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TWO NEW SPECIES AND ADDITIONAL COLLECTION RECORDS FOR THE GENUS PROTODIASPIS

(Homoptera: Coccoidea: Diaspididae)

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EVOLUTIONARY PATTERNS IN THE ARMORED SCALE INSECTS AND THEIR ALLIES

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CONTENTS (First Paper)

INTRODUCTION 133
DESCRIPTIONS OF TWO NEW SPECIES 133
Protodiaspis chichi McKenzie and Nelson-Rees, new species 135
Protodiaspis didymus McKenzie and Nelson-Rees, new species 137
ADDITIONAL COLLECTION RECORDS 137
ACKNOWLEDGMENTS 139
LITERATURE CITED 139

CONTENTS (Second Paper)

INTRODUCTION 141
TAXONOMIC REVIEW 141
CYTOLOGICAL REVIEW 143
Lecanoid System 144
Diaspidid System 144
Comstockiella System 144
Variable-D Comstockiella Systems 146
Compound Lecanoid-Comstockiella System 146
Evolutionary Sequence of Chromosomal Systems 147
Correlation of Taxonomy and Chromosome System . . . 148
THE GENERA *PROTODIASPIS* AND *ANCEPASPIS* . . 151
Pores 153
Gland Spines 153
Lobes 155
Ducts 155
Pygidial Structures 155
Exuviation 157
PHOENICOCOCCUS AND THE ASTEROLECANIIDAE . 161
XANTHOPHTHALMA 162
THE TRIBES OF THE DIASPIDIDAE 163
The Odonaspidini 164
Pupillarial Forms 165
Comstockiella 166
CONCLUSIONS 167
SUMMARY 168
LITERATURE CITED 170

EVOLUTIONARY PATTERNS IN THE ARMORED SCALE INSECTS AND THEIR ALLIES (Homoptera: Coccoidea: Diaspididae, Phoenicococcidae, and Asterolecaniidae)[1, 2]

SPENCER W. BROWN[3] and HOWARD L. McKENZIE[4]

INTRODUCTION

THE ORIGIN of the armored scale insects and the nature of the evolutionary trends within the group are problems of considerable complexity. The progression of evolutionary changes depends in part on the sustaining genetic systems. Recent studies of chromosome behavior in the armored scale insects and various other coccids have shown a diversity in this regard which implies first a diversity of genetic systems and, in turn, varying potentials for evolutionary change.

The purpose of the present report is to offer a re-evaluation of the morphological diversity as it is at present interpretable from the chromosome studies. These latter not only enable an immediate visualization of the mode of transmission of the hereditary factors, but also a picture of the chromosomal evolutionary sequence which affords another clue to ancestry and relationship irrespective of the evolutionary potentialities of the individual chromosome systems.

The method which will be followed in the present study is an analysis of the evolutionary patterns of the "higher categories" such as tribes and subfamilies and those of two problem genera, *Ancepaspis* and *Protodiaspis*, which were selected on the basis of their morphological similarity and chromosomal differences. It is believed that analysis of both "higher" and "lower" categories will lead to some measure of understanding of evolutionary patterns in the group as a whole. This information will then be in part applicable in a taxonomic reclassification of the groups concerned, and suggestions for such a revision will be offered under "Conclusions."

A proper appreciation of the problems in question requires some consideration of technical details of both taxonomy and cytology. It seems advisable, therefore, to submit these in special introductory sections. The one on taxonomy. which follows immediately, will be confined to that subject, but the cytological review will consider some of the applications that have so far been possible in problems of evolution and taxonomy.

TAXONOMIC REVIEW

With the elevation of the coccids to the rank of superfamily, the Coccoidea (Ferris, 1937;[5] Balachowsky, 1942), the various subdivisions also became

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[5] See "Literature Cited" for citations, referred to in the text by author and date.

elevated. Ferris (1937) recognized eleven families, of which one was the family of armored scale insects, the Diaspididae, equivalent to the Diaspinae or Diaspidinae of earlier authors. Balachowsky (1942) divided the superfamily into three sections, the Margaroïdae, the Lecanoïdae, and the Diaspidoïdae; in the last section he included as families the armored scale insects proper or Diaspididae and the closely allied palm scales or Phoenicococcidae, which Ferris (1937) had classed as subfamilies of the Diaspididae. Balachowsky's recognition of the major subdivisions of the coccids has been largely confirmed by recent chromosomal studies (Brown, 1959). In addition, his ranking of the categories seems to be the more acceptable one, and will therefore be followed in the present report.

Within the armored scales, Ferris (1937) recognized four tribes: the two major tribes, the Diaspidini and Aspidiotini, the relatively small Odonaspidini, and the monotypic Xanthophthalmini. Following several earlier workers, Balachowsky (1948) admitted an additional tribe, the Parlatorini, which included genera previously placed by Ferris in the Diaspidini. In his revision of *Parlatoria* and certain allied genera (nonpupillarial), McKenzie (1945) preferred to maintain these within the Diaspidini while acknowledging them to be a rather definitely distinct series of genera. The present report will not be concerned specifically with taxonomic definitions, and it is not our problem at the moment to weigh the merits of recognizing the Parlatorini as a separate tribe. However, the Balachowsky (1948) classification will be employed for ease in dealing with the phylogenetic relationships of this series of genera among the diaspidid tribes.

In his monograph on certain palm-infesting scales whose relationships had previously been obscure, Stickney (1934) proposed their inclusion in the subfamily Phoenicococcinae of the Diaspididae. This group was obviously highly specialized, on a par with the armored scale insects and the asterolecaniids. Although Stickney believed the palm scales might form a connecting link between the asterolecaniids and the armored scales, his conclusion was not generally accepted.

Taxonomists have generally agreed that the armored scales and palm scales are the most specialized of all coccids, that these two groups are probably closely related, and that the armored scales themselves are subdivisible into four or five tribes which are more or less natural groups.

There has, on the other hand, been no clear picture of the origin of the armored scales or palm scales. Balachowsky (1942), in a phylogenetic diagram, seconded Stickney's suggestion of asterolecaniid derivation, while Ferris (1957) and Mamet (1954) have favored the conchaspidids as putative ancestral types. Thus, no clear concept has emerged of an ancestral type or primitive form from which the various morphological types of armored scales and palm scales could be pictured as emanating. Even if a sequence of variation had become apparent, there would have been no way of "tying down" one end through comparison with the presumed primitive forms.

Within the armored scales the two major tribes seem, with few exceptions, to be natural groups. The existence of such genera as *Comstockiella,* which Ferris (1938) placed in the Aspidiotini while noting its anomalies, indicates a diversity which may not have merited the erection of further subdivisions

but is of significance for the evolutionary pattern. Balachowsky (1948, 1950, 1951, 1953, 1954) has proposed subtribes for all the diaspidid tribes except the monotypic Xanthophthalmini, while Ferris frequently comments on the apparent close relationship of two or more genera. Within each of the tribes there are thus clusters of similar genera which may be presumed to have a common origin. Unfortunately, Balachowsky's work was largely restricted to European and North African forms, so that the application of his subtribal classifications elsewhere in the world may not always be readily made.

It would be unfair to end this brief review without mentioning the one evolutionary process which has plagued taxonomists throughout the entire superfamily, and this is the process of reduction and loss. Two insects stemming from quite unrelated and quite distinct forms may come to resemble each other closely following the loss of characteristic anatomical structures. This problem becomes especially grievous when the further attempt is made to assign the forms under consideration to an evolutionary sequence. The animal with the poorly developed structure may represent either a primitive type, prior to the fully fledged exemplar, or a highly evolved form in which the specialized feature has begun to degenerate.

Since Balachowsky's classifications of the Diaspididae represent the attempts toward greatest refinement, a synopsis of his work will provide a fitting summary for this section.

Classification of the coccids and the armored and palm scales, according to Balachowsky (1942, 1948, 1950, 1951, 1953, 1954)

Superfamily	Coccoidea
Sections	(Margaroïdae ..... 2 families)
	(Lecanoïdae.....10 families)
	Diaspidoïdae
Families	Phoenicococcidae
	Diaspididae
Tribes	Xanthophthalmini
	Diaspidini
Subtribes	Lepidosaphedina
	Diaspidina
	Odonaspidini
	Odonaspidina
	Rugaspidiotina
	Parlatorini
	Parlatorina
	Leucaspidina
	Aspidiotini
	Pseudaonidina
	Selenaspidina
	Aonidina
	Targionina
	Aspidiotina

CYTOLOGICAL REVIEW

Three systems of chromosome behavior are known for the sexual species of the Diaspidoïdae, and these may be designated, according to the groups in which they were found first, as the lecanoid, diaspidid, and Comstockiella.

These three systems are characterized by the chromosomal behavior in the males; that of the females, as elsewhere in the coccids, has proved typical (Hughes-Schrader, 1948). It is therefore not possible to determine the antecedent system in the numerous species which reproduce parthenogenetically.

The **lecanoid system** was first discovered by Schrader (1921) and has since been found to characterize most of the families classed as lecanoid by Balachowsky (Hughes-Schrader, 1935, 1948; Brown, 1959). Because it is a highly unusual system (fig. 1), its occurrence in most of the lecanoid assemblage demonstrates the natural unity of this group while its occurrence in the armored and palm scales demonstrates the lecanoid ancestry of the Diaspidoïdae (Brown, 1959; and unpubl.).

In the lecanoid system, the paternal chromosomes become heterochromatic at the blastula stage of the male embryos and continue as such until spermatogenesis, at which juncture the paternal heterochromatic set is segregated completely from the maternal euchromatic set. Only the maternal derivatives enter into sperm formation while the paternal heterochromatic complements give rise to heteropycnotic residues which degenerate during spermiogenesis. The lecanoid male thus breeds as a true haploid, transmitting only the maternal set. As originally suggested by Schrader and Hughes-Schrader (1931), the heterochromatic set is largely inert genetically so that the male lives as a virtual haploid even though endowed with the diploid chromosome number (Brown and Nelson-Rees, 1961). With one exception, the lecanoid system exists in the Diaspidoïdae only in combination with the Comstockiella system (Brown, unpubl.); the significance of this fact for present considerations will be reviewed following the description of the Comstockiella system.

The **diaspidid system** was studied by Brown and Bennett (1957) and Bennett and Brown (1958). It is a relatively simple system in which the paternal chromosomes are eliminated at the late cleavage stage of the male embryos, which develop thereafter as true haploids. Spermatogenesis consists of a single mitotic division, both products of which yield sperm (fig. 1).

The **Comstockiella system,** which has been only briefly described (Brown, 1957), is the most complex of the three systems (fig. 1). It is identical with the lecanoid system until spermatogenesis which consists of but a single division. The difference between the heterochromatic and euchromatic sets disappears, and homologous chromosomes, one from each of the two sets, pair to form bivalents. At anaphase, the two homologues in each bivalent simply separate from each other and move to the poles. There is no evidence that the chromosomes of different origin, heterochromatic or euchromatic, tend to segregate together. Two sperm are produced by each spermatocyte and each of the two would be expected to contain a haploid set of chromosomes drawn at random from both the heterochromatic and euchromatic sets.

