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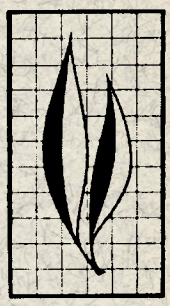
Chromosomal Survey of the Armored and Palm Scale Insects (Coccoïdea: Diaspididae and Phoenicococcidae)

Spencer W. Brown

UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES



A chromosomal survey of 140 species of 73 genera of armored and palm scale insects revealed the distribution of the 3 chromosome systems (lecanoid, Comstockiella, and diaspidid), of parthenogenesis, and of variation in chromosome number among the subdivisions of this section of the coccids, the Diaspidoïdae.

The heterochromatic Comstockiella system, with which the lecanoid system is usually associated, is the basic system of the section and is found in all the tribes for which sexual forms are known, as well as in the palm scales, however defined. The heterochromatic lecanoid system has been found only once by itself, in a species of palm scale. The diaspidid system is restricted to the two major tribes of the armored scales, the Diaspidini and Aspidiotini, where it has been found in the majority of forms.

Parthenogenesis is widespread, and unisexual strains have been newly discovered in several species previously considered sexual. Contrary to what might be expected, there is little variation in chromosome number in the parthenogenetic forms.

The basic haploid chromosome numbers are 5 for the palm scales (restricted sense) and 4 for the armored scales. A somewhat higher basic number may exist for the nude forms, such as *Phoenicococcus marlatti* (excluded here from the palm scales in the restricted sense) and *Xanthophthalma concinnum.* Chromosome numbers range from 3 to 9; there is considerably more variation in chromosome number in the Diaspidini than in the Aspidiotini. In the latter tribe, however, the Comstockiella chromosome system may be playing a more active role in evolution than in the former.

In addition, various cytological aspects, ranging from details of spermiogenesis to the formation of chromocenters in mycetocytes, have been described for certain species.

THE AUTHOR:

Spencer W. Brown is Professor of Genetics and Geneticist in the Experiment Station, University of California, Berkeley.

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Chromosomal Survey of the Armored and Palm Scale Insects (Coccoïdea: Diaspididae and Phoenicococcidae)[1, 2, 3]

INTRODUCTION

THE DIASPIDID CHROMOSOME SYSTEM

THE PURPOSE OF the present report is to offer an account of the chromosomal cytology of those species of armored scales and their closest allies, the phoenicococcids, for which such information is currently available.

Among the Homoptera, the superfamily of the coccids (Coccoïdea) is the most highly specialized morphologically; and, among the 12 to 15 rather diverse groups within the superfamily, the armored scales and the phoenicococcids have attained the highest level of specialization. For this reason, these two families, the armored scales, or Diaspididae, and the Phoenicococcidae have often been classed together in a separate section (Diaspidoïdae) of the superfamily. The specialization achieved by the armored scales has proved to be highly successful; more than fifteen hundred species are now known, including cosmopolitan types widely distributed on cultivated host plants and aggressive species found on the native vegetation throughout extensive areas. The allied family of the phoenicococcids consists of only a few genera and species, which are seemingly restricted to localized habitats in the tropics and subtropics; but one species, *Phoenicococcus marlatti* (Cockerell), has been carried around the world on the date palm. Because of their considerable importance as agricultural pests, many of the armored scales have been thoroughly studied in regard to life cycle, variation under different environmental conditions, and response to insecticides, parasites, and predators. Until recently, however, there has been relatively little information in regard to the chromosomal cytology of the armored scales.

The first observations of diaspidid chromosomes were made by Schrader (1929), who described oögenesis in the parthenogenetic (unisexual) strain of *Aspidiotus hederae* (Vallot) and reported a chromosome number of 8. The same number of chromosomes was found again by Schrader in embryos of unknown sex present in gravid females of *Aonidiella aurantii* (Maskell) supplied by Dickson (1941). The latter demonstrated that resistance to cyanide is a heritable trait in *A. aurantii* and is transmitted in a sex-linked fashion by the mothers to both sons and daughters, but by the fathers to daughters only. Dickson's work still remains the single genetic study of this sort undertaken with any of the armored scales.

[1] Submitted for publication January 28, 1964.

[2] This work was begun during the tenure of a Guggenheim Fellowship and subsequently was aided by grants from the National Science Foundation, G-4497, G-9772, and GB-413.

[3] The present publication is dedicated to Professor Dr. Hans Bauer of Tübingen on his sixtieth birthday, September 27, 1964.

More recently, Lindner (1954) reported the haploid and diploid numbers of 4 and 8 for the males and females, respectively, of *Aspidiotus* (= *Quadraspidiotus*) *perniciosus* (Comst.), and suggested that the haploid males arose from unfertilized eggs in a fashion similar to that well known in the Hymenoptera.

The results of further work with a haplodiploid system were offered by Brown and Bennett (1957) and Bennett and Brown (1958) for the peach scale, *Pseudaulacaspis pentagona* (Targ.). Eight chromosomes were present in the haploid males and 16 in the diploid females. In repeated laboratory trials, no offspring of either sex was produced by unmated females, yet these could be kept alive and fertile for many weeks. During the isolation period, the virgin female would proceed to build an accessory covering extending from one side of the original scale and differing from it in color and texture (Tremblay, 1958). After mating, the aged females soon stopped construction of the accessory covering and, a few days later, began to produce eggs. Since there was no doubt whatever of the failure of unmated females to oviposit, male haploidy could not be explained as the simple consequence of the development of unfertilized eggs.

The production of haploid males in *Psuedaulacaspis pentagona* thus required either a stimulation of the unfertilized eggs by some sort of ovarian change following mating or the operation of an entirely different type of mechanism. Observations at early embryonic stages showed the latter alternative to be true; male haploidy is the result of the elimination of one haploid set of chromosomes from an originally diploid embryo; the eliminations occur at anaphase during the mitoses of the late cleavage stage, and all or nearly all the diploid nuclei are thus simply changed to haploid.

As in other Hemiptera (Schrader, 1935), the chromosomes of the armored scales do not have a localized kinetochore or centromere but appear to be endowed with the capacity for movement on the anaphase spindle along their entire lengths. A striking validation of Schrader's concept of the hemipteran chromosome was provided by the experiments of Hughes-Schrader and Ris (1941), who used X-ray treatments to fragment coccid chromosomes; even though shattered into many small bits, the chromosomal material still showed normal mitotic behavior. Fragmented chromosomes can thus be used as genetic markers for cytogenetic studies of hereditary transmission in the Hemiptera, and an experiment of this sort was performed by Brown and Bennett (1957) with *Psuedaulacaspis pentagona*. Following X-ray treatment of the mothers, fragment chromosomes were present at post-cleavage stages in both the haploid, male embryos and the diploid, female embryos; after treatment of the fathers, fragments appeared only in the diploid embryos. These results are explicable on the assumption that the eliminated set is of paternal origin; thus, after treatment of the fathers, the paternal chromosome set containing fragmented chromosomes would be eliminated at the late cleavage stage in the ontogeny of the sons.

Haplodiploid systems in which the chromosomes of the male are of maternal origin are expected to show sex-linked hereditary transmission of *all* chromosomal hereditary factors in the same manner that all factors carried by the X chromosome show sex linkage in XX-XO systems. The results of Dickson (1941) on inheritance of resistance to cyanide in *Aonidiella aurantii* would thus conform to a haplodiploid scheme, and this species has indeed proved to be a haplodiploid.

The system of chromosome behavior in which the haploidy of the males de-

pends on chromosome elimination is the most common in the sexual species of armored scale insects and has thus been named the "diaspidid" system (Brown, 1959, as "diaspid"). Additional published information on this system includes the observation of Brown and Bennett (1957) of a slight degree of heterochromatization of the elimination chromosomes immediately prior to their ejection in *Diaspis bromeliae* (Kern) and in one other species of armored scale, and the confirmatory reports by Hughes-Schrader (1957) on the elimination process for *Psuedaulacapsis pentagona* and *D. bromeliae,* and by Tremblay (1960) for *P. pentagona.* Tremblay (1959) has also suggested that those eggs destined to yield haploid males can be identified in the young ovarioles because the associated nurse cells are lost at an early age and the egg sheath cells become grossly thickened, apparently to function as nurse cell substitutes in the nutrition of the egg. More recently, Tremblay (1961) has altered his views on this subject, leaving the problem again open.

SYNOPSIS OF THE OTHER CHROMOSOME SYSTEMS

In this section, a brief summary will be given of the chromosome systems previously described. Other aspects, not previously reported, will be described or noted for some of the species and then considered specifically following the species catalogue.

In addition to the diaspidid system, two other sexual systems are known to occur in the armored scale insects—the Comstockiella and the lecanoid. These are all illustrated in figure 1 with the more typical XX-XO system for comparison (the XX-XO system does not occur in the armored scale insects).

Lecanoid system. Probably the most common system in the coccids as a whole is the lecanoid system, well known from the pioneer work of Schrader (1921, 1923*a*) and subsequent studies of others (see Hughes-Schrader, 1948; Brown, 1959; Brown and Nelson-Rees, 1961; Nelson-Rees, 1962; Nur, 1963; Nur and Chandra, 1963). The paternal set of chromosomes becomes heterochromatic at the blastula stage in the males, and remains so throughout development. At spermatogenesis, both the heterochromatic and the euchromatic sets divide equationally during the first division, and are segregated from each other during the second to yield a quadrinucleate spermatid. Of the four nuclei, only the euchromatic derivatives form sperm, while the heterochromatic gradually diminish during early stages of spermiogenesis.

Comstockiella system. The Comstockiella system is similar to the lecanoid until spermatogenesis. One pair of homologues, the D pair, exhibits differential behavior. Behavior for the remainder of the chromosome is as follows. The heterochromatic chromosomes lose their differential aspect and pair with their euchromatic homologues during prophase; during anaphase, the pairing partners separate at random in going to the poles; only this single division occurs, and both daughter nuclei proceed to form sperm. The D chromosome pair retains the heterochromatic, euchromatic differential. The euchromatic D homologue (D^E) divides equationally, thus making a contribution to each of the two sperm, while the heterochromatic D homologue (D^H) is eliminated, the two products of its equational division forming pycnotic residues which slowly disappear during spermiogenesis.

Both the Comstockiella and lecanoid systems may occur in the same species and in the same individual; only one system, however, occurs in any one cyst. The early developmental stages of the two systems are perforce identical, and

the two can be distinguished only by examination of spermatogenesis (in some specific instances, spermiogenic stages may suffice).

In some species the D chromosome pair is not a fixed entity, but may vary from one to another pair of homologues in the diploid complement. The same pair performs the D role in any one cyst, but variation among cysts in this regard seems to be completely at random.

The Comstockiella system was described briefly in abstract by Brown (1957) and a detailed account, including a discussion of its evolution, has recently been published (Brown, 1963). The information contained in this present report has already been used in an analysis of the evolutionary patterns in the armored scales (Brown and McKenzie, 1962), and the reader is referred to this publication for a discus-

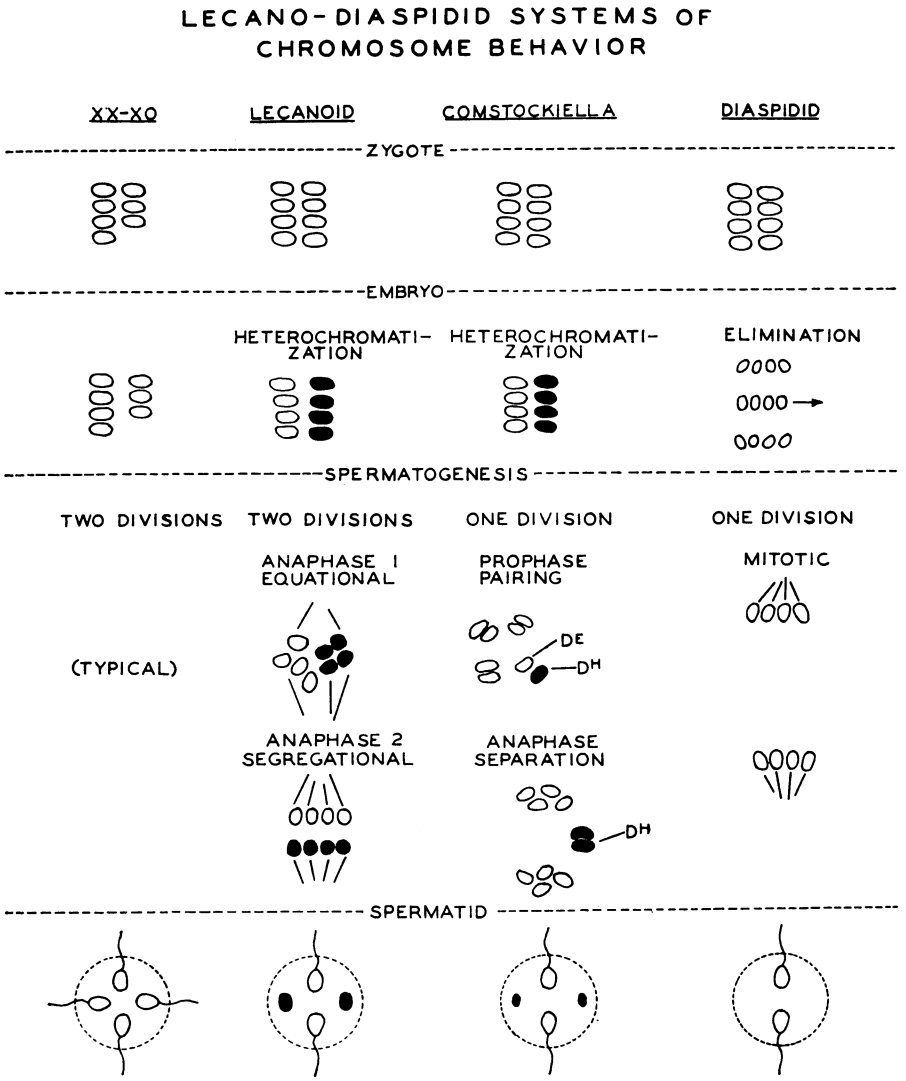


Fig. 1. Diagram of chromosome behavior in males of the Diaspidoïdae (with a typical XX-XO system for comparison). (Reprinted from Brown and McKenzie, Hilgardia 33(8) : 145.)

sion of the evolution of the insects, and to both this and the Comstockiella report (Brown, 1963) for a discussion of the evolution of the chromosome systems themselves.

In addition to the three different sexual systems occurring in the armored scales, parthenogenesis is also quite common.

Mycetocyte formation. In addition to the embryo proper, formed either from the zygote or, in the parthenogenetic races, from the zygote substitute, there is also an adjunct tissue formed by cleavage from a primary nucleus originating from the union of the two polar bodies and a cleavage nucleus. The combination of a diploid and a haploid polar body plus a diploid cleavage nucleus yields a pentaploid combination (fig. 2). This sequence may differ in parthenogenetic forms. The cells of the adjunct tissue usually contain the intracellular symbionts and thus function as mycetocytes. Mycetocyte formation in the coccids was first described by Schrader (1923*b*) for a mealybug. The sequence in the armored scale insects (Brown and Bennett, 1957; Bennett and Brown, 1958) is in general similar to that of the mealybug. One important difference, however, exists: in the mealybug, the product of the fusion of the two polar bodies undergoes several divisions to yield triploid nuclei, which then fuse either *inter se* or with cleavage nuclei (Schrader, 1923*b;* Brown and Nelson-Rees, 1961).

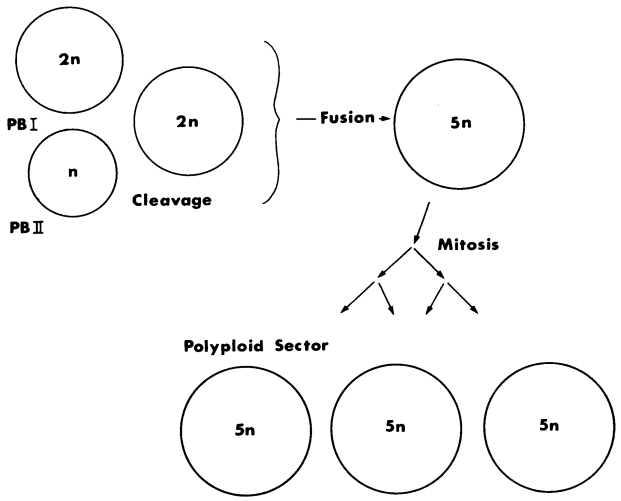


Fig. 2. Polyploid sectors in the armored scales originate from a single polyploid nucleus, which is formed by the union of both polar bodies with a cleavage nucleus. In many, but not all species, the cells formed around the polyploid nuclei will include the intracellular symbionts.

SURVEY OF THE SPECIES

Introductory notes. The cytological methods have been reported by Brown and Bennett (1957) and Brown (1959).

The species are arranged alphabetically under the family Phoenicococcidae and the five tribes of the Diaspididae—the four recognized by both Ferris (1937) and Balachowsky (1948), and the Parlatorini, recognized only by the latter.

Discussion of the validity of some of these assignments will be found in Brown and McKenzie (1962).

The information to be offered on each of the species is tabulated as follows:

(1) the name of the species, with author;
(2) *tax.*, the most readily available taxonomic reference, preferably illustrated, to the species in question:
Ferris, series (S) no. (I, II, III, IV) and page no., refers to the Ferris Atlas (1937, 1938, 1941, 1942);
Balach., series no. (IV, V, VI, VII) and page no., refers to the Balachowsky series on the Aspidiotini, Odonaspidini and Parlatorini (1948, 1950, 1951, 1953*a*); but if the symbol "Di" appears before the page no., reference is made to the separate work on the Diaspidini (1954).
The remainder of the Balachowsky references are handled as standard literature citations.
(3) *c & i.*, collected and identified by;
(4) date and place collected;
(5) *host,* the host plant;
(6) the chromosome formula:
F, the chromosome number from female tissue, usually gonial,
M, the chromosome number from male tissue, usually somatic,
E, the chromosome number or numbers occurring in the embryos (in *M* and *E,* the designation 4 + 4, etc., indicates 4 euchromatic and 4 heterochromatic chromosomes);
P, the chromosome number occurring in the polyploid sector;
(7) *sex.* or *parth.*, indicating whether the species is sexual or parthenogenetic;
(8) type of chromosome system (if sexual):
diaspidid,
Comstockiella (designated as simple when the D chromosome pair is a fixed entity, or variable-D when the D role is assumed by a different set of homologues in different instances),
lecanoid, or
heterochromatic, where a non-diaspidid system occurs but further analysis at spermatogenesis was not made;
(9) *prev. publ.*, previous reports on the cytology of the species;
(10) *results,* new information to be offered in this report unless no additional information is available.

Three species had been studied cytologically before the beginning of the present program: *Aonidiella aurantii, Aspidiotus hederae,* and *Quadraspidiotus perniciosus;* the previous work on each of these is reviewed in the species survey, and the species are starred (*).

THE PHOENICOCOCCIDAE

Reasons have recently been given (Brown and McKenzie, 1962) for a taxonomic treatment of this family quite different from that of Ferris (1942). According to the former authors, the genus *Ancepaspis* might well be included in the Diaspidini along with *Protodiaspis. Phoenicococcus,* the type genus, is quite divergent morphologically from the other genera, and should probably be associated with *Xanthophthalma.* The remaining genera seem to form a more uniform group morphologically. The chromosome systems of all the genera classed as phoenicococcids by

Ferris are heterochromatic systems, that is, Comstockiella, lecanoid, or a combination. The chromosome numbers now known conform to the suggested grouping: diploid numbers of 6 and 8 for *Ancepaspis,* of 18 for *Phoenicococcus marlatti,* and 10 for the remaining genera. However, since a formal taxonomic revision has yet to be made, the family as defined by Ferris will be used for the present study. At least one species of each of the 6 genera included in the family (Stickney, 1934; Ferris, 1942) has now been studied cytologically.

The major emphasis of the cytological analysis has been given to spermatogenic stages in order to determine the chromosome system. Consequently, there are still gaps for the entire family (however defined) in regard to certain other cytological aspects. Studies of oögenesis would undoubtedly yield little of value, especially in view of the small size of the chromosomes, but information on later behavior of the polar bodies and the formation of the polyploid sector would certainly be of interest.

Ancepaspis edentata (Ferris)

tax. Ferris SIV-435; *c.* Brown and Nelson-Rees; *i.* Wilkey; Portal, Arizona; Sept., 1960; *host, Acacia greggii.*

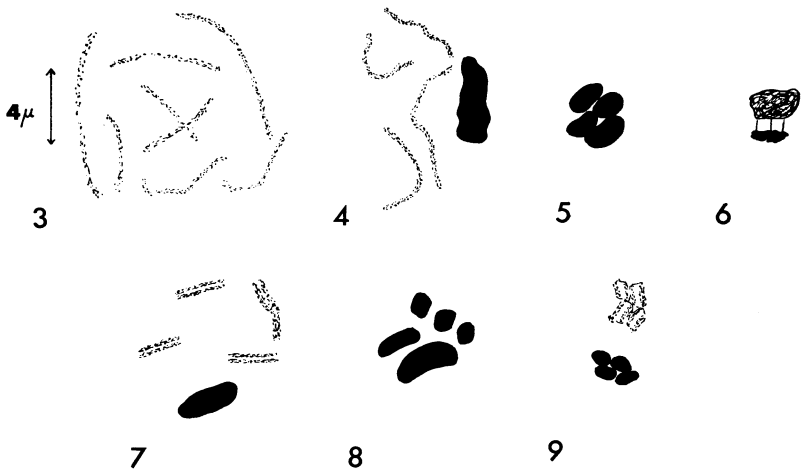
F 8 M 4+4 E 8, 4+4 P—; sex.; Comstockiella and lecanoid

prev. publ.—The chromosome number and system (as Comstockiella only) were cited by Brown and McKenzie (1962) in a comparison of *Ancepaspis* and *Protodiaspis.*

results—Males had not been recognized (Ferris, *loc. cit.*) prior to the cytological studies. The species had been described only once previously, from *Acacia greggii,* near Vail, Arizona; we were able to find it again near Portal by locating the host plant after studies of herbarium specimens at the Southwestern Research Station of the American Museum of Natural History.

Both somatic and spermatogenic division figures showed a karyotype consisting of 3 chromosomes about the same size and one considerably larger (figs. 3–5, 7–8).

Nearly all the spermatogenic stages observed showed lecanoid division figures, and all the spermiogenic stages showed the large residues expected from a lecanoid system. Only a few of the division figures were of the Comstockiella type. The various lecanoid figures observed were quite typical (figs. 7–9), but the Comstockiella figures were not. These latter consisted almost exclusively of a few prometaphases, in which there were 4 similar bivalents and no distinguishable D pair (fig. 5), displayed as separate D^E and D^H entities. Complete pairing of this sort has been observed from time to time in other Comstockiella examples (Brown, 1963). A few figures with post-telophase ejection typical of the elimination of the D^H chromosome served, however, to indicate that the Comstockiella system probably conforms to the general pattern in this species also (fig. 6). The very small percentage of cysts with the Comstockiella system, and the complete pairing in the few Comstockiella examples, indicate the desirability for further study of this species.



Figs. 3–9. *Ancepaspis edentata.* Fig. 3. Female embryo, mitotic prophase. Fig. 4. Male embryo, mitotic prophase. Figs. 5–9. Spermatogenesis. Fig. 5. Metaphase of Comstockiella sequence. Fig. 6. Post-telophase ejection of D^H chromosome, Comstockiella sequence. Fig. 7. Prophase I, lecanoid sequence. Fig. 8. Prometaphase I, lecanoid sequence. Fig. 9. Telophase II, lecanoid sequence.

Ancepaspis tridentata (Ferris)

tax. Ferris SIV-438; (1) *c.* Brown; *i.* McKenzie; La Paz, Baja California, Mexico; Oct., 1958; *host,* mesquite; (2) *c.* Brown and Nelson-Rees; *i.* Wilkey; Mitla, Oaxaca, Mexico; Aug., 1960; *host,* mesquite.

F 6 M 3+3 E 6, 3+3 P —; sex.; Comstockiella, variable-D

prev. publ.—Because of the low chromosome number and differences in chromosome size, it has been possible to demonstrate that all 3 pairs of homologues alternate in performing the D role (Brown, 1963). The chromosome number and system were also cited in the detailed comparison of *Ancepaspis* and *Protodiaspis* offered by Brown and McKenzie (1962).

results—The insects in both collections were sexual, and had the same general karyotype. Spermatogenesis was studied only in the second collection. Males had not been recognized (Ferris, *loc. cit.*) prior to the cytological observations.

Colobopyga (=*Palmaricoccus*) Brethes

Palmaricoccus was one of the new genera erected by Stickney (1934) in his monograph on the Phoenicococcidae. Synonomy with an older name was discovered by Ferris (1952) ten years after he had used *Palmaricoccus* in the Atlas. The synonomy has since been adopted by Beardsley (1963).

Colobopyga browni Beardsley

tax. Beardsley, 1963; *c.* & *i.* Beardsley (as a then undescribed species); Koolau Mts., Oahu, Hawaii; April, 1960; *host, Pritchardia* sp.

F— M 5+5 E 10, 5+5 P—; sex.; Comstockiella, simple

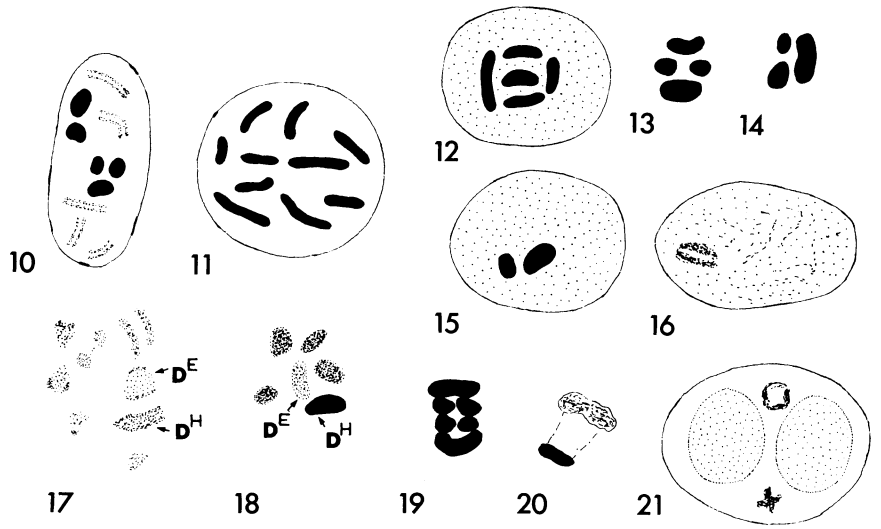
prev. publ.—none

results—Embryonic stages showed the typical differentiation between the female embryos without, and the male embryos with, heterochromatization (figs. 10–11).

During the period prior to prophase proper, the number of heterochromatic entities in each spermatocyte was reduced from five to one (figs. 12–16). As in previously described cases (Brown, 1963), there seemed to be no intermediate stages between the heterochromatic state and the assumption of an appearance indistinguishable from the remainder of the nuclear contents, which was that of the typical resting nucleus.

The earlier stages of chromosome pairing were not observed. Some bivalent formation was still in process at midprophase when the homologues were juxtaposed (fig. 17). At prometaphase, the expected 6 (n + 1) entities were present, all superficially monomeric (fig. 18). The D role was always undertaken by the largest pair of homologues, and the D^E and D^H chromosomes were sometimes identifiable at prometaphase (fig. 18), but such distinctions had completely disappeared by metaphase (fig. 19).

The D^H entities were ejected from the daughter nuclei following telophase (fig. 20). The pycnotic residues were all of the same relative size until they finally disappeared at midspermiogenesis (fig. 21). Although they assumed a variety of shapes, it was usually very easy to judge, especially from a comparison of sister, or paired, residues that the approximate volumes of the residues were uniform throughout. There was thus no evidence from either the earlier or later stages of any variation in the D role.



Figs. 10–21. *Colobopyga browni.* Fig. 10. Mitosis in a male embryo; 5 euchromatic and 5 heterochromatic chromosomes. Fig. 11. Mitosis in a female embryo; no chromatic differentiation. Figs. 12–16. Prespermatogenic reduction in number of heterochromatic entities from 5 to 1 (heterochromatic entities only in figs. 13 and 14; otherwise, whole nuclei). Fig. 17. Midprophase; homologues juxtaposed; bivalent formation just commencing. Fig. 18. Prometaphase. Fig. 19. Metaphase. Fig. 20. Post-telophase ejection of a D^H product. Fig. 21. Binucleate spermatid with two pycnotic residues, one cruciform, the other like a micronucleus.

Colobopyga pritchardiae (Stickney)

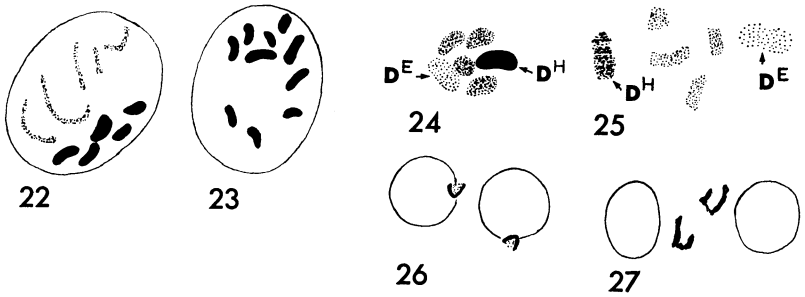
tax. Stickney, 1934; Beardsley, 1963; *c.* & *i.* Beardsley; Koolau Mts., Oahu, Hawaii; April, 1960; *host, Pritchardia* sp.

F 10 M 5+5 E 10, 5+5 P—; sex.; Comstockiella, variable-D

prev. publ.—none

results—Embryonic stages were similar to those of the congener (figs. 22–23).

Only a few individuals were in the proper stage for analysis of spermatogenesis, which showed the six (n + 1) entities expected with a Comstockiella system. The D^E and D^H chromosomes were still distinguishable at late midprophase, and the other chromosomes had completely lost all trace of their bivalent structure, appearing simply monomeric (figs. 24–25). The few examples of prophase stages showed only the largest pair of homologues functioning as the D chromosomes. However, two size classes of residues were distinguishable at later stages: a larger residue about the right size to have originated from the largest pair of homologues, and a smaller residue (figs. 26–27). In both size classes, the residues had a U-shape stemming from the division of the daughter chromatids of the D^H chromosome. Whether the D role was rotated among more than two pairs of homologues could not be determined.



Figs. 22–27. *Colobopyga pritchardiae.* Fig. 22. Somatic division in male embryo; 5 euchromatic and 5 heterochromatic chromosomes. Fig. 23. Mitosis in female embryo; 10 chromosomes, no differentiation in chromaticity. Figs. 24–25. Late prophase of spermatogenesis; n + 1 (= 6) entities present, D^H and D^E recognizable, but presumed bivalent nature of remaining elements not apparent. Figs. 26–27. Post-telophase of spermatogenesis; pycnotic residues from D^H division products; two size classes were recognized; small, fig. 26; and large, fig. 27.

Halimococcus borassi Green

tax. Stickney, 1934; *c.* & *i.* Fernando; Peradeniya, Ceylon; Jan., 1959; *host,* palmyra palm.

F— M 5+5 E 10, 5+5 P—; sex.; Comstockiella

prev. publ.—none

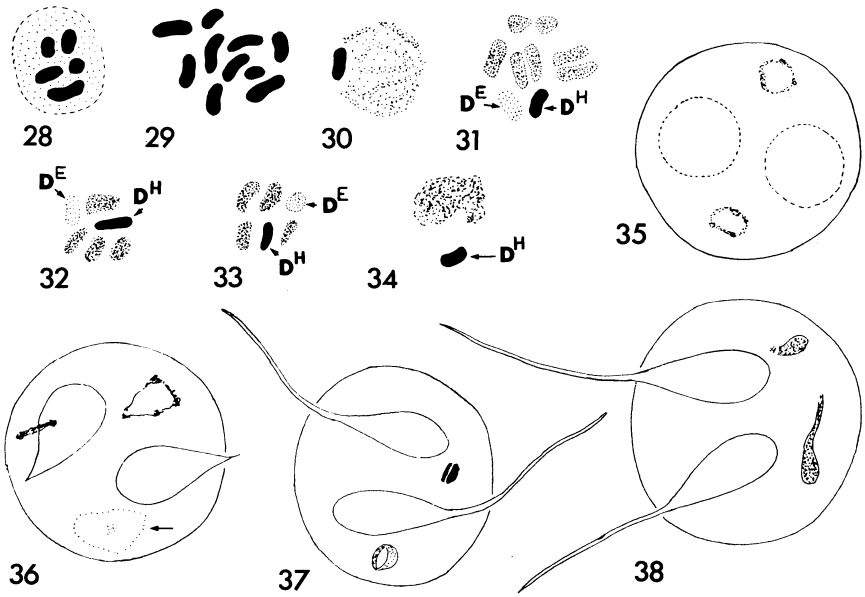
results—Typical figures with and without heterochromatization were found in the male and female embryos, respectively (figs. 28–29).

Only the Comstockiella system was observed at spermatogenesis. The number of heterochromatic elements was reduced to one prior to prophase proper of spermatogenesis (fig. 30). Pairing was largely completed by the time the chromosomes were sufficiently condensed to be individually recognizable, but some bivalents were still quite obviously bipartite at midprophase (fig. 31). At prometaphase, the expected six entities were present: the 4 bivalents and the D^E and D^H chromosomes (figs. 32–33). Both the D^E and D^H chromosomes were sometimes identifiable at prometaphase, although in most species the differential aspect had disappeared

by this stage and all entities had the same superficial appearance. The D^H chromosomes were eliminated in typical fashion at post-telophase (fig. 34).

This species was studied prior to our understanding the variable-D situation, and not studied in sufficient detail to record such variation if it occurred. The few examples illustrated here all indicate the D pair of homologues to have been one of the medium-sized pairs, but further work on this point is necessary.

Spermiogenic stages would have been useless in any event for detecting variation in D^H chromosomes from variation in the size of the residues. The pycnotic residues showed quite remarkable variation of another sort. A few maintained the highly condensed, pycnotic character of the typical D^H residue, but others soon became vesiculate, like a micronucleus, or elongate. In one instance, a residue was drawn out as though it were beginning to form a sperm. If the typical pycnotic state was maintained, the residues usually were split, but otherwise not (figs. 35–38).



Figs. 28–38. *Halimococcus borassi.* Fig. 28. Resting nucleus in male embryo showing the haploid set of 5 heterochromatic chromosomes. Fig. 29. Mitosis in female embryo; the 10 chromosomes are not differentiated. Fig. 30. Preprophase of spermatogenesis; the heterochromatic entities have been reduced in number from 5 to 1. Fig. 31. Midprophase of spermatogenesis; while the D^E and D^H chromosomes show differential behavior, the other 4 pairs of homologues are forming bivalents. Figs. 32–33. Late prophase or prometaphase. The D chromosomes are identifiable, but the bivalents appear monomeric, not bipartite. Fig. 34. Post-telophase. D^H division product (arrow) has been ejected from nucleus. Figs. 35–38. Early spermiogenesis to illustrate varied behavior of D^H residues. An adjunct structure consisting of a small center portion and large halo is illustrated in fig. 36, arrow.

In some of the spermatids it was possible to see a small, moderately densely-staining structure. Its apparent absence in others may have been actual or merely due to its small size and weak staining. It was not associated with the newly forming sperms as reported for a somewhat similar structure in another Comstockiella example (Brown, 1963). Its most noteworthy feature was its relatively huge halo.

Phoenicococcus marlatti (Cockerell)

tax. Ferris SIV-444; (1) *c.* & *i.* D. L. Lindgren; Imperial Valley, California;

Aug., 1957; *host,* date palm; (2) *c.* & *i.* Brown and Nur; Brawley, California; Feb., 1960; *host,* date palm.

F 18 M 9+9 E 18, 9+9 P —; sex.; Comstockiella, variable-D

prev. publ.—Chromosome number and system in Brown and McKenzie (1962).

