverside, for making available IBP funds to assist them in the library search.

largely on the comparative morphology of first instar nymphs, appears to have considerable merit but has not yet achieved general acceptance.

A relatively small proportion of the known species of armored scales are agricultural or horticultural pests of consequence. Schmutterer, Kloft & Lüdicke (93) listed about 135 species in their treatment of diaspidid pests. Perhaps a quarter of these can be considered as pests of major importance. Published biological and ecological information on diaspidids has been derived largely from studies on the major pest species listed in Table 1.

HOST RELATIONSHIPS

Host Specificity

Polyphagy is common among diaspidids. San Jose scale, for example, is known to infest representatives of 34 different plant families (114) while the oleander scale has been recorded from hundreds of host species in more than 100 plant families (16). On the other hand, many armored scales have either limited oligophagous or monophagous host ranges. Species of the genus *Kuwanaspis*, for example, are confined to bamboos. Closely related species sometimes exhibit very different degrees of host specificity. For example, *Carulaspis carueli* is known to attack several genera of conifer hosts, but *Carulaspis juniperi* is restricted exclusively to *Juniperus communis*. A third related species, *Carulaspis visci*, lives exclusively on the leaves of *Viscum album* (a mistletoe semiparasitic on *Pinus sylvestris*), and does not migrate to *Juniperus* even if the foliage of the two conifers are in contact (53).

With respect to varietal susceptibility of host plants, very little information is known. Agarwal & Sharma (1) studied the occurrence and abundance of *Melanaspis glomerata* on different varieties and ecotypes of sugar cane and found a direct relationship between a heavy attack and a high stomatal density of the stem. Five apple varieties studied in New Zealand exhibited no difference in susceptibility to attack of San Jose scale (91). Similarly, sour cherry hybrids tested for resistance to this scale in Hungary failed to show differences in susceptibility (62).

Host Parts Attacked

Most armored scales are eurymerous, that is, they may feed on various parts (organs) of the host plant without apparent problems (6, 115). Stenomerous species, restricted to only one plant organ, are less numerous and usually found on grasses or other herbaceous plants. Practically all plant organs, including those with a thick epidermal layer, are suitable for scale feeding and reproduction. Subterranean parts (roots, tubers, and rhizomes) are not generally attacked unless they are exposed, because armored scales are not adapted to the hypogeal environment.

When two or more species with similar feeding and settlement requirements coexist, competition between the species may affect their relative abundance and distribution on the host. Competitive displacement may occur whereby one species of scale completely displaces the other. In other instances, two species coexisting in the same host may reach a certain degree of equilibrium. Gerson (50) reported

Table 1 Principal armored scale pests of the world

	Common Name
<u>Tribe Aspidiotini</u>	
<i>Aonidiella aurantii</i> (Maskell)	California red scale ^a
<i>Aonidiella citrina</i> (Coquillett)	yellow scale ^a
<i>Aspidiotus destructor</i> Signoret	coconut scale ^a
<i>Aspidiotus nerii</i> Bouché [= <i>A. hederae</i> Vallot]	oleander scale ^a
<i>Chrysomphalus dictyospermi</i> (Morgan)	dictyospermum scale ^a
<i>Chrysomphalus ficus</i> Ashmead [= <i>C. aonidium</i> (L.) of authors]	Florida red scale ^a
<i>Hemiberlesia lataniae</i> (Signoret)	latania scale
<i>Hemiberlesia rapax</i> (Comstock)	greedy scale ^a
<i>Pseudaonidia duplex</i> (Cockerell)	camphor scale ^a
<i>Quadraspidiotus forbesi</i> (Johnson)	Forbes scale ^a
<i>Quadraspidiotus juglansregiae</i> (Comstock)	walnut scale ^a
<i>Quadraspidiotus ostreaeformis</i> (Curtis)	European fruit scale ^a
<i>Quadraspidiotus perniciosus</i> (Comstock)	San Jose scale ^a
<i>Quadraspidiotus pyri</i> (Lichtenstein)	false San Jose scale
<i>Selenaspidus articulatus</i> (Morgan)	rufous scale
<u>Tribe Parlatorini</u>	
<i>Parlatoria blanchardi</i> (Targioni-Tozzetti)	parlatoria date scale ^a
<i>Parlatoria oleae</i> (Colvee)	olive scale ^a
<i>Parlatoria pergandii</i> Comstock	chaff scale ^a
<i>Parlatoria proteus</i> (Curtis)	proteus scale
<i>Parlatoria theae</i> Cockerell	parlatoria tea scale
<i>Parlatoria ziziphi</i> (Lucas)	black parlatoria scale
<u>Tribe Diaspidini</u>	
<i>Aulacaspis rosae</i> (Bouché)	rose scale ^a
<i>Aulacaspis tegalensis</i> (Zehntner)	sugarcane scale
<i>Carulaspis carueli</i> (Targioni-Tozzetti) [= <i>C. minima</i> (T.-T.) of authors]	minute juniper scale
<i>Carulaspis juniperii</i> (Bouché)	juniper scale ^a
<i>Diaspis bromeliae</i> (Kerner)	pineapple scale ^a
<i>Diaspis boisduvalii</i> Signoret	Boisduval scale ^a
<i>Epidiaspis leperii</i> (Signoret)	Italian pear scale ^a
<i>Fiorinia fioriniae</i> (Targioni-Tozzetti)	fiorinia scale
<i>Fiorinia theae</i> Green	tea scale ^a
<i>Howardia biclavis</i> (Comstock)	mining scale ^a
<i>Ischnaspis longirostris</i> (Signoret)	black thread scale ^a
<i>Lepidosaphes bechii</i> (Newman)	purple scale ^a
<i>Lepidosaphes ficus</i> (Signoret) [= <i>L. conchiformis</i> (Gmelon) of authors]	fig scale ^a
<i>Lepidosaphes gloverii</i> (Packard)	Glover scale ^a
<i>Lepidosaphes ulmi</i> (L.)	oystershell scale ^a
<i>Phenacaspis pinifoliae</i> (Fitch)	pine needle scale ^a
<i>Pinnaspis aspidistrae</i> (Signoret)	fern scale ^a
<i>Pinnaspis strachani</i> (Cooley) [= <i>P. minor</i> (Maskell) of authors]	lesser snow scale
<i>Pseudaulacaspis pentagona</i> (Targioni-Tozzetti)	white peach scale ^a
<i>Unaspis citri</i> (Comstock)	citrus snow scale
<i>Unaspis euonymi</i> (Comstock)	euonymus scale ^a
<i>Unaspis yanonensis</i> (Kuwana)	arrowhead scale

^aEntomological Society of America approved common name.

Parlatoria pergandii to be more numerous in the summer, while *Parlatoria cinerea*, coexisting on the same citrus host, was more abundant in the winter season. A different type of accommodation is found when two species of *Aonidiella* infest citrus simultaneously: *Aonidiella aurantii* occupies all the aerial portion of the tree including trunk and branches, while *Aonidiella citrina* is restricted to the leaves and fruits (46).

McLaren (74) found that in certain areas of Victoria, Australia, red scale remains markedly more abundant on citrus than yellow scale. The intrinsic rate of natural increase (r_m) of red scale was greater at low temperatures than that of yellow scale, although the r_m of the latter was greater during the warmer summer months. The threshold of population development was 15°C for red scale and 18°C for yellow scale, which indicated that during an average year red scale would show a positive population growth rate for approximately ten months compared to six months for yellow scale. McLaren concluded that greater survival and growth rates during the colder months were largely responsible for the preponderance of red scale in these areas.