One pair of homologues may be referred to as the "D" pair because of its differential behavior. Unlike the other pairs of homologues, the D entities display a less complete loss of euchromatic-heterochromatic differentiation for the two members of the pair, which often fail to form a bivalent. The D member derived from the euchromatic set (the "D^E" chromosome) divides equationally, contributing a D^E chromosome to each sperm. The D member

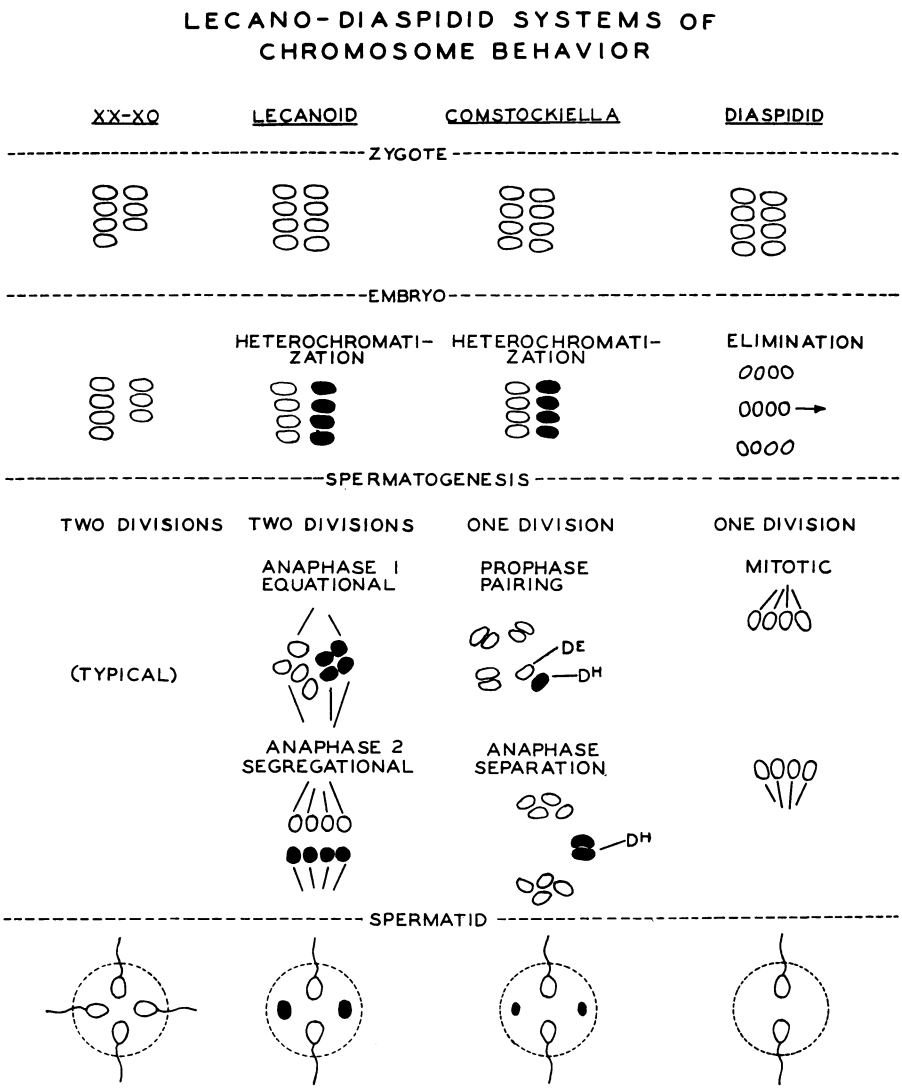


Fig. 1. Diagram of chromosome behavior in males of the Diaspidoïdae (with a typical XX-XO system for comparison).

from the heterochromatic set (the "D^H" chromosome) is eliminated from the sperm; this chromosome either lags in division so that its daughter halves never reach the poles, or it divides synchronously with the other chromosomes and its daughter halves are later ejected from the telophase nuclei. In either case, the two products of the D^H chromosome form small pycnotic residues, similar to the residues in the lecanoid system, which persist during the earlier phases of spermiogenesis.

If the heterochromatic set in the Comstockiella male is inert genetically

as it is in the lecanoid system, then the Comstockiella male must also be considered a virtual haploid. Unlike the lecanoid and diaspidid males, the Comstockiella male breeds as a diploid, not as a haploid. It would perhaps be best to consider that the Comstockiella male is a subdiploid, since it breeds as a haploid with respect to the D pair, only the D^E chromosome being transmitted. There is, however, no evidence for the formation of chiasmata during spermatogenesis, so that genetic recombination would be expected to be restricted to entire chromosomes as it is in the familiar case of *Drosophila* males.

The **variable-D Comstockiella systems** are those in which size differences of the chromosomes have permitted recognition of the fact that the D pair is not fixed or genetically determined but that the pair of homologues showing the D pattern of behavior may vary from cyst to cyst in the testis (Brown, unpubl.). There is, however, one and only one pair of chromosomes showing the D behavior, whether this pair is the longest or the shortest of the complement. Thus, the D pair is in no way analogous to a pair of sex chromosomes or to other types of genetically fixed chromosomal heteromorphisms. There is no apparent correlation of the election of a specific pair as the D pair with the morphology of the testis, and random variation from cyst to cyst throughout the testis seems to be the rule. Thus, a chromosome which is eliminated as a D^H entity in one cyst may very well not be such in an immediately adjacent cyst and therefore be transmitted. If we assume, following the situation in lecanoid males, that the heterochromatic set is of paternal origin, then any change from cyst to cyst in the D pair elected will result in that male transmitting all the paternally derived chromosomes via at least some of the cysts. For example, if a chromosome 1 pair becomes the D^H pair in some cysts and a chromosome 2 pair is so responsible in others, chromosome 2 of paternal origin will be included in the sperm of the first instance and chromosome 1 of paternal origin in that of the second.

When the chromosomes of the complement are all approximately the same size, the variable-D system cannot be demonstrated by direct observation, but should be amenable to an experimental approach involving chromosomes marked by X-ray-induced breaks. In other instances in which variation of the D pair has not yet been observed, it is obviously impossible to state that such variation never occurs. On the other hand, the possibility should be kept in mind that in some instances the D pair may have become genetically determined.

In the **compound lecanoid-Comstockiella system,** the two systems occur in the same species, frequently within the same animal and the same testis. As with the variable-D condition, the system is cyst-specific, and its determination does not seem to be correlated with any morphological features of the testis. The variable-D condition has not yet been observed in animals with both the lecanoid and Comstockiella systems. Animals with both systems will obviously breed as haploids and subdiploids simultaneously, depending upon the system in operation in the cyst from which the individual sperm was derived.

As previously mentioned, the lecanoid system has been observed to occur alone in only one of the diaspidoids studied to date. The Comstockiella sys-

tem has more often been seen independently. In neither case, however, is it possible to state that the other system would not be found if more examples were studied.

Evolutionary Sequence of Chromosomal Systems

The problem of the evolutionary sequence of the three systems found in the Diaspidoïdae can be touched upon only briefly in the present report. It seems obvious that the lecanoid system must be ancestral since it alone of the three occurs in coccids less specialized than the diaspidoids where it is the sole system found among the great majority of the lecanoid assemblage of families. That the one system has been derived from the other is amply demonstrated by the occurrence of both lecanoid and Comstockiella systems in the same individual.

The origin of the diaspidid system is not so immediately obvious. In both the lecanoid and diaspidid systems, the male breeds as a haploid; it is thus tempting to consider the former a progenitor of the latter (Schrader and Hughes-Schrader, 1931; Brown, 1958). On the other hand, the cytological features of the diaspidid system much more closely resemble those of the Comstockiella system. In both instances there is but a single spermatogenic division, while two occur in the lecanoid sequence. Chromosome elimination takes place in both the Comstockiella system, with the loss of the D^H chromosome, and in the diaspidid system, with the casting off of the paternal chromosomes at late cleavage. No such elimination is to be found in the lecanoid system; in fact, at the second division of spermatogenesis, at which time the heterochromatic set is segregated from the euchromatic, it is the former rather than the latter which shows the more active, "normal" behavior on the essentially monopolar spindle, while the euchromatic chromosomes may remain more or less passive (Schrader, 1921; Hughes-Schrader, 1935, 1948; Brown, 1959). The exclusion of the heterochromatic chromosomes from the genetic continuum in the lecanoid system is due, therefore, not to their elimination but to their failure to undergo spermiogenesis and thus to yield functional sperm.

Although the actual process of chromosome elimination in the diaspidid system may closely resemble that in certain examples of the Comstockiella system, elimination takes place at a quite different developmental stage in the latter system, at spermatogenesis rather than cleavage, and furthermore involves only one chromosome of the heterochromatic set. Studies of the variable-D Comstockiella systems have shown, however, that in these instances each of the chromosomes of the heterochromatic set is amenable, and apparently about equally so, to fulfilling the D role; in short, in the variable-D systems all the heterochromatic chromosomes are potentially susceptible to elimination. The shift in the time of development at which elimination occurs, from spermatogenesis to cleavage, does not seem a too unlikely assumption on consideration of certain other developmental shifts made by the coccids, as, for example, the achievement of sexual maturity, with no further molts, at a larval stage by all female coccids.

Finally, it should be mentioned that chromosome elimination occurs in the diaspidid system at about the same developmental stage at which heterochro-

matization occurs in the lecanoid and the Comstockiella systems. Although there is usually little or no indication of heterochromatization in the paternal chromosomes prior to or upon their elimination, at least one case is known in which the eliminative process was partially abortive, and here the chromosomes or segments which were included in the daughter nuclei were heterochromatic (Brown, unpubl.). There seems little doubt, therefore, that the diaspidid system of chromosome elimination stemmed from one, whether lecanoid or Comstockiella, in which a chromosome set became heterochromatic at early development.

In conclusion, the evolutionary sequence which seems the most likely at the present time is, therefore:

$$\text{lecanoid} \rightarrow \text{Comstockiella} \rightarrow \text{diaspidid, or}$$
$$\text{L} \rightarrow \text{C} \rightarrow \text{D}.$$

Because, with one exception, the lecanoid system does not occur independently in the Diaspidoïdae, the sequence which needs to be considered for evolutionary changes within the section is simply:

$$\text{C}(\pm\,\text{L}) \rightarrow \text{D}.$$

Correlation of Taxonomy and Chromosome System

The identification of the lecanoid system as that presumed ancestral to the systems found among the armored scales contributed nothing toward the identification of the groups antecedent to the Diaspididae. Most authors agree that the Diaspidoïdae are the end product, the most specialized of an evolutionary series beginning with the primitive pseudococcids (Balachowsky, 1942; Bodenheimer, 1944; Borkhsenius, 1958).

A sampling of nearly all the families of Balachowsky's Lecanoïdae had proved them to be lecanoid (Hughes-Schrader, 1948; Brown, 1959), except for the XX-XO system found in the genus *Puto* of the relatively primitive pseudococcids (Hughes-Schrader, 1944, 1948). According to the cytological evidence available until just recently, the Diaspidoïdae could have been derived from either of the two groups already suggested, the asterolecaniids or the conchaspidids, or, for that matter, from any of the less specialized lecanoid families.