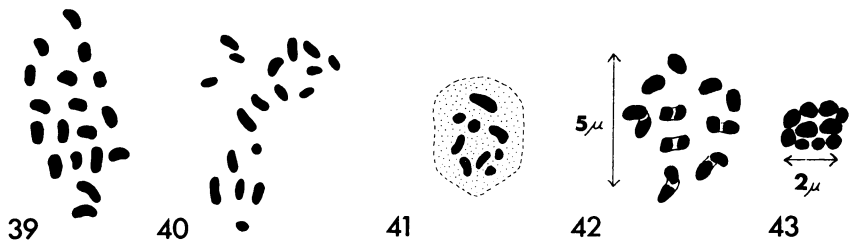
results—The insects in the first collection were all in estivation, and it was possible to obtain only mitotic division figures from the gravid females and the embryos (figs. 39–41).

Abundant young males were available at the time of the second collection, but few were at precisely the right stage for spermatogenesis. Consequently, heavily infested young date palms were transplanted to the greenhouse at Berkeley, and examinations continued during February and March.

Cytology in the maternal tissue (egg sheath cells) and in the embryos was typical.

Extensive examinations of spermatogenesis revealed only the Comstockiella sequence, quite typical even though the small size of the chromosomes made analysis of certain stages extremely difficult. Prior to prophase proper, the number of heterochromatic elements was reduced to one. The variable-D situation was evident at this stage because the single remaining heterochromatic chromosome varied in size from cyst to cyst. There was gradual gradation in size from the shortest to the longest of the 9 chromosomes. At prophase stages and during spermiogenesis, it was possible, however, to distinguish only three size classes for the D^H elements (fig. 44). Because a finer degree of discrimination would not have been possible, these observations indicated that the D role may have been performed by at least 3 different—and possibly by as many as all 9 different—pairs of homologues.

Some bipartite aspect of the bivalents was evident at late prophase. The expected 10 entities (n + 1) were present during prophase and metaphase, but the D^E and D^H chromosomes were not distinguishable at these stages (figs. 42–43). Telophase ejection of the D^H division products occurred in a typical fashion and the pycnotic residues were maintained as usual during the early phases of spermiogenesis.



Figs. 39–43. *Phoenicococcus marlatti.* Fig. 39. Mitosis, 18 chromosomes, in egg sheath cell. Fig. 40. Division figure of 18 chromosomes from female embryo. Fig. 41. Heterochromatic set of 9 chromosomes from non-dividing nucleus in male embryo. Fig. 42. Midprophase of spermatogenesis. Ten (n + 1) entities present, some obviously bipartite, D^E and D^H chromosomes not distinguishable. Fig. 43. Metaphase of spermatogenesis. Ten entities all of the same aspect.

Platycoccus tylocephalus Stickney

tax. Stickney, 1934; *c.* & *i.* Beardsley; Koolau Mts., Oahu, Hawaii; April, 1960; *host, Pritchardia* sp.

F 10 M 5+5 E 10, 5+5 P —; sex.; lecanoid

prev. publ.—none

results—The cytology of the maternal tissue and young embryos was typical (figs. 45–47).

This species is unique, as it is the only species of the Diaspidoïdae yet found which has proved to have only the lecanoid chromosome system. The material was limited, but examination of testes from 15 males at stages at which discrimination could be made gave evidence only of the lecanoid system.

The lecanoid division figures that were seen were quite typical, but only a few of the stages were available (figs. 48–49); most of the 15 males just cited were in early spermiogenic stages when the large pycnotic residues expected from a lecanoid sequence could be identified.

The chromosomes of this species were quite small and had, at spermatogenesis, an aspect different from other species in the family, as if there were a difference in reaction to the aceto-carmine stain. It was not possible to define this difference further, and the only reason for mentioning it at all is the unique cytology of the species. If this species is morphologically a true diaspidoid—and there is no evidence in Stickney's (1934) account that it is not—then it must have had ancestors with a Comstockiella chromosome system, at least in part (Brown and McKenzie, 1962), and therefore is to be regarded as a reversion to the pure lecanoid state. It seems quite unlikely

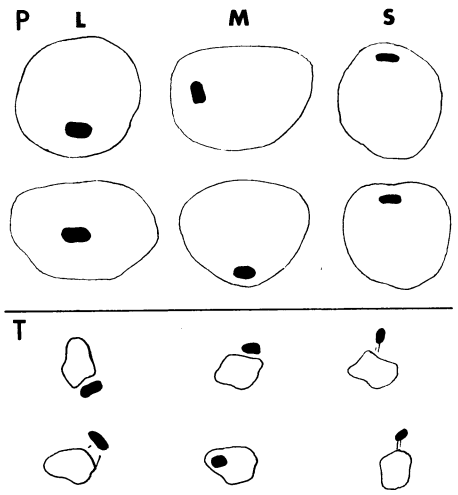
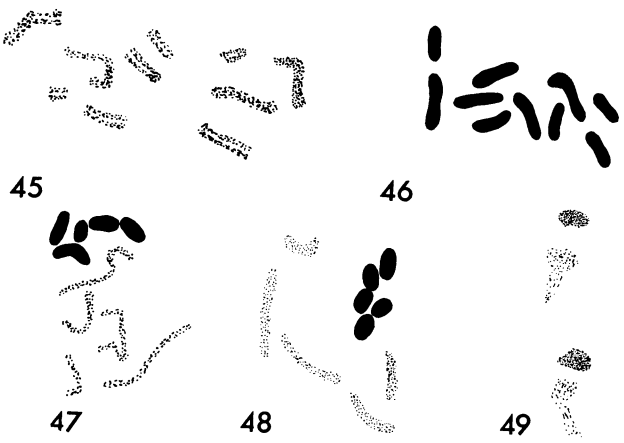


Fig. 44. *Phoenicococcus marlatti.* Spermatogenesis. The D^H chromosome at prophase (P) from two separate cells and the ejected division products of the D^H chromosome following telophase (T). Three size classes: L, large; M, medium; and S, small, were recognizable at these two stages.



Figs. 45–49. *Platycoccus tylocephalus.* Fig. 45. Prophase of mitosis in egg sheath cell. Fig. 46. Mitosis in female embryo. Fig. 47. Midprophase of mitosis in male embryo: 5 lightly stained, euchromatic and 5 densely stained, more contracted heterochromatic chromosomes. Fig. 48. Late midprophase of the first spermatogenic division, with 5 condensed heterochromatic chromosomes and 5 euchromatic. Fig. 49. Anaphase of the second spermatogenic division; this is the segregational division, and the euchromatic groups are moving away from the more condensed heterochromatic.

that convergent evolution could yield this particular species from an ancestry other than that of the remainder of the typical phoenicococcids because of its similarity in host, in general morphology, and in chromosome number to these other species. In fact, Beardsley (1963) considered *Platycoccus,* a monotypic genus, "to be an endemic Hawaiian offshoot of *Colobopyga* . . . ."; and both species of *Colobopyga* which have been studied in this regard have the Comstockiella chromosome system. At present, then, the hypothesis of a reversion to lecanoid behavior would seem more attractive than its alternative. However, it should be borne in mind that this species may be similar to *Ancepaspis edentata* in having a very low frequency of Comstockiella cysts, and that our present sample was not large enough to reveal them. Furthermore, there seems no way at present of deciding where the limit should be drawn as to the total number of cysts or testes examined before a conclusion can be reached. There are no theoretical reasons for setting a limit. At present this problem concerns us only in regard to the species at hand, with the possibilities restricted to those already mentioned.

Beardsley (1963) has recently reported abundant infestations of this species on a *Pritchardia* sp. from another Hawaiian island, so that it will be possible to make further analyses on a different population.

Thysanococcus calami Stickney

tax. Stickney, 1934; *c.* Nur; *i.* Wilkey; Castleton Botanical Garden, Castleton, Jamaica; July, 1962; *host,* palm (prob. *Calamus* sp.)

F 10 M— E— P—; parth.

prev. publ.—none

results—(Cytology by Nur.) Division figures from somatic tissue in the females yielded the chromosome number of 10, the typical diploid number for the family. The females were quite small, and only about one embryo was to be found in each gravid female; none of those inspected were young enough to yield good division figures; however, there was no evidence of heterochromatization in any of the material. Since no males were to be found and no sperm were present, the population sampled was undoubtedly parthenogenetic.

This species had previously been reported only from *Calamus* sp. and "rottang," both from Buïtenzorg (Bogor), Indonesia. Its introduction into a botanical garden, presumably from the one at Buïtenzorg, is not surprising.

Stickney (1934) was noteworthy among coccid taxonomists for his careful treatment of the males, the various stages of which he described whenever possible. In regard to *Thysanococcus calami* he had only this to say: "*Male Stages* . . . . None at hand, except one adult in poor condition, with no vestige of thoracic wing framework or of wings, with two pairs of eyes." In view of the results of the cytological study, it seems likely that this species is altogether parthenogenetic and that the one male in poor condition was a contaminant in Stickney's material. However, further study at Bogor should be undertaken before a final conclusion is reached. All that can be said for certain at present is that the Jamaican population is parthenogenetic.

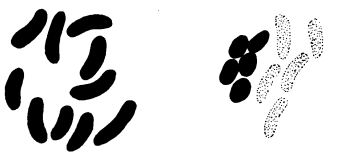
Thysanococcus pandani Stickney

tax. Stickney, 1934; *c.* Dempster; *i.* Wilkey; Bogor, Indonesia; July, 1962; *host,* *Pandanus* sp.

F— M— E 10, 5+5 P—; sex.; heterochromatic

prev. publ.—none

results—Unfortunately only females were present in the quite generous collections received, and the males must therefore have gone into pupation in considerable isolation. It was thus possible to determine only that the chromosome number was typical of the family and that the expected two types of embryos occurred in abundance (figs. 50–51).



Figs. 50–51. *Thysanococcus pandani.* Fig. 50. Midprophase in female embryo; 10 chromosomes. Fig. 51. Midprophase in male embryo; 5 condensed heterochromatic chromosomes and 5 more diffuse euchromatic.

THE DIASPIDIDAE

Gains and losses here which would result from a reshuffling of the Phoenicococcidae have already been considered under that family. There has never been any serious question about the recognition of this family as a biological entity, and our chromosomal survey, with the establishment of 4 as the basic haploid number for the entire family, certainly confirms the taxonomic treatment.

There has been some disagreement with respect to the recognition of one of the tribes, the Parlatorini, and Balachowsky's treatment will be followed, for reasons previously outlined by Brown and McKenzie (1962).

Xanthophthalmini

Xanthophthalma concinnum Cockerell and Parrott

tax. Ferris SII-174; *c.* Brown and Nelson-Rees; *i.* Wilkey and McKenzie; Allende, Coatzacoalcos, Veracruz, Mexico; June, 1960; *host,* "coyol redondo," probably *Acrocomia mexicana.*

F— M— E 16 P—; parth.

prev. publ.—The chromosome number and parthenogenetic status were reported by Brown and McKenzie (1962).

results—Because this species is the sole representative of the tribe, information as to the nature of its sexual chromosome system would have been highly desirable. Ferris (*loc. cit.*) made no comment at all in regard to the presence or absence of males. Consequently, considerable effort was made to find males at the collection site, to find sperm in the females, and to find heterochromatization in the embryos. The results were all negative; this population, at least, was parthenogenetic.

Ferris (*loc. cit.*) reported the species from two localities: Coatzacoalcos, near the site from which the above collection was made; and Bocas del Toro, Panama. Apparently on the sole basis of the wide separation of these two sites, Ferris concluded: "It is evident that this species is of wide distribution and its occurrence in the United States along the Gulf of Mexico is to be expected." Prior to the collecting at Coatzacoalcos, the author and Nelson-Rees had made a systematic search for this species along the Gulf Coast for several hundred miles to the northwest, without results. It may thus be that the wide separation of the two known sites is a relic distribution pattern. However, further efforts to obtain sexual material, for the chromosome system, would certainly be warranted because of the taxonomic position of the species.

The chromosomes were quite small, but the karyotypes of the embryonic divisions were in no way unusual (fig. 52).

Diaspidini

Brown and McKenzie (1962) have given some evidence that the Diaspidini are more primitive than the other major tribe, the Aspidiotini. Otherwise about the same, the Diaspidini show far greater variation in chromosome number than do the Aspidiotini.

52

Fig. 52. *Xanthophthalma concinnum.* Prophase of mitosis in embryo.

Africaspis chionaspisformis (Newstead)

tax. Hall, 1946; *c.* & *i.* De Lotto; Nairobi, Kenya; Sept., 1958; *host, Erythrina abyssinica.*

F— M— E 8, 4 P—; sex.; diaspidid

prev. publ.—See the following species, *Africaspis fici.*

results—No add.

Africaspis fici (Newstead)

tax. Hall, 1946; *c.* & *i.* De Lotto; Nairobi, Kenya; Jan., 1958; *host, Ficus* sp.

F 12 M— E 12, 6 P—; sex.; diaspidid

prev. publ.—The karyotype of this species has been compared with that of its congener, *Africaspis chionaspisformis,* by Brown (1960*a*), who showed that the increase in haploid chromosome number from 4 to 6 could easily be accounted for by fragmentation.

results—No add.

53 54 55

Figs. 53–55. *Aonidomytilus concolor.* Fig. 53. Diploid division figure with 12 chromosomes from female embryo. Fig. 54. Drawing eyepiece delineation of haploid division figure with 6 chromosomes from male embryo. Fig. 55. Pentaploid division figure, 30 chromosomes, from polyploid sector of embryo.

Aonidomytilus concolor (Cockerell)

tax. Ferris SI-7; *c.* Brown; *i.* McKenzie; La Paz, Baja California, Mexico; Oct., 1958; *host,* chenopodiaceous shrub.

F— M— E 12, 6 P 30; sex.; diaspidid

prev. publ.—none

results—(Cytology in part by Nelson-Rees.) Embryonic division figures revealed the expected haploid and diploid individuals as well as the pentaploid polyploid sector (figs. 53–55).

The haploid chromosome number of this species is 2 more than the basic number of 4. Relative chromosome lengths were obtained from several haploid division figures and averaged (see Brown, 1960*b*); the karyotype of this species will be compared with that of its congener, *Aonidomytilus variabilis,* in the Discussion.

Aonidomytilus variabilis Ferris

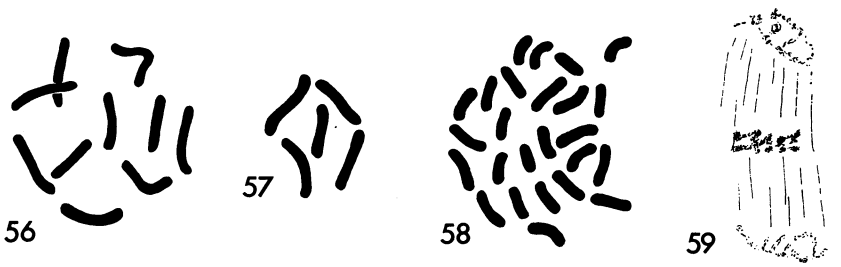
tax. Ferris SII-138; *c.* Brown and Robison; *i.* Brown; San Diego Co., California; State Highway No. 80 near Buckman Springs; May, 1962; *host, Sambucus.*

F— M— E 10, 5 P 25; sex.; diaspidid

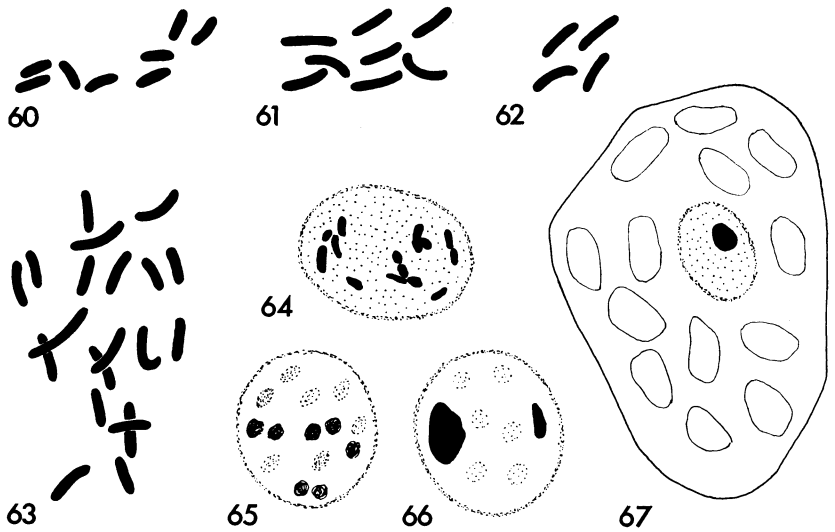
prev. publ.—none

results—(Cytology in part by Robison.) Like its congener, *Aonidomytilus concolor,* this species also departs from the basic number of 4. The typical haploid and diploid embryos and pentaploid sectors were present (figs. 56–58). Typical chromosome eliminations, resulting in densely pycnotic residues, occurred in embryos at late cleavage; but occasionally, when the elimination process was first commencing, the eliminated chromosomes showed a tendency to reconstitute an ordinary telophase nucleus (fig. 59).

As determined from numerous drawings made with a drawing eyepiece, there was very little variation in the length of the chromosomes, and therefore no evidence of a direct origin of the karyotype by fragmentation from a 4-chromosome complement. However, the derivation of the 6-chromosome complement of *Aonidomytilus concolor* from that of *A. variabilis* could have been accomplished by a simple change, and this aspect will be considered further in the Discussion.



Figs. 56–59. *Aonidomytilus variabilis.* Fig. 56. Female embryo, diploid division figure with 10 chromosomes. Fig. 57. Male embryo, haploid division figure with 5 chromosomes (drawing eyepiece). Fig. 58. Pentaploid figure, 25 chromosomes, from polyploid sector of embryo. Fig. 59. Elimination figure from embryo at start of elimination process; the eliminated chromosomes remained at the equatorial plate but were starting to reconstitute a typical resting nucleus instead of forming a pycnotic residue.



Figs. 60–67. *Aulacaspis cinnamomi.* Fig. 60. Late prophase figure from egg sheath cell. Fig. 61. Mitosis in female embryo. Fig. 62. Mitosis in male embryo. Fig. 63. Chromosomes of pentaploid division in embryo. Figs. 64–66. (Smaller scale than fig. 63.) Chromocenter formation from heterochromatic chromosomes in the polyploid sector. Fig. 67. (Smaller scale than figs. 64–66.) Mycetocyte from mother; large chromocenter in nucleus; symbionts dispersed in cytoplasm.

Aulacaspis cinnamomi (Newstead)

tax. Hall, 1946; *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Litsea glutinosa.*

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The chromosomes of the maternal tissue (egg sheath cells) and the haploid and diploid embryos occur in typical division figures (figs. 60–62). The major interest in this species stems from the polyploid sector. In the younger embryos, 20 chromosomes are to be found in the polyploid figures (fig. 63). After completion of mitotic division, the polyploid nuclei next undergo an endomitotic reduplication of the chromosomes, during which some of the chromosomes become heterochromatic and remain so, apparently throughout the remainder of development (figs. 64–66). The chromocenters are very striking in the maternal mycetocytes (fig. 67). The number of chromosomes becoming heterochromatic and the number remaining euchromatic could not be determined with accuracy in this species; presumably the same numerical relationship was present here as in the considerably clearer case of *Phenacaspis pinifoliae* (see below).

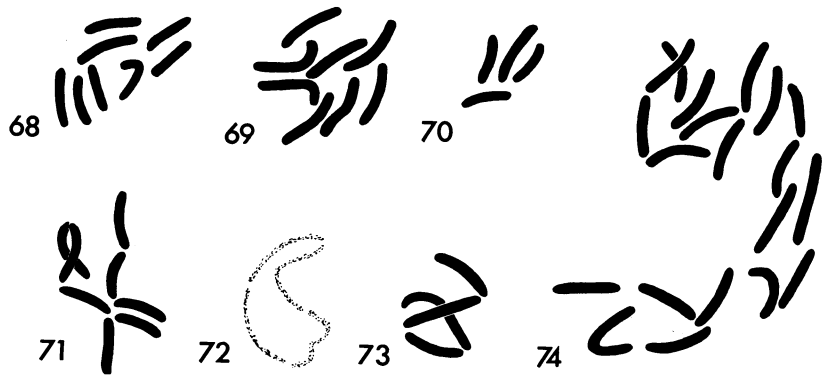
Aulacaspis rosae (Bouché)

tax. Hall, 1946; *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Litsea glutinosa.* (2) *c.* & *i.* Benassy; Antibes, France; June, 1959; *host, Rubus fruticosus.*

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Although the second collection was examined quite cursorily, chromosome conditions in both collections appeared to be the same. The division figures in the maternal tissue (egg sheath cells), haploid and diploid embryos, and poly-



Figs. 68–74. *Aulacaspis rosae.* Fig. 68. Chromosomes from maternal tissue (egg sheath cell). Fig. 69. Mitosis in female embryo. Fig. 70. Mitosis in male embryo. Figs. 71–73. Terminal associations of chromosomes in embryonic division figures. All chromosomes involved in at least one terminal association in diploid embryo, fig. 71, and haploid embryo, fig. 73. All chromosome ends associated to form a ring, haploid embryo, fig. 72. Fig. 74. Pentaploid division figure from embryo.

ploid sector all conformed to the typical pattern of the family (figs. 68–70, 74). Terminal adhesions were quite common; some prophase figures were found in which no terminal associations were present and others in which all chromosomes, and occasionally all chromosome ends, were so involved (figs. 71–73). Chromocenter formation in the polyploid cells, as reported for *Aulacaspis cinnamomi,* was not recorded; the observations on *A. rosae* were made before those of *A. cinnamomi,* and were largely restricted to early embryonic stages; there is thus the possibility that chromocenter formation occurs also in this species.

Aulacaspis spinosa (Maskell)

tax. Takagi, 1961*b; c.* Nohara; *i.* Takagi; Japan; May, 1957; *host,* undet.

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—Good embryonic figures were limited in this material. The typical maternal and embryonic figures, haploid and diploid, were obtained (figs. 75–77), but polyploid division figures were not. However, there was a suggestion of differential pycnosis in the polyploid division figures, even though none was suitable for an accurate count of the chromosomes. Further study may very well prove that *Aulacaspis spinosa* forms chromocenters in its mycetocytes like those of *A. cinnamomi.*

Figs. 75–77. *Aulacaspis spinosa.* Fig. 75. Mitosis in egg sheath cell. Fig. 76. Mitosis in female embryo. Fig. 77. Mitosis in male embryo.

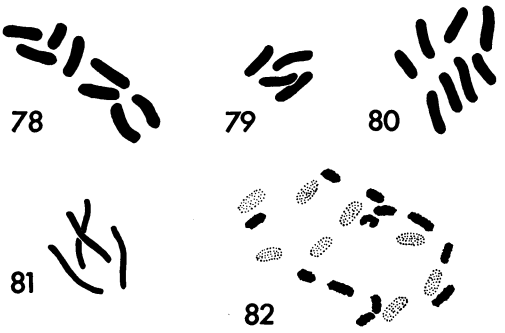
Aulacaspis tubercularis Newstead

tax. Takagi, 1961*b*; *c.* Pinto da Fonseca; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host,* mango.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—This species continued the cytological pattern of its congeners. The basic numbers appeared in male and female tissues, in embryos and polyploid sectors (figs. 78–82). Chromocenters were observed in mycetocytes of adult females and second and third instar males, and a few observations of mycetocytes in embryos indicated that chromocenter formation involves the heterochromatization of 3 of the 5 chromosome sets present in these pentaploid cells (fig. 82). This same phenomenon occurs elsewhere in the group and is explained in greater detail under *Phenacaspis pinifoliae.*



Figs. 78–82. *Aulacaspis tubercularis.* Fig. 78. Mitosis in maternal tissue (egg sheath cell). Fig. 79. Somatic division from male. Fig. 80. Mitosis in female embryo. Fig. 81. Mitosis in male embryo. Fig. 82. Stage in chromocenter formation in pentaploid nucleus (see text for further explanation).

Carulaspis minima (Targioni)

tax. McKenzie, 1956; *c.* & *i.* Brown and Nelson-Rees; Guadalajara, Jalisco, Mexico; Dec., 1957; *host,* cypress.

F— M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—Only a very limited amount of living material was available, and only embryonic division figures were obtained; these revealed nothing exceptional (figs. 83–84).

According to McKenzie (1956), *Carulaspis minima* is readily differentiated from its common congener, *C. visci,* by the absence in the former of a macroduct between the median pygidial lobes. The macroduct in question proved to be absent in the material examined.

Figs. 83–84. *Carulaspis minima.* Fig. 83. Mitosis in female embryo. Fig. 84. Mitosis in male embryo.

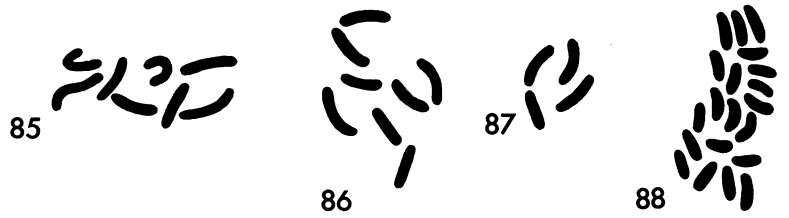
Chionaspis ortholobis Comstock

tax. Ferris SI-22; *c.* Brown; *i.* McKenzie; Portal, Arizona; June, 1958; *host,* willow.

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—Only a limited amount of material was available for study, but the maternal, embryonic, and polyploid division figures all proved typical (figs. 85–88).



Figs. 85–88. *Chionaspis ortholobis.* Fig. 85. Mitosis in egg sheath cell. Fig. 86. Chromosomes from female embryo. Fig. 87. Chromosomes from male embryo. Fig. 88. Pentaploid division figure from embryo.

Cooleyaspis praelonga (Newstead)

tax. Hall, 1946; *c.* & *i.* De Lotto; Nairobi, Kenya; July, 1958; *host, Acokanthera schimperi.*

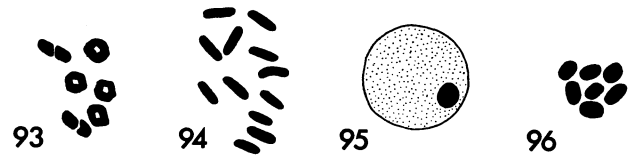
F 18 M— E 18,9 P 45; sex.; diaspidid

prev. publ.—none

results—This species is the only one yet described for the genus, which in turn belongs to a group of closely related African genera; the diploid number of 18 has been found in 3 of these genera, and these relationships will be considered further in the Discussion.

In addition to the usual cytology (figs. 89–92), this species has provided some extremely clear views of chromosome elimination in early embryogeny (plate IA, p. 285).

Figs. 89–92. *Cooleyaspis praelonga.* Fig. 89. Mitosis in maternal tissue (egg sheath cell). Fig. 90. Mitosis in female embryo. Fig. 91. Mitosis in male embryo. Fig. 92. Pentaploid division figure from embryo.



Figs. 93–96. *Costalimaspis eugeniae* (redrawn from Nur). Fig. 93. Oögenesis with 6 bivalents. Fig. 94. Mitosis from female embryo; 12 chromosomes. Fig. 95. Preprophase or early prophase in spermatogenesis; heterochromatic chromosomes reduced to 1. Fig. 96. Metaphase of spermatogenesis; n + 1 or 7 chromosomes present.

Costalimaspis eugeniae Lepage

tax. Lepage, 1937; *c.* & *i.* Pinto da Fonseca; Jardim do Luz, São Paulo, Brazil; July, 1962; *host, Eugenia* sp.

F (12) M— E 12,— P—; sex.; Comstockiella and lecanoid

prev. publ.—none

results—It was of special interest to obtain this species from the type host and type locality. Judging by the morphology of the scale, *Costalimaspis eugeniae* is the least remarkable of the 3 species described by Lepage (1937) for this genus, and it will certainly be of considerable interest to have information on the chromosome numbers and systems in the other 2 species.

Very little material was available for the cytological study, which was made by Dr. Uzi Nur. Female embryos proved to have 12 chromosomes, and 6 bivalents were present at oögenesis (figs. 93–94). At spermatogenesis in the males, the presence of but a single chromatic chromosome at the onset of prophase was the first evidence of the Comstockiella system (fig. 95). At late midprophase and metaphase, the 7 chromosomes expected in a Comstockiella system were present, but the D^H and D^E chromosomes were not identified (fig. 96).

Most of the residues observed during spermiogenesis were small, about the size to be expected following a typical D^H elimination. In a few cysts with normally elongating sperm, the residues were very much larger; it seems likely that a lecanoid sequence also occurs in this species.

Crassaspis multipora (Ferris)

tax. Ferris SI-123 and SIII-274; *c.* Brown; *i.* McKenzie; La Paz, Baja California, Mexico; Oct., 1958; *host,* mistletoe.

Figs. 97–99. *Crassaspis multipora.* Fig. 97. Mitosis in female embryo. Fig. 98. Mitosis in male embryo. Fig. 99. Mitosis in pentaploid sector of embryo.

F (8) M — E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—The chromosome number in the females is based on the observation of 4 bivalents at metaphase I of oögenesis. The embryonic division figures and the polyploid divisions were quite typical (figs. 97–99).

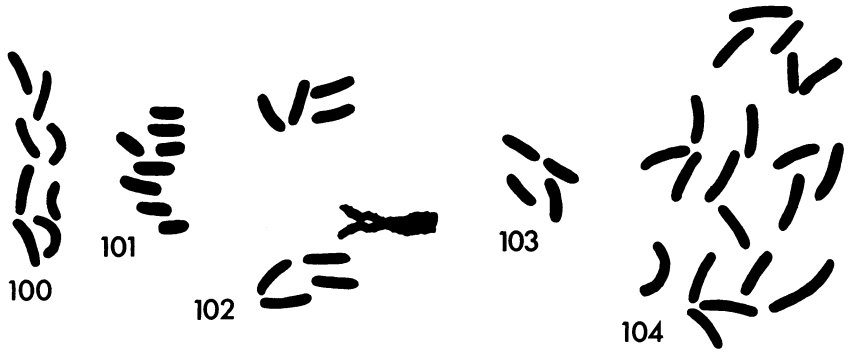
Diaspis boisduvalii Signoret

tax. Ferris SI-32; (1) *c.* Kerr; *i.* Brown; Pericicaba, Brazil; July, 1957; *host, Cattleya;* (2) *c.* & *i.* Nur; Kingston, Jamaica; Aug., 1962; *host,* banana.

F 8 M — E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—Both collections proved to have the same chromosome number; most of the observations were made on the first collection. Typical chromosome elimination was observed in the younger embryos (fig. 102), and the chromosome numbers were also typical (figs. 100–101, 103–104).



Figs. 100–104. *Diaspis boisduvalii.* Fig. 100. Mitosis in maternal tissue (egg sheath cell). Fig. 101. Mitosis in female embryo. Fig. 102. Chromosome elimination in an early embryo; eliminated chromosomes united in a pycnotic group near lower telophase group. Fig. 103. Mitosis in male embryo. Fig. 104. Chromosomes from pentaploid division in embryo.

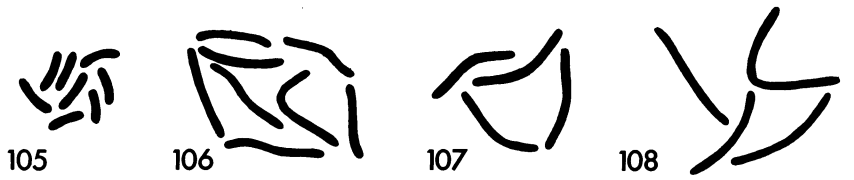
Diaspis bromeliae (Kerner)

tax. Ferris SI-33; *c.* & *i.* Bennett; St. Augustine, Trinidad; Sept., 1956; *host,* pineapple.

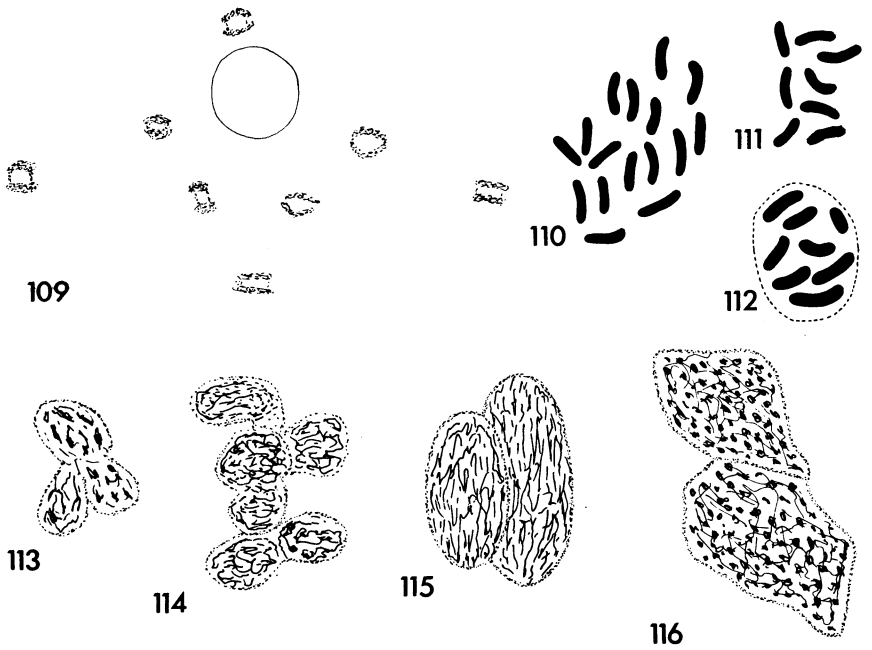
F 8 M 4 E 8,4 P —; sex.; diaspidid

prev. publ.—The chromosome numbers cited here were included in the report of Brown and Bennett (1957).

results—No illustrations of the chromosomes have been published previously for this species; the division figures were all quite typical (figs. 105–108).



Figs. 105–108. *Diaspis bromeliae.* Fig. 105. Mitosis in maternal tissue (egg sheath cell). Fig. 106. Mitosis in female embryo. Fig. 107. Mitosis in male embryo. Fig. 108. Mitosis in male (second or third instar).



Figs. 109–116. *Diaspis echinocacti.* Fig. 109. Oögenesis, 8 bivalents surrounding nucleolus. Fig. 110. Mitosis in female embryo. Fig. 111. Mitosis in male embryo. Fig. 112. Prophase of spermatogenesis, 8 univalents. Figs. 113–116. Three phases, based on size, of nuclear fusion (see text for further explanation).

Diaspis echinocacti (Bouché)

tax. Ferris SI-36; (1) *c.* & *i.* Dickson; Riverside, California; Aug., 1957; *host,* Epiphyllum; (2) *c.* & *i.* Brown; 20 mi. E. of Tucson, Arizona; June, 1958; *host,* cholla cactus; (3) *c.* & *i.* Beardsley; Oahu, Hawaii; April, 1960; *host, Opuntia.*

F 16 M 8 E 16, 8 P —; sex.; diaspidid

prev. publ.—none

results—This species has exactly double the chromosome number of the two of its congeners which have so far been subjected to cytological study. The same numbers were found in all three collections; most of the observations were made from the first. The problem of whether or not such exact doubling may be attributed to simple doubling of a chromosome set will be considered in the Discussion.

At diakinesis of oögenesis, 8 bivalents were present, each with an obviously bipartite structure (fig. 109). Sixteen chromosomes were present in the egg sheath cells, and 8 and 16 in the haploid and diploid embryos, resp. (figs. 110–111). Spermatogonial divisions and spermatogenesis offered no unusual features (fig. 112).

An exhaustive search was made to find polyploid division figures; among hundreds of embryos, about 40 at precisely the right stages were obtained from 11 females. Only the chromosome number 16 was observed, except for one embryo in which 30 to 40 chromosomes were estimated to be present in each of 4 sticky division figures. In the sectors which normally contained the polyploid nuclei, giant nuclei were observed being formed by fusion of smaller nuclei. The process seemed to commence with diploid nuclei, and there appeared to be a variety of possibilities

with aggregates of different sizes subsequently fusing (figs. 113–116). The fate of the polar bodies in this species remains unknown, as does the question of whether or not the giant fusion nuclei take over the usual function of the polyploid cells, the housing of the intracellular symbionts.