In some eurymerous species the location of the insect on the host plant may affect its morphological characteristics. Such effects sometimes are so pronounced that individual scales from different parts of the same host formerly were considered to be distinct species and sometimes were placed in different genera. Takahashi (102) recognized that certain Japanese species which had been placed in the genera *Phenacaspis* and *Chionaspis* were, in fact, site-determined morphological forms of the same species. In these species leaf-infesting individuals developed pygideal characters typical of the genus *Phenacaspis*, while bark-inhabiting individuals had the typical *Chionaspis* pygidium. Takagi & Kawai (100) reviewed the Japanese and North American species of the *Chionaspis* group and demonstrated the existence of forms intermediate between the *Chionaspis sylvatica* and *Phenacaspis nyssae* morphs of the species which is now known as *Chionaspis nyssae*. Similarly, *Aspidiotus ancylus* develops in typical form on the twigs of elm and sugar maple, but distinctly different morphological forms of this species develop on the leaves of these hosts. These differences are consistent, and the leaf-infesting forms formerly were considered separate species: *Aspidiotus howardi* on elm leaves and *Aspidiotus comstocki* on sugar maple leaves (97).

In the fig scale, *Lepidosaphes ficus*, the overwintering females on twig wood differed so greatly in size and pygideal characteristics from the summer form found primarily on the leaves that the latter was considered to be a separate species, until biological studies proved otherwise (66, 96). Danzig (34) has also demonstrated the existence of site-determined morphs, which formerly were considered distinct species, in several Russian diaspidids.

Stylet Renewal

A problem of particular interest in the biology of the armored scale insects has been the study of the processes involved in their feeding habits. For an adequate understanding of the mechanisms involved in the stylet penetration into the plant tissue,

it is necessary to examine the various processes related to the renewal of the stylet during the molt.

A diaspidid embryo, shortly before birth, shows the long maxillary and mandibular stylets separately coiled on each side of the head. During birth, the separate stylets travel down from the head, their points converging to meet at the base of the labrum where the stylets coalesce and issue as a single functional organ, the stylet fascicle. As it is extruded from the head, the stylet fascicle is stored as an elongated loop within the crumena, which is a deep membranous, cuticular invagination opening at the base of the labium (83).

The process of renewal of the stylets has been studied in detail by Heriot (56). As soon as the larva has succeeded in introducing the stylet into the plant tissue, the hypodermal cells of the base of the rostrum produce a small fold of tissue that extends like the finger of a glove on each side of the rostrum. The tip of the new stylet, which eventually will serve the second instar, begins to form at the distal end of this fold. As the new stylet is laid down from the tip, the mass of hypodermal cells lengthens out to form, subsequently, a coil in which the core of the new stylet is gradually built up. On completion of the requisite length, the creative hypodermal cells come together at the base of the rostrum to repeat the process for the subsequent instar.

Inasmuch as the stylets are simple, hollow, cuticular structures, they bear a close resemblance to other such cuticular processes. However, once they are inserted into the plant tissue, no withdrawal takes place. Consequently the stylets are never found with other cuticular processes attached to the molted exuviae (113). The old stylets are broken off during molting. Sections through the bark of twigs bearing adult female scales sometimes show the cast-off stylets of the previous two instars in their relative insertion position. The stylets of each instar can be distinguished by their relative lengths and diameters. For example, the new stylets acquired by the second instar of *Lepidosaphes ulmi* are twice the diameter and twice as long as those of the first instar (56).

Penetration of Plant Tissue

Several early workers studied feeding mechanisms of the diaspidid insects (27, 108, 118). Stylet penetration, the role of the saliva during feeding, and the reaction of the host plant, were the main subjects of interest to these investigators. The means by which insects as small as scale insects are able to penetrate even woody plant tissue with elongate hair-like feeding stylets was long considered a major entomological mystery. The explanation of Weber (117), summarized by Snodgrass (95), seems largely adequate, although Pesson (83) has questioned certain details of Weber's explanation as these apply to the Coccoidea and has suggested some modifications. It appears that some of the finer details of the process remain to be worked out.

The four stylets which comprise the stylet fascicle are intimately associated throughout their lengths so that they function as a unit. A cross section of the stylet fascicle reveals that the two mandibular stylets form the outer, lateral elements of the fascicle, enclosing the interlocking maxillary stylets between them. The inner

faces of the maxillary stylets are so formed that their juxtaposition creates two tubular canals which extend the entire length of the fascicle: a larger dorsal food channel and a smaller ventral salivary channel.

Apparently the stylets, the crumena, and the labium each play a part in the mechanics of penetration, and a repetitive sequence of events drives the stylet tips, step by step, into the host tissue. In penetration, the group of protractor muscles at the bases of each of the stylets contract sequentially. First one mandibular stylet, then the other, followed by the maxillary stylets (either together or individually), are advanced equally a short distance. The individually protracted stylets slide along the contiguous surface or surfaces of the others, but the stylet fascicle remains intact, held so by interlocking grooves and ridges in the case of the maxillary stylets, and probably also by the crumena. Pesson (83) has shown that because of its flexible nature the crumenal sac is stretched tightly around the loop of the stylet fascicle in such a way that both efferent and afferent legs of the loop are essentially individually surrounded by the adherent crumenal wall. The crumena, therefore, appears to hold the stylet fascicle together and prevents separation of the individual stylets during protraction. The elastic labial gutter may also play a similar role. The net effect therefore is to transmit the force of protraction to the tip of the protracted stylet without deforming the fascicle loop. When all four stylets have been protracted a specialized clamp-like portion of the labial gutter is closed to maintain the position of the apical portion of the fascicle while the crumenal loop is being shortened. The stylet retractor muscles are then simultaneously contracted and the protractor muscles are relaxed so that the stylet bases are returned to their original positions ready for the next series of protractions. It is the simultaneous action of the stylet retractor muscles, possibly in concert with the labial clamp mechanism, which serves to shorten the crumenal loop while the stylet tips remain in their new position in the host tissue.

Theodoro (108) found that the path of armored scale stylets in leaf tissues traveled parallel to the surface. When an obstacle such as a vascular bundle was encountered, the stylet bundle was withdrawn a little and pushed forward again in a different direction. Heriot (56) suggested that the elm scale inserts its stylets into apple twigs without directing them toward a specific tissue. Sections through the annual growth of scale-infested twigs showed stylets passing straight through the cortex, being turned aside by bundles of pericycle fibers, continuing their course through the phloem, crossing the cambium, and invading immature xylem. He suggested that tissue penetration is very slow in the elm scale as compared to the woolly apple aphid, and that the scales feed on the contents of any cells which the tips of the stylets invade.

Feeding Effects

The feeding sites of armored scales often are associated with depressions, discolorations, and other distortions of host tissues, such as leaf crinkling, etc. Splitting of bark, defoliation, dieback of twig terminals, and sometimes the eventual death of the host may follow heavy infestation. For example, heavy concentrations of *Odonaspis ruthae* were reported to cause the death of Bermuda grass in Arkansas,

while low populations weakened the grass and made it susceptible to pathogenic fungi and winter injury (32). Heavy infestations of two accidentally introduced scales, *Lepidosaphes newsteadi* and *Carulaspis juniperi* destroyed many of the native "cedars" (*Juniperus bermudiana*) of Bermuda (116).

