1.1.8 Phylogeny

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The phylogeny of the armored scale insects poses some truly fascinating questions. One of the more intriguing, and probably the most critical, centers around the sequence of events that led to the development of a scale cover and the evolutionary consequences of this structure. It is possible to envision a gradual shift from an adult female that occurs primarily under or inside of the exuviae of previous instars, to one that produces small amounts of wax attached to the exuviae, and finally to one that produces a large waxy scale cover that has small exuviae. Certainly, other scenarios are possible. With the development of the cover, there must have been changes in the pheromone delivery system for communication with the male, in the manner in which the male copulated with the female, in the way that crawlers escaped from the adult female scale cover, in the production of waste products, in the manner that such products are eliminated, etc.

REVIEW OF LITERATURE

The following chapter is a general overview of the phylogeny of armored scale insects. A review of research on Coccoidea phylogeny was presented by Miller and Kosztarab (1979) and will not be repeated here. It is our intention to concentrate our analysis on the armored scale insects and their relatives. Recent studies by Boratynski and Davies (1971), Davies and Boratynski (1979), Danzig (1980), Miller and Davidson (1981), and Miller (1983), use objective and repeatable methods of analysis that serve as a basis for developing useful hypotheses of relationship.

The characteristics that define the Diaspididae are problematical only in the more primitive forms. For most of the family these characters are clear and consistent. Characters that usually allow recognition of adult female armored scale insects include the occurrence of exuviae in the scale cover, absence of legs in the second instar and adult female, and the presence of a pygidium with specialized wax-producing and wax-molding apparatus such as lobes, gland spines, plates, and macroducts. According to Ghauri (1962), adult males are characterized by having the head fused to the thorax, absence of the tentorium except rudimentary tentorial pits, heavy sclerotization of the penial sheath forming a continuous capsule, lack of sclerotization on the head apart from ridges, near-absence of sclerotization on the abdomen, and rudimentary propleural and metapleural apophyses. Problem areas appear in diaspidoid genera such as *Ancepaspis*, *Colobopyga*, *Comstockiella*, *Halimococcus*, *Phoenicococcus*, *Protodiaspis*, *Thysanococcus*, and *Xanthophthalma*, and appear in the asterolicaniid genus *Mycetococcus*. It is interesting to note that several of these genera are pupillarial.

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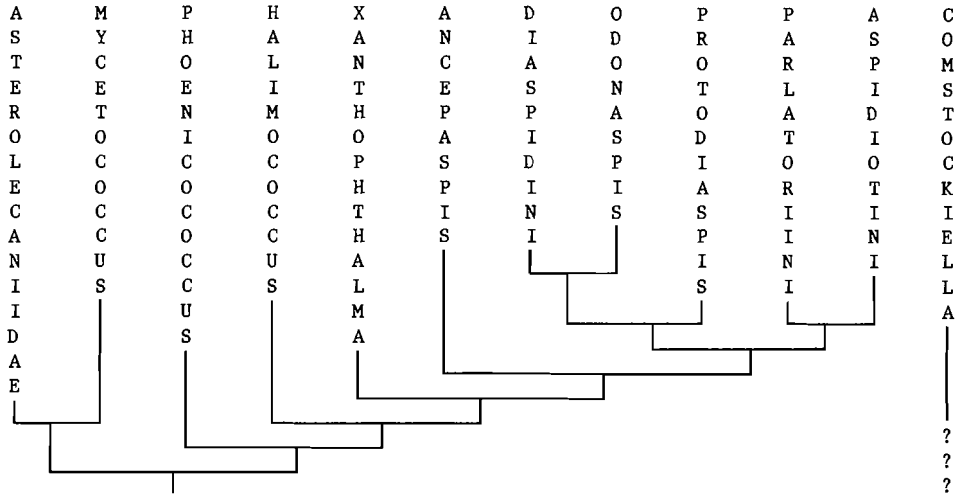

Fig. 1.1.8.2. Dendrogram of armored scale insect phylogeny according to Brown and McKenzie (1962).

Leucaspidini and the Parlatoriini and of the Aspidiotini and Parlatoriini; (2) the rank of the Chionaspidina; (3) the placement of *Rhizaspidiotus*. His dendogram is given in Fig. 1.1.8.1. It is interesting that Ghauri considered the Parlatoriini to be more closely related to the Aspidiotini than to the Diaspidini.