Duplachionaspis sicula (Lupo)

tax. Balach. Di-382; *c.* & *i.* Lupo; Aidone, Sicily; Sept., 1959; *host, Arondo plinii.*

F 8 M — E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The chromosome figures in the maternal tissue and embryos conformed to the usual pictures for the family (figs. 117–120).

Figs. 117–120. Duplachionaspis sicula. Fig. 117. Chromosome complement from egg sheath cell. Fig. 118. Mitosis in female embryo. Fig. 119. Mitosis in male embryo. Fig. 120. Mitosis in polyploid sector of embryo—pentaploid number of 20 chromosomes.

Epidiaspis leperii (Signoret)

tax. Ferris SI-51; *c.* Nucifora; *i.* Lupo; Mt. Etna, Sicily; Sept., 1959; *host,* pear.

F 8 M — E — P —; sex.

prev. publ.—none

results—In this location at least, the species appeared to overwinter as the young adult female, already fertilized. Sperm was evident in the ovaries, but no embryogenesis had commenced.

Chromosomes were available, therefore, only from mitoses in the female tissue (fig. 121).

Epidiaspis phoradendri (Cockerell)

tax. Ferris SI-53; *c.* Brown; *i.* Wilkey; Cuautla, Morelos, Mexico; June, 1962; *host,* mistletoe on *Casuarina.*

F 8 M — E 8, 4 P —; sex.; diaspidid

prev. publ.—none

results—The usual cytological determinations on maternal tissue and embryos showed that this species conforms to the typical picture for the family (figs. 122–124). Otherwise it is of interest because it is a repeat collection of a species which had been previously collected only from this host and at this locality (Ferris, *ibid.*).

Fiorinia fioriniae (Targioni)

tax. Ferris SI-55; *c.* & *i.* Pinto da Fonseca; São Paulo, Brazil; July, 1962; *host,* camellia.

F 8 M— E 8 P—; parth.

prev. publ.—none

results—(Cytology in part by Dr. Uzi Nur.) No sperm nor any evidence of male embryos was found in the ovaries; the chromosome number of every embryo observed agreed with that of the maternal tissue (figs. 125–126). This population of the species is undoubtedly parthenogenetic, but whether of the mitotic or meiotic type was not determined. Ferris (*ibid.*) reported males for this species, thus providing another example of species with both bisexual and unisexual races.

Fig. 121. *Epidiaspis leperii.* Somatic mitosis in overwintering adult female.

Fiorinia japonica Kuwana

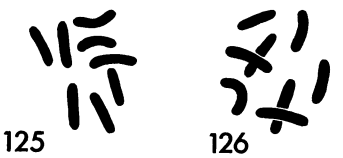
tax. Ferris SIV-394; *c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Picea excelsa* Link.

F 8 M—E 8, 4 P 20; sex.; diaspidid

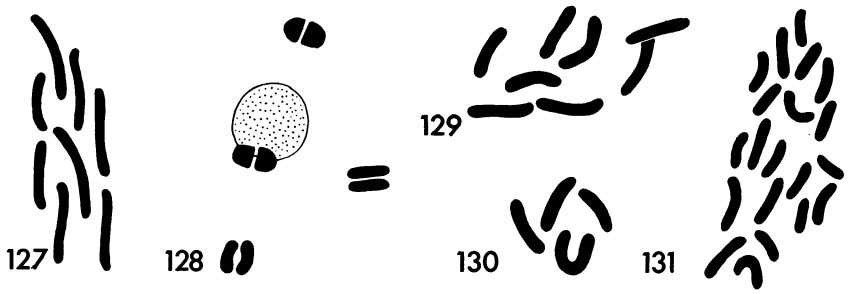
prev. publ.—none

results—Four bivalents, each visibly bipartite, were present at diakinesis of oögenesis (fig. 128). There were no noteworthy features of either the maternal or embryonic division figures (figs. 127, 129–131).

Figs. 122–124. *Epidiaspis phoradendri.* Fig. 122. Chromosome complement from egg sheath cell. Fig. 123. Mitosis in female embryo. Fig. 124. Mitosis in male embryo.



Figs. 125–126. *Fiorinia fioriniae.* Fig. 125. Mitosis in egg sheath cell. Fig. 126. Mitosis in embryo (unisexual reproduction; see text).



Figs. 127–131. *Fiorinia japonica.* Fig. 127. Mitosis in egg sheath cell. Fig. 128. Diakinesis of oögenesis, 4 bivalents and nucleolus. Fig. 129. Mitosis in female embryo. Fig. 130. Mitosis in male embryo. Fig. 131. Mitosis in pentaploid sector of embryo.

Howardia biclavis (Comstock)

tax. Ferris SI-65; (1) *c.* Simmonds; *i.* Breese; Bermuda; Jan., 1957; (2) *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Cajanus cajan;* (3) *c.* & *i.* Beardsley; Koolau Mts., Oahu, Hawaii; April, 1960; *host, Metrosideros* sp.; (4) *c.* Brown and Nur; *i.* Wilkey; Mona, Kingston, Jamaica; June, 1962; *host,* undet. leguminous tree.

F 10 M— E 10 P 20, 30; parth.

prev. publ.—Brown (1961).

results—According to Ferris (*ibid.*), this species has been reported from a long list of hosts in all parts of the world, though confined to conservatories outside the tropical and subtropical regions. The scale of the male was unknown to Ferris (*ibid.*): ". . . the species probably being entirely parthenogenetic."

The cytological studies have confirmed this. The four collections have all proved parthenogenetic, and each proved to have a chromosome number of 10 in both the maternal and embryonic tissues (plate IB, figs. 132–135).

Since 10 univalents were present at diakinesis of oögenesis, parthenogenesis in this species must be of the "mitotic" type.

Ten chromosomes were thus also expected in the only polar body which, on fusion with one—or rarely 2—cleavage nuclei would give polyploid cells with 20—or rarely 30—chromosomes.

Figs. 132–137. *Howardia biclavis.* Fig. 132. Chromosome complement from egg sheath cell. Fig. 133. Mitosis in embryo. Figs. 134–135. Mitosis in the polyploid sector of the embryo. Fig. 134. Tetraploid with 20 chromosomes. Fig. 135. Hexaploid with 30 chromosomes. Fig. 136. Complement with grossly unequal translocation; arrows indicate the chromosomes involved. Fig. 137. Same as fig. 136, but smaller translocation chromosome present twice (arrows: the long chromosome, and the two short chromosomes).

One of the major problems with the parthenogenetic forms is the stability of the karyotype, for which no compelling theoretical reasons can yet be given. Since scale chromosomes are holokinetic, fragments should be capable of perpetuating themselves indefinitely in subsequent mitoses, including that substituted for meiosis in parthenogenetic forms such as this. Yet, wherever collected, *Howardia biclavis* has proved to have the number 10. As the genus is monotypic, there is no possibility of comparing this species with a closely related one. If a related sexual form proved to have the diploid number 10, there would be excellent evidence that there had been no change in number after *H. biclavis* had become parthenogenetic. However, if the related form had the basic number 8, the number 10 could have been achieved either before or after the parthenogenetic state itself.

Fragmentation does occur in parthenogenetic forms and may be perpetuated,

although always apparently soon terminating. Brown (1961) briefly noted a grossly unequal translocation in *Howardia biclavis,* which yielded an abnormally long and an unusually short chromosome. This translocation was found in all the embryos of 2 of the 11 females examined from collection (3). The behavior of the very short chromosome was not completely regular, as occasional division figures were found in which 2 of the short chromosomes were present (figs. 136–137).

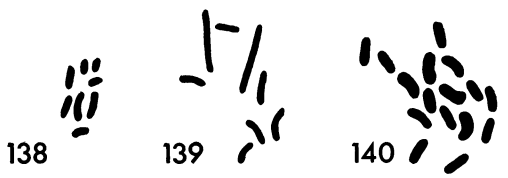
Ischnaspis bipindensis Lindinger

tax. Lindinger, 1909; *c.* & *i.* De Lotto; Nairobi, Kenya; June, 1961; *host.* undet.
F 8 M— E 8 P 16; parth.
prev. publ.—none

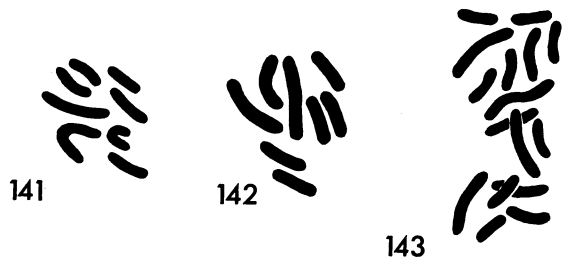
results—This species, described from central Africa by Lindinger (1909), was not recognized by Hall (1946) in his treatment of the Diaspidini from south of the Sahara.

No males were present at the collection site, and no sperm nor male embryos were present in the ovaries. The chromosome complements of the embryos were exactly like those of the mother (figs. 138–139), while the tetraploid number in the polyploid sector (fig. 140) was that expected from parthenogenetic reproduction. One pair of chromosomes was much longer than the remaining pairs of homologues, if it is fair to speak of "pairs" in a parthenogenetic form.

In all respects thus far determined cytologically, *Ischnaspis bipindensis* is like its much better-known congener, *I. longirostris* (see below). It is true that some collections of *I. longirostris* have not shown the long chromosomes, but this may well have been a secondary loss. The similarity of the two forms provides one of the few suggestions among the armored scale insects that speciation may have occurred to produce 2 species from one after parthenogenesis had supplanted sexual reproduction.



Figs. 138–140. *Ischnaspis bipindensis.* Fig. 138. Chromosome complement from egg sheath cell. Fig. 139. Mitosis in embryo. Fig. 140. Mitosis in polyploid sector of embryo.



Figs. 141–143. *Ischnaspis longirostris.* Fig. 141. Mitosis in maternal tissue (egg sheath cell). Fig. 142. Mitosis in female embryo; note the 2 long chromosomes. Fig. 143. Mitosis in polyploid sector of embryo, here tetraploid; note the 4 long chromosomes.

Ischnaspis longirostris (Signoret)

tax. Ferris SI-67; (1) *c.* Brown; *i.* Breese; St. Augustine Nursery, Curepe, Trinidad; April, 1957; *host,* dwarf coconut palm; (2) *c.* & *i.* Brown and Nelson-Rees; Veracruz, Ver., Mexico; June, 1960; *host,* palm; (3) *c.* Brown; *i.* De Lotto; Botanical Garden, Entebbe, Uganda; July, 1961; *host,* coffee; (4) *c.* Nur; *i.* Wilkey; Kingston, Jamaica; June, 1962.

F 8 M— E 8 P 16; parth.

prev. publ.—none

results—(Cytology in part by Nur.) This species is cosmopolitan. Males were reported in the original description, but Ferris (*ibid.*) stated that he had not seen them.

The cytology proved to be that of a typical parthenogenetic form (figs. 141–143). No males were observed at the collection sites; no sperm were present in the ovary; and all embryos had the same chromosome number as the maternal tissue. The tetraploid number of 16 in the polyploid sector was also evidence of parthenogenesis, which examination of oögenesis proved to be of the "mitotic" type. Eight univalents were noted at diakinesis and metaphase of oögenesis, but no drawings were made.

The karyotype is noteworthy for two long chromosomes. The fact that these can be recognized as a pair of homologues may mean that they have not been subjected to much remodeling. In one collection, no. 2 from Veracruz, the long chromosomes were not in evidence. It is probable that little evolution has occurred since the species became parthenogenetic. Thus, sexual forms of this species may possibly be uncovered or rediscovered.

Kuwanaspis bambusicola (Cockerell)

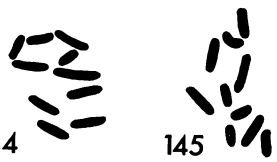
tax. Balach. Di-266; *c.* Brown and Pinto da Fonseca; *i.* Wilkey; São Vicente, Santos, Brazil; July, 1962; *host,* bamboo.

F 10 M— E 10 P—; parth.

prev. publ.—none

results—According to Balachowsky (*ibid.*), males have not been reported from this species. The absence of sperm and male embryos in the ovaries was further evidence of parthenogenesis; all embryos had chromosome complements similar to the maternal (figs. 144–145).

The chromosome number of *Kuwanaspis bambusicola* was two more than that of its congener *K. pseudoleucaspis;* likewise, the former showed greater variation in size among the chromosomes than did the latter. If the diploid number had been increased from 8 to 10 before the change from sexual to parthenogenetic, or if parthenogenesis were here of the meiotic type, exact pairs of homologues would be expected. On the other hand, increase in number following acquisition of mitotic partheno-



Figs. 144–145. *Kuwanaspis bambusicola.* Fig. 144. Mitosis in egg sheath cell. Fig. 145. Mitosis in embryo.

Figs. 146–147. *Kuwanaspis pseudoleucaspis.* Fig. 146. Mitosis in egg sheath cell. Fig. 147. Mitosis in embryo.

genesis would be accomplished simply by fragmentation without the subsequent screening by meiosis, and would yield chromosomes resembling pairs only by chance. This question is here of interest because of the difference in number between these closely related species, but must await further work for any sort of answer.

Kuwanaspis pseudoleucaspis (Kuwana)

tax. Ferris SIII-288; *c.* Benassy; *i.* Pegazzano; Antibes, France; June, 1959; *host,* bamboo.

F 8 M— E 8 P—; parth.

prev. publ.—none

results—Scales of males were reported for this species by Kuwana, but were not observed by Ferris; there is thus the possibility that a unisexual race has become the cosmopolitan representative of this species.

No stages of oögenesis nor polyploid cells were observed; it is thus not possible to make any sort of guess about the parthenogenetic mechanism here. Division figures in maternal tissues and embryos were quite typical (figs. 146–147).

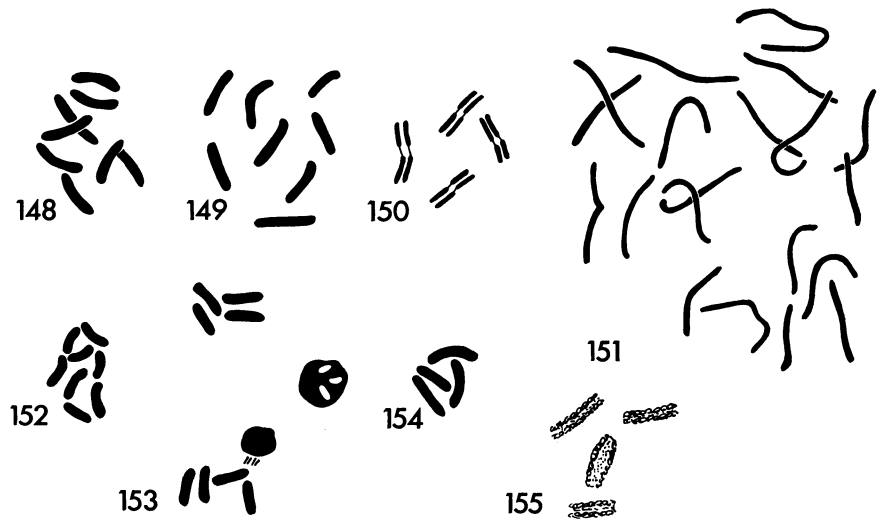
Ledaspis reticulata (Malenotti)

tax. Hall, 1946; *c.* & *i.* De Lotto; the Athi River, Kenya; Feb., 1958; *host, Balanites aegyptica.*

F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—This species is of special interest because it belongs to a genus included in a group of related genera which have proved to have the haploid chromosome number of 9; in addition, one of its congeners, *Ledaspis tenuiloba,* also proved to have 9; the problem of relationships will be considered in the Discussion.



Figs. 148–155. *Ledaspis reticulata.* Fig. 148. Mitosis in egg sheath cell, 8 chromosomes. Fig. 149. Mitosis in female embryo, 8 chromosomes. Fig. 150. Mitosis in male embryo, 4 chromosomes; note pseudocentromeres. Fig. 151. Mitosis in pentaploid sector of embryo, 20 chromosomes. Figs. 152–154. Division figures from one embryo in which chromosome elimination was occurring. Fig. 152. Pre-elimination figure with 8 chromosomes. Fig. 153. Elimination of one haploid set at anaphase; the eliminated set here had formed pycnotic clumps. Fig. 154. Post-elimination figure with 4 chromosomes. Fig. 155. Prophase of spermatogenesis.

The present species, *Ledaspis reticulata,* proved to be typically diaspidid. Maternal tissue (egg sheath cells) and diploid embryos with 8 chromosomes were present (figs. 148–149), while haploid embryos of 4 chromosomes were produced from 8-chromosome embryos by elimination (figs. 152–154). The polyploid sectors were pentaploid (fig. 151). Four chromosomes were present in the somatic tissues of the males and at spermatogenesis (fig. 155).

The species also provided a few division figures with very clear examples of pseudocentromeres (fig. 150). These last are constrictions occurring near the center of the chromosomes and presumably formed by incomplete contraction of the chromosomes, starting at both ends and moving toward, but never quite reaching, the middle of the chromosomes.

Ledaspis tenuiloba De Lotto

tax. De Lotto, 1956; *c.* & *i.* De Lotto; Nairobi, Kenya; Jan., 1958; *host, Aberia caffra.*

F— M— E 18, 9 P 45; sex.; diaspidid

prev. publ.—none

results—The chromosome number of this species agreed with those of related genera (see Discussion) but not with that of its congener, *Ledaspis reticulata.* Chromosome counts were obtained from haploid and diploid embryos and from the polyploid sector (figs. 156–158). Somewhat more variation in the size of the chromosomes was noted in the karyotype of this species than in the other 18, 9-chromosome species, *Cooleyaspis praelonga* and *Rolaspis anacantha.*

Figs. 156–158. *Ledaspis tenuiloba.* Fig. 156. Mitosis in female embryo, 18 chromosomes. Fig. 157. Mitosis in male embryo, 9 chromosomes. Fig. 158. Mitosis in pentaploid sector, 45 chromosome (2 short chromosomes overlapped by one long in upper "cross" near center).

Lepidosaphes beckii (Newman)

tax. Ferris SI-71; *c.* Bennett, Breese; *i.* Breese; St. Augustine, Trinidad; Jan., 1957; *host,* citrus.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—The chromosome numbers just cited were reported in Brown and Bennett (1957).

results—This species, as well as a congener, *L. gloverii* (Packard), is cosmopolitan on citrus. Material of *Lepidosaphes gloverii* has not been available for study. All the phases of the life cycle selected for determinations were available (figs. 159–163). There was nothing exceptional about the division figures of *L. beckii* nor the karyotype.

Figs. 159–163. *Lepidosaphes beckii.* Fig. 159. Mitosis in egg sheath cell. Fig. 160. Mitosis in female embryo. Fig. 161. Chromosomes from male embryo. Fig. 162. Chromosomes in pentaploid sector of embryo. Fig. 163. Mitosis in young male.

Lepidosaphes conchyformis f. conchyformis (Gmelin)

tax. Balach. Di-63; *c.* & *i.* Benassy; Antibes, France; May, 1960; *host,* fig.

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—This species occurs in two forms: one, *f. conchyformis,* on the twigs and stems of the fig.; the other, *f. minima,* on the leaves. The latter type is to be found only during the summer and is surprisingly different from *f. conchyformis* in pygidial architecture. Chromosomal cytology has been available only on the *Lepidosaphes conchyformis f. conchyformis,* and has shown a typical picture (figs. 164–165); it is highly doubtful that *f. minima* would show anything different.

Lepidosaphes tokionis (Kuwana)

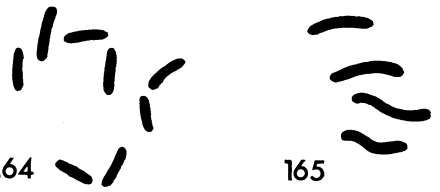
tax. Ferris SIV-398 (SII-145); *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Codiaeum* sp.

F 12 M— E 12, 6 P 30; sex.; diaspidid

prev. publ.—none

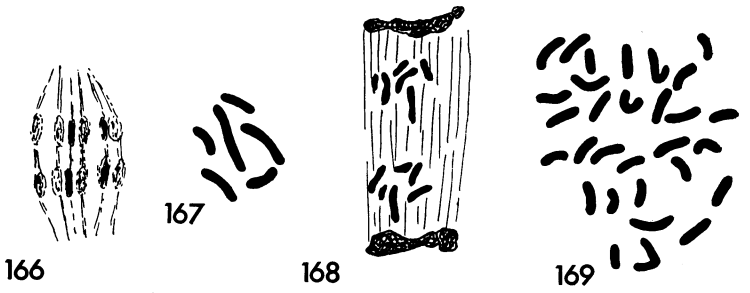
results—This species has a haploid number of two more than that of its congeners or the basic number of the family. The easiest explanation for such an increase in number is simple fragmentation, two breaks being required to increase the number from 4 to 6. The size differentiation among the karyotype was not inconsistent with such an explanation; the smallest chromosome was about half the size of the longest.

A fairly good sample of the various phases of the life cycle was obtained for this species. One example of oögenesis showed the expected 6 chromosomes, although the constituent chromatids were not resolvable (fig. 166). Egg sheath cells had the expected number of 12 (plate IC); the embryos had diploid numbers of



Figs. 164–165. *Lepidosaphes conchyformis f. conchyformis.* Fig. 164. Mitosis in female embryo. Fig. 165. Mitosis in male embryo.

12 (plate ID) and haploid numbers of 6 (fig. 167, plate IE), with the latter being achieved by the usual process of elimination by anaphase lagging (fig. 168); and the polyploid sectors showed the expected pentaploid number of 30 (fig. 169).



Figs. 166–169. *Lepidosaphes tokionis.* Fig. 166. Early anaphase I of oögenesis. Fig. 167. Mitosis in male embryo. Fig. 168. Chromosome elimination in early embryogeny of male embryo. Fig. 169. Mitosis in pentaploid sector.

Lepidosaphes ulmi (Linnaeus)

tax. Ferris SI-76, and Balach. Di-37; *c.* Brown; *i.* Pagazzano; Agay, France; June, 1959; *host, Arbutus unedo.*

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—This species is of considerable interest, as it has been recorded from a very long list of hosts throughout the world. Ferris (*ibid.*) believed the species to be strictly unisexual: "Apparently this species is parthenogenetic, no male ever having been discovered"; while Balachowsky (Di-41) stated: "*L. ulmi* L. est représenté par plusieurs races biologiques, les unes unisexuées (*unisexualis*), les autres bisexuées (*bisexualis*), dont le comportement et l'aire de répartition dans un même pays sont différents. Ces races qui possèdent des caractères morphologiques identiques ont été étudiées par divers auteurs dans l'ancien et le nouveau monde."

The material of the present collection undoubtedly belonged to the bisexual race, since haploid embryos, presumably male, were common in the ovaries. In addition, chromosomal determinations were made of maternal tissue and diploid embryos (figs. 170–172).

Figs. 170–172. *Lepidosaphes ulmi.* Fig. 170. Mitosis in egg sheath cell. Fig. 171. Mitosis in female embryo. Fig. 172. Mitosis in male embryo.

Nicholiella bumeliae Ferris

tax. Ferris SIII-299; *c.* Brown; *i.* McKenzie; Rodeo, New Mexico; July, 1958; *host, Bumelia lanuginosa* (Michx.) Pers.

F 8, M 4+4 E 8, 4+4 P —; sex.; Comstockiella and lecanoid

prev. publ.—This species was chosen to exemplify the Comstockiella-lecanoid combination in the recent detailed treatment of the Comstockiella system (Brown, 1963), and only a brief comment will be added here.

results—Males of this species had not been recognized (Ferris, *loc. cit.*) prior to the present cytological studies.

Nikkoaspis shiranensis Kuwana

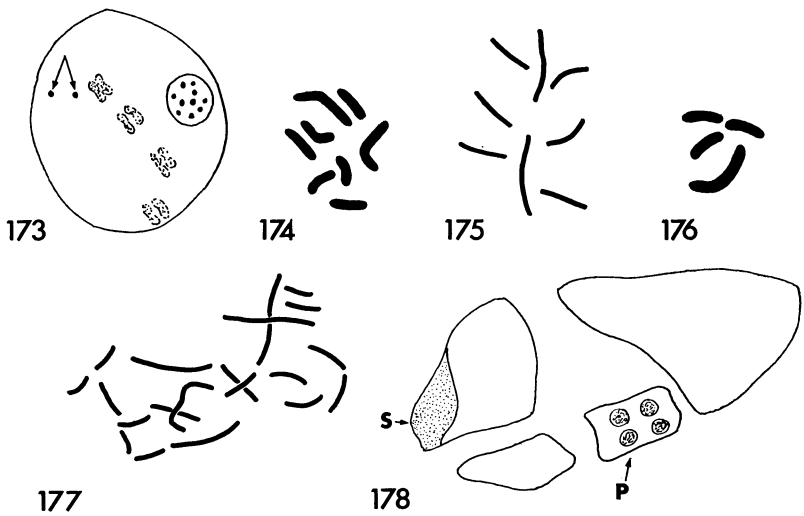
tax. Takagi, 1961*a*; *c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Sasa palmata* (Bean) Nakai.

F 8 M — E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Oögenesis showed the expected 4 bivalents and a rather unusual display of densely chromatic bodies in the nucleolus, with a few also elsewhere in the nucleus (fig. 173). In the mitotic division figures of maternal tissue and embryos, one of the chromosomes of each haploid set was obviously much longer than the other 3 (figs. 174–176), and the polyploid figures with the 5 haploid sets showed the expected 5 long chromosomes (fig. 177).

Squashes in which the entire embryo could be analyzed at early stages of development showed that the polyploid nuclei were not associated with the symbionts



Figs. 173–178. *Nikkoaspis shiranensis.* Fig. 173. Diakinesis of oögenesis; note the dense pycnotic granules in the nucleolus, and also two free in the cytoplasm (arrows). Fig. 174. Mitosis in egg sheath cell. Fig. 175. Mitosis in female embryo. Fig. 176. Mitosis in male embryo. Fig. 177. Mitosis in pentaploid nucleus; note that 5 long chromosomes are present. Fig. 178. Sketch of squash of embryo; symbionts were localized exclusively in the distal zone (*S*, stippled); 4 nuclei were present in the polyploid sector (*P*) in the middle part of the embryo.

and presumably did not, therefore, develop into mycetocytes (fig. 178). Only diploid nuclei were found in that part of the embryo which contained the symbionts, and the cells in which the symbionts were later found were relatively small, with small, presumably diploid nuclei. The development of the polyploid sector was followed to the 8-cell stage but not further; since necrosis was not noted in the polyploid sector, the pentaploid cells probably were maintained in the embryo; whether they undertook another specific role in lieu of mycetocyte formation was not determined.

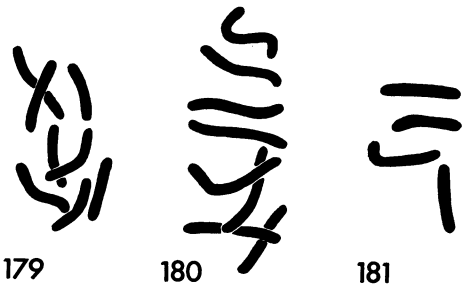
Opuntiaspis philococcus (Cockerell)

tax. Ferris SI-81; *c.* Brown and Nelson-Rees; *i.* McKenzie; Mitla, Oaxaca, Mexico; Aug., 1960; *host,* cactus.

F 8 M— E 8,4 P—; sex.; diaspidid

prev. publ.—none

results—(Cytology by Nelson-Rees.) The cytological picture here was again typical. Maternal tissue and female and male embryos were available for study (figs. 179–181). Measurements of chromosome lengths showed that, at late midprophase, the smallest chromosome was about 60 per cent the length of the longest, and the other two intermediate.



Figs. 179–181. *Opuntiaspis philococcus.* Fig. 179. Mitosis in egg sheath cell. Fig. 180. Mitosis in female embryo. Fig. 181. Mitosis in male embryo.

Phenacaspis pinifoliae (Fitch)

tax. Ferris SI-93; (1) *c.* & *i.* Bennett; Crescent City, California; *host,* pine; (2) *c.* & *i.* Brown; Portal, Arizona; June, 1958; *host, Pinus ponderosa* (see also, results); (3) *c.* & *i.* Barr; Princeton, Latah Co., Idaho; Aug., 1958; *host, Pinus ponderosa;* (4) *c.* & *i.* Brown; Pinyon Flat Camp Ground, State Highway No. 74, Riverside Co., California; April, 1962; *host, Pinus monophylla.*

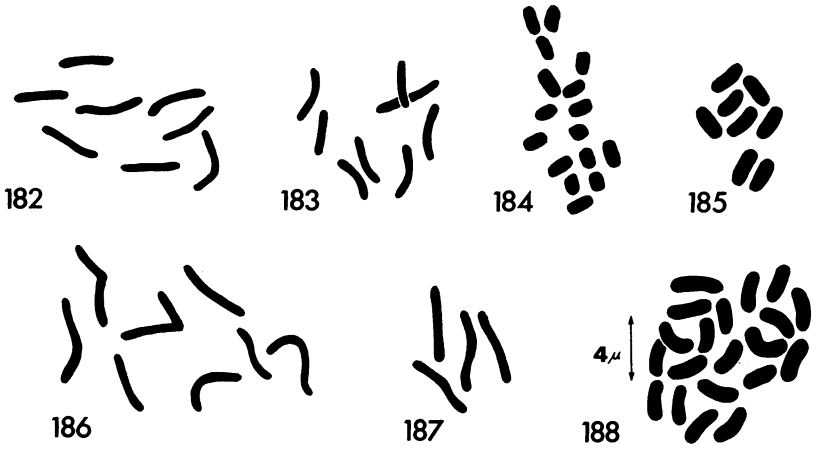
UNISEXUAL: F 8 M— E 8 P 16; parth.

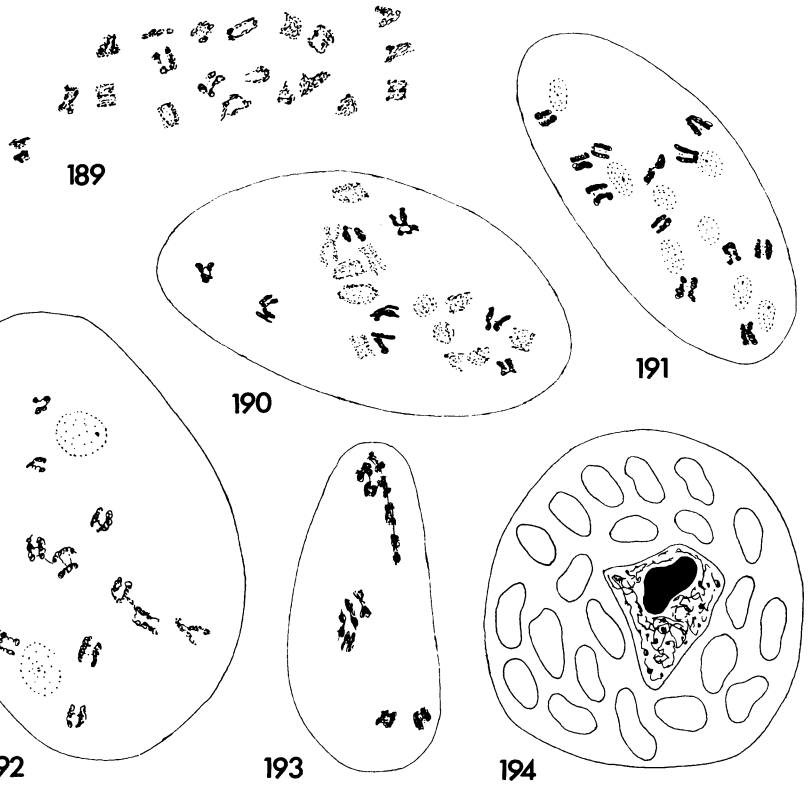
BISEXUAL: F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—The occurrence of spontaneous fragmentation in an embryo from collection (1) (unisexual, see below) has been reported and illustrated by Brown (1960*a*).

results—This species, which is extremely common on pine, exists in two races in the western United States: a unisexual (parthenogenetic) and a bisexual (sexual). Previously, only the bisexual was recognized (Ferris, *loc. cit.*), and the fact that the unisexual escaped notice was probably due to the restricting of most examinations simply to an identification based on the females.

The first three collections listed above consisted of females only, and the cytological picture in each case was that of a typical diaspidid parthenogenote. The maternal tissue and the embryos all had 8 chromosomes, while the polyploid sector showed 16 (figs. 182–184). The number 16 is the only evidence that par-





Figs. 182–194. *Phenacaspis pinifoliae*. Figs. 182–184. UNISEXUAL: Fig. 182. Mitosis in egg sheath cell. Fig. 183. Mitosis in embryo. Fig. 184. Mitosis in tetraploid sector. Figs. 185–194. BISEXUAL: Fig. 185. Mitosis in egg sheath cell. Fig. 186. Mitosis in female embryo. Fig. 187. Mitosis in male embryo. Fig. 188. Mitosis in pentaploid sector of embryo. Fig. 189. Endomitosis-like stage prior to chromocenter formation in pentaploid sector of young embryo. Fig. 190. The first differentiation of the chromosomes: 2 sets (8 chromosomes) pycnotic; 3 sets (12 chromosomes) tenuous. Fig. 191. The second differentiation of the chromosomes: 3 sets pycnotic; 2 sets tenuous. Fig. 192. Continuation of the opening up and loss of stainability of the 2 sets led to their "disappearance"; here only 2 chromosomes, swollen and very lightly staining, were still visible. Fig. 193. The 2 sets were no longer at all apparent; the chromosomes from the 3 heterochromatic sets uniting to form the chromocenter. Fig. 194. Chromocenter in mycetocyte from adult female.

thenogenesis here was of the mitotic rather than the meiotic type. Although previously illustrated, division figures from a unisexual collection will be offered here again to accompany those from the bisexual. At a rather late embryonic stage, chromocenters appeared in the mycetocytes and persisted throughout the life of the individual; Feulgen tests made by Chandra gave intensely positive results.

In addition to the 3 collections examined cytologically, samples which included no scales of males were obtained from 11 other localities in Arizona (including Clifton, Alpine, and Flagstaff), Utah, and eastern California. There is thus little doubt that the unisexual race is the only one present over wide areas in the western United States.

A bisexual collection from southern California conformed to the typical pattern for the family, with haploid and diploid embryos, diploid maternal tissue, and a pentaploid polyploid sector (figs. 185–188).

The formation of a chromocenter in the mycetocytes, already noted above for a unisexual collection, was followed in detail in the bisexual sample. The process of chromocenter formation is of special interest because of its bearing on facultative heterochromatization, which occurs in the lecanoid and Comstockiella systems.

Following typical pentaploid mitoses in the younger embryos, the polyploid nuclei enlarged, while the chromosomes therein became condensed and appeared about to begin a sequence of endoreduplication (endomitosis) (fig. 189). At this stage, the expected number of 20 chromosomes, all similar in general aspect, could be counted. Next, 8 of these chromosomes condensed, becoming strikingly different from the remaining 12, which maintained their previous tenuous appearance (fig. 190). These 8 chromosomes then lost their condensed appearance and became very enlarged and tenuous, and eventually no longer individually recognizable, while the remaining 12 chromosomes became condensed (figs. 191–192). With condensation and reversion from condensation occurring at the same time, the numerical relationships just indicated were not always apparent in each nucleus. However, as the 8 chromosomes lost their condensed appearance completely, the remaining 12 maintained a pycnotic state; these 12 then joined together to form the chromocenter (fig. 193). Shortly thereafter, the heterochromatic chromosomes united completely in a single densely pycnotic blob, which was then maintained. Figure 194 shows a mycetocyte of an adult female.

Similar chromocenter formation was observed in both male and female embryos; chromocenters were likewise present in the parthenogenetic females. The number 12 could obviously represent 3 haploid sets of 4 chromosomes each. Because 8 chromosomes remain euchromatic while 12 undergo facultative heterochromatization to form a chromocenter, the 3 sets in the latter group must have had a different past history from the 2 sets in the former. This distribution of 3 to 2 in the pentaploid nuclei is exactly that of the contributions of the polar bodies: 3 sets, and the cleavage nucleus, 2 sets, to the original polyploid nucleus. It may therefore be suggested that it is the chromosome sets stemming from the polar bodies which undergo facultative heterochromatization in these cells.