This picture has changed radically with the identification of the Comstockiella system in the asterolecaniid *Mycetococcus ehrhorni* (Cockerell) (Nur and Brown, unpubl.). This species, to be considered in detail below, undoubtedly possesses its own morphological specializations, but its otherwise typical asterolecaniid characteristics afford the necessary starting point for understanding the evolution of the armored scales. In addition, this discovery will undoubtedly stimulate the investigation of chromosome systems in other sexual asterolecaniids. To date, only two species have been analyzed: *Mycetococcus ehrhorni,* in which both the Comstockiella and lecanoid systems were found, and in the cyst-specific sort of relationship described above, and *Cerococcus quercus* Comstock, for which numerous examinations provided evidence only for a lecanoid system (Brown, 1959). The two genera are somewhat similar; the genus *Mycetococcus* was erected by Ferris (1918)

to include two species originally referred to *Cerococcus*. The chromosome numbers of the two species are different; the haploid number of *C. quercus* is 9 (Brown, 1959), while that of *M. ehrhorni* is 3 (Nur and Brown, unpubl.).

An abrupt change in chromosomal system between the Lecanoïdae, excepting *Mycetococcus*, and the Diaspidoïdae is evident from the fact that the lecanoid chromosome system seldom or never occurs alone in the latter section. Thus, within the Diaspidoïdae, as mentioned in the preceding section, there are essentially two systems to be considered, the Comstockiella, with or without the lecanoid, and the diaspidid. The Comstockiella system has

TABLE 1

THE SEXUAL SYSTEMS OF THE MAJOR DIASPIDOID GROUPS, FROM A WORLD-WIDE CYTOLOGICAL SURVEY, AND RELATIVE SIZES OF GROUPS IN NORTH AMERICA, AS SHOWN IN THE FERRIS *ATLAS*

Group	Relative size of groups in North America		Chromosome system			
			Comstockiella or lecanoid*		Diaspidid	
	Number of genera	Number of species	Number of genera	Number of species	Number of genera	Number of species
Phoenicococcidae	3	8	5	8	0	0
Diaspididae						
Xanthophthalmini†	1	1				
Diaspidini	49	176	1	1	19	32
Odonaspidini	4	15	1	1	0	0
Parlatorini‡	5	16	2	3	0	0
Aspidiotini	29	131	4	5	19(20)§	33

* In three cases, spermatogenic stages were not available, and determination was based on heterochromatization in the embryo.
† No sexual form known. See text under the head "*Xanthophthalma*."
‡ Ferris did not recognize this tribe; included genera are based on Balachowsky (1953).
§ The total of 20 includes a genus with both types of system and also tallied under the "Comstockiella" heading; i.e., a total of 23 aspidiotine genera.

been found throughout the Diaspidoïdae while the diaspidid system has been discovered in only the two major tribes where it occurs in by far the greater majority of genera and species (table 1).

The relative sizes of the taxonomic subdivisions listed in table 1 are based on the number of genera and species cited in the Ferris *Atlas*, and on only those genera and species. The genera included by Balachowsky in the tribe Parlatorini were removed from the Diaspidini, where Ferris placed them, and tallied separately in table 1. The relative sizes obtained from the Ferris *Atlas* are probably fairly accurate estimates, since Ferris himself paid particular attention to the tropical areas of North America. Finally, the present authors know of no areas in which the relative proportions of genera and species in the large and small groups would tend to be reversed.

Several conclusions may be made from the data of table 1. The Comstockiella system is undoubtedly the basic system of the Diaspidoïdae, since it occurs throughout the morphological range. The possibility that the diaspidid system is basic is untenable because of the extremely low probability

that it would then subsequently "revert" to yield both the Comstockiella and lecanoid systems.

The second conclusion is in regard to potentiality for sustaining evolution of "lower" or "higher" categories, or genera and species versus the tribes and families. The size of genera, based on the number of species per genus, is about the same for the tribes or families with only the Comstockiella system, i.e., the Phoenicococcidae, the Odonaspidini, and the Parlatorini, as it is for the two major tribes which are largely diaspidid. There is thus, from this evidence, no detectable difference, within genera, of the ability of the two systems to proliferate species.

The striking difference is seen in the number of genera in the three "Comstockiella" groups in comparison with the two major tribes. Very obviously, the diaspidid system has been much more successful in the production of large numbers of genera than the Comstockiella system, while the latter has succeeded better in the invention of new tribes and families. To this extent, the evidence may also be interpreted to indicate that the Comstockiella array was the older, and largely failed in competition with diaspidid forms when these appeared in the diaspidine and aspidiotine morphologies.

According to the interpretation of the chromosomal and taxonomic correlations which will now be presented, both these concepts will be included. The argument depends on whether the diaspidid system arose once or more than once.

If the diaspidid system arose only once, then the aspidiotine morphology was twice achieved independently (fig. 2, *A*). If it arose more than once, then a more orderly pathway of morphological change can be envisaged via the Parlatorini, which in several respects are intermediate between the Diaspidini and Aspidiotini (fig. 2, *B*). Mention has been made earlier of the changes necessary to transform a Comstockiella system into a diaspidid system. It may be noted that the changes in chromosome behavior and other cytological aspects are of an order of magnitude not much greater than that required to convert a sexual to a parthenogenetic form, and that parthenogenesis is ubiquitous in the coccids. It would not, therefore, be unreasonable to presume that the change from Comstockiella to diaspidid system could occur more than once. For these reasons, the phylogenetic pathway presented in figure 2, *B*, seems the more likely.

Finally, the question of "age" versus the potentiality for sustaining evolution by the genetic system in question cannot be answered even tentatively on the basis of the above interpretation. On the assumption of the correctness of the phylogenetic pathway represented in figure 2, *B*, the diaspidid majority of the Diaspidini could be of more recent derivation from ancestors with a Comstockiella system than the diaspidid types of the Aspidiotini. However, a consideration of the chromosomal systems themselves offers further information. The technical details will not be presented here, but only the conclusion, that the Comstockiella system, with its inclusion of the heterochromatic chromosomes at spermatogenesis, would be able to yield genetic variation at a greater rate than the diaspidid system, and thus, under certain circumstances, to provide the basis for more rapid evolution. This interpretation of the potentialities of the chromosome systems conforms with

the cytotaxonomy when the Comstockiella system is pictured as producing variation at a high rate, the diaspidid system as more successfully exploiting the numerous ecological niches.

THE GENERA *PROTODIASPIS* AND *ANCEPASPIS*

The genus *Protodiaspis* of the tribe Diaspidini is indigenous to the New World, where its species occur almost exclusively on the twigs of oak. At present, fourteen species are known from North America, a number which includes the two described in the companion report (McKenzie and Nelson-Rees, 1962, the leading paper in the present issue). Ferris characterized the genus as "a biological rather than a morphological group. The hosts, habit,

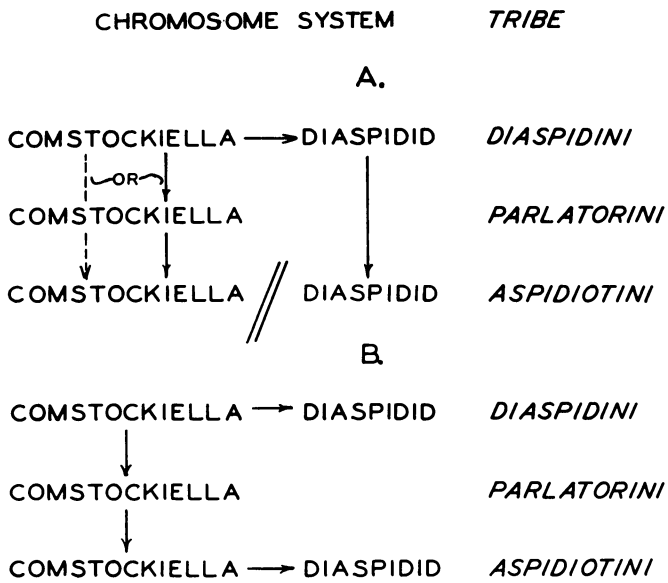


Fig. 2. Diagram of possible relationships of three tribes of Diaspididae, and their chromosome systems.

and distribution of the included species, considered in connection with similarities in the immature forms and a certain common facies of the adult females, indicate that they belong probably to a rather homogeneous common stock, in spite of the morphological vagaries of the adult female."

The following discussion is based entirely on descriptions in the Ferris *Atlas* and the paper of McKenzie and Nelson-Rees, cited above, on two new species of *Protodiaspis, P. chichi* and *P. didymus.* Consequently, the authors of the various species of this genus and *Ancepaspis* will not be cited.

The genus *Protodiaspis* is of special interest in regard to the evolutionary patterns of the Diaspidoïdae because it demonstrates a series of changes, combining losses and acquisitions, which interconnect the typical diaspidid with such exuvial types as the genus *Ancepaspis,* which Ferris (1942) placed in the Phoenicococcinae (= Phoenicococcidae). Ferris further stated that, "It is, in fact, because of the existence of this genus *Ancepaspis* and es-

TABLE 2

MORPHOLOGICAL FEATURES, CHROMOSOME NUMBER AND SYSTEM, AND HOSTS OF *PROTODIASPIS* AND *ANCEPASPIS*

+ = "present." − = "absent." ± = "intermediate." X = "not determined." Q = "on oak." L = "on leguminous (*sensu lata*) host."

Species	Ferris number*	Perivulvar pores	Spiracular pores	Lobes in adult	Second stage lobes	Number of antennal bristles	Gland spines	Nonminute ducts	Pygidium		Pupillarial	Host	Haploid chromosome number and system†
									Exserted	Resculptured			
P. agrifoliae	SI-100	+	−	−	−	−	−	+	−	−	−	Q	X
P. didymus	D	−	−	−	−	−	−	+	−	−	−	Q	4
P. colimae	SI-101	−	+	+	−	1	−	+	+	+	−	Q	X
P. emoryi	SI-102	−	−	−	−	1	−	+	+	−	−	Q	X
P. lagunae	SI-103	+	+	+	+	1	+	+	−	−	−	Q	X
P. lobata	SI-104	−	+	+	+	1	+	+	−	−	−	Q	X
P. parvula	SI-105	−	+	+	+	1	−	+	−	−	−	Q	X
P. pulchra	SI-106	−	+	−	+	1	+	+	±	−	−	Q	X
P. varus	SI-107	−	+	+	+	1	+	+	−	−	−	Q	X
P. praetexta	SIII-314	−	+	±	+	1	+	±	±	−	−	Q	X
P. signata	SIII-315	−	+	+	+	1	−	+	+	−	−	Q	X
P. infidelis	SIV-412	+	+	+	+	1	+	+	−	−	−	Q, L	3-D
P. chichi	C	+	+	+	+	1	+	+	−	−	−	Q	4-D
P. sulcata	SIV-413	−	−	−	−	X	−	−	+	+	−	Q	X
A. edentata	SIV-435	−	−	−	−	4	−	−	±	−	+	L	4-C
A. novemdentata	SIV-436	−	−	−	−	4	−	−	+	+	+	L	X
A. quadridentata	SIV-437	−	−	−	−	1	−	−	+	+	+	Q	X
A. tridentata	SIV-438	−	−	−	−	5	−	−	+	+	+	L	3-C

* C and D in this column represent new species. See the leading paper in this issue.
† Chromosome systems: C = "Comstockiella"; D = "diaspidid."

pecially of one species, *edentata,* that the Phoenicococcinae are here placed in the Diaspididae, . . ." (= Phoenicococcidae and Diaspidoïdae, respectively).