Leaf chlorosis and other localized toxic effects are commonly associated with armored scale infestations. Infestation by *Aspidiotus destructor*, for example, normally is accompanied by pronounced yellowing of affected foliage on coconut and other palms (10). Feeding on citrus leaves by the purple scale produces chlorotic spots around the insects. On the fruit, however, the tissue underneath the scale remains green while the rest of the rind approaches maturity. Likewise, when light-colored fig varieties infested with fig scale are ripening, the portions beneath and immediately surrounding the scales remain dark green as the rest of the fig turns light green and yellowish (96). Green olives infested by olive scale show purple spots which later become more pronounced and turn straw colored as the fruits mature (73). With *Melanaspis bromeliae* on pineapple leaves, Carter (29) reported that the tissue directly beneath the scale was darker green than normal leaf color, forming a dark green spot which was surrounded by a much larger chlorotic ring. Development of the dark central spot began shortly after settling of the crawler on the leaf. The chlorotic ring developed later and eventually became depressed leaving the green center as an elevated island. Carter suggested that such bizonate symptoms are due to the actions of two or more components of the saliva.

The destructive effect produced by the San Jose scale in woody tissue has been investigated by Enser (42). Sections of wood cut through the points of attachment of the insect demonstrate that the stylets penetrate the cortex into cambium. Growth of the pierced cambium ceases or is impaired. If impaired, the associated xylem and phloem cells differ in number, size, and arrangement compared to those in normal tissue. Gentile & Summers (49) indicate that the feeding of San Jose scale on peach twigs produces a characteristic halo-like discoloration which appears 24 hr after the crawlers settle on tender wood. The discolored area increases in diameter with the age of the nymph, the cortical tissue swells with accumulating sap, the bark often cracks, and finally a gradual dessication of the cortical tissue follows.

The formation of plant galls seems to be a relatively uncommon phenomenon associated with feeding by armored scales. The Australian *Maskellia globosa* is unique among diaspidids in that it produces no external scale and develops completely enclosed within globular galls on young twigs of *Eucalyptus* (47). The formation of galls on mistletoe leaves resulting from the feeding action of *Carulaspis visci* has been described by Goidanich (53). Atrophied cells are found in the vicinity of the stylets while hypertrophied tissue develops in the more distal part of the mesophyll. As a consequence, the scale becomes practically embedded in the leaf tissue. In this respect the damage produced is similar to that of the pit scale, *Asterolecanium variolosum*, on oak twig, which is also due to the enzymatic activity of the saliva (82). Information on the nature of enzymes occurring in the saliva of diaspidids is scanty. The invertase activity is greater than that of amylase in both Florida red and California red scales, and salivary composition varies according to the feeding activity and the temperature of development of the insects (60).

THE DIASPIDID DIGESTIVE SYSTEM

Armored scale insects do not excrete honeydew and lack the filter chamber type of digestive system found in most other Coccoidea. In diaspidids the esophagus opens into a large pouch-like structure termed the stomach or first ventriculus (30, 80). This is followed by a second, smaller pouch, termed the Malpighian bulb, into which the two large Malpighian tubules discharge. From the bulb the hind gut empties into an elongate rectum. The stomach is connected to the Malpighian bulb and rectum by several fine ligaments. An unusual anatomical feature of the armored scale digestive system is the apparent lack of continuity between the stomach and the hind intestine. Berlese (13) first observed that the stomach was entirely disconnected from the Malpighian bulb and rectum and correctly described both the bulb and the pair of Malpighian tubes as independent structures, separated from the stomach sac. Childs (30) and Nel (80) disputed these findings and contended that the stomach was indeed connected to the rectum, but later investigators confirmed the validity of Berlese's results (5, 7, 14, 39, 83).

Berlese (13) postulated that the products of digestion diffused from the stomach into the hemolymph and that wastes passed from the hemolymph into the Malpighian tubules and thence into the rectum. Pesson (83) suggested that the Malpighian bulb and rectum possibly have no digestive functions, and that undigested food residues are stored permanently as a fecal meconium in the hind portion of the stomach. However, histological studies in the Malpighian tubes indicate that these structures take an active part in the excretory processes (5, 39). It has been shown that the material excreted through the anus is used in the construction of the scale covering (9, 67, 101).

LIFE HISTORY

In the Diaspididae, as in all Coccoidea, the females are neotenic; except for precocious sexual maturity, the adult female is morphologically a larva. Postembryonic development in armored scales consists of three instars in females and five instars in males (88). *Pracocaspis diversa* apparently is an exception; adult females are said to develop directly from the first instar without any evident second stage (45). Generally, the sexes are indistinguishable morphologically in the first instar, although a few species (e.g. *Pseudaulacaspis pentagona*) exhibit sex-linked color differences during the crawler phase.³ Sexual dimorphism becomes manifest in the second instar. In that stage, differences in the number and distribution of secretory pores, the form of the pygidium, and the development of structures on the pygideal margin are discernible in species in which the sexes have been closely compared (18). According to Van Dinter (113) second instar males of *Chionaspis salicis* can be distinguished from females by the number of abdominal segments discernible; six in females, seven in males.

³Since this manuscript was completed, Stoetzel and Davidson (1974. *Ann. Entomol. Soc. Am.* 67:138-40) have demonstrated chaetotaxal sexual dimorphism in all stages, including the first instar, in representatives of several genera of Aspidiotini.

Toward the end of the second stadium, males become more elongated and show the beginning of ocular pigmentation spots and appendage histoblasts. The third and fourth instars in the male developmental cycle are the nonfeeding prepupal and pupal stages. The pygidium is no longer evident after the second molt, and appendage buds are enlarged. The pupal stage possesses well-defined rudimentary appendages, genital style, eye spots, and the beginnings of the imaginal thoracic sclerites (80). Bodenheimer & Harpez (17) pointed out that the metamorphosis of male Coccoidea is essentially similar to the complete metamorphosis which is characteristic of the holometabolous insect orders.

The life histories of many of the economically important diaspidids have been worked out in detail. In a particular species, the rate of development and the number of generations per year may vary substantially in different regions. Climatic conditions, particularly temperature, humidity, and rainfall, appear to be the principal controlling factors. California red scale, for example, may have anywhere from two to as many as five or six generations per year, the number being greatest in areas of relatively uniform warm, dry conditions, such as Queensland, Australia (16). In California this scale averages about two generations per year in cool coastal areas and slightly more than three generations per year in interior areas with hot, dry summers (40). With the camphor scale, Cressman et al (31) found that rate of development was closely correlated with mean temperature. Under insectary conditions they obtained indices of correlation between length of stadia and mean temperature of 0.98 for the first stadium and 0.96 for the second. These authors used average daily mean temperature as a means of predicting the date of appearance of various stages of this scale in the field.

In areas which are subject to severe winters, only scales of a particular age class may be able to survive. For example, in Quebec the oystershell scale overwinters only in the egg stage; eggs laid in September hatch the following May or June (92). In central Europe the San Jose scale overwinters exclusively as first instar nymphs in the black cap phase of development (at this stage the first instar scale has been completed but the first ecdysis has not yet taken place). This stage is extremely cold-resistant, and all other developmental stages are killed (64). In southern Europe all stages of the scale may overwinter. Melis (75) reported that in areas characterized by mild winters, as in southern Europe, true hibernation does not occur and although development may be retarded by cool weather, it does not cease. Gentile & Summers (49) found that in California's interior valley some scales overwintered as mature females, but many remained as first instar nymphs in the black-cap phase until January. They concluded that the spring brood of new adults originated principally from overwintered first nymphs. Several authors have pointed out that not only low temperatures, but also dormancy of deciduous hosts, may affect the winter development of species such as San Jose scale.