Brown and McKenzie (1962) were the first to examine the evolutionary patterns of armored scale insects as a topic in its own right. Their analysis is thought-provoking and points to the interesting, though confused, area of the primitive groups of diaspidoid scale insects. With Brown's detailed knowledge of armored scale insect genetics, an independent data set was added to the armored scale insect evolutionary hypothesis. The 'putative phylogeny' presented by Brown and McKenzie has been reorganized so that it is comparable to the other dendrograms presented in this review (see Fig. 1.1.8.2).

Asterolecaniids were believed to be most closely related to the diaspidoid groups. Evidence is given for the sequence 'Diaspidini to Parlatoriini to Aspidiotini,' from primitive to advanced. Placement of *Ancepaspis*, *Anotaspis*, *Comstockiella*, *Odonaspis*, *Protodiaspis*, and *Radionaspis* was considered to be very tentative. *Xanthophthalma* was treated as an annectent armored scale insect based on the existence of the first and second exuviae that are attached to the posterior portion of the body (please note that this is in conflict to my observations given at the end of this paper), but they pointed out the absence of several diaspidid characters such as a pygidium and scale cover, and the presence of 16 chromosomes. The occurrence of 'geminate pores,' a naked body, 16 chromosomes, and no pygidium were used to show similarity with asterolecaniids. Data were given for the distinctness of *Phoenicococcus* from the rest of the group treated by Stickney (1934) as part of the Phoenicococcidae. The suggestion was that these genera (*Colobopyga*, *Halimococcus*, *Palmaricoccus*, and *Thysanococcus*), be treated as halimococcids and that *Phoenicococcus* and *Xanthophthalma* be treated as phoenicococcids (note that the latter is paraphyletic). The paper pointed to the general trends: (1) in sex-determining systems from lecanoid to comstockiella to diaspidoid; (2) from large chromosome numbers to small; (3) from no scale cover to a cover that incorporates the exuviae. Brown and McKenzie (1962) also discussed the occurrence of pupillarial forms in the three major tribes and suggested that this character developed independently on several occasions.

The paper by Brown (1965) further developed the ideas of Brown and McKenzie (1962) and reported on a survey of the chromosome systems of 140 species of armored scale insects and phoenicococcids. The survey indicated that the