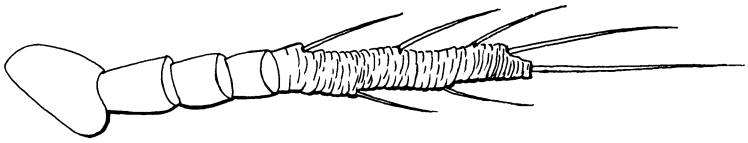
Protodiaspis is semiexuvial: the adult female is partly, but never wholly, encased within the molt of the second stage, which fragments, or ruptures in the normal, armored-scale fashion, starting at the anterior end. The genus *Ancepaspis* is truly exuvial (= pupillarial); the adult female remains completely encased in the molt of the previous stage, which ruptures at the opposite, posterior end to permit the larvae to crawl out. It is this distinction in exuviation which Ferris has made the dividing line between the armored scales, as represented by *Protodiaspis,* and the palm scales, as represented by *Ancepaspis.* That no other important criterion existed for Ferris (1942) is demonstrated by his statement that, ". . . *Protodiaspis sulcata* is of such a nature that if it were pupillarial it would seem definitely referable to *Ancepaspis.*"

The characters to be referred to in detail below are partially the result of loss, partially of acquisition. It is possible to differentiate between the two, and therefore to determine the direction of evolutionary change by comparison with large numbers of typical diaspine armored scales. These all have such structures as pygidial lobes, perivulvar pores, spiracular pores, gland spines, and ducts in a specific arrangement, and certain species of *Protodiaspis* conform to this arrangement. On the other hand, the characters newly acquired are related to the extrusion of the pygidium and its consequent and highly variable remodeling. It would take far more assumptions to derive the typical armored-scale morphology from the ancepaspine type than the reverse.

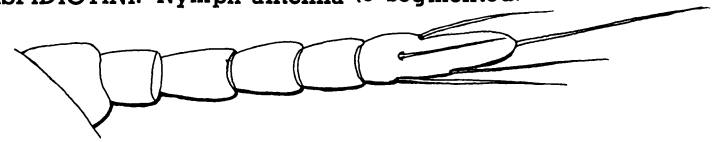
Pores. The quinquelocular pore is found in many of the lecanoid families, including the asterolecaniids. In the armored scale insects, it occurs in two places, associated with the spiracles and in an arch curving anteriorly around the vulva. Many species of armored scale have lost either or both the perivulvar or spiracular pores, or their number has been greatly reduced. Ferris throughout his work recognized the presence or absence of perivulvar pores, or a change in their number, as diagnostic of a specific difference.

In the genus *Protodiaspis,* perivulvar pores are present in four species (table 2), but are quite reduced in number in one of them, *P. agrifoliae,* which has as a companion species the newly discovered *P. didymus,* which has none at all. The pores adjacent to the anterior spiracle—the spiracle which Ferris (1937) considered to be the more revealing in this regard—are present in ten species and, as *P. agrifoliae* and *P. colimae* demonstrate, may be lost or maintained independently of the perivulvar pores. The spiracular pores are usually four to five in number, but may be reduced to one or two, as in *P. signata* or *P. lobata.* The genus thus shows reduction in number and complete loss of both types of pore.

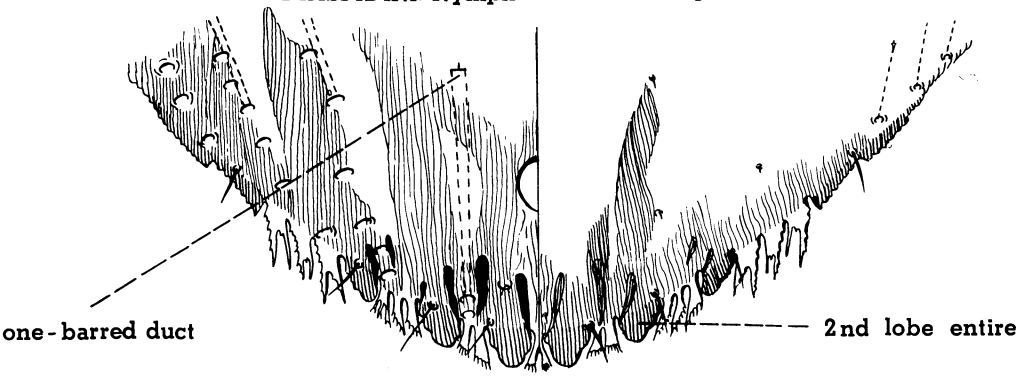
Gland Spines. The marginal gland spine or gland tubercle is common in the Diaspidini and Parlatorini but is otherwise rare. In four species of *Protodiaspis,* the gland spines form two complete marginal rows from the anterior to the posterior end. In *P. varus,* the rows are cut off about halfway down the abdomen; in *P. pulchra,* they extend only to the abdomen; while in *P.*



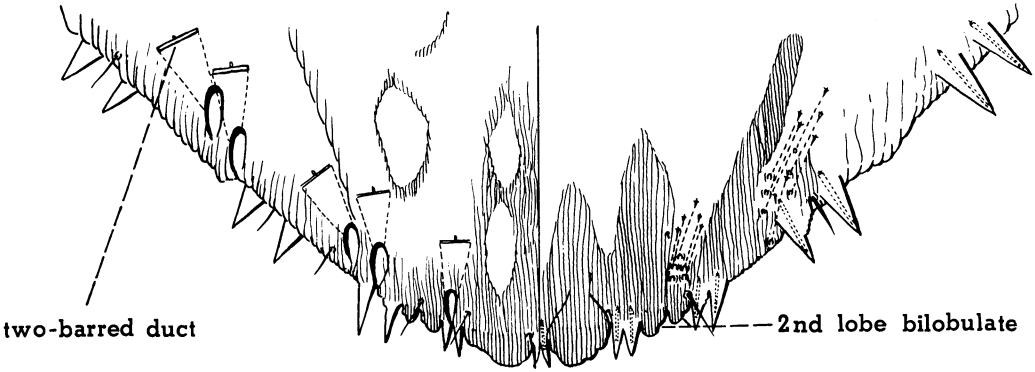
ASPIDIOTINI: Nymph antenna (5-segmented)



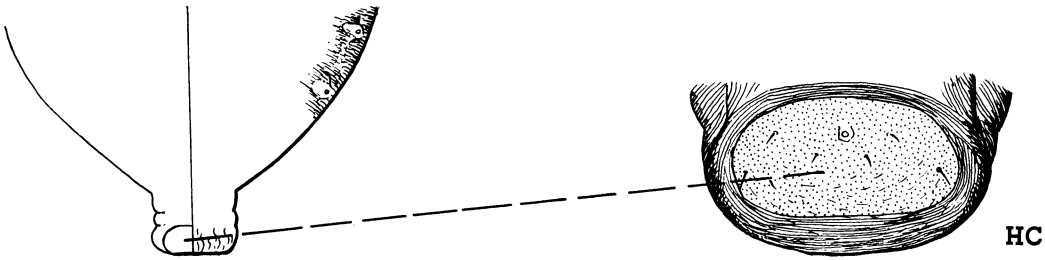
DIASPIDINI: Nymph antenna (6-segmented)



ASPIDIOTINI: Adult female pygidial fringe (after McKenzie)



DIASPIDINI: Adult female pygidial fringe (after McKenzie)



PHOENICOCOCCIDAE: Operculum of second-stage female (after Ferris)

praetexta, they are limited to but two on the head-thorax region. In the seven other species, they are completely absent (table 2).

Lobes. In the typical member of the tribe Diaspidini, the margin of the pygidium is set with two median prominences or lobes which are single structures and, anteriad along each side, two more lobes, each of which is characteristically divided (fig. 3). A fourth lobe is rarely present. The typical arrangement and double nature of the second and third lobes are shown only by *Protodiaspis infidelis,* but even here the lobes are atypical, among the Diaspidini, because of their terminal serrations. Lobes of some sort appear in adults of nine species. It may not be fair to refer to the marginal crenulations in *P. praetexta* as lobes, yet here, where no true lobes appear, the pygidial margin carries undivided median and divided second and third protuberances which clearly demonstrate their homology. Thus, nine of the species, including *P. praetexta,* have lobes of some sort in the adult (table 2).

In typical armored scales, lobes are present in both second-stage and adult females. In *Protodiaspis,* most of those species with lobes in the adult also have them in the second stage, but *P. colimae* and *P. pulchra* demonstrate that they can be lost independently at these two stages.

Ducts. Although small, the ducts of *Protodiaspis* usually are recognizably of the "two-barred" type which is characteristic of the Diaspidini (fig. 3). In *P. sulcata* and in *Ancepaspis,* they are few in number and too small to be accurately characterized. For the two genera, the ducts may, therefore, be classed as normal for the genus *Protodiaspis,* although small, or as minute (table 2).

Pygidial Structures. The typical armored-scale pygidium is a more or less sclerotized region formed by an arching of the posterior abdominal segments. It is richly endowed with ducts. The pygidium, with its attendant appendages, probably acts as a paint brush which the insect uses to apply the secretions from the highly glandular pygidial region. Dickson (1951) has made time-elapse observations of the rotations of the female *Aonidiella aurantii* (Mask.) inside her scale, and the application of the pygidium to the inside surface of the scale.

In *Protodiaspis* and *Ancepaspis,* the pygidium may be protruded somewhat beyond its normal position or may be grossly exserted. If grossly exserted, it may then be resculptured into bizarre patterns, notably in *P. sulcata, P. colimae, A. tridentata, A. quadridentata,* and *A. novemdentata* (table 2).

The relationship of the marginal lobes of the pygidium to its exsertion is quite interesting. In forms with no exsertion in evidence, such as *P. parvula* and *P. varus,* the lobes appear as ventral rather than marginal appendages, with just their tips showing in the dorsal view. In *P. lagunae,* the lobes are drawn in so far on the ventral side that they do not show at all in dorsal view. In *P. signata,* a quite typical pygidium is strongly exserted, and the lobes, although quite small, are strictly marginal. *P. colimae* is the only known species which has an exserted, resculptured pygidium and also lobes which, here again, are on the inner ventral surface rather than marginal.

Fig. 3. Characteristic morphological features of the Aspidiotini and Diaspidini; anal operculum of the Phoenicococcidae.