Summer diapause also occurs in certain armored scales. In San Jose scale, for example, it has been shown that a portion of the two overlapping summer generations remains as unmolted first instar nymphs until the end of summer. In California this condition persisted for 40 to 45 days. The factors responsible for the onset of this diapause are not known (49). Summer diapause of adult females has been reported to occur due to detrimental climatic conditions. Purple scale on citrus is

severely affected in the summer by the warm winds blowing in the Mediterranean area, and part of the females, generally those produced by the latest born individuals from the spring generation, enter diapause. These females resume activity in the fall, lay eggs, and produce young which coincide in their appearance with those normally resulting from the third annual generation of the scale (11). Winter adult diapause occurs mostly in univoltine diaspidids, the females entering into diapause before the end of the summer and recommencing activity in the next spring.

From the standpoint of controlling diaspine pests, forecasting the field appearance of crawlers acquires a great significance. Some methods developed require laboratory observations on the maturation of ova. The time of appearance of the arrowhead scale, *Unaspis yanonensis*, can be predicted about two months ahead in the first generation and one month prior to the second generation by observing the blastoderm formation and yolk formation, respectively (103).

REPRODUCTION

Reproduction in most armored scales is bisexual, although several widespread species occur as both bisexual and parthenogenetic races (e.g. *Aspidiotus nerii*, *Hemiberlesia lataniae*, and *Lepidosaphes ulmi*), and some others are known only in the parthenogenetic state (e.g. *Odonaspis ruthae*) (23). Despite some older published reports to the contrary, the occurrence of facultative parthenogenesis in the Diaspididae has not been confirmed.

Species having both uniparental and biparental races perhaps would be better treated as sibling species pairs. DeBach & Fisher (36) tested crawlers of the two such races of oleander scale and found distinctly different responses to temperature. The optimum temperature for the biparental form was 65°F, whereas 75°F appeared optimum for the uniparental form. They concluded that the differential responses of the two forms plus their obvious genetic isolation were sufficient to indicate that sibling species were involved. In Europe, the biparental and uniparental races of *L. ulmi* infest different groups of hosts. Both forms apparently have wide host ranges, but the uniparental race is reported to be the only one which occurs on fruit trees such as apple (109). Danzig (33) noted several biological differences between the two races of this species. The biparental race was the more vigorous, had a wider host range, higher fertility, and a greater resistance to adverse climatic conditions. According to Ferris (44) only the uniparental form of *L. ulmi* occurs in North America.

Adult Male Behavior

Although wingless adult males sometimes occur in a few species (e.g. *Chionaspis salicis*) (51), most armored scale males are winged and are capable of flight. However, they are tiny, fragile, and short-lived. Lacking functional mouthparts they cannot feed and the longevity of this stage generally is limited to a few hours. Development of the two sexes normally is closely correlated so that, in a given brood, adult (fifth instar) males emerge at about the same time that adult (third instar) females attain sexual maturity.

The location of receptive females by flying males probably is largely in response to female sex pheromones, although, to date, pheromones have been demonstrated in only two species, the California red scale (106) and the yellow scale (79). By exposing various dissected portions of virgin females to males, Moreno (78) showed that the probable site of pheromone origin in these scales is a pair of large internal pygideal glands, described by Nel (80), which discharge through a fine duct leading to the anal opening.

Few careful observations on the behavior of adult male scales have yet been published. Tashiro & Beavers (105) showed that longevity in adult males of California red scale was influenced neither by the presence nor the absence of virgin females. Under laboratory conditions male mortality commenced 2 hr after emergence, 50% died within 6–7 hr, and all were dead in 14 hr. Although Bodenheimer (16) believed that males of this scale were nocturnal, Tashiro & Beavers (105) found that males held in complete darkness failed to emerge. Males normally emerged during the late afternoon, apparently under influence of decreasing light intensity, at illumination levels of 350–525 fc. Emergence ceased when illumination fell below 1 fc. Moreno et al (79) suggested that males of yellow scale and California red scale must be exposed to a definite quantum of light (about 8 hr under laboratory illumination) before they are stimulated to emerge.

In dispersal tests, marked males of California red scale were recovered up to 189 m downwind and up to 92 m upwind from release points on traps baited with female pheromone (90). However, males were unable to fly upwind when wind velocities exceeded 1 mph. During colder fall and spring months maximum flight activity occurred just before sunset, and during summer it peaked between sunset and dark. A temperature of 26.7°C and relative humidity (r.h.) of $75 \pm 5\%$ were optimum for male flight under laboratory conditions. In tests with colored cards, significantly greater numbers of marked males were attracted to yellow, but when female pheromone was applied to cards all colors were equally attractive (89, 90). These results suggest that dispersing males may orient toward foliage (color) but that mate-finding is dependent ultimately upon female pheromones.

Mating Behavior

In California red scale (107) the pygidium extends behind the lateral lobes of the thorax in virgin females and can be extended to the edge of the scale covering or, occasionally, slightly beyond. Within 24 hr after mating, irreversible retraction of the pygidium commences, and, after three days, the typical reniform body shape, with lateral thoracic lobes extending posterior to the pygidium, is attained. After being inseminated females become plumper, more turgid, and attached to the scale covering. Also, rotation of the female within the scale cover ceases. During mating males orient themselves on the edge of the scale cover, facing toward its center, and insert the aedeagus under the edge by thrusting it downward and forward. In laboratory tests individual males were able to inseminate up to 30 females and the mean number inseminated was 11.9 per male. Males were able to copulate as soon as they emerged from their scales and there was no apparent difference in mating potential between males allowed to mate immediately after emergence and those

held for up to 4 hr prior to mating. Abundance of females also had no appreciable effect on male mating capacity. Female California red scales mated with as many as eight different males, but multiple matings did not influence their reproductive potential. Virgin females became attractive to males from the time the gray margin of the scale began to be formed (about 23 days after settling) and, if unmated, remained attractive up to a maximum of 107 days old. They were most attractive during the first two weeks after formation of the gray margin began. Within 24 hr after insemination females ceased to be attractive. Males placed with attractive females were capable of mating at any time of day but greatest activity occurred during the period of normal male emergence during late afternoon. The level of illumination apparently had no influence on mating. McLaren (74) reported that delayed mating of overwintering virgin females of this scale caused an initial high spring natality and suggested this was due to continued ovulation in unfertilized females which resulted in a large initial output of crawlers once mating occurred.

Virgin females which are prevented from mating for long periods may exhibit unusual behavior. Ezzat (43) reported that unmated olive scale females produced abnormal elongate scales. Later they exerted their pygidia from beneath the edge of the scale, and ultimately vacated the scale covering entirely. Extension of the pygidium beyond the scale covering was also observed in unmated females of San Jose scale (49) and white peach scale (112). Virgin females of the latter species eventually vacated their scales and produced an anomalous external mass of secretory filaments. The habit of exerting the pygidium may serve to increase the attractiveness of female scales through the discharge of sex pheromones directly into the atmosphere, but vacating the scale entirely does not appear to have any obvious survival value and is difficult to explain.