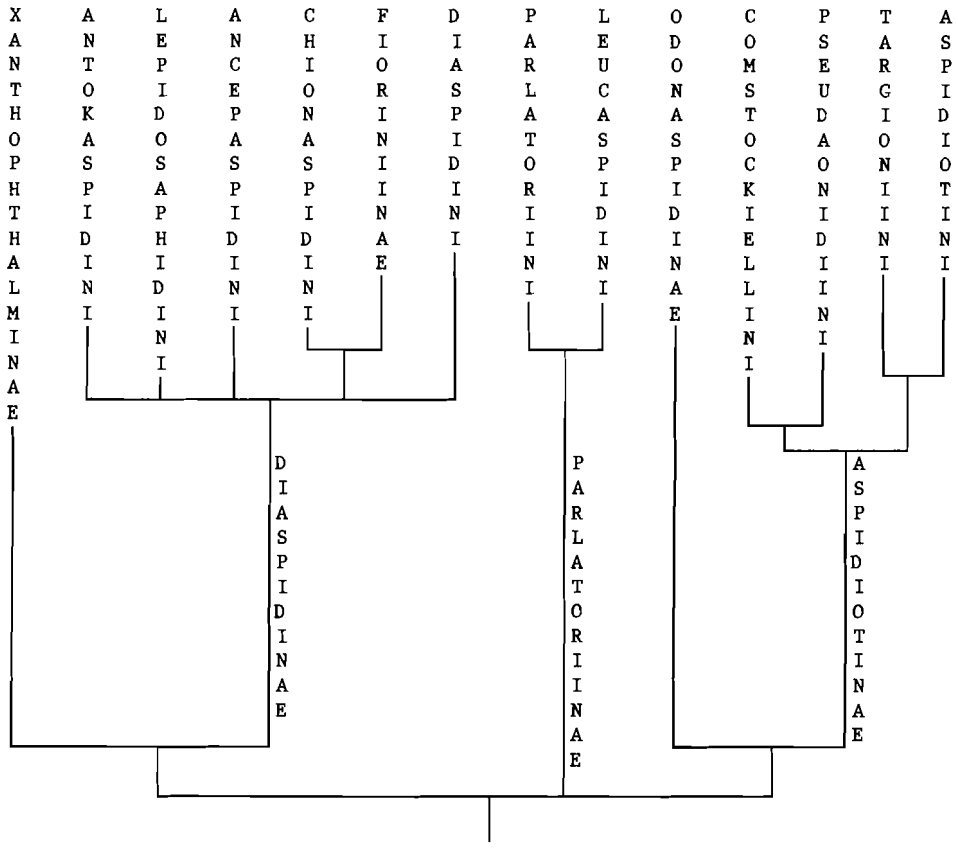

Fig. 1.1.8.3. Dendrogram of armored scale insect phylogeny according to Borchsenius (1965).

comstockiella system or comstockiella–lecanoid systems were primitive and were the only sex-determining systems in the Parlatoriini, Odonaspidini, and 'phoenicococcid' genera *Ancepaspis*, *Colobopyga*, *Halimococcus*, *Phoenicococcus*, *Platycoccus*, and *Thysanococcus*. The diaspidid system was confined to the Diaspidini and Aspidiotini although each of these tribes has a few peculiar members with the comstockiella system. The diaspidid system was independently derived on at least two occasions. The basic chromosome number for diaspidids was eight and was predominant in the Diaspidini, Parlatoriini, Odonaspidini, and Aspidiotini. *Xanthophthalma* and *Phoenicococcus* have 16 chromosomes, *Comstockiella* has ten, as do *Colobopyga*, *Halimococcus*, *Platycoccus*, and *Thysanococcus*, and *Ancepaspis* has six or eight. Although Brown suggested the possibility of a pupillarial ancestor of the armored scale insects, he discounted the idea since he could not envision independent evolution of the scale cover and the series of plates, wax glands, and lobes that form the cover.

The study of Borchsenius (1965) gives a very detailed classification of the armoured scale insects, dividing many of the groups mentioned by Ferris and Balachowsky into subtribes. Although the system is intuitive, it relied on Borchsenius' perception of phylogenetic relationships and presented several interesting observations concerning armored scale insect evolution not considered by previous authors. His system of armored scale insects (subtribes not included) is given in Fig. 1.1.8.3. Note that the general order of taxa on the tree is similar to the dendrograms of previous authors, but the root is located between the Diaspidinae and Aspidiotinae with the Parlatoriinae being more basal. This is similar to the tree of Ghauri, although he considered the Aspidiotini and Parlatoriini to be sister groups; Borchsenius tentatively con-

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sidered the parlatoriines to be basal, the sister group of a combined unit of the odonaspidine-aspidiotines. Although his dendrogram did not depict the Xanthopthalminae as the most primitive group of armored scale insects, he did state this belief in the text.

Borchsenius depicted the primitive armored scale insect as one that lacked a pygidium, did not produce a definite scale cover, used the relatively large 1st and 2nd-instar exuviae as a cover, and had a small adult female that was elongate and laid few eggs. The scale covers of primitive groups that contained wax were characterized as constructed of loosely congealed wax, unlike the solid covers of the more-advanced groups. Male covers were considered to be primitive if they resembled the cover of the female; the advanced forms have ridges and are of a different texture than the female. The adult males were considered to be more conservative in their evolutionary change since they are not subject to as many of the changing conditions of the environment as are the females. He supported the belief that pupillarial forms have independently evolved on several different occasions.

The study of Takagi (1969) included a general discussion of his higher classification system of armored scale insects and gave a detailed description of its phylogenetic basis. Information on adult females, second-instar males and females, and first instars was given in considerable detail. Unfortunately, it is difficult to organize this information into a dendrogram consistent with Takagi's discussion. His classification system is as follows:

- Family Halimococcidae (including *Halimococcus*, *Thysanococcus*, *Colobopyga*)
- Family Diaspididae
  - Group Diaspididae parlatoriformes
    - Tribe Leucaspidinii (*Leucaspis*, *Lopholeucaspis*, etc.)
    - Tribe Parlatoriini (*Parlatoria*, *Parlatoreopsis*, etc.)
    - Tribe Rugaspidiotiini (*Rugaspidiotus*, *Discodiaspis*, etc.)
    - Tribe Odonaspidini (*Odonaspis*, *Circulaspis*, etc.)
    - Tribe Aspidiotini (*Aspidiotus*, *Aonidiella*, etc.)
  - Group Diaspididae lepidosaphidiformes
    - Tribe Diaspidini (*Diaspis, Carulaspis,* etc.)
    - Tribe Lepidosaphidini (*Lepidosaphes, Andaspis,* etc.)