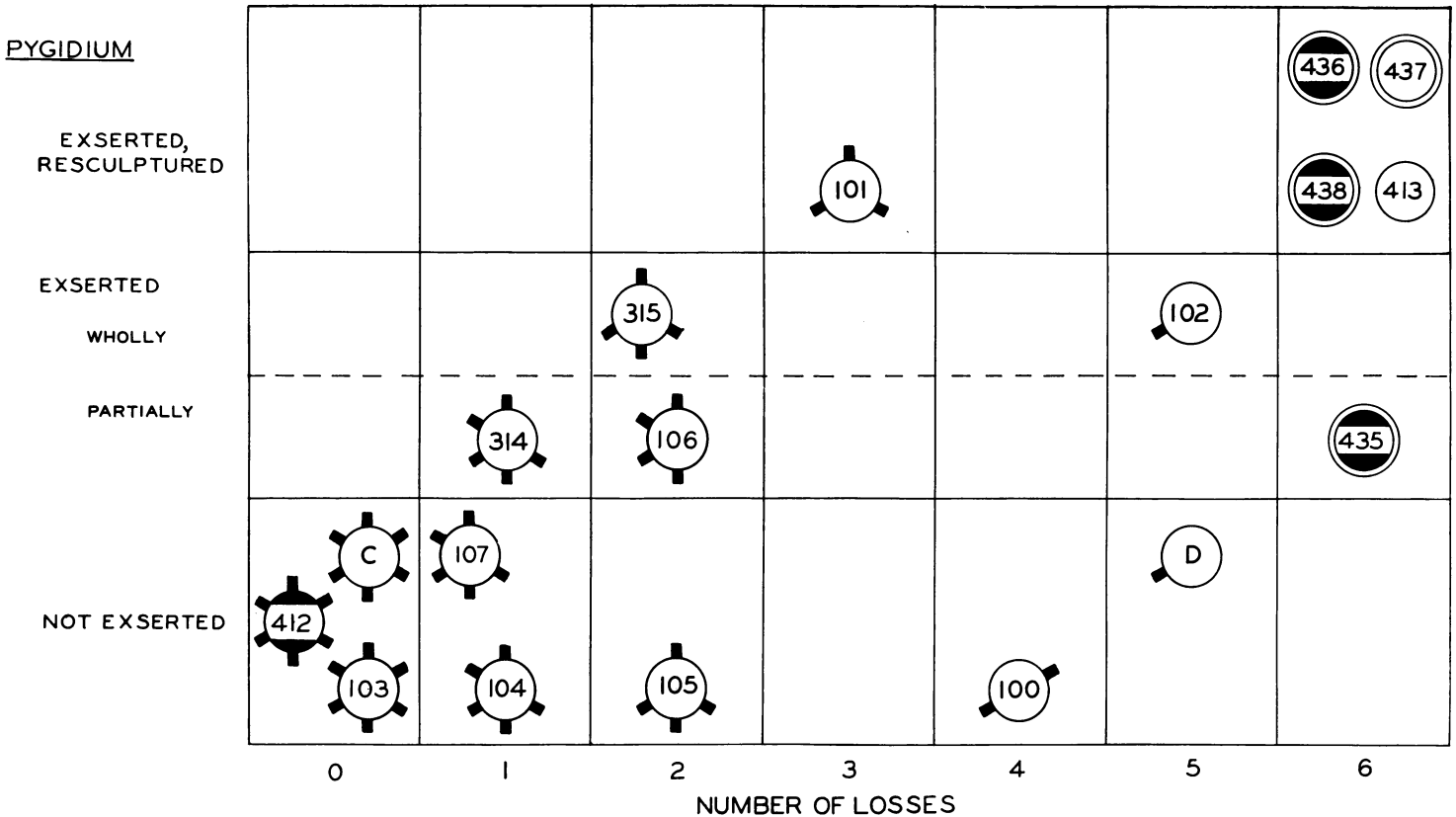


Fig. 4, *A*. Diagram of losses of parts (horizontal) and reshaping of pygidium (vertical) in *Ancepaspis* and *Protodiaspis*. The numbers refer to the species descriptions in the Ferris *Atlas*. *C* refers to *P. chichi* and *D* refers to *P. didymus* (McKenzie and Nelson-Rees, 1962; the leading paper in the present issue). See also table 2.

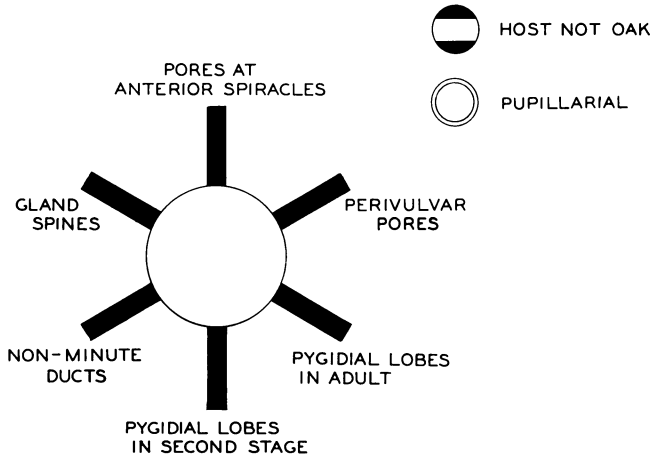


Fig. 4, *B*. Key to the circular symbols used in figure 4, *A*.

Exuviation. As already mentioned in the introductory remarks of this section, *Ancepaspis* but not *Protodiaspis* is a true exuvial type. On the basis of this difference, Ferris (1942) assigned the two genera to distinct families.

At this juncture it will be well to consider briefly the significance of the above morphological changes. These seem to be simply adaptations to exuvial existence. If the adult female is to remain largely enclosed in the exuvia of the second stage, then the ducts and lobes and gland spines would cease to be of use in the secretory processes, and would be subject to loss. On the other hand, an extruding pygidium would presumably have the function of inducing or aiding the exuvia to crack, or to widen further if already cracked, in order to permit the egress of the larvae. Thus, both the losses and gains described above can be explained simply as adaptations to exuvial existence.

The scales formed by the insects correspond in general to the type of exuviation. Species of *Protodiaspis* usually form a typical scale which includes the first-stage exuvia and secretionary material; inside this scale, the adult female remains partially covered by the second-stage exuvia. Altogether, Ferris, in his key of the Diaspidini, includes eleven genera which are truly pupillarial; *Protodiaspis,* which is semiexuvial, is not included in this list. Two of these eleven genera form very poor scales, consisting of only a small amount of waxy material which is readily lost to expose the sclerotized exuvia. Only a first start toward this condition is present in *Protodiaspis*; the scales may consist of loosely consolidated wax or fluffy, threadlike material rather than a more definite structure, and variation in this characteristic may occur within a species. On a superficial, subjective basis, there is apparently no correlation between loss of pygidial characteristics and type

of scale formed, but information in addition to the rather general descriptions offered by Ferris might change this conclusion. There is no available information on the scale of the critical species, *P. sulcata.* In *Ancepaspis,* the amount of secretionary material is very small or absent altogether, as in *A. quadridentata,* in which species the first molt is usually lost; the second exuvia, which therefore constitutes the only protective covering, is strongly sclerotized.

As was abundantly obvious in the consideration of the individual characters (table 2), the various losses and gains were individually independent, except for the true exuvial types, which always showed all six of the losses under consideration (fig. 4). However, the same six losses were also shown by one of the nonexuvial types.

Figure 4, *A,* may be viewed as a correlation diagram between the losses, ordinate, and gains, abscissa. The typical armored-scale type of *Protodiaspis,* with no losses and no gains, is in the lower left section while the typical *Ancepaspis,* with all the losses and gains, is in the upper right. The diagram thus shows a rough correlation between losses and gains. Figure 4, *B,* acts as a key to the circular symbols in figure 4, *A.*

This information may now be considered in view of the previous taxonomic treatment of the two groups. Ferris (1942) discussed his assignments and doubts regarding them in his notes on the genus *Ancepaspis.* Following Stickney's (1934) point of view that there are unmistakable affinities between *Ancepaspis* and the Phoenicococcinae (= Phoenicococcidae), Ferris placed the genus in this subfamily. The assessment was based on the fact that in *Ancepaspis* and in Stickney's phoenicococcine genera, the pygidium contains no abdominal segment anterior to the sixth, while the fifth, and frequently the fourth, segment is included in the true armored scales; the segmentation, however, has been quite difficult to analyze accurately. On the other hand, the affinities of *Ancepaspis* with the true armored scales were simultaneously noted by Ferris: "It is, in fact, because of the existence of this genus *Ancepaspis* and especially of one species, *edentata,* that the Phoenicococcinae are here placed in the Diaspididae, . . ." (as quoted before).

The problem of the relationship of *Ancepaspis* and *Protodiaspis* is clearly brought out in the penultimate paragraph of the notes: "A fifth species, *Ancepaspis quadridentata,* is here described as new. And here doubt arises in the author's mind. This new species is from oak. The genus *Quercus* harbors a group of species which herein are referred to the genus *Protodiaspis* and some of which present difficulties in their generic assignment. None of the species of *Protodiaspis* retains the adult female within the second exuvia at maturity, as do all the species here referred to *Ancepaspis,* but some of them in their pygidial characters strongly suggest some species of *Ancepaspis.* For example, the species herein described as *Protodiaspis sulcata* is of such a nature that if it were pupillarial it would seem definitely referable to *Ancepaspis.* But, on the other hand, this species connects through a series of forms to the typical species of *Protodiaspis.*"

It may also be noted that the one species of *Ancepaspis* which occurs on oak, i.e., *A. quadridentata,* is the sole member of the genus to have but a single bristle on the antenna, while the other species have four or five (table

2). Thus, in two characteristics, host preference and antenna structure, *A. quadridentata* conforms to the characteristics of *Protodiaspis* rather than *Ancepaspis.*

Only a few species of *Protodiaspis* and *Ancepaspis* have so far been examined cytologically, but in each, the haploid numbers of 3 and 4 occur (table 2). Four is by far the most frequent number for the Diaspididae and should be regarded as basic; the number 3 has not been found in the Diaspidoïdae except in these two genera. In regard to chromosome system, the species studied for *Protodiaspis* have the diaspidid system while those of *Ancepaspis* have the Comstockiella system. The data are limited, and those for such critical species as *A. quadridentata* and *P. sulcata* are missing.

In view of the above evidence, the genera *Protodiaspis* and *Ancepaspis* should probably be regarded as products of a single complex evolutionary series or of two closely parallel series, in either case with ultimate derivation of all forms from typical pygidial armored scales. The difference in chromosome system presents no problem for the assumption of two parallel series. If one complex series is assumed, however, then the corollary assumption must be made that the species with the Comstockiella system were more specialized because they either began earlier, or their chromosome system enabled more rapid advancement, or both.

Recently, Brimblecombe (1959) has assigned a series of Australian species to the genus *Ancepaspis.* Of these, five were collected from *Casuarina* spp. (Casuarinaceae), the sixth from *Acacia* (Leguminosae). Three of the species strongly resemble *Ancepaspis edentata* in that the pygidium is entire and not strongly exserted; a fourth has an exserted but entire pygidium. The remaining two species are of special interest; bars are present reminiscent of the teeth of *A. novemdentata* or *A. tridentata* but do not extend, or only slightly so, beyond the margin of the pygidium. The differences and similarities of the American and Australian forms raise highly intriguing questions of relationship and evolutionary pattern, but much further work will be required before an evaluation can be attempted.

Borkhsenius and Bushchik (1959) have described a new genus, *Protancepaspis,* from *Rubus* (Rosaceae), in southwest China, which may well, as its name implies, be characteristic of the forms antecedent to *Ancepaspis.* (The authors are grateful to Mr. Uzi Nur for calling to their attention the English translation of this article.) The one species is pupillarial with sparse secretionary material, but both spiracular and perivulvar pores are present, the latter in considerable number. Tubular marginal ducts are present on the pygidium, which is grossly exserted. Of special interest is the terminal structure of the pygidium, which consists of two somewhat sclerotized lobes formed by a deep apical cleft; the lobes are lightly serrated on the exterior margin, while the marginal ducts are to be found almost to the ends of the lobes. These lobes seem much more reminiscent of the median lobes of a typical armored-scale pygidium than they do of either the unique types present in most of the species of *Ancepaspis* or of the strongly sclerotized lobes present at the end of the abdomen of *Mycetococcus ehrhorni* (Cockerell) (Ferris, 1955; see below). This recently described genus, therefore, offers some additional evidence that the ancestors of *Ancepaspis* were structurally like the typical armored scale.