Neither numerical relationships nor other details of chromocenter formation are available for the parthenogenetic populations of this species. However, the fact that chromocenters were observed in the parthenogenotes indicates that a contribution from the male is in no way necessary for inducing or stimulating heterochromatization in this instance and thus helps to support the claim that the 12 chromocenter chromosomes in the sexual forms were derived from the polar bodies. (In the parthenogenetic form, the polyploid sector had 16 chromosomes,

of which 8 presumably stemmed from the one and only polar body, and 8 from a cleavage nucleus. In the mycetocytes, an 8 : 8 distribution of the chromosomes between euchromatic and heterochromatic types would thus be expected rather than an 8 : 12, as in the sexual forms.)

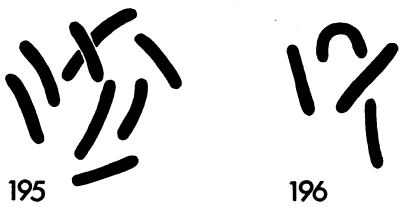
Phenacaspis platani (Cooley)

tax. Ferris SI-94; *c.* Brown and Nelson-Rees; *i.* Wilkey and McKenzie; Monterrey, Nuevo León, Mexico; June, 1960; *host,* plane tree.

F— M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—(Cytology by Nelson-Rees.) Only division figures from the embryos were available for study, and the haploid and diploid complements proved quite typical (figs. 195–196).



Figs. 195–196. *Phenacaspis platani.* Fig. 195. Mitosis in female embryo. Fig. 196. Mitosis in male embryo.

Pinnaspis aspidistrae (Signoret)

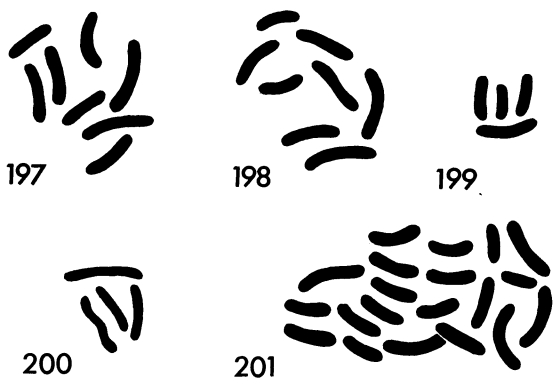
tax. Ferris SI-97; *c.* Nucifora; *i.* Lupo; Catania, Sicily; Sept., 1959; *host, Aspidistra.*

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The various stages of the life cycle available for this species permitted the chromosome formula to be worked out completely (figs. 197–201). The division figures were typical, while a longer and a shorter chromosome were readily distinguishable from the other members of the complement.

Heterochromatic chromocenters were noted in the mycetocytes of moderately advanced embryos and adult females, but were not studied further.



Figs. 197–201. *Pinnaspis aspidistrae.* Fig. 197. Mitosis in maternal tissue. Fig. 198. Mitosis in female embryo. Fig. 199. Mitosis in male embryo. Fig. 200. Mitosis in somatic tissue of young male. Fig. 201. Mitosis in pentaploid sector of embryo.

Figs. 202–205. *Pinnaspis buxi* (Redrawn from Nur). Fig. 202. Four bivalents at diakinesis of oögenesis. Fig. 203. Eight chromosomes, female somatic tissue. Fig. 204. Mitosis in embryo. Fig. 205. Mitosis in polyploid (tetraploid) sector of embryo.

Pinnaspis buxi (Bouché)

tax. Ferris SI-98; *c.* Brown and Becker; *i.* Wilkey; Rio de Janeiro, Brazil; July, 1962; *host,* philodendron.

F 8 M— E 8 P 16; parth.

prev. publ.—none

results—(Cytology by Nur.) According to Ferris (*ibid.*), males are not known for this species; the cytology revealed "meiotic" parthenogenesis. Four bivalents were present at oögenesis (fig. 202), 8 chromosomes in female soma and the only class of embryo (figs. 203–204) and 16 in the polyploid sector—thus, here tetraploid (fig. 205). No record was made as to whether or not chromocenters were present in the mycetocytes.

Pinnaspis strachani (Cooley)

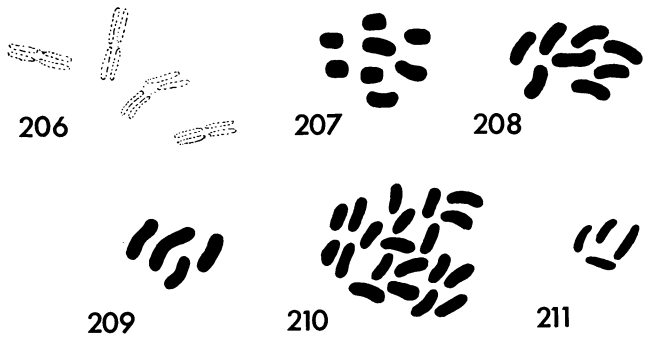
tax. McKenzie, 1956; (1) *c.* Brown; *i.* McKenzie; La Paz, Baja California, Mexico; Oct., 1958; *host,* leguminous shrub; (2) *c.* Brown and Nelson-Rees; *i.* McKenzie; Progreso, Yucatán, Mexico; July, 1960; *host,* cotton; (3) *c.* Brown and Nelson-Rees; *i.* Wilkey; Hacienda Barron, near Mazatlán, Sinaloa, Mexico; Aug., 1960; *host,* cuca; (4) *c.* Brown and Nur; *i.* Wilkey; Kingston, Jamaica; June, 1962; *host,* Barbados Pride, *Caesalpinia pulcherrima;* (5) *c.* Brown and Becker; *i.* Wilkey; Viçosa, Brazil, July, 1962; *host,* grapefruit; (6) *c.* Brown; *i.* Wilkey; Lima, Peru; July, 1962; *host,* citrus.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

(1) F 8 M— E 8, 4 P— (La Paz, Baja California)
(2) F— M— E 8, 4 P 20 (Progreso, Yucatán)
(3) F 8 M— E— P— (Mazatlán, Sinaloa)
(4) F 8 M 4 E 8, 4 P— (Kingston, Jamaica)
(5) F— M— E 8, 4 P 20 (Viçosa, Brazil)
(6) F 8 M 4 E 8, 4 P— (Lima, Peru)

prev. publ.—none

results—Since this species has been collected for cytological study at more different sites than any other sexual armored scale, the results of each are cited above as an example of the usual vicissitudes encountered in the present cytological survey. For none of the collections was it possible to obtain the complete chromosomal formula, yet all were essentially in agreement with regard to chromosome number and—except for coll. no. 3, which consisted of young females—with regard to sexuality and system. Figure 206, of oögenesis, was obtained from coll. no. 5; figures 207–209, of egg sheath cell and mitosis in haploid and diploid embryos, from coll. no. 1; figure 210, of a polyploid mitosis, from coll. no. 2; and



Figs. 206–211. *Pinnaspis strachani.* Fig. 206. Diakinesis of oögenesis, 4 bivalents. Fig. 207. Mitosis in egg sheath cell. Fig. 208. Mitosis in female embryo. Fig. 209. Mitosis in male embryo. Fig. 210. Mitosis in polyploid sector of embryo. Fig. 211. Mitosis in somatic tissue of young male.

figure 211, of a somatic figure in the male, from coll. no. 4. The mycetocytes in the adult female did *not* have chromocenters.

Protodiaspis agrifoliae Essig

tax. Ferris SI-100; *c.* Brown; *i.* Wilkey; Tecate, Baja California, Mexico; April, 1963; *host,* otherwise undet. oak.

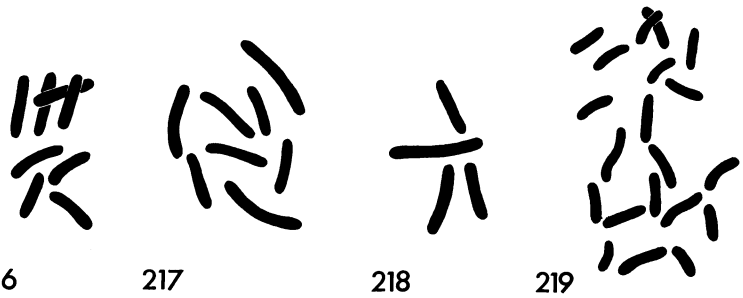
F 8 M— E 8, 4 P —; sex.; diaspidid

prev. publ.—none

results—(Cytology by Robison.) This species is the type of one of the most interesting genera of the armored scales; within the limit of a relatively few species the genus shows a remarkable range of variation, an encapsulated evolutionary series reaching from a more or less typical armored scale to forms quite similar to those of the quite atypical *Ancepaspis* (Brown and McKenzie, 1962).

A species quite similar to *Protodiaspis agrifoliae* but lacking perivulvar pores has recently been described (*P. didymus;* McKenzie and Nelson-Rees, 1962) and its chromosome number determined. As far as can be told, the cytology of the two is also similar; the figures which were seen in the *P. agrifoliae* material were in general quite typical (figs. 212–214). One chromosome, somewhat longer than the others, had a weak, relatively less chromatic zone, about a third from the end. This zone somewhat resembled a pseudocentromere; and on squashing, the two segments of the chromosome were sometimes separated to give the appearance of 5 entities instead of 4 in the haploid embryos, and 9 or 10 instead of 8 in the diploid embryos. The nucleolus had usually disappeared by the time the chromosomes were sufficiently condensed for study, but a few figures indicated that the achromatic zone in question may have been associated with the nucleolus (fig. 215).

Figs. 212–215. *Protodiaspis agrifoliae.* Fig. 212. Mitosis in egg sheath cell. Fig. 213. Mitosis in female embryo. Fig. 214. Mitosis in male embryo. Fig. 215. Mitosis in male embryo; nucleolus near achromatic gap in longest chromosome.



Figs. 216–219. *Protodiaspis chichi.* Fig. 216. Mitosis in egg sheath cell. Fig. 217. Mitosis in female embryo. Fig. 218. Mitosis in male embryo. Fig. 219. Mitosis in polyploid sector.

Protodiaspis chichi McKenzie and Nelson-Rees

tax. McKenzie and Nelson-Rees, 1962; *c.* Nelson-Rees and Brown; *i.* McKenzie and Nelson-Rees; Sololá Province, Guatemala; July, 1960; *host, Quercus crassifolia* H. and B.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Chromosome number cited in McKenzie and Nelson-Rees (*ibid.*) and Brown and McKenzie (1962).

results—(Cytology from type collection by Nelson-Rees.) In all respects the cytology here was that of a typical armored scale with a diaspidid system (figs. 216–219). One chromosome appeared appreciably longer than the other 3 in the haploid set; but when more fully contracted, as in the polyploid or egg sheath cells, the chromosomes did not manifest such differences in size.

Protodiaspis didymus McKenzie and Nelson-Rees

tax. McKenzie and Nelson-Rees, 1962; *c.* Nelson-Rees and Brown; *i.* McKenzie and Nelson-Rees; 25 mi. N. of Clifton, Arizona; Sept., 1960; *host, Quercus grisea* Liebm. × *Q. turbinella* Greene.

F 8 M— E— P—; sex.

prev. publ.—Chromosome number cited in Brown and McKenzie (1962).

results—(Cytology on type collection by Nelson-Rees.) The only material available consisted of young females already fertilized and apparently destined to overwinter in this condition. The chromosome number was available only from maternal tissue.

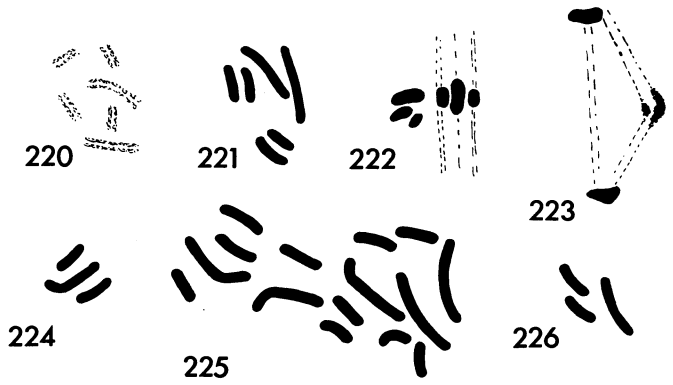
Protodiaspis infidelis Ferris

tax. Ferris SIV-412; *c.* Nelson-Rees and Brown; *i.* McKenzie and Nelson-Rees; 2 mi. S. of Panajachel, Lake Atitlán, Guatemala; July, 1960; *host, Quercus castanea* Nee.

F 6 M 3 E 6, 3 P 15; sex.; diaspidid

prev. publ.—Chromosome number and system cited in McKenzie and Nelson-Rees (1962) and Brown and McKenzie (1962).

results—Not only was *Protodiaspis infidelis* the first species of this important genus to be studied cytologically, but its chromosome number was unusual. Therefore, every effort was made not only to make a complete determination as far as the chromosome formula was concerned but also to verify without question, by demonstrating chromosome elimination at cleavage, that the chromosome system

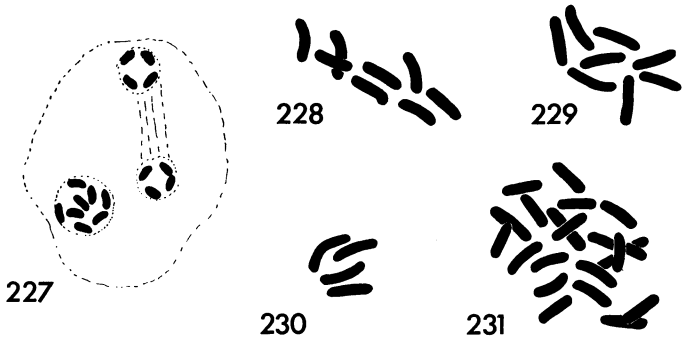


Figs. 220–226. *Protodiaspis infidelis.* Fig. 220. Mitosis in somatic tissue of female. Fig. 221. Mitosis in female embryo. Figs. 222–223. Elimination of one haploid chromosome set at late cleavage of embryogeny. Fig. 224. Mitosis in male embryo. Fig. 225. Mitosis in polyploid sector. Fig. 226. Somatic mitosis in young male.

was, as indicated by the numerical relationships, actually diaspidid (figs. 220–226). The longest of the chromosomes was a little over twice the length of the shortest, which was just distinguishable from the third member of the complement. One embryo was found with a sector with 4 and 7 chromosomes, the extra chromosome being a small fragment, presumably of maternal origin, since it survived the elimination process. In the polyploid figure (pentaploid, 15 chromosomes), drawn as an example, the chromosomes showed an unusual arrangement; the 5 representatives of the long chromosome formed somewhat of a row down the middle; the 5 representatives of the shortest chromosome were all on one side and those of the intermediate chromosome on the other (fig. 225).

Protodiaspis signata Ferris

tax. Ferris SIII-315; (1), (2), and (3) *c.* Nelson-Rees and Brown; *i.* McKenzie; (1) 8 mi. N. of Nueva Ixtapan, Mexico, Mexico; (2) and (3) 5 mi. W. of Carapan, Highway 15, Michoacán, Mexico; (1), (2), and (3) Aug., 1960; *host* (1) and (2), *Quercus obtusata* H. and B.; (3) *Q. castanea* Nee.



Figs. 227–231. *Protodiaspis signata.* Fig. 227. The 3 products of oögenesis in their common periplasm; the 8-chromosome polar body I, the 4-chromosome polar body II, and the egg; the latter two cannot be distinguished from one another here. Fig. 228. Mitosis in egg sheath cell. Fig. 229. Mitosis in female embryo. Fig. 230. Mitosis in male embryo. Fig. 231. Mitosis in pentaploid sector, 20 chromosomes (overlapping at 3 o'clock; 2 long chromosomes over 2 short).

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—Chromosome number and male haploidy in McKenzie and Nelson-Rees (1962).

results—(Cytology by Nelson-Rees.) Cytology from the three collection sites was essentially similar, and the information will be combined. Maternal tissue and embryos gave typical mitoses, and a typical meiotic figure was found in one egg (figs. 227–231).

Pseudaulacaspis pentagona (Targioni)

tax. Ferris SI-108; (1) *c.* & *i.* Bennett; St. Augustine, Trinidad; fall, 1956; laboratory culture on potatoes; (2) *c.* & *i.* Francis (via Bedford); Pietermoritzburg, Natal, S. Africa; April, 1958; (3) *c.* Nur; *i.* Wilkey; Mona, Kingston, Jamaica; July, 1962; *host, Nerium;* (4) *c.* Brown; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host, Erythrina* sp.

F 16 M 8 E 16,8 P 40; sex.; diaspidid

prev. publ.—This species was the first in which the diaspidid system of chromosome behavior was recognized and has been the subject of extensive work by Brown and Bennett (1957), Hughes-Schrader (1957), Bennett and Brown (1958), and Tremblay (1959, 1960, 1961).

results—Tremblay's (*ibid.*) reports on the Italian material, as well as further collections (nos. 2–4 above), confirmed the original work on the Trinidad material. *Pseudaulacaspis pentagona* has now been sampled fairly well around the world, except in the area where it originated, the Orient.

Pseudoparlatoria

This New World genus includes a number of species which are just beginning to be understood. Of the three reported here, one has just recently been described. Cytological data has been previously reported for the undetermined collections, which all demonstrate a haploid number of 5, or derivation therefrom.

Pseudoparlatoria browni McKenzie

tax. McKenzie, 1963; *c.* Brown; *i.* McKenzie; La Paz, Baja California, Mexico; Oct., 1959; *host,* undet.

F— M— E 8,4 P 20; sex.; diaspidid

prev. publ.—Brown, 1960*a,* under *Pseudoparlatoria* sp.

results—This species is of special interest because its karyotype was apparently derived from a 5-chromosome ancestral form. When first reported (Brown, *ibid.*), no congeners had been definitely determined, and it was therefore not possible to evaluate with certainty the derivation of the karyotype. Since data have become available for the two other species, *Pseudoparlatoria ostreata* and *P. parlatorioides,* both wide-ranging and both having 5 chromosomes, there seems little doubt that the 4-chromosome complement has been derived from one of 5. The double-sized member in the 4-chromosome complement presumably arose from a grossly unequal reciprocal translocation as described by Brown (1960*b,* 1961).

Fig. 232. *Pseudoparlatoria browni.* Mitosis in polyploid or pentaploid sector of embryo; note that the double-length chromosome is represented five times.

Photographs of the haploid and diploid figures have been published (Brown, 1960*b*); a camera lucida drawing is presented of mitosis in a polyploid sector, in which the double-length chromosome is represented five times (fig. 232).

Pseudoparlatoria ostreata Cockerell

tax. Ferris SIV-416; (1) *c.* Nur; *i.* Wilkey; Kingston, Jamaica; June, 1962; *host, Piper nigrum;* (2) *c.* Brown and Becker; *i.* Wilkey; Viçosa, Brazil; July, 1962; *host,* magnolia; (3) *c.* Nur and Brown; *i.* Wilkey; 2 mi. S. of Ocho Rios, Jamaica; Aug., 1962; *host,* undet. tree; (4) *c.* Nur and Brown; *i.* Wilkey; Lucea, Jamaica; Aug., 1962; *host,* coleus.

F 10 M 5 E 10, 5 P 25; sex.; diaspidid

prev. publ.—none

results—(Cytology by Nur.) Chromosomal conditions were seemingly the same in all 4 collections, and the results will therefore be combined. The maternal tissue and one class of embryos showed 10 chromosomes, while the other class of embryos and the young males had 5; the polyploid sector, as expected, was pentaploid with 25 chromosomes (figs. 233–237). Several figures of oögenesis showed 5 bivalents at diakinesis.

Figs. 233–237. *Pseudoparlatoria ostreata* (redrawn from Nur). Fig. 233. Mitosis in egg sheath cell. Fig. 234. Mitosis in female embryo. Fig. 235. Mitosis in male embryo. Fig. 236. Mitosis in pentaploid sector. Fig. 237. Mitosis in fourth instar male.

Pseudoparlatoria parlatorioides (Comstock)

tax. Ferris SI-117; *c.* Brown and Becker; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host, Eugenia jaboticaba.*

F 10 M— E 10, 5 P 25; sex.; diaspidid

prev. publ.—none

results—As in *Pseudoparlatoria ostreata,* the haploid complement consisted of 5 chromosomes; the various tissues displayed complements as expected (figs. 238–241).

Figs. 238–241. *Pseudoparlatoria parlatorioides.* Fig. 238. Mitosis in egg sheath cell. Fig. 239. Mitosis in female embryo. Fig. 240. Mitosis in male embryo. Fig. 241. Mitosis in pentaploid sector of embryo.

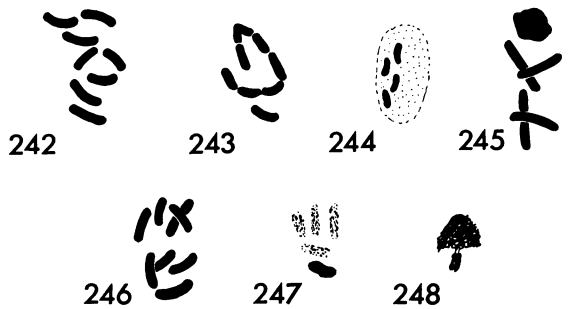
Radionaspis indica (Marlatt)

tax. Ferris SII-153 and SIV-422; *c.* Nur; *i.* Wilkey; Kingston, Jamaica; June, 1962; *host,* mango.

F 8 M—E 8, 4 + 4, P—; sex; Comstockiella (and lecanoid?)

prev. publ.—none

results—(Cytology in part by Nur.) Maternal tissue and early embryonic stages were typical of the heterochromatic systems (figs. 242–246). The n + 1, here 5, elements, characteristic of the Comstockiella system, were observed at prometaphase of spermatogenesis (fig. 247), and typical eliminations at telophase (fig. 248). No lecanoid figures were seen at this stage, but larger residues in an occasional cyst indicated that the lecanoid system may also occur; although the larger residues were bigger than would have been expected from D^H-elimination in the Comstockiella system, further study will be required before this question can be resolved.



Figs. 242–248. *Radionaspis indica.* Fig. 242. Mitosis in egg sheath cell. Fig. 243. Mitosis in female embryo. Fig. 244. Non-dividing nucleus in male embryo with four heterochromatic chromosomes. Fig. 245. Prophase of mitosis in male embryo; 4 euchromatic chromosomes and one, as yet unresolved, chromocenter of heterochromatic chromosomes. Fig. 246. Late prophase of mitosis in male embryo; the 4 euchromatic and 4 heterochromatic chromosomes now similar. Fig. 247. Late prophase of spermatogenesis, Comstockiella system; 5 (i.e., n + 1) elements present, the D^H but not the D^E identifiable. Fig. 248. Telophase of spermatogenesis, Comstockiella system; D^H elimination.

Rolaspis anacantha De Lotto

tax. De Lotto, 1956; *c.* & *i.* De Lotto; Nairobi, Kenya; Feb., 1958; *host, Oxyris weightiana.*

Figs. 249–251. *Eolaspis anacantha.* Fig. 249. Mitosis in male embryo. Fig. 250. Mitosis in female embryo. Fig. 251. Chromosomes of the secondary oöcyte; separation into chromatids not detectable.

F (18) M— E 18,9 P—; sex.; diaspidid

prev. publ.—none

results—The diploid chromosome number of 18 for the adult female was derived from the haploid number of 9 from a secondary oöcyte; the resolution into dyads of the individual chromosomes was not clear in this figure (fig. 251). Haploid embryos with 9 and diploid embryos with 18 chromosomes were observed (figs. 249–250), but no polyploid figures suitable for counts.

This species belongs to a group of closely related genera which will be considered further in the Discussion.

Situlaspis yuccae (Cockerell)

tax. Ferris SI-125; *c.* Brown; *i.* McKenzie; Tucson, Arizona; June, 1958; *hosts,* box elder and mesquite.

F 10 M 5 E 10,5 P—; sex.; diaspidid

prev. publ.—Brown (1960*a*) reported an example of a transmitted fragment and also discussed the significance of the 5-chromosome karyotype in the relationship of this species to others in western North America.

results—The samples came from 2 collections in and near Tucson, only one of which, from mesquite, was determined by McKenzie. Since they agreed both in morphology and cytology, there seems little likelihood that they were not the same species.

The chromosome complements for normal male and female embryos, as well as the fragmentation examples, have been pictured by Brown (1960*a*).

Unachionaspis bambusae (Cockerell)

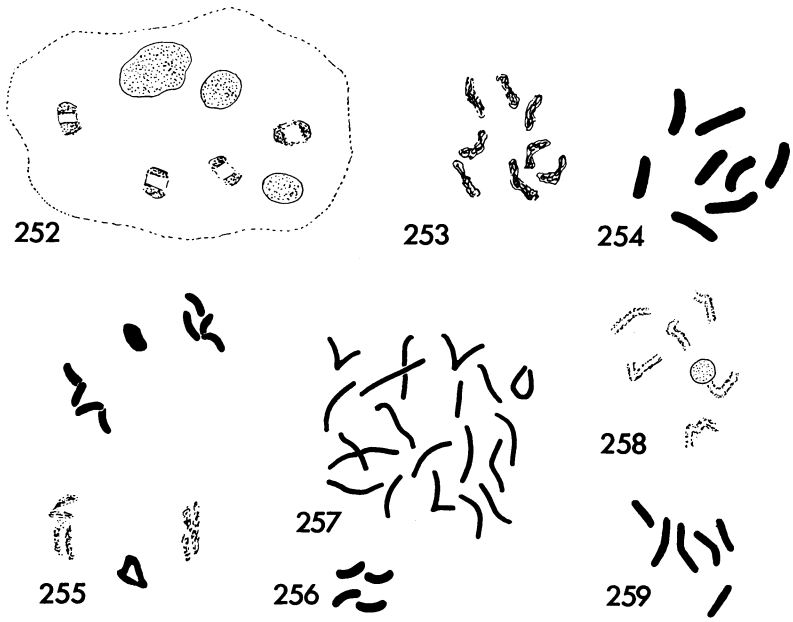
tax. Takagi, 1961*a; c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Sasa palmata* (Bean) Nakai.

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—A fairly complete record was obtained for this species. Four bivalents were observed at diakinesis of oögenesis (fig. 252). Eight chromosomes were evident in mitoses in maternal tissue and female embryos (figs. 253–254), and 4 in the male (fig. 256). Typical elimination figures were observed at late cleavage to yield the haploid embryos (fig. 255). As expected, 20 chromosomes were to be found in the pentaploid division figures (fig. 257).

Two division figures with 6 chromosomes each (figs. 258–259) were noted in an otherwise apparently normal haploid embryo, in which several 4-chromosome fig-



Figs. 252–259. *Unachionaspis bambusae.* Fig. 252. Diakinesis of oögenesis; 4 bivalents and 3 nucleolar fragments. Fig. 253. Mitosis in egg sheath cell. Fig. 254. Mitosis in female embryo. Fig. 255. Chromosome elimination, 2 adjacent telophase figures; 4 chromosomes at each pole; eliminated chromosomes in blob at equatorial plate. Fig. 256. Mitosis in male embryo. Fig. 257. Mitosis in pentaploid sector of embryo. Figs. 258–259. Six-chromosome division figure in otherwise haploid (i.e., 4-chromosome) embryo (see text for further explanation).

ures were counted. These division figures were quite well isolated from each other on opposite sides of the embryo; they could not, therefore have been produced simultaneously as an artifact by, for example, disrupting a 4-chromosome figure so that 2 of its chromosomes intruded into one adjacent figure and 2 into another, making them both appear as 6-chromosome figures. In addition to the wide spatial separation, the 2 were at separate phases of the mitotic cycle. In brief, it seems most likely that non-disjunction occurred during early embryogeny to produce an original 6-chromosome nucleus, which in turn contributed a few scattered descendants to this embryo at early blastula.

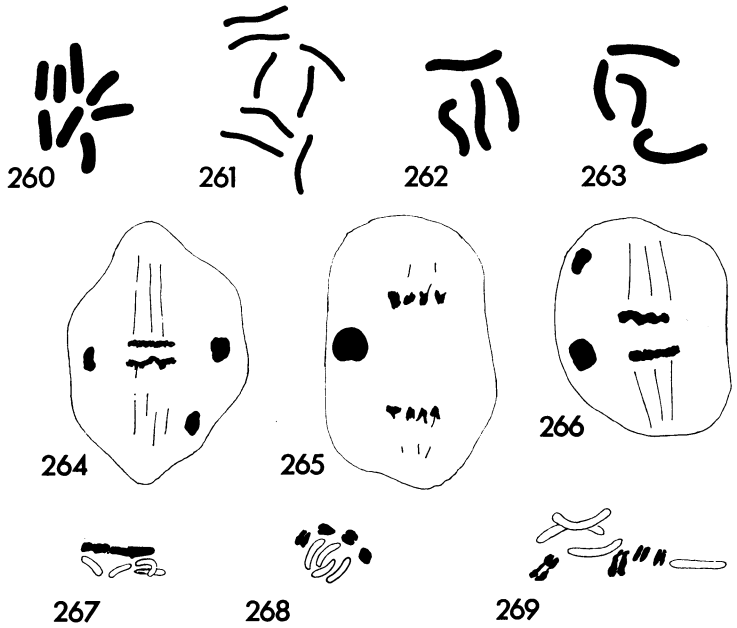
Unaspis citri (Comstock)

tax. Ferris SI-129; *c.* Brown; *i.* Breese; St. Augustine, Trinidad; April, 1957; *host,* lime.

F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—In regard to size relationships and number, the cytological pictures from maternal tissue, embryos and males conformed to the usual picture (figs. 260–263). Pentaploid division figures were also observed, but not drawn. Of special interest in this species was the occurrence of chromosome elimination after delineation of cell boundaries. According to a very rough estimate based on cell size and number, the delineation was occurring at an earlier than usual stage in this species rather than the converse, a later elimination. The residues were thus trapped for a while



Figs. 260–269. *Unaspis citri.* Fig. 260. Mitosis in egg sheath cell. Fig. 261. Mitosis in female embryo. Fig. 262. Mitosis in male embryo. Fig. 263. Mitosis in somatic tissue of young males. Figs. 264–266. Retention in cell of pycnotic residue following chromosome elimination in young male embryo. Figs. 267–269. Differentiation of 2 haploid chromosome sets at late prophase, prior to elimination at the immediately succeeding anaphase, in young male embryo.

in the cell of origin (figs. 264–266), but eventually were cut off in small cells containing little cytoplasm in addition. Immediately prior to elimination, the 2 haploid sets become differentiated, the more densely pycnotic of the 2 being that eliminated (figs. 267–269). Occasionally, the pycnotic set assumed hypercontracted, bizzare shapes and the individual chromosomes were strikingly split (fig. 269).

Unaspis euonymi (Comstock)

tax. Ferris SI-130; *c.* Brown; *i.* Lupo; Ischia, Naples, Italy; Aug., 1959; *host,* undet. shrub.

F 8 M 4 E 8, 4 P —; sex.; diaspidid

prev. publ.—none

results—The routine cytological determinations on this species agreed with the basic pattern of the family (figs. 270–273).

Figs. 270–273. *Unaspis euonymi.* Fig. 270. Mitosis in egg sheath cell. Fig. 271. Mitosis in female embryo. Fig. 272. Mitosis in male embryo. Fig. 273. Mitosis in somatic tissue of young male.

Xerophilaspis prosopidis (Cockerell)

tax. Ferris SI-136; *c.* & *i.* Brown; La Paz, Baja California, Mexico; Oct., 1958; *host, Prosopis* sp.

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—In spite of the rather unusual morphology of the species, the chromosome complement of 4 (or 8) proved to be quite typical (figs. 274–276). Two stages of oögenesis were observed, and these also were typical. Males had not previously been recognized. The cytology here establishes this as a sexual species; not only were typical male, i.e., haploid, embryos present in the ovaries but abundant sperm also.

Figs. 274–276. *Xerophilaspis prosopidis.* Fig. 274. Mitosis in egg sheath cell. Fig. 275. Mitosis in female embryo. Fig. 276. Mitosis in male embryo.

Parlatorini

The genera included in this tribe are based on Balachowsky's (1953*a*) definition. Although not recognized by Ferris in the Atlas or by McKenzie (1945) in his revision of Parlatoria and allied genera, the tribal status aids appreciably in coping with this group of genera as an evolutionary entity (Brown and McKenzie, 1962). In regard to chromosome number, the Parlatorini conform to the basic diploid number of 8. In regard to chromosome system, the few sexual species sampled have all proved to have a heterochromatic system, whereas the Diaspidini, with which these genera have been kept united by Ferris and others, have only a very few species with such a system.

In his listing of the various genera to be included, Balachowsky (*ibid.*) pointed out that *Pseudoparlatoria* was not a member of this tribe but a typical member of the Diaspidini.

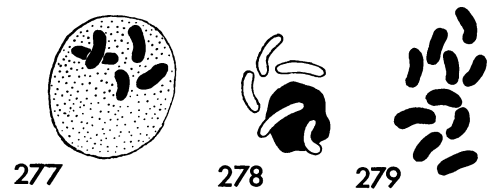
Gymnaspis aechmeae Newstead

tax. Ferris SI-63; *c.* Brown; *i.* Wilkey; Rio de Janeiro, Brazil; July, 1962; *host,* a bromeliad.

F 10 M— E 10, 5 + 5 P—; sex.; heterochromatic

prev. publ.—none

results—Female tissue and embryos only were available for study. Although the embryos showed the typical lecanoid-Comstockiella heterochromatization (figs. 277–279), spermatogenic stages were not available for determination of the system. This species was not particularly favorable even for embryonic division, since there were only one to 3 embryos present per female. In addition to the typical



Figs. 277–279. *Gymnaspis aechmeae.* Chromosomes in male embryo. Fig. 277. The heterochromatic set in the resting nucleus. Fig. 278. Prophase, 5 euchromatic chromosomes and clump of heterochromatic chromosomes. Fig. 279. Ten chromosomes at late prophase. No differentiation between the euchromatic and heterochromatic sets.

male heterochromatization, the presence of copious sperm left no doubt as to the bisexuality of the population.

Leucaspis loewi Colvée

tax. Balach. VII-868; *c.* Benassy; *i.* Pegazzano; Antibes, France; June, 1959; *host,* pine.

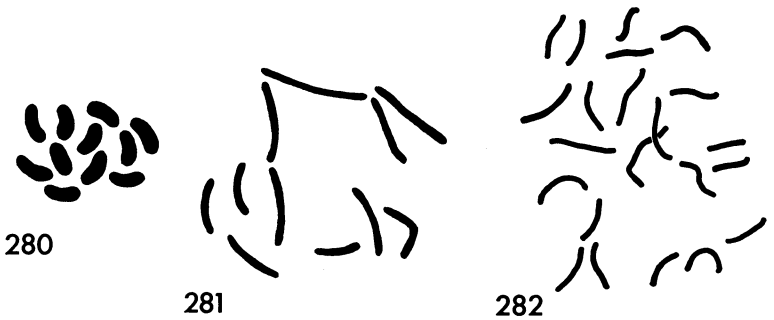
F 11 M— E 11, P 22 and 33; parth.

prev. publ.—none

results—The type of parthenogenesis occurring in this collection was probably that of a mitotic rather than a meiotic oögenic sequence. It is difficult to see how an uneven chromosome number could be maintained in the meiotic type, but there would obviously be no problem if oögenesis consisted of a single mitotis-like division. The numbers found in the polyploid division figures were tetraploid and hexaploid rather than pentaploid, and these would also conform to expectation from a mitotic type (figs. 280–282).

The "diploid" number of 11 in this collection deserves special comment. In the first place, parthenogenetic strains and species have departed much less than sexual types from the basic number of the Diaspididae. Most of the parthenogenetic collections have been of the mitotic type and, as indicated in the preceding paragraph, these should be free to vary in regard to chromosome number. Secondly, even though the one congener studied had the basic diploid number of 8, another genus in this tribe, *Gymnaspis,* had a basic number of 10. One break only would be required to convert 10 to 11, whereas 3 would be necessary for the change from 8.

Balachowsky (*ibid.*) has described male puparia for this species. He stated further that the species is widely distributed in Europe, from Sweden to the



Figs. 280–282. *Leucaspis loewi.* Fig. 280. Mitosis in egg sheath cell. Fig. 281. Mitosis in embryo. Fig. 282. Mitosis in polyploid sector.