He discussed the following character systems as important in evaluating 'evolutionary patterns' in the Diaspididae: abdominal disc pores; spiracular disc pores; tubular ducts in the crawlers, second-stage males, and adult females; number of antennal segments in the crawler; number of setae on the antennae of the adult female; marginal processes on the abdomen with emphasis on the plates, gland spines, and lobes; sexual dimorphism in second instars; and cytological information. He was uncertain of the placement of *Ancepaspis*, *Comstockiella*, *Costalimaspis*, *Crassaspis*, *Nicholiella*, and *Radionaspis*. Although it is placed in the Aspidiotini, he pointed to unusual characteristics of *Furchaspis*. He reiterated the position of others that the pupillarial forms developed independently on several occasions. He suggested that there are two main stocks in the armored scale insects, one that includes the Parlatoriini and Aspidiotini (the Diaspididae parlatoriformes stock) and a second that includes the Diaspidini and Lepidosaphedini (Diaspididae lepidosaphediformes stock). Within the former, the Leucaspidini was most similar to the ancestral form of the lineage although he did not believe that this ancestor was pupillarial. The ancestor had three processes on the margin of each abdominal segment, and these processes developed into gland spines, plates, and single and double lobes through evolutionary time.

The presentation of Boratynski and Davies (1971) used the data of Ghauri

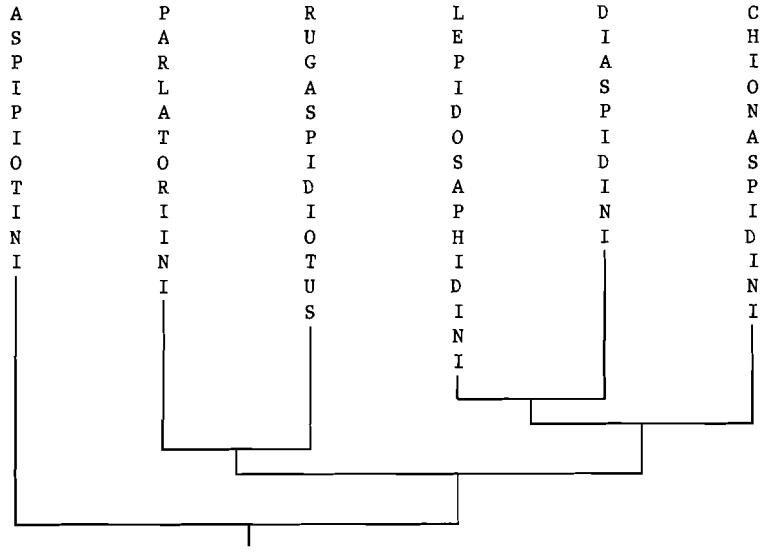

Fig. 1.1.8.4 Dendrogram of armored scale insect phylogeny according to Boratynski and Davies (1971).

(1962) and analyzed it with a series of phenetic methods. Although no phylogenetic implications were intended, dendrograms and principal component clusters were given to show total similarity relationship. Results of an average linkage analysis is illustrated in Fig. 1.1.8.4. Note that the Parlatoriini is more closely related to the Diaspidini than to the Aspidiotini and that *Rugaspidiotus* is closer to the parlatorines. A distance coefficient phenogram is given in Fig. 1.1.8.5. In this case the Parlatoriini is more closely related to the Aspidiotini, and *Rugaspidiotus* is basal to all of the other armored scale insects.