Sex Ratio and Sex Determination

Published data on sex ratios in biparental armored scales indicate that within a given species considerable variation frequently occurs. Sex ratios often vary with season; for example, widely different ratios have been reported for California red scale at different times of year (63, 80), although when calculated for the entire year the ratio may approach unity (16, 63). Also, individual females within a given population may yield progeny of widely varying sex ratios in some species (e.g. *Aspidiotus simulans*) (25).

The factors which control sex determination, and therefore govern sex ratios in armored scales, are as yet poorly understood. In most armored scales adult males are haploid, yet in all bisexual forms which have been carefully studied unmated females produce no progeny of either sex, thus ruling out the usual type of haploid parthenogenesis. In the white peach scale (24) and in numerous other species (23), males develop from embryos in which the paternal chromosome set is eliminated during early embryogeny, and males continue development as haploids. Other chromosome systems occur in a few species (22, 23) but in every case there is no clear-cut genetic determination of sex. A general explanation for widely varying sex ratios which are encountered among those Coccoidea which lack sex chromosomes (such as the Diaspididae) was offered by Hughes-Schraeder (58) who suggested that

sex may be determined by rather weak genetic factors which are easily overridden by environmental influences. The identification of these environmental influences and how they affect sex determination appears to be a promising area for future research.

In the white peach scale the deposition of eggs by an individual female is sexually dichronistic (12, 24). The insect first produces a series of coral-colored eggs containing female embryos, followed by a series of pinkish-white, male-containing eggs. Furthermore, aging of females prior to mating resulted in a marked increase in the proportion of male progeny produced. In this species it appears that the sex of progeny is predetermined by ovarian conditions which change with aging. Therefore, a scarcity of males which could result in the delayed mating of many females, might be expected to cause a relative abundance of males in the generation following. Sexual dichronisms of this nature have not been reported in other armored scales, but may have been overlooked in forms which lack the easily observed sexual color differences characteristic of white peach scale embryos. Direct effects by external environmental factors on sex ratio in progeny of armored scales have not been well documented, although they probably occur. In the citrus mealybug, which also lacks a clear-cut genetic mechanism of sex determination, relative humidity had a minor influence on sex ratio of progeny of females which were aged prior to mating (61).

DISPERSAL

There are two principal ways by which scale insects spread: by passive transport on infested plant material and as unsettled first instar nymphs (crawlers). Spreading by crawlers generally has been assumed to be limited to relatively short distances, although a recent paper (54) places doubt on the universal validity of this assumption. Long-range dispersal, at least over distances of several hundred kilometers or more, probably almost always results from transport of infested host material, principally in the form of viable propagative stock.

Dispersal by Infested Plant Material

The majority of economic problems involving armored scales result from spread of pest species into new geographical areas, and relatively few species have become serious pests in areas where they are indigenous. Most of the major diaspidid pests have achieved wide geographical distribution through the activities of man. The spread of pest species resulting from transport of infested plant material has been well documented. The San Jose scale, for example, apparently is indigenous to northern China (70). This pest, which spread chiefly on infested nursery stock, now occurs in deciduous fruit-growing areas throughout temperate and subtropical regions of the world (3). Similarly, the California red scale, which probably originated in Southeast Asia, now occurs virtually everywhere citrus is grown commercially (4). The promulgation and enforcement of plant quarantine and nursery inspection regulations has materially slowed the spread of many pest scales. However, despite quarantines, some species have continued to expand their ranges. The olive scale,

for example, was discovered in California near Fresno in 1934 and soon became a serious pest (73). The sugar cane scale, *Aulacaspis tegalensis*, which probably is indigenous to Indonesia, recently has become a serious pest in East Africa where it was unknown until 1946 (2). The coconut scale, *Aspidiotus destructor*, appeared in the Hawaiian Islands for the first time in 1968 (10). These examples, and others, suggest that many pest scales are destined to extend their ranges until they occupy virtually all regions where suitable host plants and favorable climate occur. A single gravid female may be all that is necessary to initiate an infestation. The small size and sessile habits of armored scales make incipient infestations difficult to detect, and usually by the time a scale pest is discovered in a new region it is already too widespread to warrant an eradication attempt; or, as in the case of the olive scale in California, its potential seriousness is not sufficiently apparent to generate the support necessary for an effective eradication campaign (73). That eradication may at times be feasible was demonstrated in the southwestern US with the parlatorial date scale (20). However, the heroic measures which were necessary to eliminate this relatively isolated infestation of a species confined largely to a single host are not often likely to be applied.

Infested plant material can be responsible for local as well as long-range dispersal. For example, Williams (118) has shown that the sugar cane scale may be spread into new fields by planting scale-infested setts. The local spread of pest scales on infested nursery stock has been documented repeatedly.

The probability of armored scales being spread by means of nonpropagative plant material such as fruits, edible tubers, cut flowers, and the like, appears to be low, as establishment requires the chance placement of infested material in close proximity to suitable growing hosts. Schweig & Grunberg (94) found that infested fruit was of little or no importance in spreading Florida red scale in citrus orchards in Palestine, and regarded infested seedlings as the principal means of spread to new areas. Infested fruit piled under clean trees did not result in infestation except where branches were low enough to sweep the ground. These authors believed fallen infested leaves blown by the wind were of greater importance in spreading the scale within orchards than was infested fruit. Similarly, Melis (75, 76), after testing the ability of crawlers to cross exposed soil, concluded that infested fruits were of no importance in spreading San Jose scale unless fruit was placed in direct contact with susceptible hosts.

Crawler Behavior

The unfed first instar or crawler is the primary dispersal phase in the life cycle of all Coccoidea. Although many soft scales, mealybugs, and the like are able to move from one feeding site to another at various times during their developmental cycles, armored scales are incapable of further wandering once they have settled and commenced feeding. Dispersal of armored scale crawlers is accomplished mainly by active wandering and by wind. Occasionally other agencies such as birds, insects, and other animals, including man, may serve as accidental carriers. A report (69) that San Jose scale crawlers fasten themselves to legs and other parts of ants, and are transported in a phoretic manner, needs to be confirmed.

The free-living crawler is possibly the most vulnerable stage in the developmental cycle of most armored scales. Mortality, particularly that due to abiotic factors, must be very high for most species, although data dealing with crawler mortality are few. Oda (81) calculated 89% mortality in crawlers of the white peach scale, while mortality during the period between settling and the onset of oviposition was about 30% of the survivors. The principal hazards which crawlers face include extremes of temperature, low humidity, rain, and lack of suitable settling sites (54, 57). Wind is both a mortality agent and a dispersal agent. Large numbers of crawlers may be dislodged by wind, but a few eventually may be deposited on suitable hosts which they otherwise would be unable to colonize. There are virtually no data available on the viability of wind-borne crawlers, a parameter which has important bearing on the problem of long-range dispersal.

Newly hatched crawlers generally remain sequestered for a time beneath the maternal scale, although this period may be very brief. Jones (63) reported that in California red scale the period between the birth of crawlers and their emergence from beneath the female scale, varied from half an hour to more than two days and was dependent upon external environmental conditions. Delayed emergence coincided with unfavorable climatic conditions such as low temperature or very high relative humidity. Gentile & Summers (49) found that San Jose scale crawlers began to migrate between 2 min and 24 hr after birth, but those which remained beneath the mother for a long period often died without settling. Bliss et al (15) state that crawlers of the camphor scale seldom emerged at night and tended to emerge earlier on warm days than on cool. When the mean temperature between 9 AM and noon was 25°C, 80% of the daily emergence occurred during that time, but when temperature during this period was 31°C, so many crawlers emerged before 9 AM that the portion emerging later in the morning was reduced to 40% of the total.