Mediterranean and that it is the most common species on pine in Central and Western Europe.

Undoubtedly this species merits much further study.

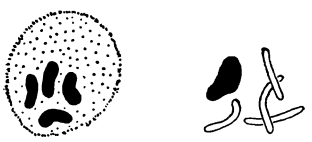
Leucaspis pusilla Loew

tax. Balach. VII-860; *c.* & *i.* Pegazzano; Florence, Italy; July, 1959; *host,* pine.

F 8 M— E 8, 4+4 P—; sex.; heterochromatic

prev. publ.—none

results—In addition to typical heterochromatization of one set in certain embryos (figs. 283–284), the other embryonic and maternal cytology conformed to the usual pattern. Later stages of the male were not available for determination of the chromosome system.



283 284

Figs. 283–284. *Leucaspis pusilla.* Chromosomes in the male embryo. Fig. 283. The haploid set of heterochromatic chromosomes in the resting nucleus. Fig. 284. Prophase. Four euchromatic chromosomes and the heterochromatic chromosomes in a clump.

Parlatoria crotonis Douglas

tax. Ferris SIV-401; *c.* Nur; *i.* Wilkey; Kingston, Jamaica; July, 1962; *host, Codiaeum.*

F 8 M 4+4 E 8, 4+4 P 20; sex.; Comstockiella and lecanoid

prev. publ.—none

results—(Cytology by Nur.) Typical heterochromatization was observed in the male embryos, and the polyploid embryonic sectors showed the expected pentaploid division figures. Lecanoid and Comstockiella sequences were observed in the same testis. The lecanoid sequence was identified by the occurrence of metaphase plates with the diploid number of 8 chromosomes and the characteristic segregational division of anaphase II. The Comstockiella sequence was identified by the occurrence of prophases in which the number of heterochromatic entities had been reduced from 4 to one.

Parlatoria oleae (Colvée)

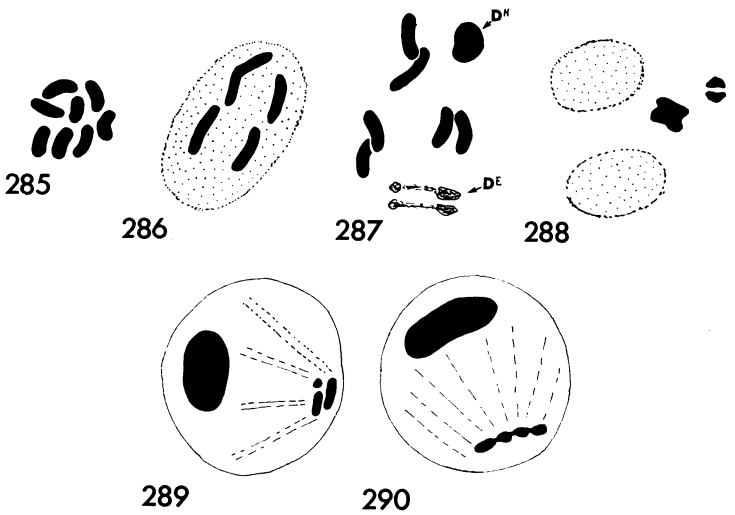
tax. Ferris SI-87; (1) *c.* & *i.* Dickson; Riverside, California; August, 1957; *host,* plum; (2) *c.* & *i.* Doutt; from laboratory culture on Irish potato, Albany, California; Oct., 1957.

F 8 M 4+4 E 8, 4+4 P—; sex.; Comstockiella

prev. publ.—See below, *results;* also, Brown (1960*a*) for karyotype in female embryo and example of spontaneous fragmentation.

results—A detailed experimental analysis of the Comstockiella system, with *Parlatoria oleae* as the subject, has been undertaken by Mr. W. Gerald Robison, and some of his preliminary results have been cited by Brown (1963). Because the species has been under intensive study by Mr. Robison, little attempt has been made to complete the cytological observations for the purposes of the present report; and of those which have been made, only a few will be mentioned.

Cytology of embryos and maternal tissue conformed to the typical heterochromatization pattern (figs. 285–286). Studies of spermatogenesis, collection 2, showed for the most part a quite typical Comstockiella sequence. Bivalents were obvious at late prophase, and in some instances the three different types of chromosomes—



Figs. 285–290. *Parlatoria oleae.* Fig. 285. Mitosis in egg sheath cell. Fig. 286. Heterochromatic set in resting nucleus of male embryo. Fig. 287. Spermatogenesis, midprophase, 3 bivalents, the D^E and the D^H chromosomes. Fig. 288. Post-spermatogenesis (or early spermiogenesis). Normal and fragment D^H residues. Fig. 289–290. Post-telophase. Cytokinesis has followed telophase; the eliminated D^H products show abnormal "spindle fiber" formation.

bivalents, D^E, and D^H—could each be clearly distinguished at prometaphase (fig. 287).

Early spermiogenic stages yielded some examples of aberrancies associated with the D^H chromosome. In one instance, one of the two residues was markedly reduced in size, as though only a small terminal segment had been ejected from the telophase nucleus (fig. 288). In another animal, in telophase cells of one cyst, fibers or strands, like astral or spindle fibers, radiated outward from the pycnotic residues (figs. 289–290).

Parlatoria proteus (Curtis)

tax. Ferris SI-89; (1) *c.* Kerr; *i.* Breese; Brazil; Feb., 1957; *host,* palm; (2) *c.* Brown; *i.* Wilkey; Rio de Janeiro, Brazil; *host,* palm; July, 1962.

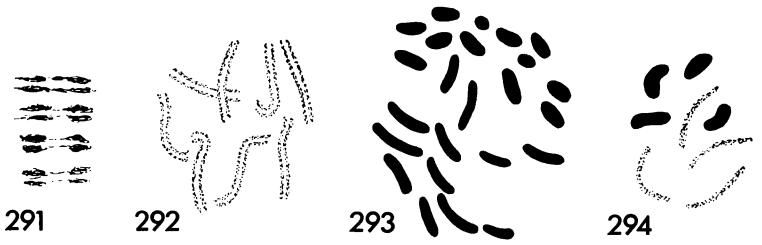
UNISEXUAL: F 8 M — E 8 P (12?); parth. (meiotic)
BISEXUAL: F 8 M — E 8, 4+4 P —; sex.; Comstockiella and lecanoid

prev. publ.—none

results—(Cytology on (2) by Nur and Brown.) Notes on the specific locality of the first collection have been lost, but the collection was made in the general region of São Paulo—that is, in the same major geographical area as the second.

According to Ferris (*ibid.*), the species is known from a long list of hosts all around the world in tropical and subtropical areas. The material described by Ferris included males and was obtained from the host *Sansevieria,* near Los Angeles, California.

The first collection proved to be unisexual: the examination of many embryos (fig. 292) showed only the one chromosome number and no heterochromatization. No sperm were found in the females. In the oöcyte, the haploid number of bivalents



Figs. 291–294. *Parlatoria proteus.* Figs. 291–293. Parthenogenetic strain. Fig. 291. Oögenesis, early anaphase, 4 bivalents. Fig. 292. Mitosis in embryo. Fig. 293. Mitosis in polyploid sector (see text for further explanation). Fig. 294. Sexual strain. Male embryo, differentiation of euchromatic and heterochromatic sets at midprophase.

was found at first division (fig. 291). Meiosis, therefore, occurred. The diploid number of the embryos could have been achieved either by an interruption of meiosis after the first division (the secondary oöcyte substituting for the zygote) or by reunion of haploid products following completion of the meiotic sequence. Some evidence that it was the latter process came from the only polyploid nucleus found (fig. 293); this "nucleus" consisted of two triploid complements in different stages of condensation. The most likely interpretation is that two products of polar body fusion were themselves fusing; that is, polar body I (diploid) had united with polar body II (haploid) to yield a triploid nucleus, division products of which were forming the figure in question. Whether this particular figure should be interpreted as fusion or not, the existence of triploidy indicates that meiosis had gone to completion, since interruption at the end of the first division would have yielded two diploid products only.

The second collection was bisexual and showed typical heterochromatization in the male embryos (fig. 294), and again 4 bivalents in the female, at diakinesis. The chromosomes of the male were not studied per se—but the two chromosome systems were identified on the basis of some cysts observed immediately prior to spermatogenic prophase, in which the number of heterochromatic entities had been reduced from 4 to 1 (typical of the Comstockiella system), and on the basis of other cysts, observed during spermiogenesis, in which the pycnotic residues were quite large and must have originated from a lecanoid, rather than a Comstockiella sequence.

Parlatoria ziziphus (Lucas)

tax. Ferris SI-90; *c.* & *i.* Benassy; Antibes, France; originally from Algiers; June, 1959; *host,* grapefruit in laboratory culture.

F 8 M 4+4 E 8, 4+4, P —; sex.; Comstockiella and lecanoid

prev. publ.—none

results—Embryonic stages, male and female tissue showed typical division figures (figs. 295–296).

The determinations of the chromosome systems were based on quite limited observations. The reduction in number of heterochromatic entities from 4 to one prior to the onset of true prophase indicated the occurrence of a Comstock-

Figs. 295–296. *Parlatoria ziziphus.* Fig. 295. Mitosis in female embryo. Fig. 296. Spermatogonial cell, the 4 heterochromatic chromosomes at interphase.

iella sequence in this species. The presence of two size classes of pycnotic residues during spermiogenesis, one very much larger than the other, indicated the occurrence of both Comstockiella and lecanoid systems. Variation in size of residues due to variable-D behavior is limited to variation in size among the chromosomes of the complement, which was here quite insufficient to account for that observed in the residues.

Odonaspidini

Of the 4 diaspidid tribes recognized by Ferris (1942), the Odonaspidini was the only one about which he expressed serious doubts. Although the typical genus obviously does not belong in either of the two major tribes, other genera resembling it closely have characteristics suggestive of either one or the other of the major tribes. The evolutionary position of the tribe has been discussed by Brown and McKenzie (1962). It is to be very much regretted that more information on chromosome numbers and systems is not available for this group. However, the data now existing conform to the general picture of the family in regard to chromosome number; some other cytological features, such as the formation of mycetocytes from diploid nuclei (see *Odonaspis penicillata* below), may eventually help resolve the problem of phylesis.

Odonaspis penicillata Green

tax. Ferris SII-164; *c.* Hieb; *i.* Brown; Fiji; Jan., 1960; *host,* bamboo.

F — M 4+4 E 8, 4+4 P 20; sex.; Comstockiella, variable-D

prev. publ.—A detailed description of the Comstockiella spermatogenic sequence as well as an illustration of a pentaploid division figure has been reported by Brown (1963).

results—In addition to the Comstockiella sequence, this species is of interest for one or two cytological aspects not included in the report just cited. The embryo has a somewhat different organization than that typical of the family; diploid nuclei occur in association with the symbionts at the distal end of the embryo, while the pentaploid nuclei are few in number and do not occur in the symbiont area.

Odonaspis ruthae Kotinsky

tax. Ferris SII-165; (1) *c.* & *i.* Dickson; Riverside, California; Aug., 1957; *host,* Bermuda grass; (2) *c.* & *i.* Beardsley; Wailupe Valley, Oahu, Hawaii; April, 1960; *host,* Bermuda grass.

F 8 M — E 8 P 16; parth.

prev. publ.—none

results—Both of the above collections gave the same cytological picture. Ferris (*ibid.*) based his description of the species on material from Honolulu, Hawaii, presumably from Bermuda grass and included a drawing and description of the scale of the male. There is no doubt that the material examined cytologically came

Figs. 297–299. *Odonaspis ruthae.* Fig. 297. Mitosis in egg sheath cell. Fig. 298. Mitosis in embryo. Fig. 299. Mitosis in polyploid sector.

from parthenogenetic populations; the problem now remaining is the rediscovery of the sexual forms.

No details are known of the type of parthenogenesis, but the chromosome number of the polyploid sector is 16, or tetraploid, and thus is typical of the forms with a mitotic type of oögenesis. The somatic chromosome number of the sexual congener just cited is the same for the female, or 8; but 20, or pentaploid, as expected, in the polyploid sector (figs. 297–299).

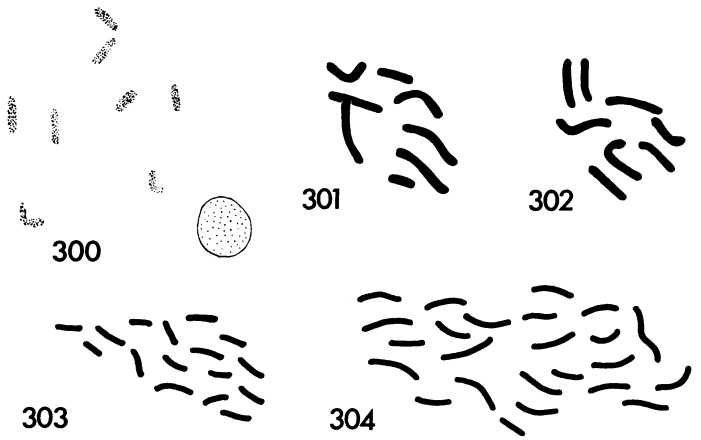
Poliaspoides formosana (Takahashi)

tax. Takahashi, 1930 and Mamet, 1946; (1) *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Bambusa multiplex;* (2) *c.* & *i.* De Lotto; Nairobi, Kenya; June, 1961; *host,* bamboo.

F 8 M— E 8— P 16, 24; parth.

prev. publ.—none

results—Both collections gave essentially the same results. Males were not observed at the collection site and the cytological picture further demonstrated parthenogenesis.



Figs. 300–304. *Poliaspoides formosana.* Fig. 300. Oögenesis; 8 univalents at diakinesis and nucleolus. Fig. 301. Mitosis in egg sheath cell. Fig. 302. Mitosis in embryo. Figs. 303–304. Mitosis in polyploid sector (see text for further explanation).

Eight chromosomes were observed in the egg sheath cells and all embryos proved to have the same number (figs. 301–302). Oögenesis was essentially mitotic with 8 univalents (fig. 300). In the collection from Mauritius, the polyploid sectors typically had 24 chromosomes; one such figure had an extra chromosome for a total of 25. A hexaploid level in this species could readily have been achieved by the fusion of 2 cleavage nuclei with a polar body. In the collection from Kenya, the polyploid sector had the tetraploid number usually found in species with "mitotic" parthenogenesis. Whether or not this difference is consistent or otherwise of significance is not known (figs. 303–304).

Aspidiotini

Presumably the most advanced of the tribes (Brown and McKenzie, 1962), the Aspidiotini are noteworthy for their monotonous adherence to the basic chromosome number of 4, in marked contrast to the Diaspidini.

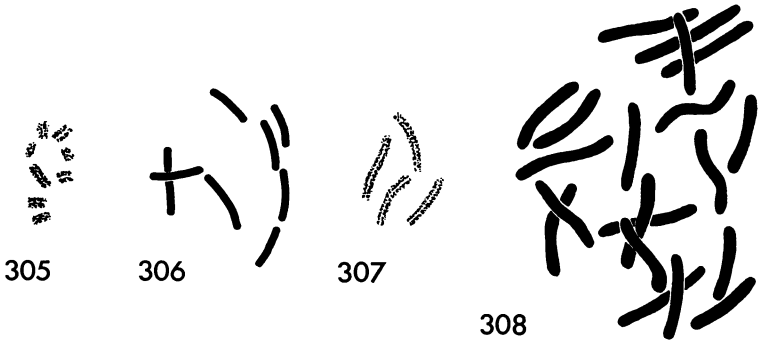
Abgrallaspis (=*Hemiberlesia*) *cyanophylli* (Signoret)

tax. Ferris SII-237; *c.* Nucifora; *i.* Lupo; Catania, Sicily; Aug., 1959; *host, Opuntia* sp.

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—The division figures in this species showed the complements quite clearly; these were typical of the family with nothing exceptional about them (figs. 305–308).



Figs. 305–308. *Abgrallaspis cyanophylli.* Fig. 305. Mitosis in egg sheath cell. Fig. 306. Mitosis in female embryo. Fig. 307. Mitosis in male embryo. Fig. 308. Mitosis in pentaploid sector.

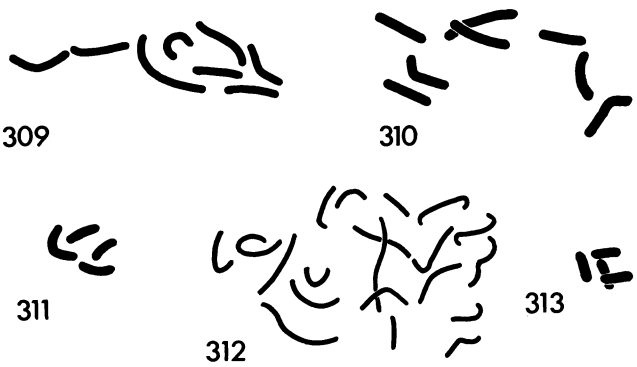
Abgrallaspis flavida De Lotto

tax. De Lotto, 1957; *c.* & *i.* De Lotto; Nairobi, Kenya; Sept., 1958; *host, Elaeodendron* sp.

F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—This species proved similar to its congener in chromosomal characteristics. The clear cytology enabled the chromosomal formula to be completed (figs. 309–313).



Figs. 309–313. *Abgrallaspis flavida.* Fig. 309. Mitosis in egg sheath cell. Fig. 310. Mitosis in female embryo. Fig. 311. Mitosis in male embryo. Fig. 312. Mitosis in polyploid sector. Fig. 313. Mitosis in young male.

Figs. 314–317. *Acutaspis perseae.* Fig. 314. Mitosis in egg sheath cell. Fig. 315. Mitosis in female embryo. Fig. 316. Mitosis in male embryo. Fig. 317. Mitosis in polyploid sector (5n).

Acutaspis perseae (Comstock)

tax. Ferris SIII-332; *c.* Brown and Becker; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host,* undet. tree.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Clear division figures (figs. 314–317) enabled the ready demonstration of a typical complement and typical behavior.

Aonidia lauri (Bouché)

tax. Ferris SII-176; (1) *c.* & *i.* Benassy; Antibes, France; June, 1959 et seq.; *host, Laurus nobilis;* (2) *c.* & *i.* Brown; Daphni, Greece; July, 1959; *host, Laurus nobilis.*

F 8 M 4+4 E 8, 4+4 P ca. 20; sex.; Comstockiella

prev. publ.—The chromosomal conditions at spermatogenesis have been quite recently described (Brown, 1963), and further observations will not be offered at this time.

results—Chromosomal conditions in the embryos proved to be the same in both collections.

Aonidia shastae (Coleman)

tax. Ferris SII-177; *c.* Brown; *i.* McKenzie; near Chiricahua National Monument, Arizona; July, 1958; *host, Juniperus* sp.

F 8 M 4 E 8, 4 P —; sex.; diaspidid

prev. publ.—The normal diploid complement and another showing fragmentation have already been illustrated (Brown, 1960*a*).

results—This species is of particular interest because its congener, *Aonidia lauri*, has a Comstockiella system. The significance of this relationship will be considered in the Discussion. The chromosomes proved typical at all stages available for study (figs. 318–320).

Figs. 318–320. *Aonidia shastae.* Fig. 318. Mitosis in female embryo. Fig. 319. Mitosis in male embryo. Fig. 320. Mitosis in young male.

Aonidiella andersoni (de Charmoy)

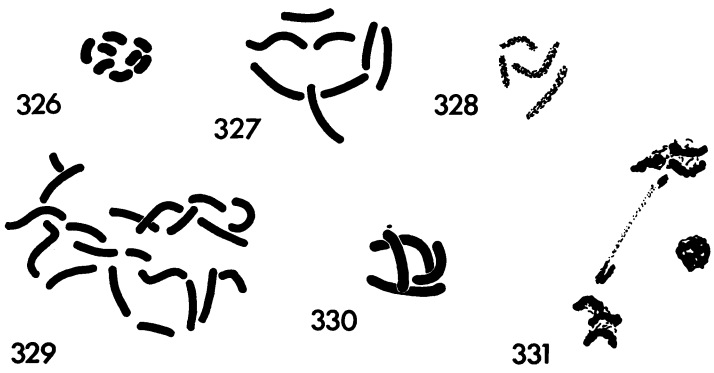
tax. McKenzie, 1938, 1939; Balachowsky, 1953*b*; *c.* Graham; *i.* De Lotto; Kitui, Kenya; June, 1958; *host, Ricinus communis.*

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—The diploid complement of this species, as well as examples of chromosome erosion, has been published under the name *Aonidiella simplex* (Charm.) (Brown, 1960*a*). Balachowsky (1953*b*) has determined the synonomy for this species, which had previously been illustrated by McKenzie (1939).

results—Opportunity will be taken at this juncture to illustrate the normal chromosome picture of *Aonidiella andersoni.* The usual diaspidid picture was observed at the various stages examined (figs. 321–325).

Figs. 321–325. *Aonidiella andersoni.* Fig. 321. Mitosis in egg sheath cell. Fig. 322. Mitosis in female embryo. Fig. 323. Mitosis in male embryo. Fig. 324. Mitosis in polyploid sector. Fig. 325. Mitosis in soma of young male.



Figs. 326–331. *Aonidiella aurantii.* Fig. 326. Mitosis in egg sheath cell. Fig. 327. Mitosis in female embryo. Fig. 328. Mitosis in male embryo. Fig. 329. Mitosis in polyploid sector. Fig. 330. Mitosis in young male. Fig. 331. Chromosome elimination, with chromosome bridging in young male embryo.

**Aonidiella aurantii* (Maskell)

tax. Ferris SII-179; *c.* & *i.* DeBach; Riverside, California; Aug., 1957; *host,* laboratory culture on Irish potato.

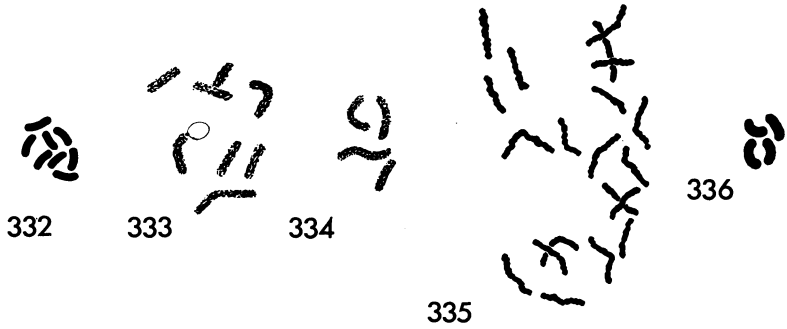
F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—A chromosome number of 8 was reported by Dickson (1941) from counts in embryos of unknown sex, made on his material by Prof. Franz Schrader.

results—This species proved to be typical, with haploid males and diploid females (figs. 326–330). An interesting case of a chromosome bridge in an elimination figure was observed in one embryo (fig. 331). One chromosome had apparently failed to divide properly and was stretched out between the telophase groups; the break in the bridge near one side may have been caused by squashing.

Aonidiella citrina (Coquillett)

tax. Ferris SII-179; *c.* & *i.* DeBach; Riverside, California; Aug., 1957; *host,* laboratory culture on squash.



Figs. 332–336. *Aonidiella citrina.* Fig. 332. Mitosis in egg sheath cell. Fig. 333. Mitosis in female embryo. Fig. 334. Mitosis in male embryo. Fig. 335. Mitosis in pentaploid sector. Fig. 336. Mitosis in young male.

* See last paragraph in Introductory Notes on page 194.

F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—According to Ferris (*ibid.*, who in turn cites McKenzie), this species is very much like *Aonidiella aurantii*, and the two can be separated only by careful determination of delicate sclerotizations. Chromosome complements and behavior have offered nothing of significance here; the complement of *Aonidiella citrina*, like that of *A. aurantii*, proved quite typical (figs. 332–336).

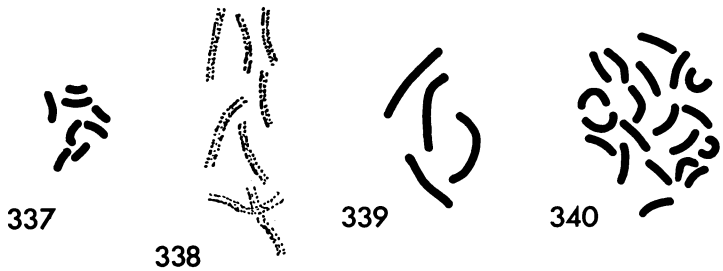
Aspidaspis arctostaphyli (Cockerell and Robbins)

tax. Ferris SII-182; *c.* & *i.* Dickson; Cajon Summit, San Bernardino Co., California; Aug., 1957; *host, Arctostaphylos.*

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results.—The chromosomes in the various tissues studied again proved typical of the family (figs. 337–340).



Figs. 337–340. *Aspidaspis arctostaphyli.* Fig. 337. Mitosis in egg sheath cell. Fig. 338. Mitosis in female embryo. Fig. 339. Mitosis in male embryo. Fig. 340. Mitosis in polyploid sector.

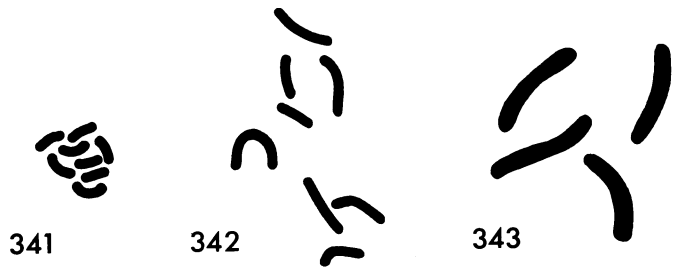
Aspidaspis densiflorae (Bremner)

tax. Ferris SII-183; *c.* Hawthorne; *i.* Wilkey; Fairplay, El Dorado Co., California; May, 1960; *host, Quercus* sp.

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—Like its congener, *Aspidaspis densiflorae* also proved to have typical chromosomal cytology (figs. 341–343).



Figs. 341–343. *Aspidaspis densiflorae.* Fig. 341. Mitosis in egg sheath cell. Fig. 342. Mitosis in female embryo. Fig. 343. Mitosis in male embryo.

Figs. 344–346. *Aspidiella hartii.* Fig. 344. Mitosis in female embryo. Fig. 345. Mitosis in male embryo. Fig. 346. Mitosis in pentaploid sector.

Aspidiella hartii (Cockerell)

tax. Ferris SII-188; *c.* & *i.* Bennett; St. Augustine, Trinidad; Sept., 1956; *host,* yam.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Chromosome numbers and system were recorded by Brown and Bennett (1957).

results—Illustrations are offered here to supplement the previous report (figs. 344–346).

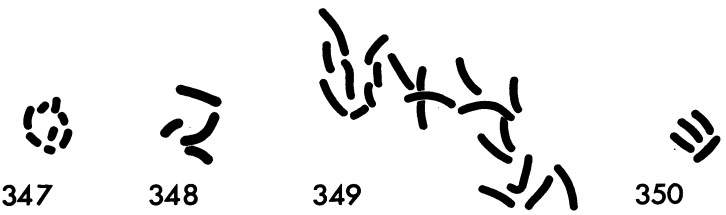
Aspidiella sacchari (Cockerell)

tax. Ferris SII-189; *c.* Brown; *i.* Breese; St. Augustine, Trinidad; April, 1957; *host, Setaria* sp.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The quite clear chromosomal cytology enabled the chromosome formula to be completed; the drawings (figs. 347–350) do not include a complement from the female embryo.



Figs. 347–350. *Aspidiella sacchari.* Fig. 347. Mitosis in egg sheath cell. Fig. 348. Mitosis in male embryo. Fig. 349. Mitosis in polyploid sector. Fig. 350. Mitosis in young male.

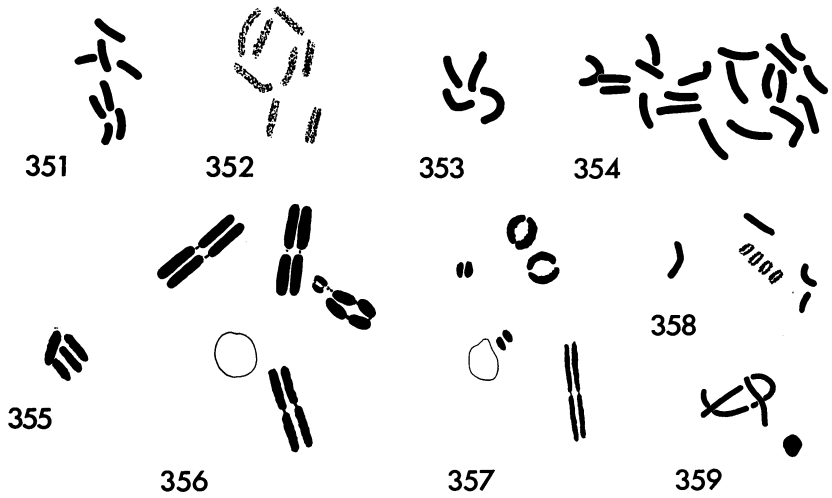
Aspidiotus cryptomeriae Kuwana

tax. Takagi, 1957; *c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Taxus cuspidata* Siebold et Zuccarini.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Both the normal and aberrant chromosomal cytology of this species have been described in considerable detail (Brown, 1960*b*).

results—No add.



Figs. 351–359. *Aspidiotus destructor*. Fig. 351. Mitosis in egg sheath cell. Fig. 352. Mitosis in female embryo. Fig. 353. Mitosis in male embryo. Fig. 354. Mitosis in polyploid sector. Fig. 355. Mitosis in young male. Fig. 356. Oögenesis, fragment univalent attached to one bivalent, nucleolus present. Fig. 357. Oögenesis; one pair of homologues has failed to form a bivalent; nucleolus present. Figs. 358–359. Elimination figures in young male embryos. Fig. 358. Set to be eliminated grouped together, individual chromosomes divided. Fig. 359. Eliminated set forming pycnotic residue.

Aspidiotus destructor Signoret

tax. Ferris SII-191; (1) *c.* Brown; *i.* Breese; St. Augustine, Trinidad; Sept., 1956; *host,* poinsettia; (2) *c.* Maharaj; *i.* Bennett; St. Augustine, Trinidad; May, 1958; *host,* coconut; (3) *c.* Nur; *i.* Wilkey; Palisadoes, Kingston, Jamaica; June, 1962; *host, Terminalia catappa.*

F 8 M 4 E 8,4 P 20; sex.; diaspidid

prev. publ.—Chromosome numbers and system were reported by Brown and Bennett (1957). A comparison of the cytology of *Aspidiotus destructor* with that of *A. simulans* was made briefly by Brown and De Lotto (1959), but no details were noted. A case of simple fragmentation has also been observed by Brown (1960*a*).

results—The various collections showed similar results, and the observations will therefore be combined. Divisions in males, females and embryos revealed quite usual complements (figs. 351–355). Several clear examples of oögenesis were found; in one of these a small fragment, obviously bipartite, was attached to a bivalent by a delicate strand (fig. 356); in another, bivalent formation had failed for one pair, which was represented by two univalents (fig. 357). Rather typical chromosome elimination figures were noted in some instances (figs. 358–359, plate II A–C).

**Aspidiotus hederae* (Vallot)

tax. Ferris SII-192; UNISEXUAL: (1) *c.* & *i.* DeBach; Riverside, California; Aug., 1957; *host,* laboratory cultures on potato; (2) *c.* & *i.* Brown; Ischia, Napoli, Italy; Aug., 1959; *host,* unident. BISEXUAL: (1) *c.* & *i.* Brown; Auburn, California; Aug., 1958; *host, Arctostaphylos* sp.; (2) *c.* & *i.* Nur; 'Ein Harod, Israel; Sept.,

* See last paragraph in Introductory Notes on page 194.

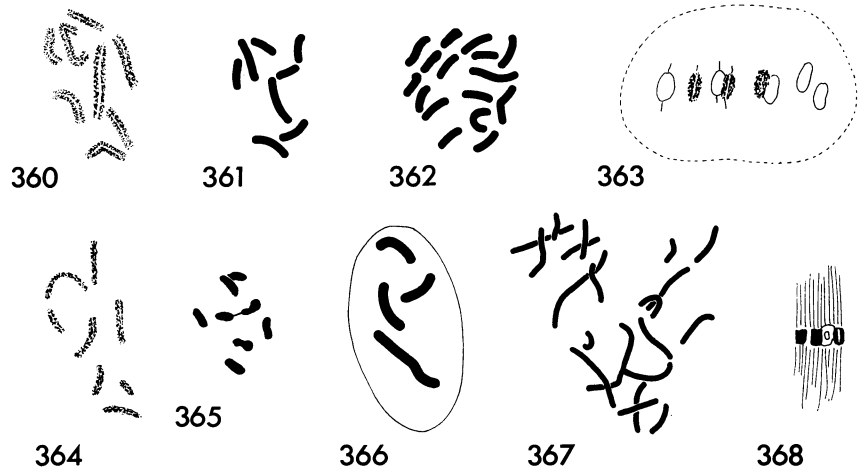
1958; *host, Dodonaea* sp.; (3) *c.* Brown and Becker; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host,* undet. tree.

UNISEXUAL: F 8 M— E 8 P 16; parth.

BISEXUAL: F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—The unisexual form of *Aspidiotus hederae* was the first armored scale to be studied cytologically, by Schrader (1929), who reported the mitotic type of parthenogenesis.

results—Efforts have been made to distinguish the unisexual from the bisexual strain of this species, but no morphological criteria have proved successful. The chromosome complements of both strains are typical of the family and therefore similar to each other. In the unisexual form, all the embryos had the same chromosome number, 8, found in the maternal tissue; the polyploid sectors had 16 chromosomes, and 8 univalents were present at oögenesis (figs. 360–363). In the bisexual form, haploid as well as diploid embryos were present; the polyploid division figures revealed a pentaploid number of 20 rather than a tetraploid number of 16 chromosomes, and 4 bivalents were present in oögenesis (figs. 364–368). In addition, sperm were to be found in the ovaries of the females of the bisexual strain. These various cytological differences have permitted an easy and rapid determination of the strain in the collections made to date and should be generally useful for this purpose.



Figs. 360–368. *Aspidiotus hederae.* Figs. 360–363. UNISEXUAL: Fig. 360. Mitosis in egg sheath cell. Fig. 361. Mitosis in female embryo. Fig. 362. Mitosis in polyploid sector. Fig. 363. Oögenesis, metaphase with 8 univalents. Figs. 364–368. BISEXUAL: Fig. 364. Mitosis in egg sheath cell. Fig. 365. Mitosis in female embryo. Fig. 366. Mitosis in male embryo. Fig. 367. Mitosis in polyploid sector. Fig. 368. Oögenesis, metaphase with 4 bivalents.

Aspidiotus hedericola Lindinger

tax. Balach. IV-285; *c.* Nucifora; *i.* Lupo; Catania, Sicily; Sept., 1959; *host, Hedera.*

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—The chromosomes again showed the family characteristics in the haploid and diploid embryos, diploid maternal tissue and pentaploid sectors in the embryos (figs. 369–372).

Figs. 369–372. *Aspidiotus hedericola.* Fig. 369. Mitosis in egg sheath cell. Fig. 370. Mitosis in female embryo. Fig. 371. Mitosis in male embryo. Fig. 372. Mitosis in polyploid sector; most of the chromosomes divided.

Aspidiotus simulans De Lotto

tax. De Lotto, 1957; *c.* & *i.* De Lotto; Nairobi, Kenya; Feb., 1958 et seq.; *host,* various.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—This species first attracted attention because it is to date the only coccid known in which individual females have been observed, in one of several populations, to produce either all male or all female offspring. The cytology of the species has therefore been carefully examined (Brown and De Lotto, 1959); chromosome number, morphology and behavior proved to be typical except for chromosome elimination in the development of the male (see below). In addition, *Aspidiotus simulans* has also provided some extremely clear examples of chromosome erosion (Brown, 1960*a*).

results—Descriptions and illustrations of the cytology at the various stages in the life cycle have been reported already by Brown and De Lotto (1959). The present review, however, provides an opportunity for photographic illustration of the elimination process. In general, the chromosomes which were being eliminated showed less than typical condensation and pycnosis and more activity on the spindle. Plate III illustrates some of the variation in the elimination process observed in this species.