The principal component analyses give similar answers. There were three distinct clusters of species, i.e., the Parlatoriini, Aspidiotini, and Diaspidini. The relative position of *Rugaspidiotus* was variable; it formed a 'cluster' independent of other species. In the general discussion of 'probable relationships, Boratynski and Davies considered the Conchaspididae to be the ances-

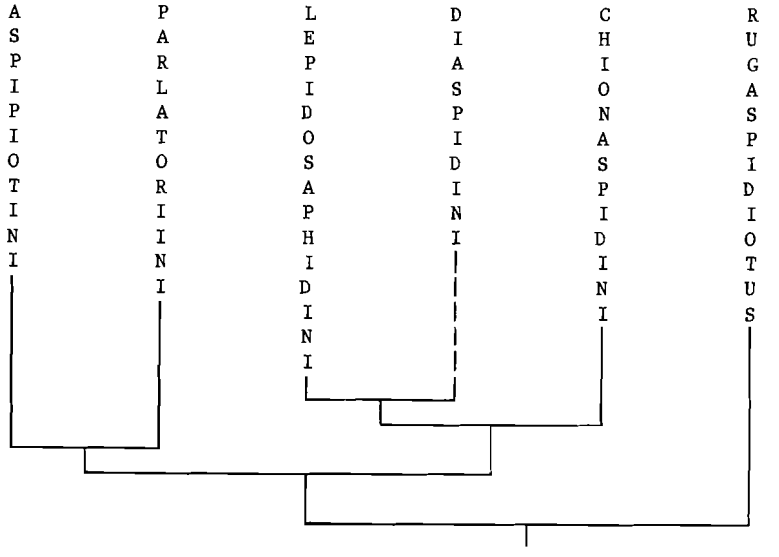

Fig. 1.1.8.5. Distance coefficient phenogram relating the Parlatoriini more closely with the Aspidiotini (cf. Fig. 1.1.8.4).

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tors of the armored scale insects, although the possibility of an asterolecaniid ancestor was suggested. It is interesting that they considered the Phoenicococcidae to be more advanced than the Diaspididae.

CURRENT RESEARCH

A study currently is under way to make a detailed phylogenetic analysis of the diaspidoid groups and their relatives. The character systems involved will include morphological features of the adult females, first instars, second instars, adult males, and available data on life history and chromosome systems. Unfortunately, this project is in a preliminary state and therefore, only general observations will be discussed here.

The analysis is being performed using the PHYSYS program of Farris and Mickevich. Representative species (number in parentheses) of 33 higher-level taxa were analyzed; where placement of a species into a higher-level taxon was questionable, the species was treated as a separate entity. The taxa treated are: *Ancepaspis* (4) (Diaspididae); Aspidiotini (3) (Diaspididae); *Asterolecanium caudatum, As. proteae* (Asterolecaniidae); *Beesonia dipterocarpi* (Beesoniidae); *Cerococcus* (4) (Cerococcidae); Chionaspidini (5) (Diaspididae); *Colobopyga attaleae* (Halimococcidae); *Comstockiella sabalis* (Diaspididae); Conchaspididae (2); Diaspidini (3) (Diaspididae); Eriococcidae (10); *Fagisuga triloba* (Conchaspididae); *Fiorinia* (3) (Diaspididae); *Halimococcus borassi, H. lampas* (Halimococcidae); Lecanodiaspididae (6); Lepidosaphidini (6) (Diaspididae); Leucaspidini (5) (Diaspididae); *Melanaspis* (2) (Diaspididae); *Mycetococcus* (2) (Asterolecaniidae); Odonaspidini (11) (Diaspididae); Parlatoriini (3) (Diaspididae); *Phoenicococcus marlatti* (Phoenicococcidae); *Platycoccus tylocephalus* (Halimococcidae); *Pollinia pollini* (Asterolecaniidae); *Protodiaspis* (3), *Pr. colimae* (Diaspididae); Rugaspidiotini (2) (Diaspididae); *Thysanococcus chinensis, T. pandani, T. squamulatus* (Halimococcidae); *Xanthophthalma concinnum* (Diaspididae). At the present time, 70 characters have been examined including morphological data from adult females, first instars, and second instars. Decisions on character-state polarity were made using the Eriococcidae as the outgroup.