The dispersal and settling behavior of crawlers following emergence appears to be controlled primarily by three types of factors: 1. innate behavior patterns which initiate wandering and settling; 2. availability of acceptable settling sites; and 3. ambient environmental conditions such as illumination, temperature, humidity, wind velocity, etc. Numerous workers have attempted to measure behavioral parameters such as speed of crawler movement, distance traveled, duration and orientation; and to assess the influences of various environmental factors on these. Much of such work has been based upon laboratory experiments under artificial conditions and the results are sometimes difficult to relate to field situations. The literature is also replete with conjectural explanations for field-observed behavioral phenomena.

The duration of wandering differs from species to species and is influenced strongly by such factors as temperature and humidity, nature of the substrate, and sex of the crawlers. Jones (63) reported that the wandering period of California red scale crawlers in Southern Rhodesia lasted from one half to three days, but that the majority usually settled within one day. In one experiment 91.8% of the crawlers which eventually settled did so during the first day, 8% the second day, and 0.2% in the third day. Bodenheimer (16) suggested that crawlers of this scale which are still wandering after the second day have little chance of settling suc-

cessfully. Gentile & Summers (49) observed that most San Jose scale crawlers settled within 1-4 hr after leaving the mother.

The speed and distances which crawlers travel are highly dependent upon the nature of the substrates over which they move. In laboratory tests on relatively smooth surfaces such as frosted glass or smooth paper, crawlers have been clocked at rates ranging from a few millimeters to a few centimeters per minute (15, 16, 65, 71, 84). Quayle (85) calculated the hypothetical maximum distance which purple scale and red scale crawlers might traverse as 444 feet, assuming a maximum active life of 4 days, an optimum temperature of about 90°F, and a constant speed of about 23 mm per minute. It seems likely that the maximum distance which could be covered by a walking crawler in nature would be far less than this value.

Various authors have suggested that the crawler wandering generally serves to disperse young scales away from the mother onto new growth of the same host (12, 21). Except for wind transport, movement between plants seldom occurs unless the crowns of such plants are in contact (16). There is considerable evidence that diaspidid crawlers can move across sand or bare soil only very short distances and with great difficulty. Mathis (71), for example, reported that Florida red scale crawlers required a minimum of 2 hr to cross a 6 inch circle of sandy soil. Melis (76) found that San Jose crawlers were unable to migrate more than about 1.5 inches over soil. Quayle (85) obtained similar results with California red scale and purple scale crawlers crossing sand, but red scale crawlers were able to travel up to 2.3 feet across a compacted irrigation furrow.

Temperature influences both the initiation and rate of crawling, as well as crawler survival, and probably also affects direction of movement and selection of settling sites. The threshold for crawler activity appears to be between 13 and 20°C in most species studied (48, 71). Bodenheimer (16) states that in California red scale crawler activity occurs between 14 and 39°C, with 25-32°C being the optimum range. He suggested that temperature preferences of settling crawlers may determine distribution of scales within the crowns of trees, and cites California red scale which settles more densely in the shaded inner part of citrus in the hot Jordan Valley than it does in the cooler coastal plain. Florida red scale tends to settle in shaded parts of trees during hot summer months and on sunny parts during cooler periods of the year (94). These findings suggest possible directional responses to temperature gradients on the part of scale crawlers. However, such responses might just as well be attributed to humidity gradients or be due to combinations of temperature and humidity stimuli. Although desiccation would seem to be an important factor in crawler mortality, there have been few studies designed to assess the influence of humidity upon crawler behavior and survival. Greathead (54), experimenting with *Aulacaspis tegalensis* crawlers, showed that both high temperature and low humidity increased crawler mortality; but even under the most unfavorable conditions which he tested (30°C, 30% r.h.), 50% of crawlers survived for 8 hr. He found also that very high humidity inhibited crawler activity in this scale. DeBach & Fisher (36) found that mortality of oleander scale crawlers due to raising the temperature from 65 to 80°F was much greater than that attributable to lowering relative humidity from 80 to

40%. Avoidance of direct sunlight, reported for crawlers of several species (16, 49), may well be a response to high temperature rather than to light.

Light appears to be a major factor influencing the direction of wandering in scale crawlers. Bennassy (11) concluded that, after the temperature threshold had been reached, phototaxis played the dominant role in dispersal of white peach scale crawlers. The two-sexes of crawlers of this species responded differently to light, but in total darkness both sexes tended to settle in the immediate vicinity of the mother. Hulley (59) reported a definite positive orientation toward a directional light source in purple scale crawlers, although the accuracy of orientation was not great. In his experiments an increasing percentage of crawlers responded as light intensity was increased from 0 to about 42 m-candles, when 100% response was obtained. He found no clearcut threshold response to light, and in nondirectional light, crawler movement appeared to be random. Experiments with camphor scale crawler (15) also showed a definite, but somewhat irregular movement toward light. *Aulacaspis tegalensis* crawlers also proved to be positively phototactic, moving upwards toward light during the morning. However, in darkness they moved downward (54).

The nature of the substrate over which crawlers move not only affects the rate and direction of movement, but also has a profound influence on the duration of wandering. In some species it appears that settling behavior may be initiated as soon as a suitable site is encountered, while in others a definite period of wandering appears to be necessary before settling can be induced (11). In scales which utilize crevices, other surface irregularities or contact surfaces, or which normally occur in closely packed aggregations, settling may be induced largely by thigmotaxis (11, 28).

It has been often noted that heavy scale infestations frequently occur in the presence of deposits of dust or other particulate matter on host foliage. The most commonly accepted explanation for this phenomenon is that such particles interfere with the activities of natural enemies (35). Dust particles also affect crawler behavior and, therefore, scale distribution and density. Hulley (59) reported that the average wandering time of purple scale crawlers on dusty orange leaves was 63.8 ± 3.9 min at 28°C, and 91.0 ± 8.8 min on clean leaves. In species with thigmotactically induced settling behavior, such as purple scale, dust patches on foliage may result in crawlers settling where they otherwise would not, and the shortening of wandering time also may result in the settling of crawlers which otherwise might be dislodged by wind (59).

Geotactic responses of scale crawlers seldom have been investigated. In purple scale, no clearcut response could be demonstrated (59). However, McLaren (74) states that the majority of California red scale crawlers settled on upper surfaces of peripheral citrus leaves because of a negative geotaxis. Chemotactic phenomena in scale crawlers also have received little attention. Bodenheimer (16) concluded that citrus odor had a positive effect upon California red scale crawlers causing them to move more rapidly in the majority of his tests, but no directional effect was demonstrated. Tests with purple scale crawlers failed to demonstrate any chemotactic reaction to juices of orange pulp and orange rind (59).