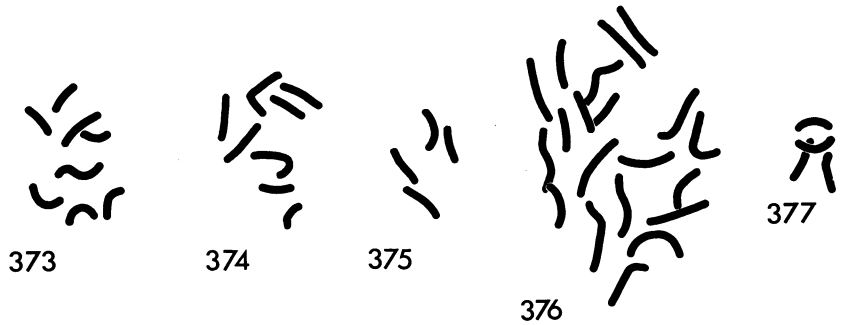
Chrysomphalus bifasciculatus Ferris

tax. Ferris SII-199; *c.* & *i.* McKenzie; Sacramento, California, Sept., 1957; *host, Aspidistra.*

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Ample material and clear cytology demonstrated a typical condition in each of the tissues studied (figs. 373–377).



Figs. 373–377. *Chrysomphalus bifasciculatus.* Fig. 373. Mitosis in egg sheath cell. Fig. 374. Mitosis in female embryo. Fig. 375. Mitosis in male embryo. Fig. 376. Mitosis in polyploid sector. Fig. 377. Mitosis in young male.

Figs. 378–380. *Chrysomphalus dictyospermi.* Fig. 378. Mitosis in egg sheath cell. Fig. 379. Mitosis in embryo. Fig. 380. Mitosis in polyploid sector.

Chrysomphalus dictyospermi (Morgan)

tax. Ferris SII-200; *c.* Brown and Nelson-Rees; *i.* Brown; Puerto Vallarta, Jalisco, Mexico; Dec., 1957; *host,* coconut.

F 8 M— E 8,— P 16; parth.

prev. publ.—none

results—The cytology of this species was that of a typical parthenogenetic armored scale. Only one class of embryos was observed with chromosomes identical to those of maternal tissue, and only the tetraploid number was to be found in the polyploid sector (figs. 378–380). In addition, no sperm were seen in the ovaries and no males at the collection site. Ferris (*ibid.*) reported males for this species, which probably represents another example of a species with both unisexual and bisexual forms.

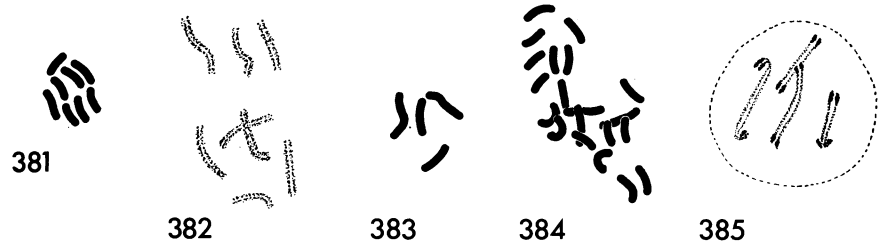
Chrysomphalus ficus Ashmead

tax. Ferris SII-201; (1) *c.* & *i.* Breese; St. Augustine, Trinidad; Oct., 1956; *host,* citrus; (2) *c.* Brown and Nelson-Rees; *i.* McKenzie; Guadalajara, Jalisco, Mexico; Dec., 1957; *host,* unident. tree.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—Brown and Bennett (1957) recorded the chromosome number.

results—Both collections showed a similar and quite typical cytology (figs. 381–385); in addition, elimination figures were observed in this species, and these also were typical.



Figs. 381–385. *Chrysomphalus ficus.* Fig. 381. Mitosis in egg sheath cell. Fig. 382. Mitosis in female embryo. Fig. 383. Mitosis in male embryo. Fig. 384. Mitosis in polyploid sector. Fig. 385. Mitosis in young male.

Chrysomphalus pinnulifer (Maskell)

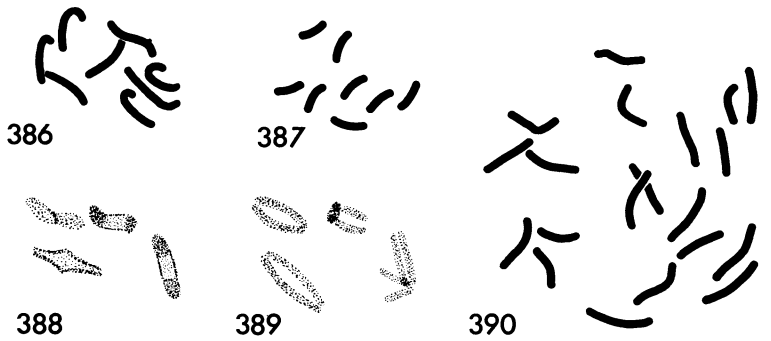
tax. Green, 1923; *c.* & *i.* De Lotto; Nairobi, Kenya; Feb., 1958; *host, Canna* sp.

F 8 M— E 8 P 20; parth.

prev. publ.—none

results—This species proved to be an example of meiotic parthenogenesis. Eight chromosomes were present in the maternal tissue and embryos (figs. 386–387, plate IV A–B), and 4 bivalents at oögenesis (figs. 388–389, plate IV E). The division figures in the polyploid sector were pentaploid with 20 chromosomes (fig. 390). The restoration of diploidy—in other words, the origin of the zygote substitute—was not determined. However, the numerical relationships could be accounted for if the egg nucleus divided to give two products which then fused to provide a diploid zygote substitute. The two polar bodies would thus be uninvolved in this process and remain intact to fuse with a cleavage nucleus to achieve the observed pentaploid level.

Two interesting anomalies were also observed in embryonic divisions. In one instance one chromosome was lagging (plate IV C); in another, the spindle was tripolar (plate IV D).



Figs. 386–390. *Chrysomphalus pinnulifer.* Fig. 386. Mitosis in egg sheath cell. Fig. 387. Mitosis in female embryo. Figs. 388–389. Oögenesis, prometaphase with 4 bivalents. Fig. 390. Mitosis in polyploid sector.

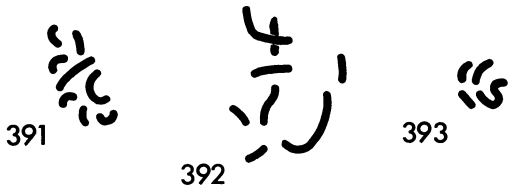
Clavaspis coursetiae (Marlatt)

tax. Ferris SII-203; *c.* Brown; *i.* McKenzie; Tucson, Arizona; June, 1958; *host,* box elder.

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—Cytology was typical as far as it could be followed in the limited sample (figs. 391–393).



Figs. 391–393. *Clavaspis coursetiae.* Fig. 391. Mitosis in egg sheath cell. Fig. 392. Mitosis in female embryo. Fig. 393. Mitosis in male embryo.

Clavaspis texana Ferris

tax. Ferris SII-210; *c.* Brown and Nelson-Rees; *i.* Wilkey; Monterrey, Nuevo León, Mexico; June, 1960; *host,* undet. tree.

F—M—E8, 4 P—; sex.; diaspidid

prev. publ.—none

results—As was the case with its congener, this species also showed the usual picture as far as could be determined from limited material (figs. 394–395).

394 395

Figs. 394–395. *Clavaspis texana.* Fig. 394. Mitosis in female embryo. Fig. 395. Mitosis in male embryo.

Comstockiella sabalis (Comstock)

tax. Ferris SII-213; *c.* Hughes; *i.* Simmonds; Bermuda; spring, 1957; *host,* Sabal palm.

396 397

Figs. 396–397. *Diaspidiotus aesculi.* Fig. 396. Mitosis in female embryo. Fig. 397. Mitosis in male embryo.

F 10 M 5 + 5 E 10, 5 + 5 P —; sex.; Comstockiella

prev. publ.—This species was the first in which the Comstockiella system was observed and therefore the source of its name; the system has been described once in an abstract (Brown, 1957) and more recently in greater detail (Brown, 1963).

results—No add.

Diaspidiotus aesculi (Johnson)

tax. Ferris SII-215; *c.* Brown; *i.* McKenzie; Southwest Research Station, Portal, Arizona; June, 1958; *host,* maple.

F 8 M 4 E —2 P 20; sex.; diaspidid

prev. publ.—An example of fragmentation in a pentaploid cell was reported by Brown (1960*a*).

results—Only young males and females were available in the population sampled; these gave the results expected in a diaspidid system (figs. 396–397).

Furcaspis biformis (Cockerell)

tax. Ferris SII-231; *c.* Nur; *i.* Wilkey; Duncan, Jamaica; Aug., 1962; *host, Pedilanthus latifolius.*

F 6 M 3 + 3 E 6, 3 + 3 P 21, 42; sex.; Comstockiella

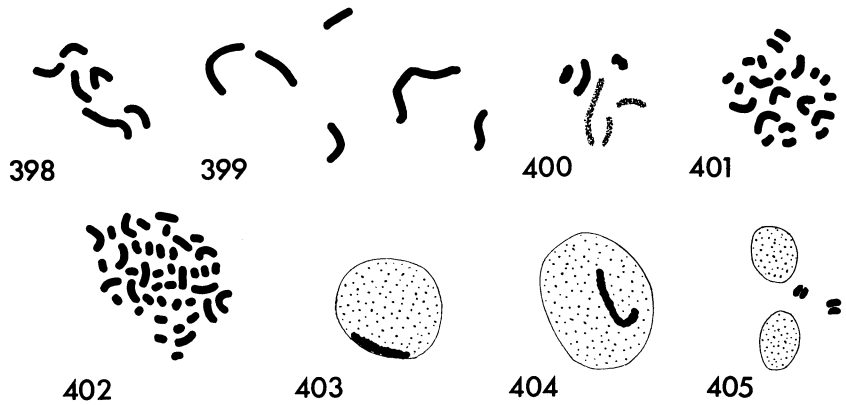
prev. publ.—none

results—According to Ferris (*ibid.*), this species is to be found only on orchids. The present collection, therefore, represents a violation of host specificity.

The species proved to be quite remarkable cytologically in the combination of the Comstockiella system, the chromosome number, and the level of polyploidy in the mycetocytes.

The haploid number of the species was 3, with one of the chromosomes considerably longer than the other two. All euchromatic chromosomes were observed in maternal tissue and female embryos (figs. 398–399). In the male embryos, one set of chromosomes showed typical heterochromatization (fig. 400).

Many division figures were observed in the polyploid sectors, and all had rela-



Figs. 398–405. *Furcaspis biformis.* Fig. 398. Mitosis in egg sheath cell. Fig. 399. Mitosis in female embryo. Fig. 400. Mitosis in male embryo. Fig. 401. Mitosis in polyploid sector, 21 chromosomes or 7-ploid. Fig. 402. Mitosis in polyploid sector, 42 chromosomes or 14-ploid. Figs. 403–405. Spermatogenesis. Figs. 403–404. Preprophase with heterochromatic complement reduced to the single long chromosome. Fig. 405. Post-elimination of the D^H chromosome; both residues split.

tively high chromosome numbers. No pentaploid figures were observed. The lowest number was 7-ploid with 21 chromosomes (fig. 401); in these figures the expected 7 long chromosomes were quite obvious. The other number determined with accuracy was the 14-ploid, with 42 chromosomes and again with 14 long chromosomes (fig. 402). The formation of the initial nuclei was not observed, but the numbers may be readily explained on the basis of extra nuclear fusions: the union of 2 cleavage nuclei, instead of one, with the polar bodies would yield a 7-ploid nucleus, and fusion of 2 of 7-ploids would give a 14-ploid. An alternative explanation, that a cycle of endomitosis intervened to produce the 14-ploid from the 7-ploid, seems unlikely, since endomitosis was not observed.

A complement similar to that of the male embryo was observed in the somatic tissue of the older males. Only a few males were in the right stage for the determination of any aspects of spermatogenesis; these few showed evidence only of a Comstockiella system. In preprophase, the heterochromatic elements were reduced to one, and in 2 testes from one animal, this single element was elongate, either appearing as a "cap" at one end of the nucleus (fig. 403) or laterally (fig. 404). Prespermiogenic and spermiogenic stages revealed pycnotic residues, always of uniform size within the testes, and judged from the prespermiogenic example to be about the size expected from elimination of a single chromosome rather than an entire set (fig. 405). Only the Comstockiella system, and without variation in the D chromosome, was thus found in this limited sample.

Furcaspis capensis Green

tax. Brain, 1918; *c.* & *i.* Annecke; Pretoria, Transvaal; Feb., 1958; *host, Aloe* sp.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Microfragmentation was reported by Brown (1960*a*).

results—In striking contrast to its congener, this species was typically diaspidid. The chromosome number was that typical of the family, and haploid males were present after the earliest developmental stages of the embryos (figs. 406–408).

Figs. 406–408. *Furcaspis capensis.* Fig. 406. Mitosis in female embryo. Fig. 407. Mitosis in male embryo. Fig. 408. Mitosis in polyploid sector.

Helaspis mexicana McKenzie

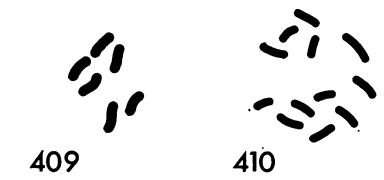
tax. McKenzie, 1963; *c.* Brown and Nelson-Rees; *i.* McKenzie; Hacienda Barron, Mazatlán, Sinaloa, Mexico; Aug., 1960; *host,* undet. tree; locally called "zorillo."

F— M— E 12, 6 P—; sex.; diaspidid

prev. publ.—none

results—Only limited material was available, so that it was not possible to determine more than the chromosome numbers of the male and female embryos (figs. 409–410). The diploid number of 12 found here is the highest yet recorded for the Aspidiotini and, except for the anomalous *Comstockiella sabalis,* is the only departure above the basic number of 8.

The material did not permit accurate determination of chromosome lengths, but at any rate there was no evidence of recent fragmentation to establish the higher number. In fact, the recognition of this form as the type of a new genus is indicative of a long-standing separation from any other known species; change in chromosome number could, as far as is known, have occurred at any time, recent or long past, in its evolutionary history.



Figs. 409–410. *Helaspis mexicana.* Fig. 409. Mitosis in male embryo. Fig. 410. Mitosis in female embryo.

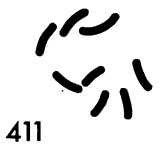


Fig. 411. *Hemiberlesia cupressi.* Mitosis in embryo.

Hemiberlesia

The present report has not been consistent in the treatment of this genus, which has been more narrowly defined by Balachowsky (1948), with *Hemiberlesia lataniae* and *H. rapax* retained in it but many of the others reassigned to his new genus, *Abgrallaspis.* The chromosomes of *H. cyanophylli* (Ferris SII-237) have been described under *Abgrallaspis cyanophylli* in the present report, while *palmae* has been retained in *Hemiberlesia.* Balachowsky did not include *cupressi, howardi,* or *quercicola* under either genus, and no attempt will be made here to suggest where these might be housed if evicted from *Hemiberlesia.*

Hemiberlesia cupressi (Cockerell)

tax. Ferris SII-236; *c.* Brown and Nelson-Rees; *i.* McKenzie; Quezaltenango, Guatemala; July, 1960; *host, Cupressus* sp.

F 8 M— E 8 P—; parth.

prev. publ.—none

results—Males have been reported for this species (Ferris, *ibid.*), but the population sampled proved to be parthenogenetic. All embryos were diploid and thus like the maternal tissue (fig. 411); there were no haploid embryos nor any with heterochromatization; and, finally, there were no sperm in the ovaries.

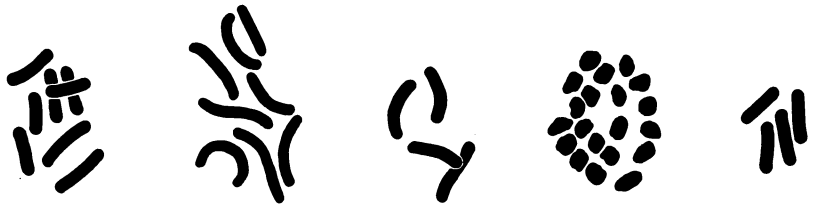
Hemiberlesia howardi (Cockerell)

tax. Ferris SII-240; *c.* Brown and Nelson-Rees; *i.* Wilkey and McKenzie; Monterrey, Nuevo León, Mexico; June, 1960; *host,* olive.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Ample material enabled the completion of the chromosome formula for this species, again a typical diaspidid (figs. 412–416).



Figs. 412–416. *Hemiberlesia howardi.* Fig. 412. Mitosis in egg sheath cell. Fig. 413. Mitosis in female embryo. Fig. 414. Mitosis in male embryo. Fig. 415. Mitosis in polyploid sector. Fig. 416. Mitosis in young male.

Hemiberlesia lataniae (Signoret)

tax. Ferris SII-241; UNISEXUAL: (1) *c.* & *i.* Finney; lab culture, Biol. Control, Albany, California; July, 1957; *host,* Irish potato; (2) *c.* Newcombe; *i.* McKenzie; Guadalupe Island, Baja California, Mexico; Dec., 1957; *host, Photinia* sp.; (3) *c.* Brown and Nelson-Rees; *i.* McKenzie; Puerto Vallarta, Jalisco, Mexico; Dec., 1957; *host,* palm; (4) *c.* & *i.* Brown; La Paz, Baja California, Mexico; Oct., 1958; *host,* leguminous shrub; (5) *c.* & *i.* Beardsley; Oahu, Hawaii; April, 1960; *host,* sandalwood; (6) *c.* Brown and Nelson-Rees; *i.* Brown; Veracruz, Ver., Mexico; June, 1960; *host,* palo mulatto; (7) *c.* Brown; *i.* De Lotto; Entebbe Botanical Garden, Entebbe, Uganda; July, 1961; *host, Acacia* sp.; (8) *c.* Nur; *i.* Wilkey; Kingston, Jamaica; July, 1962; *host, Mimosa pudica;* BISEXUAL: (1) *c.* Brown and Nelson-Rees; *i.* Wilkey and McKenzie; Mexico D. F., Mexico; June, 1960; *host,* fagaceous tree.

UNISEXUAL: F 8 M— E 8 P 16; parth.

BISEXUAL: F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—Cases of uncomplicated fragmentation have been reported by Brown (1960*a*) from the first two collections of the unisexual strain.

results—This species, according to Ferris (*loc. cit.*), has been "... recorded from an endless series of hosts in all tropical and subtropical parts of the world.... It is the commonest species in the collections at hand from Texas and Mexico." Ferris also recognized its parthenogenetic nature, no males having been reported. Our list of collections again indicates the ubiquity of this species which, in all but one case, proved to be typically parthenogenetic, with the diploid number present in all embryos, maternal tissues, and as univalents at diakinesis (figs. 417–418, plate V); the tetraploid number was to be found in the polyploid sector (fig. 419).

One collection, from Mexico City, was bisexual. The tentative identification, made in the field at the same time the chromosomes were examined, was *Diaspidiotus ancylus* (Putnam) (see Ferris SII-216). Because of the ubiquity of *Hemiberlesia lataniae,* there is always the chance that individuals of this species may be found as contaminants in other collections. However, *D. ancylus* and *H. lataniae* (Signoret) are sufficiently alike that we may have mistaken the latter for the former in our hasty field identification, especially since we knew that *H. lataniae* was "supposed" to be parthenogenetic. (It should also be noted that our field taxonomy was done quite casually in most instances, since specimens were almost always saved for accurate determinations by specialists.) The cytology of the Mexico City collection proved to be typically that of a sexual diaspidid, and the collection proved adequate for completing the chromosome formula (figs. 420–424). Undoubtedly, further work should be done in the Mexico City area before a final conclusion is reached that a bisexual race of *H. lataniae* exists.

Figs. 417–424. *Hemiberlesia lataniae.* Figs. 417–419. UNISEXUAL: Fig. 417. Mitosis in egg sheath cell. Fig. 418. Mitosis in female embryo. Fig. 419. Mitosis in polyploid sector (tetraploid). Figs. 420–424. BISEXUAL: Fig. 420. Mitosis in egg sheath cell. Fig. 421. Mitosis in female embryo. Fig. 422. Mitosis in male embryo. Fig. 423. Mitosis in polyploid sector (pentaploid). Fig. 424. Mitosis in somatic tissue of young male.

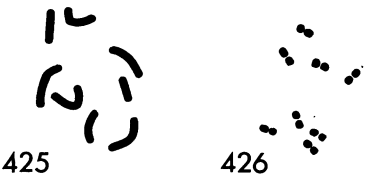
Hemiberlesia palmae (Cockerell)

tax. Ferris SII-242; *c.* Brown and Becker; *i.* Wilkey; São Paulo, Brazil; July, 1962; *host,* undet. tree.

F— M— E 8 P—; parth.

prev. publ.—none

results—The cytology (by Nur) confirmed Ferris' (*ibid.*) report that the male was unknown; only diploid embryos were found and 8 univalents were present during prophase of the first oögenic division (figs. 425–426).



Figs. 425–426. *Hemiberlesia palmae.* Fig. 425. Mitosis in embryo. Fig. 426. Eight univalents at diakinesis-like stage of oögenesis.

Hemiberlesia quercicola Ferris

tax. Ferris SIII-344; *c.* Brown; *i.* McKenzie; Paradise, Arizona; June, 1958; *host, Quercus arizonica.*

F — M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—Brown (1960*a*), fragmentation in polyploid sector.

results—Although the scale of the male had not been recognized by Ferris (*ibid.*), this species proved, on this subsequent collection, to be sexual. Young males were found, and the cytology was otherwise in agreement with a sexual, diaspidid system (figs. 427–429).

Figs. 427–429. *Hemiberlesia quercicola.* Fig. 427. Mitosis in female embryo. Fig. 428. Mitosis in male embryo. Fig. 429. Mitosis in somatic tissue of young male.

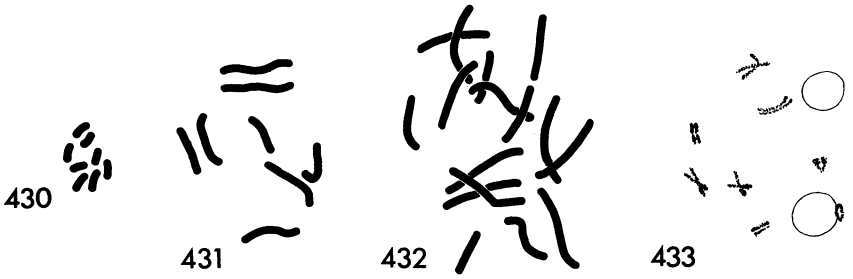
Hemiberlesia rapax (Comstock)

tax. Ferris SII-244; (1) *c.* & *i.* Finney; Gill Tract, Albany, California; July, 1957; *host,* camellia; (2) *c.* & *i.* Bennett; Campus, University of California, Berkeley, California; Nov., 1957; *host,* undet. shrub; (3) *c.* Nucifora; *i.* Lupo; Catania, Sicily; Sept., 1959; *host, Euonymus;* (4) *c.* Brown and Nelson-Rees; *i.* McKenzie; Quezaltenango, Guatemala; July, 1960; *host,* alder; (5) *c.* Brown; *i.* Wilkey; 15 mi. S. of Ensenada, Baja California, Mexico; April, 1963; *host, Ceanothus* sp.

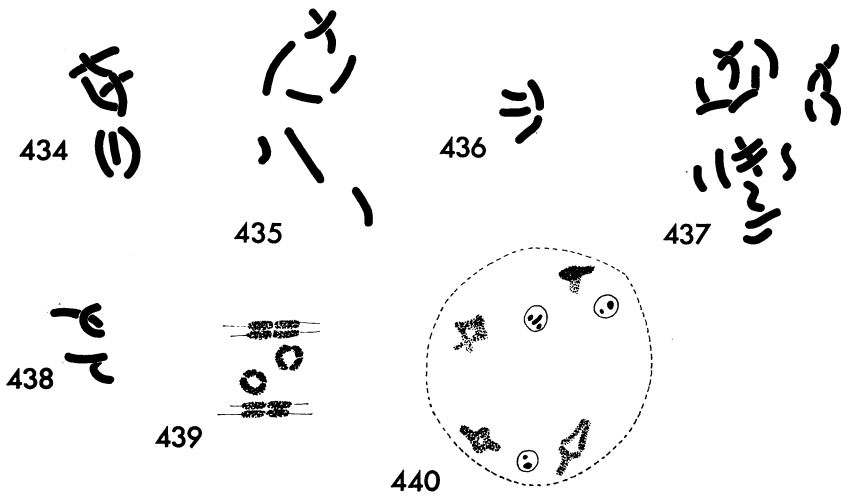
F 8 M — E 8 P 16; parth.

prev. publ.—none

results—Like its congener, *Hemiberlesia lataniae, H. rapax* is also widely distributed and parthenogenetic; and, in fact, the two have been recognized as "twin" species (Ferris, *ibid.*). The cytology of the two is also similar, the chromosome number and behavior of *H. rapax* repeating that of *H. lataniae* (figs. 430–433).



Figs. 430–433. *Hemiberlesia rapax.* Fig. 430. Miotsis in egg sheath cell. Fig. 431. Mitosis in embryo. Fig. 432. Mitosis in polyploid sector. Fig. 433. Diakinesis, oögenesis, 8 univalents and 2 nucleoli.



Figs. 434–440. *Lindingaspis opima.* Fig. 434. Mitosis in egg sheath cell (8 chromosomes, 2 in terminal adhesion). Fig. 435. Mitosis in female embryo. Fig. 436. Mitosis in male embryo. Fig. 437. Mitosis in polyploid sector. Fig. 438. Mitosis in somatic tissue of young male. Fig. 439. Early metaphase of first oögenic division. Fig. 440. Diakineses of oögenesis, 4 bivalents and 3 nucleoli with dense inclusions.

Lindingaspis opima (Silvestri)

tax. McKenzie, 1950; *c.* & *i.* De Lotto; Nairobi, Kenya; Feb., 1958; *host, Acokanthera schimperi.*

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The cytology of this species was quite clear, and excellent examples of several stages were obtained. Typical diploid figures were to be seen in egg sheath cells (fig. 434, plate VI C) and in the female embryos (fig. 435). During elimination, the discarded chromosomes were usually left as a pycnotic clump on the equatorial plate (plate VI E), but sometimes showed marked response to the spindle instead (plate VI F). Following elimination, typical haploid sets were to be found in the male embryos (fig. 436) and later in the young males (fig. 438). The chromosome number in the polyploid sector of the embryos was pentaploid, with 20 chromosomes (fig. 437, plate VI D). Especially clear figures of oögenesis were available for study. One example at mid-diakinesis indicated that two chiasmata may occasionally be present (fig. 440). At this stage, densely pycnotic granules of unknown nature were present in the nucleoli (fig. 440, plate VI A). The bivalents appeared bipartite at late diakinesis (plate VI A) and became quadripartite at metaphase (fig. 439). In the secondary oöcyte, the oöcyte nucleus proper and the first polar body could not be distinguished in the squashes since the squashing process destroyed the orientation; both clearly showed a haploid number of dyads (plate VI B).

Lindingaspis rossi (Maskell)

tax. Ferris SII-246; (1) *c.* & *i.* Brookes; Waite Inst., Adelaide, S. Australia; Dec., 1958; *host, Laurus nobilis;* (2) *c.* Brown; *i.* Wilkey; Lima, Peru; July, 1962; *host, Araucaria angustifolia.*

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

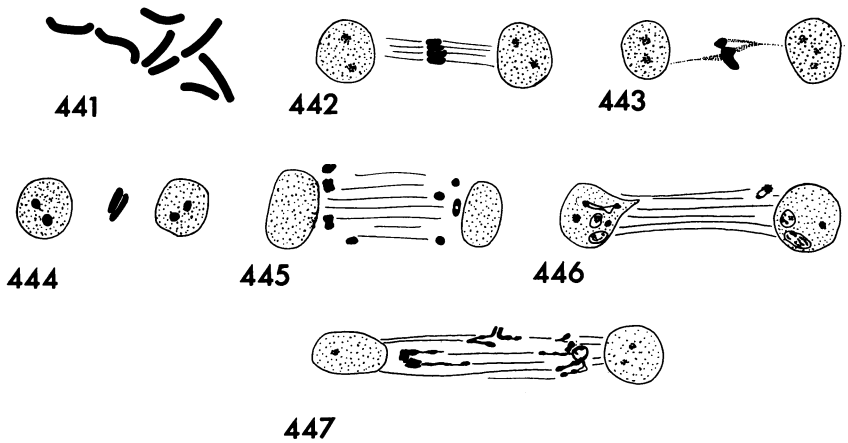
prev. publ.—Brown (1960*a*), fragmentation in polyploid complement and microfragment in haploid figure.

results—The diaspidid system of the armored scale insects has unquestionably been derived from one in which heterochromatization occurs in one set in the males, yet very little tendency toward heterochromatization has been observed in the diaspidid system, and that relatively weak and immediately prior to elimination. The elimination process in *Lindingaspis rossi* is therefore of special interest.

The maternal tissue and male and female embryos showed the expected diploid and haploid sets (fig. 441, plate VII A, B, and C). Twenty chromosomes occurred in the polyploid sector (plate VII D), which must have been formed from the polar bodies in the usual fashion; but the mycetocytes were apparently derived from diploid nuclei, which then underwent endomitosis (plate VII E). There was thus otherwise nothing particularly noteworthy about the general cytology of *Lindingaspis rossi*. These aspects were the same in both collections, and elimination was studied only in the first.

Chromosome elimination was first recognized as the mechanism responsible for the production of male haploidy in the diaspidid system by Brown and Bennett (1957). At that time the process was described as involving the clumping of the chromosomes to be eliminated into one or two chromatic blobs. These were then ejected laterally from the anaphase division spindle, and remained free in the cytoplasm.

The *Lindingaspis rossi* material provided additional information and a few exceptions to previous observations of chromosome elimination. In this case elimination started earlier than usual in embryonic development and was incomplete, the chromosomes destined for eventual elimination frequently becoming included in one of the daughter nuclei, where they became heterochromatic. In addition to clumping and lagging on the metaphase plate (fig. 442), some chromatin would sometimes stretch out toward the daughter nuclei (fig. 443). In other instances,



Figs. 441–447. *Lindingaspis rossi*. Fig. 441. Mitosis in egg sheath cell. Figs. 442–447. Elimination in young male embryos. Fig. 442. Elimination chromosomes clumped on equatorial plate. Fig. 443. Chromatin bridging from eliminated group. Fig. 444. Two of the 4 elimination chromosomes eliminated, 2 as heterochromatic entities in daughter nuclei. Fig. 445. All elimination chromosomes divided and scattered near daughter nuclei. Fig. 446. Elimination chromosomes forming pycnotic vesicles in and near the daughter nuclei. Fig. 447. Elimination with considerable activity on the spindle.

and in the same embryos, the elimination chromosomes would remain partially or completely as discrete entities (figs. 444–445); and these, being included in the daughter nuclei, would remain completely pycnotic or form obviously denser vesiculi (fig. 446). In addition, the type of lagging pictured for *L. opima,* in which the chromosomes showed some activity on the spindle and were stretched between the two daughter nuclei, was not uncommon (fig. 447; compare with plate VI F).

A series of photographs (plate VII F–I) illustrates the sequence of changes during early prophase in the nuclei with the heterochromatic elimination chromosomes. In the resting nuclei these form a dense clump on one side (plate VII F), as expected if they were lagging behind the remainder of the chromosomes in the preceding division, and this orientation is maintained during prophase (plate VII G–I). It is impossible to compare exactly the various prophase changes in euchromatin and heterochromatin, because the state of the latter undoubtedly varied considerably from cell to cell. The heterochromatin is strikingly different in earlier stages (plate VII G–H), but at late midprophase the elimination set is differentiated only by its more snarled aspect, presumably from its failure to uncoil during interkinesis.

Melanaspis inopinatus (Leonardi)

tax. Balach. VI-580; *c.* Nucifora; *i.* Lupo; Catania, Sicily; Sept, 1959; *host, Pistacia vera.*

F 8 M— E— P—; sex.

prev. publ.—none

results—The fact that this species was sexual was evident from the abundant sperm in the ovary; the species presumably hibernated as the young, mated female, with embryonic development commencing the following spring. Since only maternal tissue was available, the diploid chromosome number (fig. 448), but not the system, could be determined.

448

Fig. 448. *Melanaspis inopinatus.* Mitosis in egg sheath cell.

Melanaspis lilacina (Cockerell)

tax. Ferris SIII-357; *c.* Brown; *i.* McKenzie; Chiricahua National Monument, Arizona; July, 1958; *host, Quercus emoryi.*

F— M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—The limitations of the collections restricted the chromosomal observations to embryos, where the picture conformed to the diaspidid pattern (figs. 449–450).

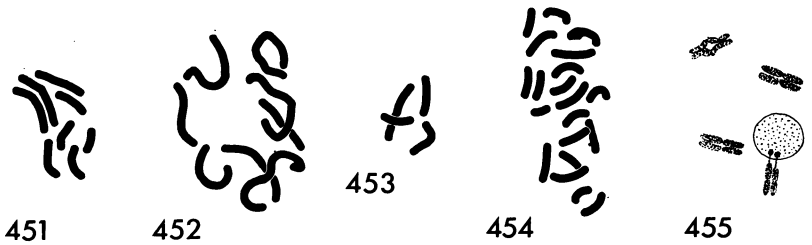
449 450

Figs. 449–450. *Melanaspis lilacina.* Fig. 449. Mitosis in female embryo. Fig. 450. Mitosis in male embryo.

Melanaspis paulista (Hempel)

tax. Hempel, 1900; McKenzie, 1939; *c.* & *i.* Pinto da Fonseca; São Paulo, Brazil; March, 1958 and July, 1962; *host,* undet.

F 8 M— E 8, 4 P 20; sex.; diaspidid



Figs. 451–455. *Melanaspis paulista.* Fig. 451. Mitosis in somatic tissue of adult female. Fig. 452. Mitosis in female embryo. Fig. 453. Mitosis in male embryo. Fig. 454. Mitosis in polyploid sector. Fig. 455. Oögenesis, diakinesis, nucleolus present (redrawn from Nur).

prev. publ.—none

results—Like its congeners, this species proved also to have the basic diaspidid chromosome number; fairly complete cytology showed that it also conformed in regard to chromosome behavior, including oögenesis (figs. 451–455).

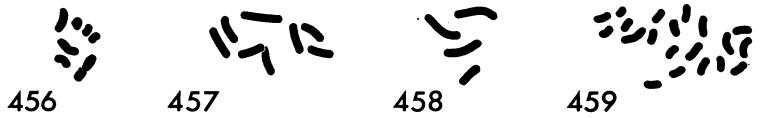
Morganella longispina (Morgan)

tax. Ferris SII-249; (1) *c.* Simmonds; *i.* Simmonds and Breese; Bermuda; Jan., 1957; *host,* oleander; (2) *c.* Nur; *i.* Wilkey; Hope Botanical Gardens, Kingston, Jamaica; July, 1962; *host, Nerium oleander.*

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Uncomplicated fragmentation in a diploid complement (Brown, 1960*a*).

results—Both collections showed similar chromosomal cytology, which conformed to the most common pattern (figs. 456–459).



Figs. 456–459. *Morganella longispina.* Fig. 456. Mitosis in somatic tissue of young female. Fig. 457. Mitosis in female embryo. Fig. 458. Mitosis in male embryo. Fig. 459. Mitosis in polyploid sector.

Mycetaspis juventiae Lepage and Gianotti

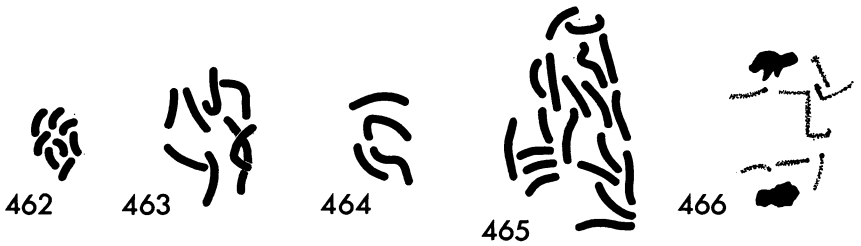
tax. Lepage and Giannotti, 1944; *c.* & *i.* Pinto da Fonseca; São Paulo, Brazil; July, 1962; *host, Erythrina* sp.