Based on a preliminary analysis that produced three, equally parsimonious, trees, the conchaspidids (including *Fagisuga*) form the sister group of the remaining taxa in the study (excluding the eriococcid outgroup). The asterolecaniid groups (*Asterolecanium*, Cerococcidae, Lecanodiaspididae, *Pollinia*) form a monophyletic unit that is the sister group of the diaspidoids plus *Mycetococcus* and *Beesonia*. There is no clear break that sets the 'typical' diaspidids (those groups currently considered to be armored scale insects) apart from the seemingly annectent groups. *Mycetococcus* is closely related to *Phoenicococcus* and does not seem to belong in the Asterolecaniidae. The general sequence from primitive to advanced taxa is not worked out well enough to be presented in any detail, but the current overall pattern is similar to that suggested by other authors. The sequence of taxa from halimococcids to typical diaspidids includes a series of intermediate steps that gives reasonable data on transitional phases of some characters. For example, most halimococcids lack any special wax-forming structures that are homologous to the wax-forming structures on typical diaspidids (although some species of *Colobopyga* have large flattened setae on the posterior body margin that may serve the same function as lobes on typical armored scale insects); however, one species, *Thysanococcus squamulatus*, has projections on the pygidium margin that appear to be homologous to gland spines. Apparent annectents between gland spines and plates occur on *Melanaspis, Furchaspis,* and *Crenulaspidiotus*. There is a reasonably clear sequence of anal-opening transition from a ring

with several setae, to one with only one or two very small setae, to one without setae.

The sequence that led to the development of the scale cover is not obvious, and needs further study. There are a few clues that, hopefully, can be pieced together with a detailed phylogenetic analysis.

(1) Most of the primitive, pygidium-possessing scales are pupillarial, suggesting the possibility that pupillarial forms were ancestral to armored scale insects. Detailed analysis is required to ascertain homologies of pupillarial forms. It seems clear that the pupillarial condition has arisen more than once; there are distinct differences among pupillarial groups in regard to completeness of enclosure of the adult female, methods of escape of crawlers, production of wax, structure of the anal area, etc. Of the typical armored scale insects that also are pupillarial, *Ancepaspis* appears to be the most primitive. It is interesting to note that, in some species of *Ancepaspis*, the first-instar exuviae remains attached to the second-instar female, while the first-instar exuviae of the male is incorporated into the scale cover. There is a striking similarity between certain species of *Protodiaspis*, which is not pupillarial, and *Ancepaspis*.

(2) *Xanthophthalma concinnum* is small in size compared with typical armored scale insects; the cover usually is composed of two exuviae with a narrow waxy area around the perimeter. The surface of the exuviae is noticeably rough, with distinct segmentation. The second instar produces a white, almost filamentous, secretion around the edge of the body. The adult female apparently adds to this secretion, but the first instar contributes little or no secretory material. The exuviae of the first instar may or may not remain attached to the cover, but the second-instar exuviae is an integral part of the cover. The adult female is clearly visible through the dorsal surface of the second exuviae and the head and thorax of the adult remain inside the exuviae. The ventral portion of the second exuviae is absent posteriorly, and the protruding portion of the abdomen of the adult is covered by the white wax that surrounds the second exuviae. The exuviae of the first instar is only slightly smaller than that of the second instar, and the same is true of the second exuviae and the adult female.

(3) The cover of species of *Parlatoria* is similar to *Xanthophthalma* except that the exuviae and body of the adult female are relatively large, the wax is not filamentous, the surface of the exuviae is smooth, and the exuviae of the second instar splits along the juncture between dorsum and venter.

(4) The cover of *Comstockiella* is quite different from other diaspidoid scales. A smooth waxy cover is produced by each of the instars and at first glance appears like the cover of most typical armored scale insects. However, close examination of the cover reveals that the exuviae are not visible on the surface. When slide preparations are made of the cover, there appears to be no particular pattern of incorporation. The exuviae apparently do not serve any important function in the cover and appear to be incorporated accidentally. The first exuviae is nearly always part of the cover, but the second exuviae usually is separate.

CONCLUSION

It seems likely that the diaspidoid scale insects are closely related to the asterolecaniids. The annectent forms such as the halimococcids, phoenicococcids, *Ancepaspis*, *Protodiaspis*, and *Xanthophthalma* have not been studied sufficiently to definitely establish their position in the diaspidoid classification system, but it is clear that they are basal lineages in the phylogeny of the group. In addition to completing a detailed phylogenetic analysis of the diaspidoids,

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it will be of value to concentrate research efforts on the diaspidoids of palms since most of the annectent forms occur on these hosts, including the halimococcids, phoenicococcids, *Xanthophthalma*, and *Comstockiella*. There are two different types of annectent scale covers, the comstockiella type and the xanthophthalma type. There seem to be many similarities between the xanthophthalma cover and the parlatorine and diaspidine cover, whereas the comstockiella cover seems to be closer to the aspidiotine cover. The significance of these similarities must await further analysis with the question of scale cover evolution left as a puzzling but intriguing area of inquiry.

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