Male and female crawlers of the same species often exhibit different patterns of behavior which result ultimately in separation, or at least nonrandom mixtures, of the sexes on the host. Behavioral differences between sexes have been observed in phototactic and thigmotactic responses, as well as in duration of wandering behavior. Priesner (84) suggested that a differential response to light resulted in the preponderance of male Florida red scales on upper surfaces of leaves where this surface was directed toward light. Geier (48) found that female crawlers of *Epidiaspis leperii* were negatively phototactic and sought sheltered or hidden settling sites in the immediate vicinity of the mother, whereas male crawlers dispersed and eventually settled on young shoots and fruit. In the white peach scale, male crawlers tend to settle quickly after leaving the mother, as soon as a suitable locality is encountered; whereas female crawlers undergo a definite wandering period lasting several hours (11, 12). Brown (21) showed that the average distance traveled before settling was four times as great with female pine needle scales than with males. This explained why nearly all male scales occurred on old growth, while most of the females were on the new growth. Benassy (11) in controlled experiments on white peach scale crawlers showed that females tended to settle in a random manner on the surface of smooth potato tubers, although showing preference for eyes or other surface irregularities. Male crawlers, on the other hand, tended to form definite aggregations. He suggested that after one male crawler settles (usually a thigmotactic response to some surface irregularity), others aggregate with it because of some gregarious instinct. Aggregations of male scales occur in many diaspidids, particularly in genera such as *Phenacaspis*, *Pinnaspis*, and related forms. The nature of the gregarious instinct of these males is unknown. The possibility that pheromones may be involved has not been investigated. Perhaps aggregation results merely from the thigmotactically induced settling of males as, by chance, they encounter previously settled males.

Hulley (59) divided the usual settling behavior of purple scale crawlers on orange leaves into five stages. During stage one, crawlers walked fast with little turning. At the onset of stage two, there was a sudden decrease in speed often accompanied by increased turning. Usually after a short period of stage two crawlers began to walk in a peculiar manner in which the tarsi were put down at almost the same spot where they were lifted. This behavior was accompanied by much turning and little progress in any direction (stage three). After a short time, crawlers came to a complete halt, making only slight pawing movements (stage four). In stage five, final settling, the antennae were folded back against the body and the crawler flattened itself against the leaf surface. The legs were then withdrawn beneath the body and the crawler remained motionless. Within 50 min to 3 hr characteristic wax threads, which indicated the beginning of scale formation, began to appear. Sometimes this sequence was broken at some point with a reversion to an earlier stage of behavior. Thus, even after flattening (stage five), reversion to stage one occasionally occurred.

Wind Dispersal

Air currents have long been recognized as being of probable importance in the dispersal of armored scale crawlers, at least over short distances (as within orchards)

(16, 59, 63). Crawlers of virtually all Coccoidea possess a broad, flat body form and long fine caudal setae. These features appear to be morphological adaptations for maximum buoyancy in air currents, although armored scale crawlers have been observed to use the caudal setae to right themselves when overturned (59). Even though positive trapping data indicated crawlers of other Coccoidea, such as mealybugs and soft scale, (87, 98) were wind dispersed, relatively little attention had been given to this mode of spread in armored scales until recently. In wind tunnel experiments Brown (21) found that crawlers of the pine needle scale traveled a maximum horizontal distance of 72 inches while falling through an average vertical distance of 7.5 inches in a 4.0 km/hr wind. Using the formula for small bodies: distance traveled = (horizontal wind speed/terminal velocity) X initial height above surface, he calculated the terminal velocity as 0.42 km/hr (0.12 m/sec). A vertical component of wind velocity in excess of this value would keep such a body aloft indefinitely. In field trapping experiments large numbers of crawlers were carried for short distances (up to 30 feet) showing the importance of wind in intrastadial dispersal of pine needle scale. Small numbers of crawlers were trapped up to 2.8 km (the maximum distance tested) downwind from the nearest source. Timlin (111) using spaced greased plates to trap windborne crawlers showed that *Parlatoria pittospori* was spread downwind into apple orchards for 250 yards from infested shelter belts of *Pinus radiata*. Data from trapping tests designed to measure aerial density of crawlers of the sugar cane scale, *Aulacaspis tegalensis*, in East Africa (54) showed that crawler distribution conformed to the pattern expected from similar experiments with airborne aphids and the like, i.e. log density was inversely proportional to log height above crop. Below the upper level of the crop the pattern of crawler density was complicated by eddy currents, but tended to approach expected values at higher wind velocities. Crawler density increased with increasing wind speed up to about 2.0 m/sec. Observed departures from expected velocity-density relationships were attributed to reduced crawler activity during periods of very high humidity. Densities of airborne crawlers below the upper surface of the crop ranged between 0.03 and 5.0/m³ and the author concluded that such densities were more than sufficient to explain the spread of scales across roads between blocks of sugar cane. Densities at the crop surface were in the range of 0.1–2.0/m³ and it was calculated that the crawler emission rate from the crop surface ranged between 500 and 2.5 X 10⁶/m²/hr. The previously cited formula employed by Brown to estimate the distance a crawler will be carried does not take into account vertical components of wind velocity. Greathead stated that with turbulent air conditions characteristic of East Africa *A. tegalensis* crawlers, which have a low terminal velocity of 0.12 m/sec, could be carried upward and eventually become distributed to the level of inversion close to the cloud base. He postulated that under certain atmospheric conditions, such as in converging winds associated with storm fronts, airborne crawlers might be concentrated and deposited over a relatively small area some distance from their source. He suggested that such long-range dispersal of airborne crawlers may have initiated *A. tegalensis* infestations at localities 150 and 260 km inland from known infestations on the Kenya Coast. Crawlers of this species appear to possess a distinctive behavior pattern which favors wind dispersal. The crawlers,

most of which emerge during the morning, move upward from infested stalks to cane leaves where part of the population is detached by wind. The remaining crawlers move downward at night and settle on the stalks beneath leaf sheaths. Greathead suggested that behavior patterns favoring wind dispersal may occur in other diaspidid crawlers, particularly those which infest relatively short-lived hosts such as grasses and herbs.

THE SCALE COVERING

A major advance in the evolution of the armored scales was the development of the pygidium, the organ responsible for the formation of the external scale covering (26). The pygidium is composed of the more or less fused and sclerotized posterior abdominal segments. This structure bears the openings of secretory glands of various sizes and shapes, the anus, and usually, variously shaped marginal lobes and special marginal gland spines or flattened fringe plates. All of these structures function in the construction of the external scale. The number, type, and arrangement of these pygidial structures are of paramount importance in the taxonomy of the diaspidids (110). A well-developed pygidium is present in nearly all armored scale insects, although occasionally it is reduced or largely unsclerotized, and sometimes lacks marginal lobes, gland spines, or fringe plates, as in *Protodiaspis agrifoliae* which produces an external scale of unconsolidated filaments. Normally the pygidium includes the fifth abdominal segment (sometimes also the fourth) and those posterior to it, but occasionally it contains no segments anterior to the sixth (e.g. *Ancepaspis* spp.) (45).

The scale coverings of female diaspidids are formed from three basic materials: 1. loose fibers secreted mainly by the pygideal glands, 2. a fluid material discharged from the anus which is thought to bind the fibers together, and 3. the two larval exuviae which are incorporated into the scale at each molt (39). Sometimes fragments of the host plant epidermis also may become incorporated into the scale around its margins (38). The so-called mining scales, such as *Howardia biclavus* and *Psuedaonidia claviger*, bury themselves almost completely beneath the epidermal layer of host twigs and the host epidermis becomes intimately associated with the dorsal scale covering (37). In most species the mature female scale is composed of three distinct segments corresponding to the three instars of the female developmental cycle. The first and second segments consist of secretory products plus the dorsal exuviae of the first and second instars, respectively. The third or outer segment, laid down by the adult female, is composed entirely of secretory materials.

In addition to the dorsal scale most diaspidids also produce a membranous ventral scale which separates the insect from direct contact with the plant surface. The ventral scale is formed of secretions from ventral pygideal glands, plus incorporated ventral exuvial residues. In some Lepidosaphini, the ventral scale forms an internal fold which serves as an incubation chamber (86). In some other diaspidids (e.g. Odonaspidini), it is nearly as thick as the dorsal portion, but in many scales it is extremely delicate or not detectable.