The genus *Ancepaspis* should, therefore, be retained in the Diaspidini and regarded simply as a specialized group with affinities for *Protodiaspis*. Although assigned to this family by Ferris, the genus *Ancepaspis* is clearly distinct from other members of the Phoenicococcidae in several important respects. Among this family, the genus *Phoenicococcus* is the only one which is not pupillarial and is also unlike the others in several important respects. *Phoenicococcus* itself will be considered in the next section; in the present section, reference to the Phoenicococcidae may be understood to indicate that family *not* including *Phoenicococcus*, as well as *Ancepaspis*, even though certain characters may also be common to these genera.

The major morphological difference between the genus *Ancepaspis* and members of the Phoenicococcidae (Ferris, 1942) is the presence in the latter of a flat anal plate, an operculum, which is surrounded by a heavily sclerotized rim (fig. 3). Furthermore, the ducts in the Phoenicococcidae are more apt to reveal a clear 8-shaped or geminate structure. The differences in the ducts are strikingly apparent in the drawings of *Ancepaspis* and the Phoenicococcidae in the Ferris *Atlas*. Stickney (1934), however, refers to such a variety of ducts as 8-shaped that it becomes difficult to decide about similarities and differences.

In addition to the morphological differences, there are those of host range. *Ancepaspis* occurs on *Quercus* (Fagaceae), and especially on members of the subfamily Mimusoideae, family Leguminosae, while the Phoenicococcidae occur exclusively on palms. The haploid chromosome number of the four species (three genera) of the Phoenicococcidae so far examined has proved to be 5. The chromosome system was either Comstockiella or, in one case, only lecanoid.

Borkhsenius and Bushchik (1959) include *Protancepaspis* along with *Ancepaspis* in the Phoenicococcidae, although their description of the insect, as outlined above, as well as its host, *Rubus*, would indicate that this genus would belong with the phoenicococcids even less than *Ancepaspis*.

The Phoenicococcidae proper may be looked upon as the products of another evolutionary series terminating in adaptation to the pupillarial type of existence and, therefore, parallel to that (or those) of *Ancepaspis* and *Protodiaspis*. There is no evidence, however, that the phoenicococcid series originated from forms with a true armored-scale type of pygidium, and this series may therefore have evolved from early forms with an ill-defined pygidium. At present, there seems no guide to certainty. However, the antiquity of the phoenicococcids is suggested by their world-wide distribution and the presence of geminate pores.

Both Ferris (1942) and Stickney (1934) were convinced of the alliance of the phoenicococcids to the true armored scales. Stickney based his beliefs largely on the geminate pores and looked upon the phoenicococcids as a possible transitional group between the armored scales and the asterolecaniids, for which the geminate pore is the prominent diagnostic feature. Both Ferris and Stickney looked upon the sclerotization which extended from the anal, or eighth, abdominal segment to include the seventh and sometimes the sixth segment as representing the phoenicococcid pygidium. This structure is, however, strikingly different from that of *Ancepaspis*,

which much more closely resembles a true pygidium even though it includes no more abdominal segments. Fortunately, the ideas of Ferris and Stickney have been confirmed by the fact that the Comstockiella chromosome system occurs in the Phoenicococcidae; the relation of this small family to the armored scales is no longer in dispute, and the morphological differences may now be emphasized in order to gain an understanding of the evolutionary pathways.

PHOENICOCOCCUS AND THE ASTEROLECANIIDAE

The recent discovery that an asterolecaniid species also has the Comstockiella chromosome system (Nur and Brown, unpubl.) opens the possibility for further elucidation of the origins of the armored scales. The asterolecaniid species *Mycetococcus ehrhorni* (Cockerell) is typical of the family in regard to the geminate pores which, however, are somewhat invaginated.

In several respects, *M. ehrhorni* (see Ferris, 1955) would conform to expectation of an ancestral type for the armored scale. The only types of ducts and pores present are the geminate and quinquelocular; the tubular duct with the lateral internal process or terminal flexure, common in other asterolecaniids but absent in diaspidoids, is also absent in *M. ehrhorni.* Furthermore, the quinquelocular pores of *M. ehrhorni* are found only immediately adjacent to the spiracles; this is their typical position, in addition to the perivulvar, in the diaspidoids.

In certain of the asterolecaniids, as well as in other families, the abdomen terminates in two lobes. In *M. ehrhorni,* the development of these lobes is highly exaggerated and they are sclerotized. In live specimens of *M. ehrhorni* recently examined, the entire distal portion of the abdomen may be seen to protrude in a long, narrow limb with the sclerotized lobes at the tip. Very superficially, the terminal structures of *M. ehrhorni* resemble those of the "dentate" species of *Ancepaspis.* Although there is no real resemblance between the terminal structures of *M. ehrhorni* and a pygidium, these may be a reflection of one of various experiments in terminal structure which led to the invention of the pygidium by the ancestors of the armored scales. Furthermore, *M. ehrhorni* is embedded in waxy filaments; there is no sclerotization of the membranes and no tendency for these to remain associated with later stages. Thus, *M. ehrhorni* shows neither tendencies toward exuvial existence nor toward building a scale and is easily separated from its secretionary product in a completely naked state. The sclerotized abdominal tip and the protrusion of the abdomen may, however, have an adaptive role to play; in addition to its own secretionary material, the insect is sometimes enveloped by a fungus, and the abdominal apparatus may help to form a channel for the egress of larvae. (All the material of *M. ehrhorni* examined by Ferris [1955] occurred in association with fungus, but that obtained by Nur in 1961 from oak in Berkeley, California, did not.)

Phoenicococcus marlatti Cockerell is the single species of the genus for which the family was named, but differs widely from the others and appears to be about as closely related to *Mycetococcus ehrhorni* as to any of the diaspidoids. It is also a naked form, occurring embedded in waxy filaments but without associated fungus. The quinquelocular pores of *P. marlatti* are

confined to the proximity of the spiracles but are more neavily sclerotized than those of *M. ehrhorni,* while the geminate "pores" of *P. marlatti* are so deeply invaginated that they should rather be considered ducts.

Phoenicococcus marlatti exhibits no abdominal lobes, protrusions, or heavy sclerotizations other than those restricted to the anal ring. Unlike the anal ring of other diaspidoids, that of *P. marlatti* exhibits a primitive characteristic in bearing setae, although these are short and only two in number.

The Comstockiella chromosome system occurs in both *P. marlatti* and *M. ehrhorni,* but the chromosome numbers are quite different; that of the former is 9 (haploid) and that of the latter is only 3. Furthermore, *M. ehrhorni* occurs on *Quercus* and *Lithocarpus* (Fagaceae), while *P. marlatti* is restricted to the genus *Phoenix* (the date palm and its allies).

If the main evolutionary series of the armored scale insects is looked upon as involving invention of the pygidium and true scale, then both *P. marlatti* and *M. ehrhorni* must be regarded as lateral series, either maintaining a primitive condition of nudity or secondarily achieving it. Since both species have certain specialized characteristics, such as the terminal abdominal structures of *M. ehrhorni* and the invaginated antennae of *P. marlatti,* the two species should probably be regarded as relics of their individual evolutionary series.

A word should be added about *Mycetococcus corticis* (Townsend and Cockerell), which also infests oak (and mistletoe) and has abdominal lobes resembling those of its congener. This species, which has not been examined cytologically, has several other characteristics quite divergent from those of *M. ehrhorni,* and Ferris (1955) believed that they "might very well be referred to different genera." Thus, all comparisons for the present should be confined to *M. ehrhorni.*

Mycetococcus was separated from *Cerococcus* by Ferris (1918), but the two genera seem to have much in common. The one asterolecaniid species for which a sexual chromosome system is known is *Cerococcus quercus* Comstock, and this proved to have a haploid chromosome number of 9 and, on extensive examination, only the lecanoid chromosome system (Brown, 1959).

XANTHOPHTHALMA

The genus *Xanthophthalma* contains a single species, *X. concinnum* Cockerell and Parrott, which has been collected from palms and a dicotyledonous tree in Mexico and Panama. This genus is sufficiently distinct that Ferris (1938) gave it tribal status as the Xanthophthalmini.

Morphologically, the insect is intermediate between *Phoenicococcus* and a typical armored scale. The posterior portion of the abdomen is lobed in a fashion reminiscent of the armored scales; however, no true scale is formed; the first and second exuviae remain attached to the posterior portion of the body but are separate from each other and form independent flaps which do not cover the body of the adult. A small amount of wax may be associated with the exuviae. The tubular ducts are few in number and distinctly geminate at the anterior end. *X. concinnum* has thus progressed farther toward simple nudity than any other diaspidoid.

A collection of *X. concinnum* from Coatzacoalcos, state of Veracruz, Mex-

ico, proved to have a diploid chromosome number of 16; the females were reproducing parthenogenetically, so that a determination of the sexual system of chromosome behavior was not possible.

It seems likely that *X. concinnum* represents the sole surviving member of an evolutionary branch parallel to that of *Phoenicococcus marlatti* but, because of the rudimentary pygidium and persistent exuviae, stemming from ancestors more closely related to those of modern armored scales than were those of *P. marlatti.*

THE TRIBES OF THE DIASPIDIDAE

Certain aspects of the evolutionary patterns within the Diaspididae may now be considered. As mentioned in the section headed "Correlation of Taxonomy and Chromosome System," the Parlatorini are intermediate in morphology between the Diaspidini and the Aspidiotini. The ducts are two-barred and relatively broad and short in the Parlatorini as they are in the Diaspidini, while those of the Aspidiotini are long and narrow. On the other hand, in the Diaspidini the second, and frequently the third, pygidial lobes are double structures, while those of both the Aspidiotini and the Parlatorini are single. Finally, the Aspidiotini and Parlatorini are again alike in the presence along their pygidial margins of fringed plates, which are less developed in the Diaspidini (fig. 3).

Because the pygidium is used as a paint brush or plasterer's trowel in the construction of the scale covering (Dickson, 1951), the greater development of the pygidial fringe in the Parlatorini and the Aspidiotini indicates that these two tribes are more highly adapted to the armored-scale mode of life than are the Diaspidini. In addition, it is possible to cite two other characteristics which point to the same conclusion. These are the number of antennal bristles and the presence or absence of spiracular pores. These two characteristics have the advantage that they are not pygidial, can vary from species to species within a genus, and have, therefore, been little used, unlike the pygidial characteristics, for taxonomic assessment. If the same conclusion can be reached from a study of characters which have not been considered to be of taxonomic significance as from those which have been so considered, then the conclusion will be more than a restatement of the prior categorizations. Furthermore, in this instance, it is possible to utilize *Mycetococcus ehrhorni* as reflecting the ancestral type.