F 8 M 4 E— P —; sex.; diaspidid

prev. publ.—none

results—Only young individuals of the two sexes were available for study; the males proved to be haploid, the females diploid (figs. 460–461).

Figs. 460–461. *Mycetaspis juventiae.* Fig. 460. Mitosis in somatic tissue of young male. Fig. 461. Mitosis in somatic tissue of young female.



Figs. 462–466. *Mycetaspis personata.* Fig. 462. Mitosis in egg sheath cell. Fig. 463. Mitosis in female embryo. Fig. 464. Mitosis in male embryo. Fig. 465. Mitosis in polyploid sector. Fig. 466. Chromosome elimination in young male embryo.

Mycetaspis personata (Comstock)

tax. Ferris SIII-372; *c.* Brown and Nelson-Rees; *i.* McKenzie; Veracruz, Ver., Mexico; June, 1960; *host,* palo mulatto.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—An adequate collection enabled the chromosome formula to be completed except for mitosis in the male (figs. 462–465). Chromosome elimination proved somewhat atypical, with the eliminated chromosomes in one instance lying scattered over much of the spindle; the chromatids had obviously separated fairly cleanly but had not succeeded in reaching the poles (fig. 466).

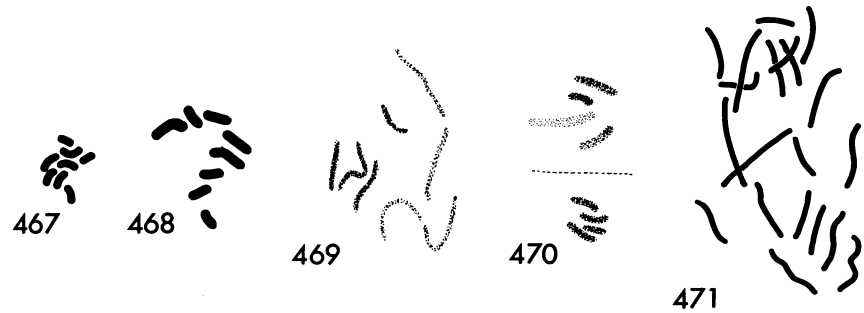
Neomorgania eucalypti (Maskell)

tax. MacGillivray, 1921; *c.* & *i.* Brookes; Waite Inst., Adelaide, S. Australia; Feb., 1959; *host, Acacia* sp.

F 8 M— E 8, 4+4 P 20; sex.; heterochromatic

prev. publ.—none

results—Because only embryos were available for study of the male, it was not possible to determine the chromosome system other than as one involving facultative heterochromatization. Heterochromatic sets of chromosomes were present in one class of embryos, where they showed interesting examples of differential contraction (figs. 469–470), while the remainder of the embryos, maternal tissue and polyploid sectors contained only euchromatic sets (figs. 467–468, 471).



Figs. 467–471. *Neomorgania eucalypti.* Fig. 467. Mitosis in egg sheath cell. Fig. 468. Mitosis in female embryo. Fig. 469. Mitosis in male embryo, one set of 4 heterochromatic, the other euchromatic. Fig. 470. Mitosis in male embryo; heterochromatic sets from two adjacent nuclei, both at interkinesis; in one all elements are similarly contracted, in the other there is a marked differential. Fig. 471. Mitosis in polyploid sector.

472 473 474

Figs. 472–474. *Neoselenaspidus kenyae.* Fig. 472. Mitosis in female. Fig. 473. Mitosis in embryo. Fig. 474. Mitosis in polyploid sector (tetraploid).

Neoselenaspidus kenyae Mamet

tax. Mamet, 1958; *c.* & *i.* De Lotto; Nairobi, Kenya; Jan., 1959; *host, Euphorbia* sp.

F 8 M— E 8— P 16; parth.

prev. publ.—none

results—The cytology of this species proved to be that of a typical parthenogenetic race, with only one class of embryos and tetraploid polyploid sectors (figs. 472–474).

Neoselenaspidus silvaticus (Lindinger)

tax. Mamet, 1958; *c.* & *i.* DeLotto; Nairobi, Kenya; Dec., 1957; host, *Aberia caffra.*

F 8 M— E 8 P 16; parth.

prev, publ.—A detailed description of chromosome erosion (fragmentation) has been offered by Brown (1960*a*), the species then being included under *selenaspidus.*

results—In view of the rather complete picture already provided, only the tetraploid polyploid figure will be illustrated here (fig. 475).

475

Fig. 475. *Neoselenaspidus silvaticus.* Mitosis in polyploid sector (tetraploid).

Nuculaspis apacheca Ferris

tax. Ferris SIII-376; *c.* Brown and Nelson-Rees; *i.* McKenzie; Quezaltenango, Guatemala; July, 1960; *host,* pine.

F 8 M— E 8, 4 P—; sex.; diaspidid

prev. publ.—none

results—Only one collection site, the type locality, was cited by Ferris (*ibid.*) in his description of this species. It was obtained in the Chiricahua Mountains of Arizona, and Ferris (*ibid.*) believed that it might extend into northern Mexico.

476 477 478

Figs. 476–478. *Nuculaspis apacheca.* Fig. 476. Mitosis in egg sheath cell. Fig. 477. Mitosis in female embryo. Fig. 478. Mitosis in male embryo.

A second collection from Guatemala raises at once the question of geographical distribution. McKenzie believed that, for the present, the identification of this species as *apacheca* should remain somewhat tentative.

Chromosome figures from maternal tissue and embryos showed the familiar diaspidid picture (figs. 476–478). Its inclusion in the present report seems justifiable on the basis that it is extremely close to *apacheca,* if not actually this species, and undoubtedly not *californica,* the only other species of the genus.

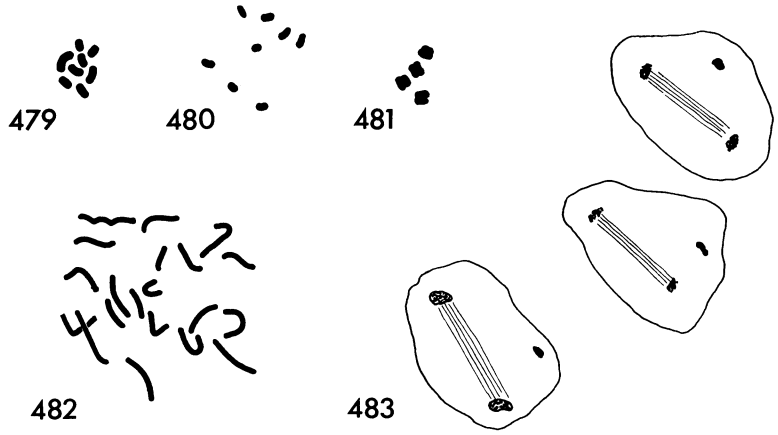
Nuculaspis californica (Coleman)

tax. Ferris SII-251; *c.* & *i.* Dickson; Crestline, San Bernardino Co., California; Aug., 1957; *host, Pinus ponderosa.*

F 8 M— E 8,4 P 20; sex.; diaspidid

prev. publ.—none

results—Like its congener, this species showed a typical diaspidid picture (figs. 479–482) with the exception of chromosome elimination in male embryogeny; cell boundaries were delineated prior to elimination, and the pycnotic residues remained briefly trapped (fig. 483).



Figs. 479–483. *Nuculaspis californica.* Fig. 479. Mitosis in egg sheath cell. Fig. 480. Mitosis in female embryo. Fig. 481. Mitosis in male embryo. Fig. 482. Mitosis in polyploid sector. Fig. 483. Elimination in embryogeny of male embryo; cell delineation occurred prior to elimination, and the residues of the eliminated chromosomes were trapped.

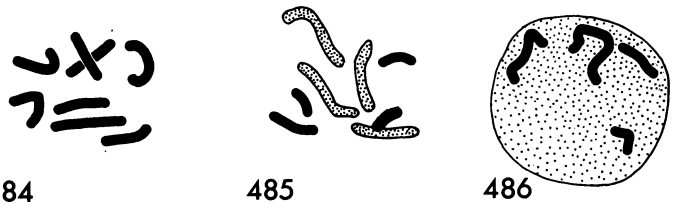
Pseudaonidia baikeae (Newstead)

tax. Newstead, 1914; *c.* & *i.* De Lotto; Nairobi, Kenya; Aug., 1958; *host, Chaetachme aristata.*

F 8 M— E 8,4+4 P —; sex.; heterochromatic

prev. publ.—none

results—Examination of the maternal tissue and embryos (figs. 484–486) showed that a heterochromatic system was present in this species; somewhat more complete results were obtainable with its congener, *Pseudaonidia trilobitiformis.*



Figs. 484–486. *Pseudaonidia baikeae.* Fig. 484. Mitosis in somatic tissue of adult female. Fig. 485. Mitosis in male embryo, the 4 heterochromatic and 4 euchromatic chromosomes at midprophase. Fig. 486. Male embryo, the 4 heterochromatic chromosomes in an interkinetic nucleus.

Pseudaonidia trilobitiformis (Green)

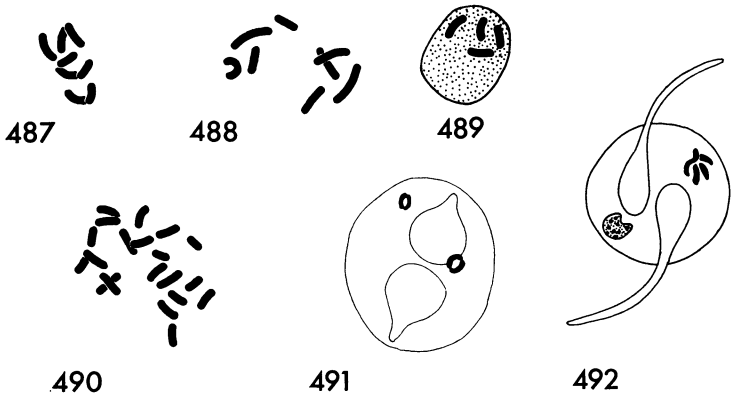
tax. Brain, 1919; (1) *c.* Kerr; *i.* Williams; southeast Brazil; several collections, April–Sept., 1957; *host, Heavea* sp.; (2) *c.* & *i.* Mamet; Mauritius; Nov., 1957; *host, Ficus* sp.; (3) *c.* Brown and Becker; *i.* Wilkey; Viçosa, Brazil; July, 1962; *host, Lecythis pisonis.*

F 8 — E 8, 4+4 P 20; sex.; Comstockiella, lecanoid

prev. publ.—none

results—Maternal and embryonic tissues showed the usual picture of a heterochromatin system (figs. 487–490).

No detailed examination of spermatogenesis was possible, because none of the males were in the right stage, even though several collections had very kindly been provided by Dr. Kerr. The marked differences in size and constitution of the pycnotic residues at early spermiogenesis left no doubt that both the Comstockiella (fig. 491) and lecanoid (fig. 492) systems were occurring.



Figs. 487–492. *Pseudaonidia trilobitiformis.* Fig. 487. Mitosis in egg sheath cell. Fig. 488. Mitosis in female embryo. Fig. 489. Male embryo, the 4 heterochromatic chromosomes in an interkinetic nucleus. Fig. 490. Mitosis in polyploid sector (pentaploid). Fig. 491. Early spermiogenesis, small bipartite pycnotic residues typical of Comstockiella system. Fig. 492. Early spermiogenesis, large pycnotic residues sometimes displaying the constituent 4 elements expected from the lecanoid system.

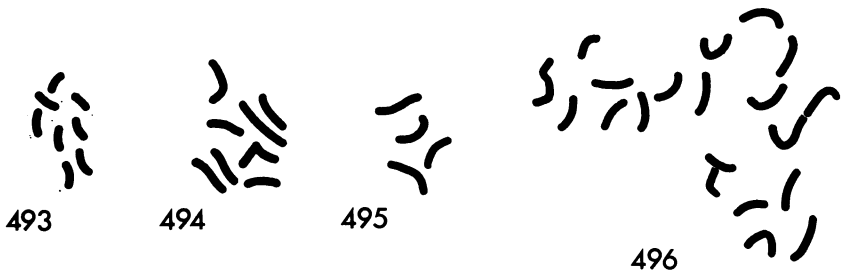
Pseudischnaspis bowreyi (Cockerell)

tax. Ferris SIII-383; *c.* Nur; *i.* Wilkey; Hope Botanical Gardens, Kingston, Jamaica; July, 1962; *host, Yucca* sp.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—(Cytology by Nur.) The usual diaspidid picture was here once more repeated (figs. 493–496).



Figs. 493–496. *Pseudischnaspis bowreyi.* Fig. 493. Mitosis in egg sheath cell. Fig. 494. Mitosis in female embryo. Fig. 495. Mitosis in male embryo. Fig. 496. Mitosis in polyploid sector.

Quadraspidiotus lenticularis (Lindinger)

tax. Balach. V-433; *c.* & *i.* Brookes; Mypolgona, S. Australia; Dec., 1958; *host,* pear tree.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—A typical diaspidid picture (figs. 497–500) was present in this species, which often showed terminal adhesions of chromosomes during early embryonic stages—in one instance resulting in a ring form when one end had become stuck to the opposite end of the same chromosome (fig. 499).

Figs. 497–500. *Quadraspidiotus lenticularis.* Fig. 497. Mitosis in egg sheath cell. Fig. 498. Mitosis in female embryo. Fig. 499. Mitosis in male embryo; note terminal adhesions. Fig. 500. Mitosis in polyploid sector.

Quadraspidiotus ostreaeformis (Curtis)

tax. Ferris SII-258; *c.* Nucifora; *i.* Lupo; Botanical Garden, Catania, Sicily; Sept., 1959; *host,* fig.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The maternal tissues and embryos (including polyploid sectors) again showed the most common chromosome numbers (figs. 501–504). The elimination process showed several aspects of interest; it apparently occurred with unusual rapidity, since pycnotic residues were sometimes already formed by early metaphase (fig. 505) and under circumstances in which squashing could not have introduced such a residue as an artifact from elsewhere. Secondly, the elimination process was sometimes incomplete, as testified by heterochromatic chromosomes in the daughter nuclei (fig. 506).

Figs. 501–506. *Quadraspidiotus ostreaeformis.* Fig. 501. Mitosis in egg sheath cell. Fig. 502. Mitosis in female embryo. Fig. 503. Mitosis in male embryo. Fig. 504. Mitosis in polyploid sector. Fig. 505. Chromosome elimination, pycnotic residue (arrow) formed by late prophase or earliest metaphase. Fig. 506. Heterochromatic chromosome in interkinetic nucleus, presumably consequent to incomplete elimination.

**Quadraspidiotus perniciosus* (Comstock)
(= *Aspidiotus perniciosus* Comstock)

Of the three species which were studied prior to our current program, this is the only one that has not also been collected again. Lindner (1954) reported haploidy in the males (4 chromosomes) but believed that these originated from unfertilized eggs. The finding of the elimination process in a congener, Quadraspidiotus ostreaeformis, *leaves little doubt that members of this genus are regularly diaspidid.*

Quadraspidiotus zonatus Frauenfeld

tax. Balach. V-418; *c.* & *i.* Benassy; Antibes, France; May, 1960; *host, Ficus* sp.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—Chromosome number and behavior were in general similar to those of the congener *Quadraspidiotus ostreaeformis* (figs. 507–510). In one egg all the products of oögenesis were displayed, so that each could be readily recognized (fig. 511). During chromosome elimination at early embryogeny, the eliminated set was usually left on the metaphase plate (fig. 512), but sometimes these chromosomes divided and moved a considerable distance toward the poles (fig. 513).

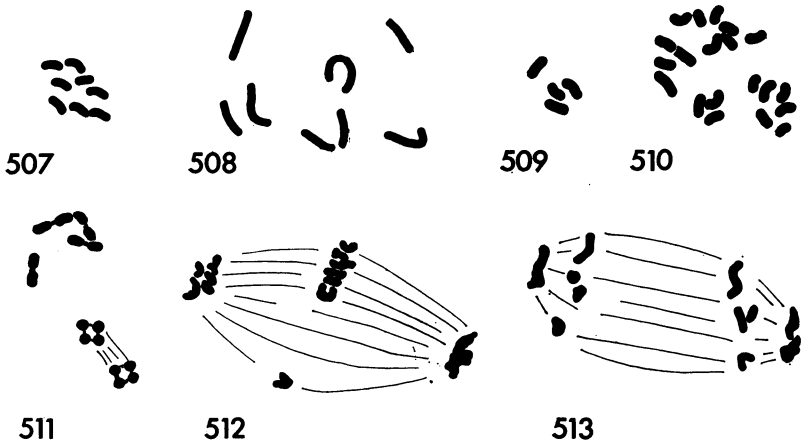
Rhizaspidiotus dearnessi (Cockerell)

tax. Ferris SII-263; *c.* Brown; *i.* Wilkey; Highway No. 3, 5 mi. S. of Tecate, Baja California, Mexico; April, 1963; *host, Adenostoma.*

F 8 M— E —, 4 P —; sex.; diaspidid

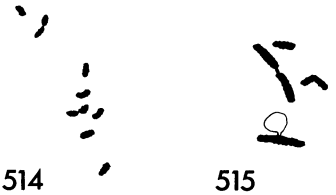
prev. publ.—none

* See last paragraph in Introductory Notes on page 194.



Figs. 507–513. *Quadraspidiotus zonatus.* Fig. 507. Mitosis in egg sheath cell. Fig. 508. Mitosis in female embryo. Fig. 509. Mitosis in male embryo. Fig. 510. Mitosis in polyploid sector. Fig. 511. Oögenesis, telophase II; the 4 dyads of polar body I (above) have not yet fallen apart to yield 8 chromosomes; all 3 nuclei were in a common periplasm. Fig. 512. Chromosome elimination; eliminated set retained on metaphase plate. Fig. 513. Chromosome elimination; eliminated set separated and moved part way to the poles.

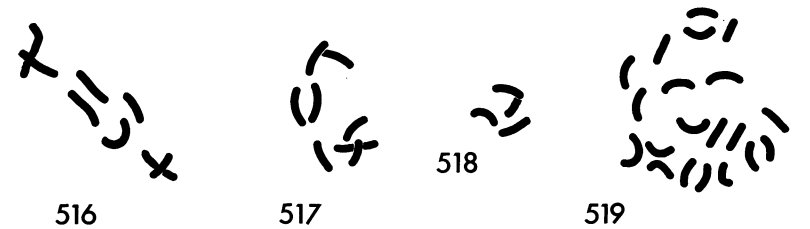
results — (Cytology by Robison.) Only a few females were available for study, and these contained only a few male embryos as determined on comparison with maternal tissue (figs. 514–515). The longest chromosome had a pronounced median constriction, which sometimes led to its appearing to be two chromosomes instead (fig. 514). This constriction was not, however, associated with the nucleolus or its organizer (fig. 515).



Figs. 514–515. *Rhizaspidiotus dearnessi.* Fig. 514. Mitosis in egg sheath cell; note pronounced median constriction in the longest pair of chromosomes. Fig. 515. Mitosis in male embryo; note that the nucleolus-forming zone is not in the longest chromosome.

Selenaspidus articulatus (Morgan)

tax. Ferris SII-265; (1) *c.* Bennett; *i.* Breese; St. Augustine, Trinidad; Oct., 1956; *host,* citrus; (2) *c.* Nur; *i.* Wilkey; Kingston, Jamaica; June, 1962; *host, Blighia sapida;* (3) *c.* Brown; *i.* Wilkey; Lima, Peru; July, 1962; *host, Calliandra carbonaria.*



Figs. 516–519. *Selenaspidus articulatus.* Fig. 516. Mitosis in egg sheath cell. Fig. 517. Mitosis in female embryo. Fig. 518. Mitosis in male embryo. Fig. 519. Mitosis in polyploid sector.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—Brown and Bennett (1957) reported the chromosome numbers in embryos of both sexes and maternal tissue.

results—The three samples gave essentially similar pictures and the results are combined. To supplement the previous information, illustrations of the chromosomes, including the polyploid figures, are offered here (figs. 516–519).

Selenaspidus incisus Lindinger

tax. Mamet, 1958; *c.* & *i.* De Lotto; Nairobi, Kenya; Sept. 1958; May, 1959; *host, Aberia caffra.*

F 8 M— E 8 P 16; parthenogenetic

prev. publ.—A very striking example of transmitted fragments has been reported for this species (Brown, 1960*a*).

results—Mamet (1958) is here cited as the taxonomic reference, even though his monograph of this group of genera dismisses *Selenaspidus incisus* as an incompletely described species.

No further illustrations or comments will be offered at this juncture.

Spinaspidiotus fissidens (Lindinger)

tax. Lindinger, 1909; MacGillivray, 1921; Balachowsky, 1958; (see also Mamet, 1946); *c.* & *i.* De Lotto; Thika, Kenya; Feb., 1958; *host, Ficus* sp.

F 8 M 4 E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—All stages of the life cycle which were studied gave quite typical pictures (figs. 520–524).

Figs. 520–524. *Spinaspidiotus fissidens.* Fig. 520. Mitosis in egg sheath cell. Fig. 521. Mitosis in female embryo. Fig. 522. Mitosis in male embryo. Fig. 523. Mitosis in polyploid sector. Fig. 524. Mitosis in somatic tissue of young male.

Targionia bigeloviae (Cockerell)

tax. Ferris SII-267; *c.* Brown; *i.* Wilkey; Highway No. 3, 20 mi. E. of Ensenada, Baja California, Mexico; April, 1963; *host,* undet. shrub.

F 8 M— E 8— P 32; parth.

prev. publ.—none

results—(Cytology by Robison.) This species was a further example of diploid female parthenogenesis following a reduction division. No sperm were found in the ovaries, and the chromosome complements of the single class of embryos were identical to those in maternal tissue (figs. 525–526). Only one polyploid figure was analyzed; it proved to have an octoploid chromosome number, which could have been achieved by several fusions (or doublings) from the diploid, but could not have included the typical pentaploid level as a step in its formation. Oögenesis

Figs. 525–528. *Targionia bigeloviae* (redrawn from Robison). Fig. 525. Mitosis in egg sheath cell. Fig. 526. Mitosis in an embryo. Fig. 527. Oögenesis, diakinesis, all chiasmata terminalized. Fig. 528. Oögenesis, diakinesis, one chiasma not terminalized. (Note nucleolar-like bodies in figs. 527 and 528.)

provided some extremely clear examples of diakinesis (figs. 527–528). Small nucleolus-like blebs were usually attached to the bivalents.

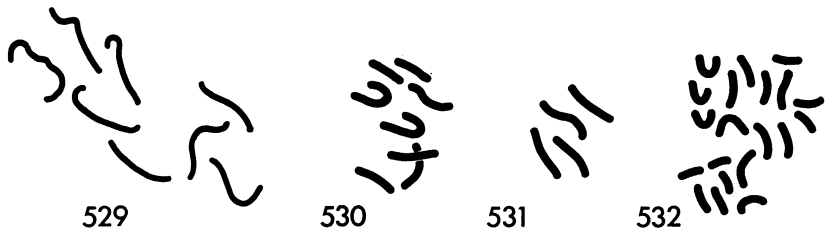
Targionia nigra Signoret

tax. Balach. VI-634; *c.* Brown; *i.* Pegazzano; Agay (Esterel), France; June, 1959; *host,* dusty miller.

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—none

results—The stages examined showed that a typical diaspidid system was present in this species (figs. 529–532).



Figs. 529–532. *Targionia nigra.* Fig. 529. Mitosis in egg sheath cell. Fig. 530. Mitosis in female embryo. Fig. 531. Mitosis in male embryo. Fig. 532. Mitosis in polyploid sector.

Targionia vitis Signoret

tax. Balach. VI-638; *c.* & *i.* Pegazzano; Florence, Italy; July, 1959; *host,* grape.

F 8 M— E —, 4 P —; sex.; diaspidid

prev. publ.—none

results—The living females in the sample obtained were all rather old and "laid out," the few remaining embryos being all haploid (figs. 533–534).

Targionia yuccarum (Cockerell)

tax. Ferris SII-268; *c.* & *i.* Brown; Portal, Arizona; June, 1958; ***host, Atriplex canescens.***

F 8 M— E— P—; (sex.)

prev. publ.—none

results—The small sample available was badly parasitized. Since a male scale of the type of this species was found with the female, this sample was probably sexual, as reported by Ferris (*ibid.*) for the species. No sperm were found in the one unparasitized female examined. However, since she was quite large and contained no embryos, she provided further evidence that parthenogenesis was not occurring here. It seems that she simply had not yet been fertilized. The chromosome number was 8 (fig. 535).

533

534

Figs. 533–534. *Targionia vitis.* Fig. 533. Mitosis in egg sheath cell. Fig. 534. Mitosis in male embryo.

535

Fig. 535. *Targionia yuccarum.* Mitosis in egg sheath cell.

536

Fig. 536. *Tsugaspidiotus tsugae.* Mitosis in egg sheath cell.

Tsugaspidiotus pseudomeyeri (Kuwana)

tax. Takahashi and Takagi, 1957; *c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Chamaecyparis pisifera.*

F 8 M— E 8, 4 P 20; sex.; diaspidid

prev. publ.—A detailed analysis of explosive chromosome fragmentation or erosion has been reported for this species (Brown, 1960*b*).

results—No add.

Tsugaspidiotus tsugae (Marlatt)

tax. Takahashi and Takagi, 1957; *c.* & *i.* Takagi; Sapporo, Hokkaido, Japan; June, 1959; *host, Picea excelsa* Link.

F 8 M— E— P—; sex.

prev. publ.—none

results—The presence of sperm in the ovaries indicated that this species was sexual, but embryonic development had not yet commenced in the females sampled, and the only chromosome counts obtainable were from maternal tissue (fig. 536).

DISCUSSION

A total of 140 species of armored and palm scales has now been examined cytologically; it has been possible to determine at least the chromosome number and usually to obtain some information about the chromosome system as well. The three chromosome systems of the armored and palm scales have been described in the introductory sections and illustrated in figure 1. The evolutionary significance of the changes in chromosome system have been discussed by Brown and McKenzie (1962) and Brown (1963). The information contained in the present report has formed the basis for many of the conclusions of the earlier papers, particularly that of Brown and McKenzie (1962), and these will not be repeated in detail. The present survey provides the most complete statistical summary yet available, as well as information necessary for detailed comparisons of species and genera.

In the present report, the Ferris-Balachowsky taxonomic scheme has been followed. However, Brown and McKenzie (1962) have pointed out that the Phoenicococcidae are heterogeneous on the basis of morphology and chromosome number, and that both the type genus, *Phoenicococcus* itself, and *Ancepaspis* should be placed elsewhere. These two genera have consequently been listed separately under the Phoenicococcidae in table 1. All the groups listed under the Phoenicococcidae in table 1 have a chromosome system involving heterochromatization as in the lecanoid and Comstockiella systems. Since a heterochromatic system, the Comstockiella, is the basic system for the Diaspidoïdae as a whole, its uniform presence within a group is thus not evidence of taxonomic homogeneity. On the contrary, the occurrence in a species of the elimination, or diaspidid, system would place it, on the basis of present evidence, in one of the two major diaspidid tribes, the Aspidiotini or the Diaspidini.

The Comstockiella system also occurs in the two major tribes, and it has been pointed out by Brown and McKenzie (1962) that the independent origin of the diaspidid system, at least once for each tribe, is by far the simplest way of accounting for the sequence of changes. Within both tribes, the Comstockiella system might be expected, therefore, to be associated with the most primitive morphology. On the other hand, forms with the Comstockiella system would be continuing to evolve, so that the Comstockiella system would also occur in the most advanced species. In general, the evolutionary sequence of the three largest tribes conforms to this picture: the Diaspidini are believed to be the most primitive, with the Parlatorini transitional between them and the Aspidiotini (Brown and McKenzie, 1962). The Comstockiella system, often with the lecanoid associated, occurs in each tribe and exclusively in the Parlatorini.

Chromosome system. On closer inspection, the problem becomes quite complex. Two of the Diaspidini, *Nicholiella* and *Radionaspis,* and one of the Aspidiotini, *Aonidia,* are pupillarial and also endowed with a Comstockiella system. There is no particular difficulty

TABLE 1

SUMMARY OF CHROMOSOME DETERMINATIONS IN 140 SPECIES OF 73 GENERA OF ARMORED AND PALM SCALES*†

Total Examined		Taxonomic Group	Chromosome Numbers	No. of Species	CHROMOSOME SYSTEMS OF THE SPECIES							
					Sexual						Parthenogenetic	Unknown
Genera	Species	Family Tribe Genus			Diaspidid	Heterochromatic	Lecanoid	Comstockiella and Lecanoid	Comstockiella	Undetermined		
6	9	**Phoenicococcidae**										
		Phoenicococcus	18	1					1			
		Ancepaspis	6	1					1			
			8	1				1				
		Other genera	10	6		1	1		3		1	
		Diaspididae										
1	1	Xanthophthalmini	16	1							1	
31	56	Diaspidini	6	1	1							
			8	40	30			1	1‡	2	6	
			10	6	4						2	
			12	4	3				1‡			
			14	0								
			16	2	2							
			18	3	3							
			(Total)	56	43			1	2	2	8	
3	7	Parlatorini	8	5		1		3	1			
			10	1		1						
			11	1							1	
			(Total)	7		2		3	1		1	
2	3	Odonaspidini	8	3					1		2	
30	64	Aspidiotini	6	1					1			
			8	61	45	2		1	1	2	9	1
			10	1					1			
			12	1	1							
			(Total)	64	46	2		1	3	2	9	1

* Including 3 species examined by other workers; see the Survey of the Species for further comments on *Aspidiotus hederae*, *Aonidiella aurantii*, and the one not re-examined in the present study, *Quadraspidiotus perniciosus*.
† If a species contained both sexual and parthenogenetic races, it is listed once according to its sexual system.
‡ Also a suggestion of, but as yet no clear evidence of, a lecanoid system.

in picturing the primitive armored scales as pupillarial and having a Comstockiella system. But if the completely logical conclusion is drawn, then the major evolutionary stem of the armored scales consisted of forms which were both pupillarial and Comstockiella—in other words, the major morphological characteristics of the three tribes, the Diaspidini, Parlatorini, and Aspidiotini, were evolved by pupillarial forms which independently, in each instance, gave rise to the non-pupillarial types. That the Comstockiella system and the pupillarial condition could be lost independently is evident from the numerous

non-pupillarial genera in the Aspidiotini and Parlatorini, which still have the Comstockiella system; and from the pupillaria genus *Xerophilaspis*, a diaspidine with a diaspidid system. If the evolutionary main stem consisted of pupillarial forms, then the beautifully definitive pygidial architecture of the non-pupillarial adult forms of the three tribes in question must be a secondary manifestation of pygidial evolution which had been confined to the second stage female. This last objection would seemingly be a serious obstacle to accepting the above picture of the evolutionary pattern. Suffice it to say for the present that further attention to chromosome systems in pupillarial forms is certainly warranted.

The Diaspidini seem to be less specialized than the Aspidiotini; in other words, the latter have more recently evolved. In regard to chromosome number, there is very much more diversity in the Diaspidini than in the Aspidiotini; possible reasons for the greater diversity will be considered below. Three species (three genera) of the Diaspidini have a Comstockiella (or heterochromatic) system, while six (five genera) are known for the Aspidiotini. This difference may be significant, because two of the Diaspidini are of the same type, pupillarial, while the five aspidiotine genera represent quite diverse forms. The two major tribes thus seem to represent opposing conditions. In the Diaspidini, the Comstockiella system is associated with a few species with some primitive characteristics, while most of the evolution has been carried out by forms with a diaspidid system; the evolution has been in progress long enough for chance to lead to the establishment of a wide array of chromosome numbers. In the Aspidiotini, on the other hand, the Comstockiella system is present in a wide array of morphological types and the chromosome number is largely restricted to the basic number, 8, for the family. Two facts lend credence to the idea that the Comstockiella system is, to a considerable extent, in the lead in the Aspidiotini. First, two of the three departures from the basic chromosome number are in species with the Comstockiella system. (Even if *Comstockiella* itself is is not a true aspidiotine, the logic of the argument would still be the same.) Secondly, in two genera, *Aonidia* and *Furcaspis*, one of the species sampled had a diaspidid, the other a Comstockiella system. This last is excellent evidence of the multiple origin of the diaspidid system.

Chromosome number. The chromosomal survey has established two basic chromosome numbers and provided some evidence of a third. The haploid number of 4 is the basic number for all the tribes of the armored scales except the Xanthophthalmini and may therefore be considered the basic number of the family Diaspididae. The haploid number of 5 is the characteristic number of the Phoenicococcidae with the exception of *Ancepaspis* and of *Phoenicococcus* itself. The ideas of Brown and McKenzie (1962) on the reassignment of these genera have already been mentioned. The chromosome numbers of 4 and 3 in *Ancepaspis* conform to those of *Protodiaspis*, a diaspidine genus believed to represent a parallel to *Ancepaspis* (Brown and McKenzie, 1962). *Xanthophthalma* and *Phoenicococcus* should possibly be lumped together; the chromosome number of 8 (16, diploid parthenogenote) for the former and 9 for the latter may indicate a higher basic number for these essentially nude forms. However, the occurrence of a relatively high chromosome number in two relic species may mean very little.

Increases and decreases of 1 or 2 in chromosome number among related forms seem to involve simple fracture or fusion of the chromosomes in the coccids (Brown, 1960*a*, 1960*b*, 1961). In the three instances known in which the haploid number is 3, *Ancepaspis tridentata*, *Protodiaspis infidelis*, and *Furcaspis*

biformis, 1 of the 3 chromosomes is considerably longer than the other 2; it is a "double-length" chromosome which could well have been formed by fusion of 2 members of a 4-chromosome complement. Such fusions are presumably accomplished by grossly unequal reciprocal translocations in which the terminal segments of 2 chromosomes unite to form a very small chromosome, and the main body of each unites to form a "double-length" chromosome; on loss of the small chromosome, the number is decreased by 1, while the double-length entity provides evidence for the mechanism of the decrease as long as it is maintained as such (Brown, 1960*b,* 1961).

A similar mechanism may very well be responsible for the double-length chromosome in *Pseudoparlatoria browni;* the condition in this species has previously been described under *Pseudoparlatoria* sp., by Brown (1960*a,* 1961). It is now known that 2 other species of this genus have the haploid number of 5. Thus the explanation that the condition in *P. browni* is not the basic condition but a secondary derivation from an ancestral 5-chromosome complement would seem reasonable.

For the other species with haploid numbers of 5 and 6, the possible derivation of the 6-chromosome complement from a 4 has already been described for the 2 species of *Africaspis* (Brown, 1960*a*); the one karyotype is derivable from the other by simple fragmentation. For most of the other examples with 5 and 6, closely related forms are not known, and such comparisons are therefore impossible to make. Of special interest, however, is the comparison of *Aonidomytilus variabilis* with 5, and *A. concolor* with 6, chromosomes. The karyotype of the latter is not directly derivable from that of the former on a simple assumption of fracture of one chromosome. Idiograms of the two karyotypes are shown in figure 537A. It may be noted that, even without the small chromosome 6, there is greater size variation in *A. concolor* than in *A. variabilis,* thus indicating a fairly extensive reshuffling of chromosomal material. The simplest way of homologizing the two karyotypes is by assuming an incomplete reciprocal translocation (fig. 537B). If chromosomes 2 and 4 of *A. variabilis* were both broken and the smaller segments of each united while the larger segments remained free, a karyotype like that of *A. concolor* would have been produced. A similar result could have been produced in two steps: first, the fragmentation of chromosome 2; secondly, at some later time, a grossly unequal translocation, which would shift about a third of chromosome 4 onto the smaller segment from the chromosome 2 fracture, but very little in return. This sort of sequence is considered less likely than the single-step derivation because either of the smaller segments, that from chromosome 2 or chromosome 4, would be very close to the minimum size necessary for mitotic stability (Brown, 1960*b*).