Soon after a diaspidid crawler has settled and inserted its stylets, secretory filaments begin to issue from gland orifices on the pygidium and elsewhere on the body. In the red scale, the material from the pygideal glands is forced out by periodic contractions of the abdomen (9). In the oystershell scale the newly settled crawler produces a mass of thread-like fluff which exudes from abdominal gland spines and pores, and from wax pores in the region of the head. When this secretion is complete only the head region of the insect remains uncovered (92). Subsequently, the body of the insect becomes flattened and the dorsal skin hardens and thickens to form the first scale. Observations on newly settled purple scales indicated that this species first produces two long tangled threads extending from the anterior part of the body, over and around the insect. These threads (presumably produced from a pair of large cephalic ducts which are present in the first instar in the Lepidosaphini and some other tribes) serve to support the more compact covering which is produced later (86).

In describing the formation of the dorsal shield of the red scale, Dickson (38) stated "The insect uses its pygidium much as a plasterer uses a trowel, in this case a self-feeding trowel that continually produces its own plaster." The scale covering is enlarged by the insect "pressing the tip of the pygidium against an area at the edge and slowly shoving outward, building a flatly triangular extension the size and shape of the pygidium. The pygidium is then drawn back, the body rotates, the pygidium is reapplied, and another portion of the edge of the covering extended."

Except for minor modifications due to crowding, irregularities in the substrate, and the like, the form of the external covering is quite uniform within a given species. In general, the shape of the female body is reflected in the form of the external scale, i.e. species with elongate bodies tend to produce elongate scales, whereas short-bodied species tend to produce circular or oval scales. There are exceptions, however (e.g. the circular scale produced by *Aulacaspis greeni*, an elongate-bodied species) (101).

Several workers have discussed the movements executed by the pygidium during the formation of the secretory portions of the scale covering (9, 38, 39, 72, 101). In general these movements appear to be oscillatory in nature, i.e. the pygidium is moved through an arc as the insect pivots around the inserted stylets and the scale is built up of concentric arcuate strips added to the margin. The length of the arcs described by the pygidium and their alignment determines the shape of the scale. In species with long, narrow scales the pygidium describes narrow arcs which are generally aligned in one direction. In the case of circular scales with central or subcentral exuviae, the process of formation has been called rotation by some authors (72), although the insects do not rotate continuously in one direction. Such scales are formed of a series of arcuate segments. Disselkamp (39), describing the formation of the dorsal shield of the female San Jose scale, stated that the pygidium is first rotated through an arc of approximately 320° during which a strip of loose fibers from the pygideal glands is laid down. The insect then agglutinates these fibers with the anal discharge while rotating the pygidium in the opposite direction. During this process one droplet of anal secretion is deposited every one or two

minutes. The sequence is then repeated to lay down additional arcs of scale material. By shifting the starting point of successive arcs, a circular or oval scale eventually is formed. This method of scale formation is somewhat different than the deposition of discontinuous segments described for red scale (38). Takagi & Tippins (101) postulated an evolutionary trend toward forms which produce circular scales by rotational types of pygideal movements. Scales of this type are characteristic of the advanced tribe Aspidiotini but have evolved independently in a few species in other tribes.

The scales of male diaspidids are formed during the feeding stages, which are the first and second instars in that sex. Therefore, only the first stage exuviae are incorporated into the scales. Male scales are smaller and usually distinctly different in shape, and often in color and texture, from those of females of the same species. For example, in many Diaspidini, Aspidiotini, and Parlatorini in which the female scales are circular or oval, the male scales are more or less elongate. In some genera (e.g. *Chionaspis*, *Diaspis*) the surface of the male scales are frequently decorated with one or more longitudinal raised ridges. Disselkamp (39) described differences in the pygideal movements in second instar San Jose scales which resulted in sexual differences in scale shape. In male scales the first bands of secretory material laid down are broad arcs forming a complete ring, as in the female, but later bands cover an arc of only about 180° so that the final resulting scale is oblong.

Information on the chemical composition of diaspidid scale covering is still meager. Many early workers referred to the waxy nature of these coverings. Green (55) for example described the scales as formed of "waxy, fibrous or resinous matter." Manlik (68), while attempting to use wax solvents to improve insecticides for scale control, tested various solvents and concluded the scale covering of *Lepidosaphes ulmi* probably was not a wax. Disselkamp (39) found that the secretory fibers of the shield of San Jose scale were composed of extremely resistant chitin-like secretion products which were insoluble in organic solvents such as xylene, methanol, ether, acetone, and chloroform. These fibers did dissolve almost completely in hot concentrated sulfuric and nitric acids. By paper chromatography, the presence of serine and tyrosine in the fibers was established.

It appears that the scales of most diaspidids do contain at least some waxy materials. Chloroform-soluble substance in the covering of the white peach scale amounted to about 35% (104), and approximately 50% in the Florida red scale (41). Metcalf & Hockenyos (77) extracted the scale coverings of a number of species with hot carbon tetrachloride and found that waxes accounted from 31 to 58% of the weight of the scales tested. Dickson (38) reported that the covering of California red scale was about 45% waxes, 47% proteinaceous material, and 8% exuviae.

The nonwaxy fraction has been found to be proteinaceous in nature and does not contain chitin, except for the exuviae incorporated into it. Spectrophotometric studies in Florida red scale showed that the scale material contained 3.7% nitrogen, and amino acids accounted for only 15% of the total weight. The nonwaxy component did not contain DNA, RNA, or carbohydrate. The bulk of this fraction was composed of material with a molecular weight of at least 200,000, and its chemical composition was similar to that of melanin and polyphenol polymers. The possible

identification of a polyphenol polymer suggests that hardening of the shield may result from enzymatic polymerization of tyrosine (41).

The amount of polyphenol polymers must undoubtedly vary among the various species, as reflected by the different quality and texture of the shield. Very little information exists on the density and permeability of the scale covering. The production of waxy filaments coming through the shield in young stages is considered to be a result of the scale permeability. The diffusion of plant volatile materials through the shield of the fir scale, *Dynaspidiotus abietis*, has been reported by Goidanich (52).

PUPILLARIAL FORMS

In several specialized genera (e.g. *Ancepaspis*), females do not shed the exuviae during the second molt, but remain enclosed within the hardened second stage skin. Such species are referred to as pupillarial or exuvial. Glandular structures associated with scale formation are often much reduced or absent in pupillarial species, except in the second stage males which produce a scale of normal form (26). It appears that in most pupillarial species the second stage exuvium is ruptured along its posterior margin by the mature female within to accommodate mating and the egress of the crawlers. In several species of *Ancepaspis*, the pygidia of mature females are exerted from the second stage exuviae. In such forms the posterior parts of the pygidia are strongly sclerotized with pronounced, tooth-like, apical lobes (26). In species of *Fiorinia* the pupillarial females generally retain a few glandular pygideal structures and may make some secretory additions to the second stage exuviae (44). Species of *Protodiaspis* are semieuxual, as the adult female is partly, but never completely, enclosed within the second stage molt which fragments or ruptures in the normal fashion (26).

Brown & McKenzie (26) presented evidence that pupillarial or partly pupillarial forms such as *Ancepaspis* and *Protodiaspis* represent a specialized, derived condition rather than a primitive ancestral one.

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