In *Mycetococcus ehrhorni,* quinquelocular pores are grouped immediately adjacent to the spiracles, while in the presumably related genus *Cerococcus,* such pores form restricted bands terminating at the spiracles. Pores are also to be found restricted to the area immediately adjacent to the spiracles in other groups of coccids. The presence of spiracular pores may thus be looked upon as a primitive characteristic; they are to be found in 82.6 per cent of the Diaspidini but in only 6.3 per cent of the Aspidiotini (table 3, column 2 plus column 4). Considering the small sample size, the percentages for the Odonaspidini and Parlatorini agree fairly well with those for the Diaspidini but not at all with those for the Aspidiotini. In this respect, the Parlatorini are on a par with the Diaspidini and not intermediate between them and the Aspidiotini.

A similar situation is to be found with the antennal bristles. The antennae of *Mycetococcus ehrhorni,* of *Cerococcus,* and of the armored scales in general are small tubercles bearing one or more stout setae or bristles. Those of *M. ehrhorni* and *Cerococcus,* as well as of other coccids with reduced appendages, bear several bristles, sometimes as many as six. More than one antennal bristle is to be found in 45.9 per cent of the Diaspidini but in only 4 per cent of the Aspidiotini, while the Odonaspidini with 20 per cent and the Parlatorini with 25 per cent fall between the two major tribes (table 3, column 3 plus column 4).

TABLE 3

SPIRACULAR PORES AND ANTENNAL BRISTLES IN SPECIES OF THE TRIBES OF THE DIASPIDIDAE

Tribe	Per cent of species with:*				Total species	Incomplete description
	Spiracular pores present	More than one antennal bristle	Spiracular pores present and more than one antennal bristle	Spiracular pores absent and one antennal bristle		
Xanthophthalmini...	....	....	....	100.0	1	..
Diaspidini.....	48.3	11.6	34.3	5.8	172	4
Odonaspidini.....	66.7	0.0	20.0	13.3	15	..
Parlatorini.....	75.0	6.2	18.8	0.0	16	..
Aspidiotini.....	4.7	2.4	1.6	91.3	127	4

* Based exclusively on the Ferris *Atlas* but with genera assigned to the Parlatorini as defined by Balachowsky (1953).

In conclusion, the sequence, Diaspidini-Parlatorini-Aspidiotini, derived from pygidial characters used in taxonomy, is confirmed by a study of non-pygidial characters not used in taxonomy. This analysis almost completely exhausts the morphological information available for any sizable body of scale insects; the adult female has a paucity of parts, and other phases of the life cycle, including larvae and males at various stages of development, have not been recorded in any comprehensive fashion. The Ferris *Atlas,* however, does offer detailed figures of larval antennae, which usually have six segments in the Diaspidini but only five in the Aspidiotini (fig. 3). It may be noted that five are also commonly found in the Parlatorini and Odonaspidini.

The Odonaspidini

Ferris (1942) expressed considerable doubt as to the validity of the odonaspidine tribe. For the present purposes, suffice it to say that it does not appear to be involved in the major sequence of the diaspidid tribes just considered. The presence of the two-barred ducts indicates an affinity with the Diaspidini, and it may be looked upon, to the extent that it is a biological reality, as an independent offshoot from that tribe. The data of table 3, to the extent that such relatively small samples can be trusted, indicate that the Odonaspidini and Parlatorini have progressed beyond the Diaspidini to about the same extent in regard to loss of antennal bristles. It is possible, however, that the tribe as it now stands may include some species which were otherwise derived. The absence of definitive pygidial lobing and the

small size of the ducts (with the bars for that reason obscured) are characteristics that could be achieved by loss and reduction from the Aspidiotini or Parlatorini as well as the Diaspidini.

The one sexual odonaspidine species so far studied cytologically proved to have a Comstockiella system; further work on this aspect of the problem may well help in the understanding of the group.

TABLE 4

PUPILLARIAL SPECIES IN THE TRIBES DIASPIDINI, PARLATORINI, AND ASPIDIOTINI*

Tribes and species	Spiracular pores present (+)	One antennal bristle (+)	Typical pygidial structures; absent (−) to fully present (++++)†	
			Second-stage	Adult
Diaspidini				
Anotaspis particula	+	−	±	−
Exuviaspis enceliae	+	+	+++	−
Fiorinia externa	−	+	+++	++
fioriniae	−	+	+++	++
japonica	−	+	+++	++
theae	−	+	+++	+±
Fissuraspis ulmi	+	+	+	±
Nicholiella bumeliae	+	+	++	+
Pelliculaspis durapyga	+	−	++	++
pellita	+	−	++	++
Radionaspis indica	−	+	−	−
Vinculaspis inclusa	−	+	++	+++
laniata	+	+	++	++
mendicula	+	−	++	++
virgata	+	+	++	++
Parlatorini				
Gymnaspis aechmeae	+	−	+++	±
Leucaspis cockerelli	+	+	+++	+++
japonica	+	+	+++	+++
portaeaureae	+	+	+++	+++
Aspidiotini				
Aonidia atlantica	−	−	+++	++
lauri	−	+	+++	+
shastae	−	−	+±	+

* Data from the Ferris *Atlas*.
† Subjective scoring, on comparison with other species of the same tribe.

Pupillarial Forms

In addition to the pupillarial types already considered, there are several others among the Diaspidini, Parlatorini, and Aspidiotini (table 4). In nearly all the species listed there is unmistakable evidence of the origin of the pupillarial type from that characteristic of the tribe, if not for the adult female at least for the second stage, and in many of the examples the pygidial structures are nearly as well developed as in related nonpupillarial forms. The failure of the adult females to lose the typical pygidial features indicates that most of these species have been relatively recently derived from related nonpupillarial forms. In addition, spiracular pores and more than one antennal bristle are to be found in proportions that might be expected in small samples of the tribes in question.

The two genera *Radionaspis* and *Anotaspis* were placed by Ferris (1938, 1941) in the Diaspidini because of general similarities to certain other forms definitely belonging to this tribe; these forms, however, were not designated by Ferris, and it is impossible at this time to guess which he had in mind. In both genera the single known species is almost completely devoid of characteristic pygidial features; the ducts are too small to be of diagnostic value. *Radionaspis indica* has a distinctive marginal fringe of low lobes and longer processes; the latter are similar to the characteristic diaspidid pygidial lobes in number and spacing but appear more as marginal protuberances than definite structures. In both species there is little or no wax secreted by the second stage and consequently no scale covering, and the insects, as in *Ancepaspis,* are protected only by the second exuvia. *Radionaspis indica,* according to Ferris (1938), is restricted to mango and is therefore of Asian origin, while *Anotaspis particula* (Ferris, 1941) is known only from a single collection from an undetermined tree in Panama. Ferris (1941) noted at least a superficial resemblance between the two genera. Nothing further is known about either species. These two genera apparently represent one (or two) evolutionary divergences parallel to *Ancepaspis* and the pupillarial phoenicococcids. We have only Ferris' (1938, 1941) suggestions of a diaspidine affinity to indicate the point of departure from the main pathway. Finally, it should be noted that the pygidial appendages of *R. indica* seem to follow an aspidiotine rather than a diaspidine developmental pattern, since both the second and third appendages are single rather than double structures.

Comstockiella

The genus *Comstockiella* was assigned to the Aspidiotini by Ferris (1938) on the basis of its long, slender glands and their arrangement in poriferous furrows, but Ferris also pointed out that the genus differed from the typical aspidiotine in the presence of six rather than five segments in the larval antenna, the presence of spiracular pores which are otherwise quite rare in the tribe, and of ducts of neither the one-barred (aspidiotine) nor the two-barred (diaspidine) type. The pygidium is completely devoid of lobes and plates, and in this respect resembles those of the Odonaspidini. Morphologically, *Comstockiella* may be pictured as an evolutionary offshoot from primitive aspidiotine forms which has advanced parallel with the Odonaspidini. In addition, in the odonaspidine genus *Circulaspis,* long, narrow ducts lead into a specially modified median furrow, while shorter, usually broader, ducts are present in abundance elsewhere on the pygidium.

The haploid chromosome number of *Comstockiella* is 5, and it was the first species in which the Comstockiella chromosome system was identified (Brown, 1957). If the evolutionary interpretation based on the morphology is correct, then the primitive aspidiotines had a Comstockiella system, as already suggested (fig. 2, *B*). On the other hand, *Comstockiella* may actually belong to the Odonaspidini rather than being the sole representative of a parallel branch. And the Odonaspidini are extremely difficult to picture as putative ancestors of the Aspidiotini.

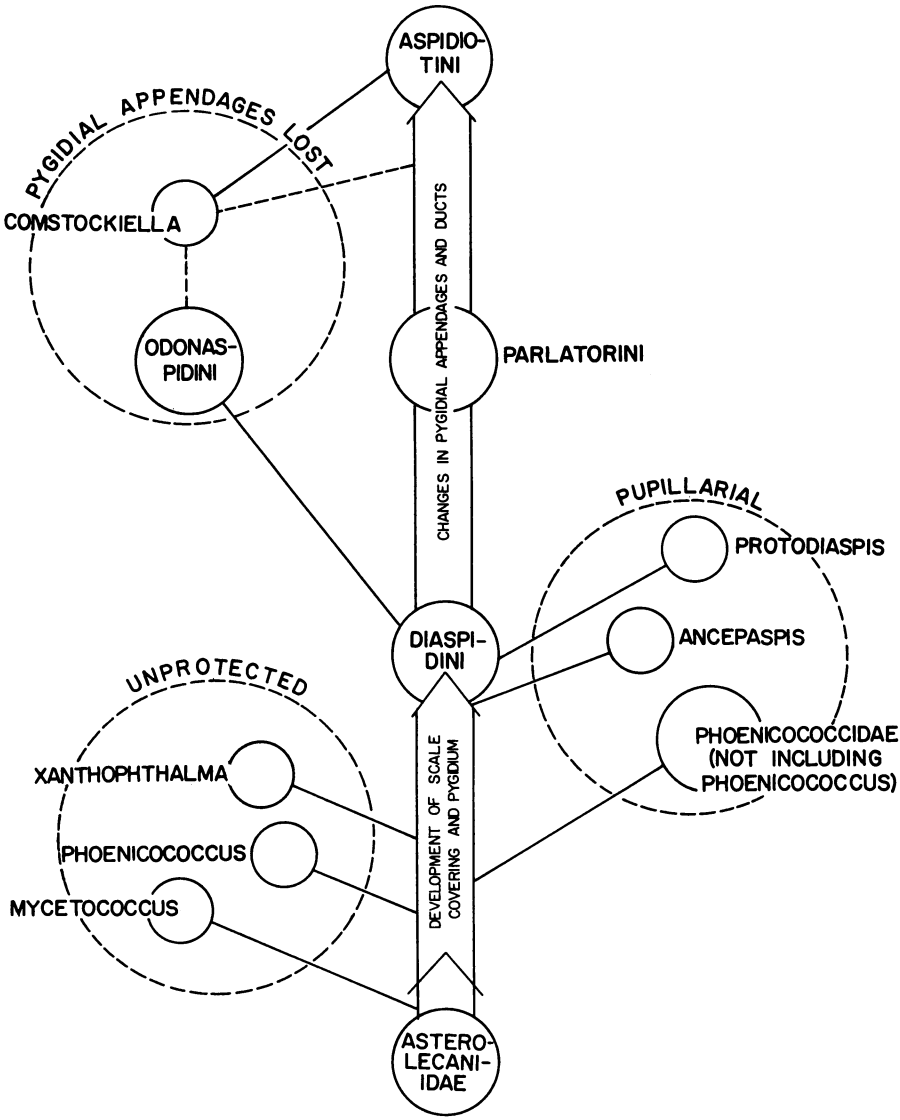


Fig. 5. Putative phylogeny in the armored scale insects and their allies. The pupillarial genera *Radionaspis* and *Anotaspis*, as well as other pupillarial forms with well-defined scale coverings (see text), are not included in the above diagram.