There are two examples in which the number is an exact doubling of the basic. For *Diaspis echinocacti,* with $2n = 16$, congeners are known with the basic number, $2n = 8$; while, on the basis of related genera, the same may also prove true for *Pseudaulacaspis pentagona,* with $2n = 16$. The difficulties of accounting for an exact doubling of number, on each of several hypotheses, have already been mentioned (Brown, 1960*a,* 1961), and it is to be hoped that eventually two sufficiently closely related species will be found where the chromosome morphology test suggested by Brown (1960*a*) may be applied.

Chromosome numbers and relationships in the African genera Cooleyaspis, Ledaspis, and Rolaspis. The following discussion of taxonomic relationships is based on Hall's (1946) treatment of the Ethiopian Diaspidini. One of the three main groups of diaspidine species consisted of forms which closely

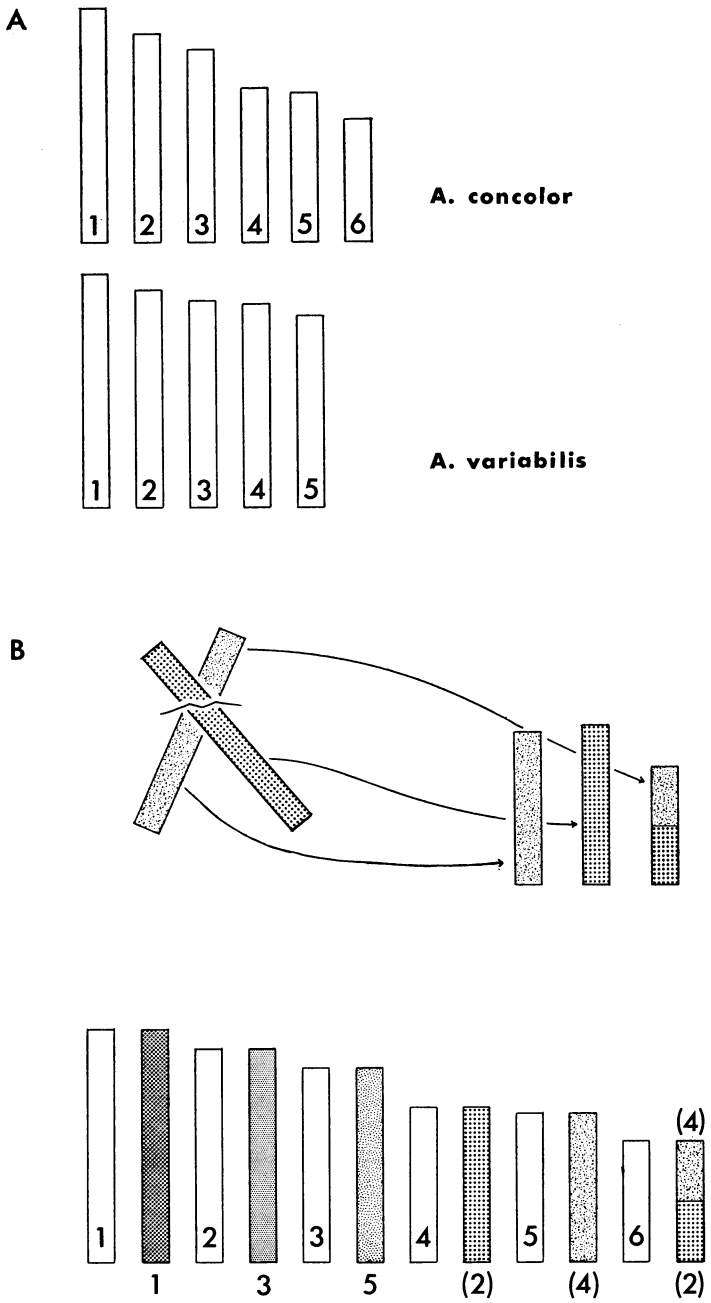


Fig. 537. A. Idiograms of the 6-chromosome haploid complement of *Aonidomytilus concolor* and the 5-chromosome complement of *A. variabilis*. B. The 6-chromosome complement is derivable from that of *A. variabilis* by an incomplete reciprocal translocation. If chromosomes 2 and 4 of *A. variabilis* are fractured so that the longer segments are equal to chromosomes 4 and 5, respectively, of *A. concolor*, then the shorter segments, on uniting, will just equal chromosome 6 of *A. concolor*.

resembled *Phenacaspis* Cooley and Cockerell, and many had been assigned to this genus. According to Ferris (1937), the genus is largely Oriental. Hall (1946) believed that, of the two species assigned to *Phenacaspis* itself, one—*P. dilatata* Green—was introduced, while the other—*P. kenyae*—was of dubious affinity.

Hall (1946) therefore erected several new genera to accommodate the *Phenacaspis*-like complex of species and recognized one pre-existing genus as also belonging to this complex, to make a total of 6 genera and 27 or 28 species, as follows:

Cooleyaspis MacGillivray (1 species)
Ledaspis Hall (5 species)
Moraspis Hall (1 species)
Rolaspis Hall (8 or 9 species)
Tecaspis Hall (9 species)
Voraspis Hall (3 species)

Hall further offered some suggestions as to relationship: *Ledaspis* seemed to be most like *Tecaspis,* which in turn was most like *Rolaspis;* but by no means was any phyletic scheme implied.

Cytogolical information is now available on 4 of these species, from 3 different genera. Three of these 4 have a haploid chromosome number of 9, a unique occurrence not duplicated elsewhere in the Diaspididae. (The same number does occur in the Phoenicococcidae in *Phoenicococcus marlatti.*) The common possession of such an unusual characteristic undoubtedly indicates common ancestry and that the genera in question are a bona fide biological group.

The basic haploid chromosome number of the Diaspididae is 4. A chromosome number of 9 might theoretically be obtained either by chromosome breakage, chromosome doubling, or a combination. Five breaks would be required to obtain 9 chromosomes from 4. A doubling of 4 would yield 8 and a break also would be required to change 8 to 9. Doubling in a hybrid between 4-chromosome and 5-chromosome forms would also yield 9. The change from 4 to 9 does not seem, therefore, to be one that would be quickly accomplished and must have had a considerable evolutionary history.

Because of the uniqueness of the chromosome number and the close morphological affinities of these species, it seems highly unlikely that the number 9 was achieved more than once. All species with this number must therefore have a common ancestry. Sufficient diversification to yield several different genera would thus also have required considerable evolutionary history *after* the establishment of the number 9.

One of the species of the genus *Ledaspis* proved to have the basic chromosome number of 4; this was *L. reticulata,* which is readily separable from the remainder of the species on the basis of reticulated pattern in the sclerotized dermis of the anterior half of the body.

It would certainly be pushing the evidence much too far at the present moment to claim that *Ledaspis reticulata* represented the antecedent 4-chromosome group from which all the 9-chromosome types were derived. A variety of other possibilities could be suggested, including that of a different taxonomic assignment for *L. reticulata.* With such an invaluable index of common ancestry as that afforded by the odd chromosome number, it would seem that further taxonomic analysis of this group of genera would be highly rewarding. There is as yet very little evidence as to how close a guide morphological criteria will be to phylogeny within the major familial divisions, the tribes. The African group of genera should prove, when sufficient chromosomal evidence is collected, to be an excellent model of the potentialities of a limited evolutionary series.

Mycetocyte formation. During the course of the chromosomal survey, an attempt was usually made to determine the chromosome number in the polyploid sector, and in sexual forms this proved to be typically pentaploid. Since

the pentaploid level is that expected (see figure 2), it was presumed that mycetocyte formation in these instances followed the pattern previously described by Brown and Bennett (1957) for the armored scales. It should be emphasized that the chromosomal survey revealed exceedingly few examples of the fusion of the polar bodies with a cleavage nucleus, but that exhaustive searches were believed not to be warranted because the chromosome number evidence continued to indicate that the typical process was occurring among the various species. What seemed especially conclusive was the finding of a pentaploid number in cases in which, as in *Lindingaspis rossi,* mycetocyte formation was taken over by diploid nuclei, which in turn formed polyploid nuclei by endomitosis, while the pentaploid cells were relegated elsewhere in the embryo to perform a yet to be determined function. To conclude, the formation of a pentaploid sector in sexual species seems to be a stable characteristic with sometimes further additions, such as an extra cleavage nucleus to yield a 7-ploid sector or still other fusions, as in *Furcaspis biformis.*

One striking modification in the pentaploid mycetocytes occurs when some of the chromosomes become heterochromatic during the first endomitotic cycle. The heterochromatization is of special interest for two reasons. First, it occurs in both males and females, whereas heterochromatization in the soma of the armored scales (in the Comstockiella system) is restricted to the male sex. Second, it has been a common observation in our laboratory that polyploid somatic tissues, in males with heterochromatization, usually lack the heterochromatic chromocenter. Since the polyploid state in the somatic tissues is achieved by endomitosis, we have an example of this process in the one instance—the mycetocytes—bringing out facultative heterochromatization; and in the other—polyploid somatic tissue—restoring the heterochromatized chromosomes to their previous euchromatic condition.

Mycetocyte chromocenters are apparently restricted to a small group of genera in the Diaspidini, *Phenacaspis, Pinnaspis,* and probably also *Aulacaspis.* They may therefore provide another clue to phylogeny within groups of genera. It seems likely that a relationship could be assumed on the basis of this characteristic, but, since there is no evidence yet as to how easily it could be lost, absence should not be taken to indicate lack of relationship.

Parthenogenesis. Two types of parthenogenesis have been observed in the armored and palm scales: that in which a normal, reductional oögenesis is followed by some mechanism for restoring diploidy, and that in which an essentially mitotic division replaces the reductional divisions. The former process has not yet been followed in detail in any species; and it is not known, therefore, how diploidy is restored in any such instance. The mitotic-type parthenogenesis is easily recognized by the presence of the diploid number of univalents at oögenesis; it usually results in a tetraploid polyploid sector, since the fusion of a single, diploid polar body with a diploid cleavage nucleus would result in tetraploidy. This sequence, however, has not been followed in detail, and would be extremely difficult to do in squashes, since the various nuclei would all be diploid and therefore could only be distinguished from each other with certainty by spatial relationships which, of course, are distorted in the squashes.

The majority of examples of parthenogenesis in the armored scales seem to be of the mitotic type, whereas those in the pseudococcids are almost exclusively of the meiotic (Brown, Beardsley, and Nur, unpubl.). However, the type of parthenogenesis is yet to be determined for many of the examples in the armored scales.

One of the most surprising aspects of the parthenogenetic strains is their conformity to the basic chromosome number. The holokinetic nature of the chromosomes permits fragments of any appreciable size to survive. The substitution, in many parthenogenetic strains, of a mitosis-like division for the usual reductional sequence would preclude the hazards of elimination at meiosis. Yet, in spite of these presumably favorable aspects of parthenogenesis, the parthenogenetic strains show far less variation in chromosome number than do the sexual species. In one instance (Brown, 1960*a*), a clone demonstrated the sort of behavior expected on chromosome breakage, but the fragment-bearing clone was quite restricted. In only one instance, therefore, that of *Leucaspis loewi,* is there any evidence for a propagation in nature of a number different from that of the sexual progenitor. Here the number 11 may have been derived by one fragmentation from 10, or by 3 fragmentations from 8 chromosomes. Again, however, only a restricted sample has been obtained for this species, and no certain information is available as to the number of the sexual diploid progenitor.

It may be noted at this juncture that this same situation prevails with both *Howardia biclavis* and *Kuwanaspis bambusicola,* parthenogenetic forms with 10 chromosomes each. Here also, the number 10 may have characterized the sexual diploid progenitor.

The evidence in general seems clear that little or no significant increase in chromosome number has taken place following the change from sexual reproduction to mitotic-type parthenogenesis. Two general types of explanation may be offered. The first assumes that fragmented chromosomes are as able, or better able, to become established in parthenogenetic strains as in sexual ones, but that the parthenogenetic strain has a relatively short evolutionary history and usually dies out before a fragment strain can replace the types with the original chromosome number. A converse of this explanation may be that chromosome number changes in the sexual forms may occur only during speciation, to erect a reproductive barrier, which, of course, would be meaningless for the parthenogenetic type.

In contradistinction to long-range evolutionary processes, attention may be directed to the immediate consequences of the chromosome breaks involved in karyotype changes. In numerous experiments using irradiation on female mealy bugs in our laboratory at Berkeley, we have not yet been able to produce a chromosome aberration which is not lethal in male offspring (effectively haploid). The suggestion may thus be made that chromosome breakage usually induces a deleterious change at the point of breakage, and that only with sexual recombination can the aberration be placed in a new combination of genes where it will no longer be disadvantageous. As mentioned above, there might be sufficient advantage during speciation to compensate for what, under usual circumstances in the sexual form and always in the parthenogenetic, would simply remain a deleterious change. It should also be noted that we have yet to find sexual species polymorphic for chromosome number, even though the colonial population pattern and extremes of geographical isolation would presumably favor such changes in these species.

Parthenogenetic strains or races. Taxonomists of the armored scale insects have varied considerably in the attention they have devoted to the males, and there may even be considerable difference from species to species in the same treatise. Consequently, we cannot at this juncture offer more than a few particular instances in which the cytological picture has enabled an extension of the earlier observations.

Three types of species are known in regard to sexuality per se: the bisexual,

the unisexual (reproducing by female parthenogenesis), and the dimorphic (with both bisexual and unisexual strains), of which *Aspidiotus hederae* provides the classic example. With taxonomic attention given almost exclusively to the female, the species may be described with no certain record of its sexuality. However, collections are sometimes scanty and will not include males for reasons quite beyond the control of the collector. Cytological techniques are of considerable value in assessing species. The presence of sperm will, for example, immediately indicate sexuality, while the observation of a diploid number of univalents at the stage of the first oögenic division will likewise indicate, without further question, a mitotic-type parthenogenesis.

The cytological survey has resulted in the discovery of males in species not previously recognized as sexual; usually this has been the result merely of further, more intensive collecting. Species falling into this category are: *Ancepaspis edentata, A. tridentata, Nicholiella bumeliae, Xerophilaspis prosopidis,* and *Hemiberlesia quercicola.* In only one instance, that of *Hemiberlesia lataniae,* has a sexual strain of a widespread parthenogenetic species been revealed, and this example undoubtedly warrants further study.

Parthenogenetic races have been identified in 10 species previously reported as sexual, and these examples present rather diverse situations. *Thysanococcus calami* was presumed to be sexual and reported only from the Botanical Garden at Bogor, Indonesia. The only other collection, on a host imported from Indonesia to a botanical garden in Jamaica, proved parthenogenetic. *Odonaspis ruthae* has been repeatedly examined for males, even when not checked cytologically, in many localities, including Hawaii, where it was first described, without any evidence of males. Other species for which males have been reported but which the present survey indicates have parthenogenetic races are: *Leucaspis loewi, Lepidosaphes ulmi, Fiornia fiorniae, Chrysomphalus dictyospermi, Hemiberlesia cupressi, Targionia bigeloviae, Parlatoria proteus,* and *Phenacaspis pinifoliae.*

A very limited start has been made in defining the distribution of the unisexual and bisexual forms of the last species just cited, *P. pinifoliae.* Sexual forms are known only from central and southern California, whereas repeated collections from elsewhere in California, Arizona and Utah have uniformly yielded unisexual forms.

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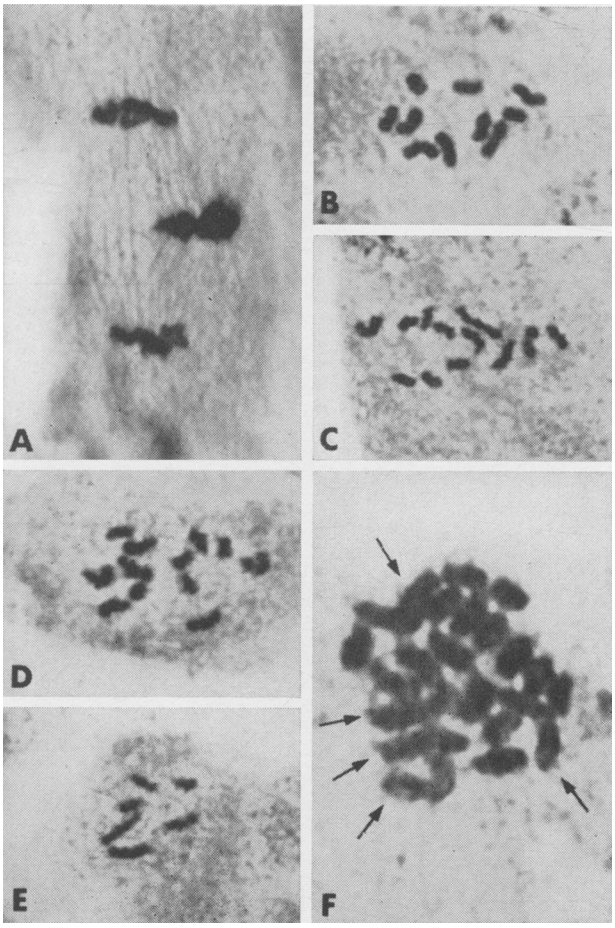

Plate I. Fig. A. *Cooleyaspis praelonga.* Chromosome elimination in young male embryo. Fig. B. *Howardia biclavis.* Mitotic prophase, 10 chromosomes. Figs. C, D, and E. *Lepidosaphes tokionis.* Fig. C. Mitosis in egg sheath cell, 12 chromosomes. Fig. D. Mitosis in female embryo, 12 chromosomes. Fig. E. Mitosis in male embryo, 6 chromosomes. Fig. F. *Pseudoparlatoria browni.* Mitosis in polyploid sector, pentaploid with 20 chromosomes; arrows: the 5 double-length chromosomes.

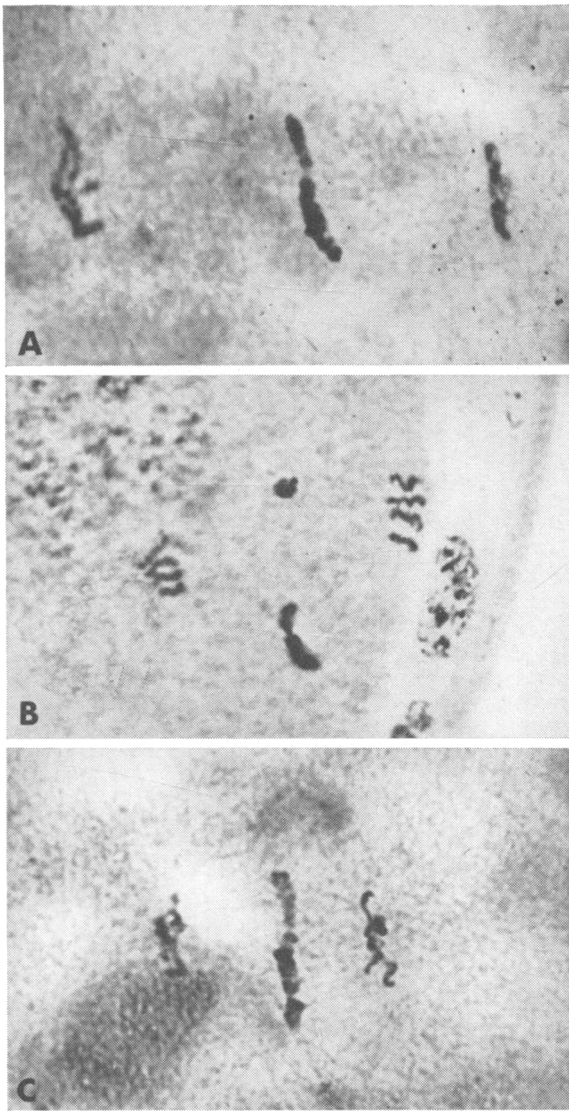

Plate II. *Aspidiotus destructor*. Figs. A, B, and C. Elimination figures in young male embryos.

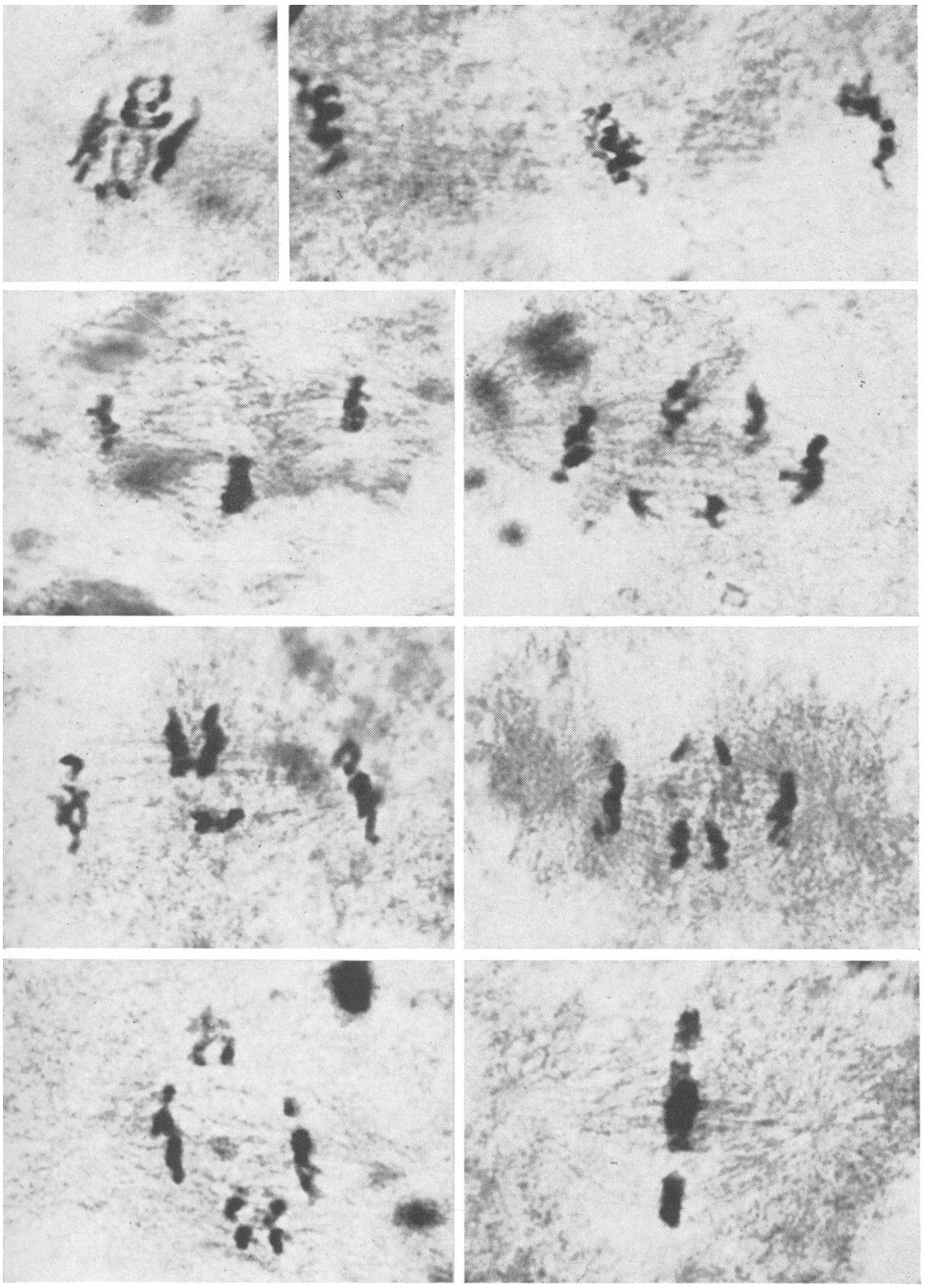

Plate III. *Aspidiotus simulans.* Elimination figures. Note variability of chromosomal activity.

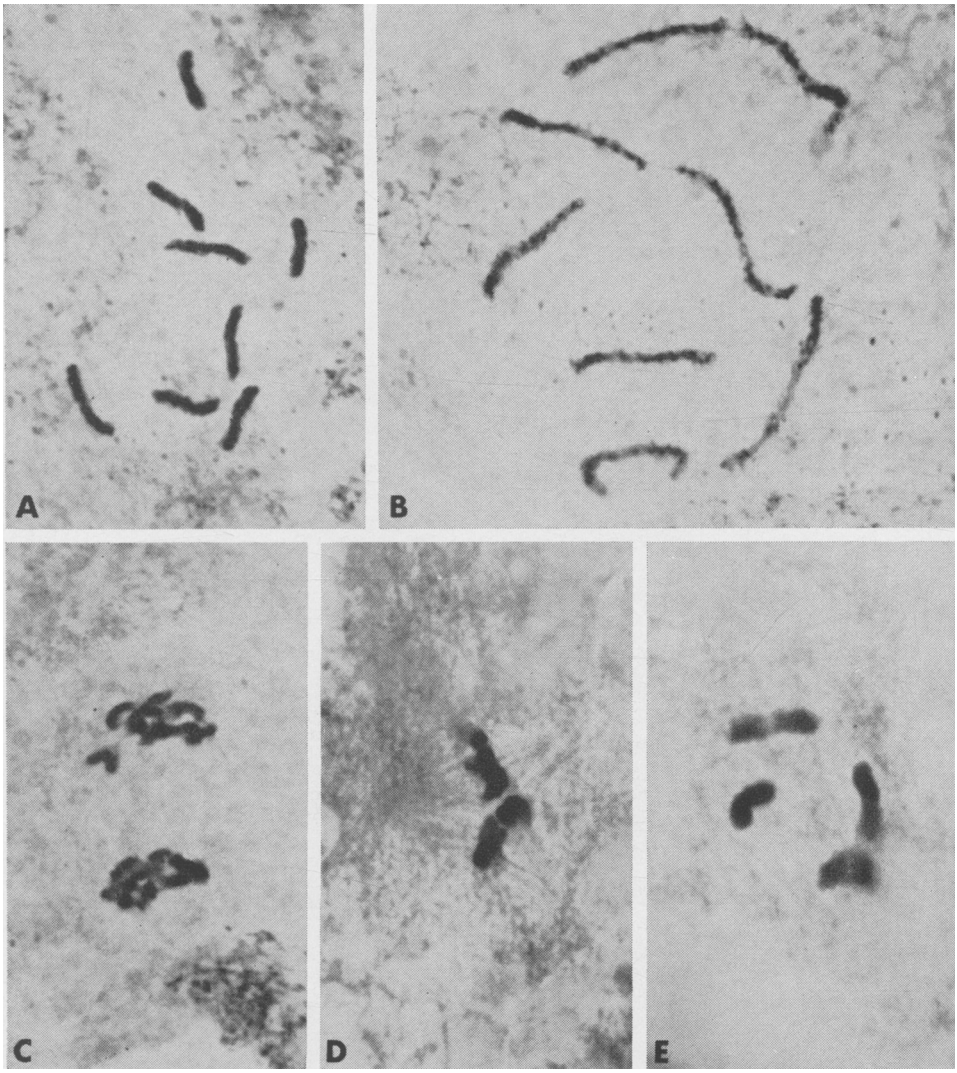

Plate IV. *Chrysomphalus pinnulifer*. Figs. A and B. Mitotic prophases in embryos. Fig. C. Lagging chromosome, attached to one telophase daughter group, mitosis in embryo. Fig. D. Tripolar spindle in mitosis in embryo. Fig. E. Oögenesis, prometaphase, 4 bivalents.

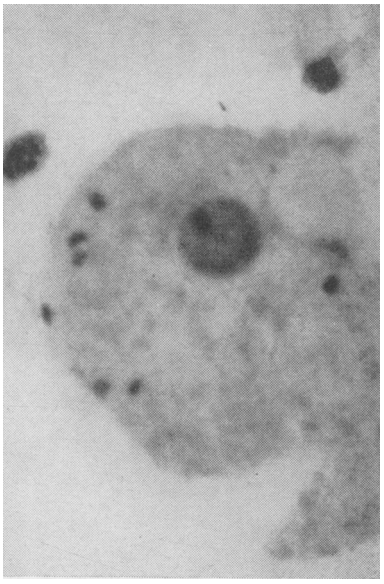

Plate V. *Hemiberlesia lataniae.* Oögenesis, prophase of first division, 8 univalents.

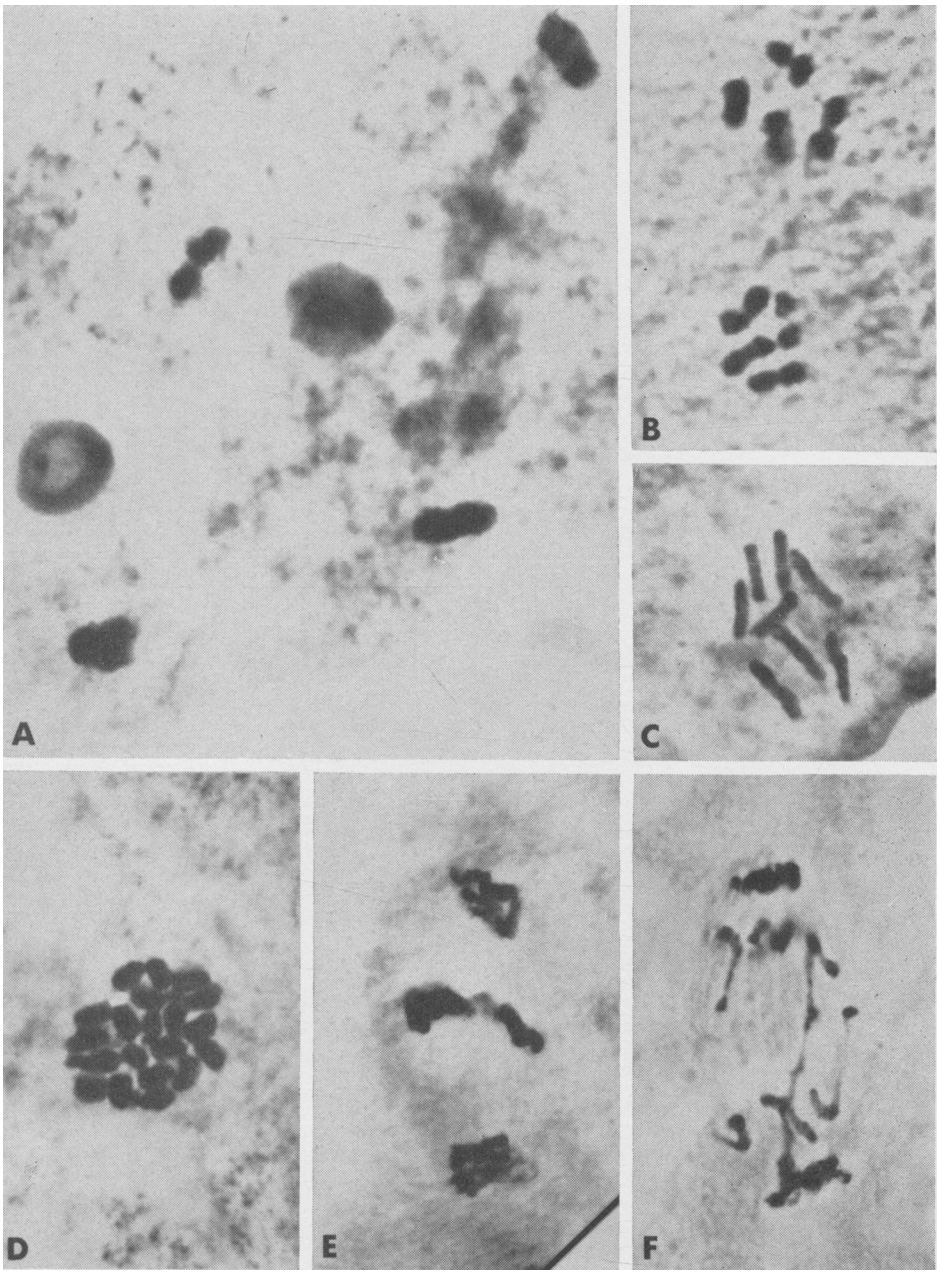

Plate VI. *Lindingaspis opima.* Figs. A and B. Oögenesis. Fig. A. Late first prophase with 4 bivalents; note structure in lower nucleolus. Fig. B. Late second prophase or prometaphase; secondary oöcyte and first polar body not distinguishable, 4 dyads in both. Fig. C. Egg sheath cell with 8 chromosomes. Fig. D. Polyploid division figure, pentaploid with 20 chromosomes. Figs. E and F. Chromosome elimination in young male embryos.

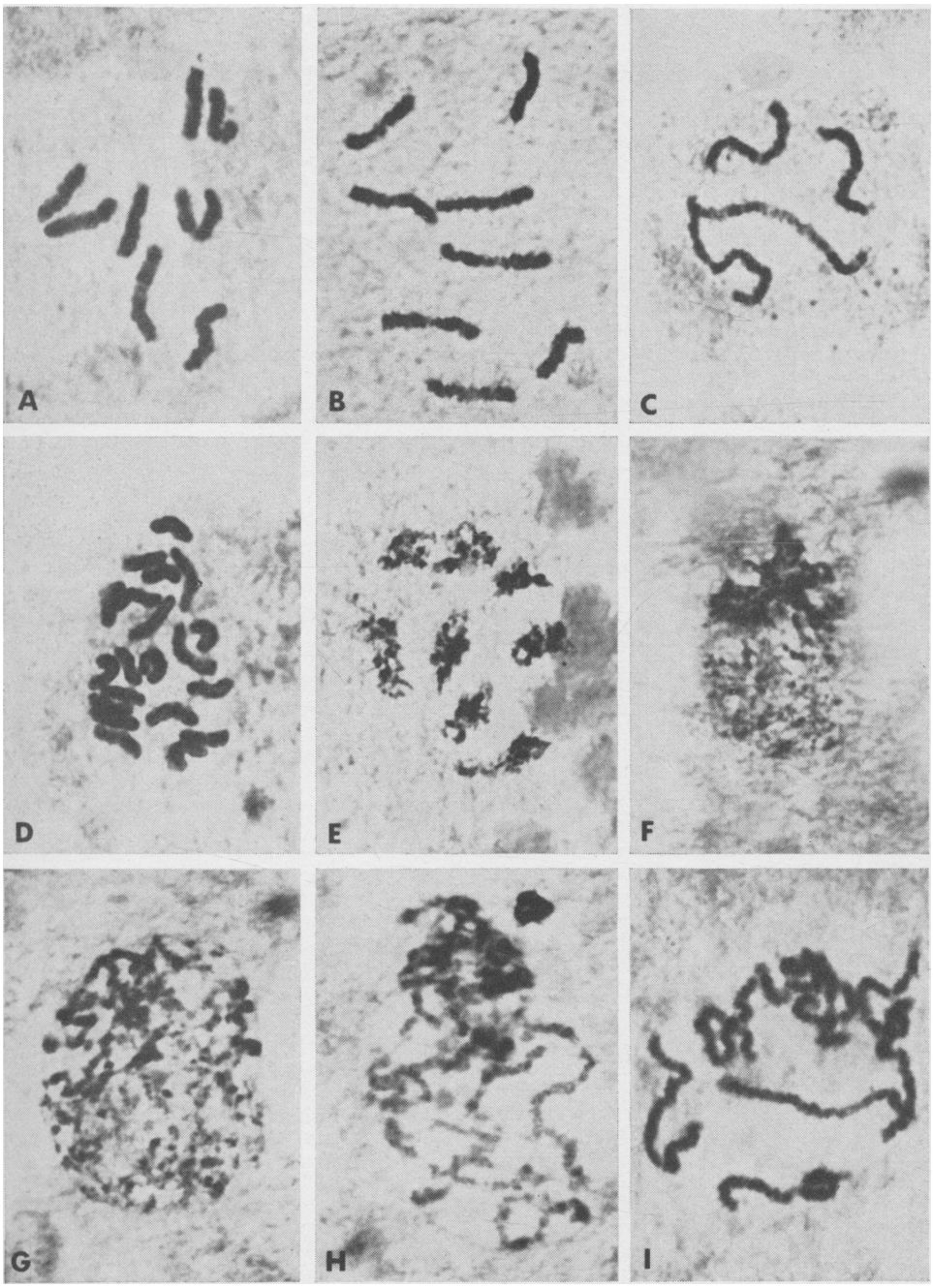

Plate VII. *Lindingaspis rossi.* Figs. A and B. Mitosis in female embryo. Fig. C. Male embryo. Fig. D. Polyploid sector. Fig. E. Endomitotic mycetocyte. Figs. F, G, H, and I. Sequence of prophase stages showing the heterochromatic set.

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