CONCLUSIONS

The major evolutionary progress of the armored scale insects has been in the development of a pygidium for use in the construction of a scale. On cytological evidence, the armored scales originated from the Asterolecaniidae, which lack pygidia and scale coverings. No primitive pygidial forms have been identified, and it is concluded that these have been replaced by the modern scale insects.

The surviving forms with poorly developed pygidia represent lateral divergences from the main evolutionary pathway. These forms, as represented by such groups as the Phoenicococcidae, Xanthophthalmini, and others, have proved to be taxonomic problems because loss of characteristic structures has resulted in apparent convergence. A reassessment of the morphological evidence from this point of view, in connection with cytological evidence, can be used to obtain a picture of the evolutionary pattern, which, though admittedly tentative, is logical and subject to revision on this basis. The gist of the conclusions can therefore be represented in a diagram of the pattern (fig. 5).

The above conclusions would result in some taxonomic reshuffling. A formal attempt in this direction will not be made here; its proper place is in a taxonomic monograph. We should like, however, to mention the retentions and changes which seem desirable. The section Diaspidoïdae should be maintained and include three families, the Phoenicococcidae, the Halimococcidae, and the Diaspididae. The Phoenicococcidae would contain only the two genera *Phoenicococcus* and *Xanthophthalma,* which may or may not deserve separate tribal status. The other genera assigned by Stickney (1934) to the Phoenicococcidae, i.e., *Thysanococcus, Platycoccus, Palmaricoccus,* and the only one theretofore named, *Halimococcus,* would then comprise the Halimococcidae. Within the Diaspididae, six tribes should be recognized, the Diaspidini, Aspidiotini, and Odonaspidini as defined by Ferris; the Parlatorini as defined by Balachowsky; and two new tribes, yet to be defined, one each for the genera *Ancepaspis* and *Comstockiella.* The genera *Radionaspis* and *Anotaspis* might well be left unassigned pending further investigation of Central American and Asian scale insects. The suggested changes are few in number and involve only the problem groups, which include but a very small percentage of the total number of armored scale insects and close allies. It is of interest to note that the interpretations presented above, which stem from points of view quite different from those of Ferris, Stickney, and Balachowsky, leave the bulk of their work quite unaltered. The over-all conclusion that the groups in question are natural entities would therefore be the more reliable.

SUMMARY

Problems of relationship in the armored scale insects and their allies have been complicated because loss of characteristic structures leads to apparent convergence. The results of a chromosomal survey, combined with a new interpretation of data previously presented by taxonomists, have permitted a new assessment of various problem groups and identification of the probable origins of evolutionary series.

The armored scale insects originated from the Asterolecaniidae. The noteworthy innovations were the protective scale covering and the pygidial apparatus used in its construction. Primitive pygidial forms, if any exist, have not been identified as such and have probably been replaced by modern forms. The various problem groups are believed to be lateral divergences from the main, or "pygidial," evolutionary series, and may have originated from ancestors either before or after the pygidium was developed.

One set of problem groups, the genera *Protodiaspis, Ancepaspis,* and those of the Phoenicococcidae other than *Phoenicococcus* itself, represent pupillarial specializations in which the adult female remains encased in the second molt. The genus *Protodiaspis* represents a well-defined series in which the primitive members are typical pygidial types, while the more advanced members closely resemble species of *Ancepaspis.* The genus *Ancepaspis* probably includes the surviving members of an evolutionary series closely parallel to but, on the basis of its chromosome system, probably independent of that of *Protodiaspis.* The genera of the Phoenicococcidae, other than *Phoenicococcus,* are a pupillarial group which could have arisen from either a pygidial form or a prepygidial type; there is no closely parallel series by which to judge.

In the opposite direction, *Phoenicococcus* and *Xanthophthalma* are protected by neither a scale covering nor the second molt. Loss of a protective scale covering on the one hand and substitution of the second molt for a scale covering on the other could well have resulted in convergence from ancestors with distinctive pygidial characteristics to descendants with none, and therefore of similar appearance. The two genera may possibly be related and, if not, are the relics of two parallel series. If the latter is the case, then *Xanthophthalma,* with retained first and second molts, probably originated from farther along the main evolutionary path than did *Phoenicococcus.*

The major tribes of the Diaspididae may be arranged in an evolutionary series, Diaspidini-Parlatorini-Aspidiotini, on the basis of pygidial characteristics used in taxonomy. A comparison of the number of antennal bristles and the presence or absence of spiracular pores indicates that the Diaspidini are much more like the Asterolecaniidae in these two characters and therefore are at the lower end of the series. If this picture is correct, then the most common chromosome system in the armored scale insects must have originated at least twice from its antecedent, at least once in the Diaspidini and once in the Aspidiotini.

The tribe Odonaspidini seems to be a second derivative from the Diaspidini. Although a well-defined scale is present, the pygidium has lost its characteristic marginal appendages. The Odonaspidini could thus include convergent elements from several tribes. The monotypic genus *Comstockiella* has characteristics which may be interpreted as derivable rather remotely from a primitive aspidiotine; the possibility must also be considered that it is, instead, related to the odonaspidines.

No formal taxonomic reclassification of the section Diaspidoïdae is made, but the way in which the above interpretations could be so applied is indicated. Although the problem groups would undergo some reshuffling, the majority of the armored scale insects and their allies would remain as classified at present.

LITERATURE CITED

BALACHOWSKY, A. S.
1942. Essai sur la classification des cochenilles (Homoptera: Coccoidea). Grignon Ec. Natl. Agr. Ann. (sér. 3) **3**:34–48.
1948. Les cochenilles Diaspidinae (première partie). Aspidiotini. Act. Sci. et Ind. No. 1054. 154 pp. (Hermann et Cie., Paris.)
1950. Les cochenilles Diaspidinae (deuxième partie). Aspidiotini. Act. Sci. et Ind. No. 1087. 163 pp. (Hermann et Cie., Paris.)
1951. Les cochenilles Diaspidinae (troisième partie). Aspidiotini (fin). Act. Sci. et Ind. No. 1127. 162 pp. (Hermann et Cie., Paris.)
1953. Les cochenilles Diaspidinae (quatrième partie). Odonaspidini-Parlatorini. Act. Sci. et Ind. No. 1202. 207 pp. (Hermann et Cie., Paris.)
1954. Les cochenilles paléarctiques de la tribu des Diaspidini. Mem. Sci. Inst. Pasteur. 450 pp. (Paris.)

BENNETT, F. D., and S. W. BROWN
1958. Life history and sex determination in the diaspine scale *Pseudaulacaspis pentagona* (Targ.) (Coccoidea). Canad. Ent. **90**:317–25.

BODENHEIMER, F. S.
1944. A conchaspid from Kurdistan and its importance in the phylogeny of the Diaspidae (Hemiptera). Proc. Roy. Ent. Soc. London. Sec. B: Taxonomy **13**:4–5.

BORKHSENIUS, N. S.
1958. On the evolution and phylogenic interrelations of Coccoidea (Insecta: Homoptera). (English summary.) Zool. Zhurn. **37**:765–80.

BORKHSENIUS, N. S., and T. N. BUSHCHIK
1959. Notes on the Coccoidea of China. V. A new genus and species of scale insects (Homoptera: Coccoidea: Phoenicococcidae) from the province of Szuch'uan. (Scientific results of the Sino-Soviet expeditions of 1955–57 in southwest China). Ent. Obozrenie **38**(1):160–63. (English translation, "Entomological Review," A.I.B.S., Washington, D.C. **38**(1):143–46.)

BRIMBLECOMBE, A. R.
1959. Studies of the Coccoidea. 10. New species of Diaspididae. Queensland Jour. Agr. Sci. **16**:381–407.

BROWN, S. W.
1957. Chromosome behavior in *Comstockiella sabalis* (Comstk.) (Coccoidea: Diaspididae). (Abstract.) Genetics **42**:362–63.
1958. Haplodiploidy in the Diaspididae—confirmation of an evolutionary hypothesis. Evolution **12**:115–16.
1959. Lecanoid chromosome behavior in three more families of the Coccoidea (Homoptera). Chromosoma **10**:278–300.

BROWN, S. W., and F. D. BENNETT
1957. On sex determination in the diaspine scale *Pseudaulacaspis pentagona* (Targ.) (Coccoidea). Genetics **42**:510–23.

BROWN, S. W., and W. A. NELSON-REES
1961. Radiation analysis of a lecanoid genetic system. Genetics **46**:983–1007.

DICKSON, R. C.
1951. Construction of the scale covering of *Aonidiella aurantii* (Mask.). Ann. Ent. Soc. Amer. **44**:596–602.

FERRIS, G. F.
1918. Notes on Coccidae. II. (Hemiptera.) Canad. Ent. **50**:323–32.
1937. Atlas of the scale insects of North America (series I). The Diaspididae (part I). Stanford University Press, California.
1938. Atlas of the scale insects of North America (series II). The Diaspididae (part II). Stanford University Press, California.
1941. Atlas of the scale insects of North America (series III). The Diaspididae (part III). Stanford University Press, California.
1942. Atlas of the scale insects of North America (series IV). The Diaspididae (part IV). Stanford University Press, California.

1955. Atlas of the scale insects of North America (volume VII). Stanford University Press, California.

1957. Notes on some little-known genera of the Coccoidea. Microent. **22**:59–77.

HUGHES-SCHRADER, SALLY

1935. The chromosome cycle of *Phenacoccus* (Coccidae). Biol. Bul. **69**:462–68.

1944. A primitive coccid chromosome cycle in *Puto* sp. Biol. Bul. **87**:167–76.

1948. Cytology of the coccids (Coccoidea: Homoptera). Adv. in Genetics **2**:127–203.

MCKENZIE, H. L.

1945. A revision of *Parlatoria* and closely allied genera (Homoptera: Coccoidea: Diaspididae). Microent. **10**:47–121.

MCKENZIE, H. L., and W. A. NELSON-REES

1962. Two new species and additional collection records for the genus *Protodiaspis* (Homoptera: Coccoidea: Diaspididae). Hilgardia **33**(4):133–139. (Leading paper in the present issue.)

MAMET, R.

1954. A monograph of the Conchaspididae Green (Hemiptera: Coccoidea). Trans. Roy. Ent. Soc. Lond. **105**:189–239.

SCHRADER, F.

1921. The chromosomes of *Pseudococcus nipae*. Biol. Bul. **40**:259–70.

SCHRADER, F., and SALLY HUGHES-SCHRADER

1931. Haploidy in metazoa. Quart. Rev. Biol. **6**:411–38.

STICKNEY, F. S.

1934. The external anatomy of the red date scale, *Phoenicococcus marlatti* Cockerell, and its allies. U.S.D.A. Tech. Bul. No. 404. 162 pp.

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