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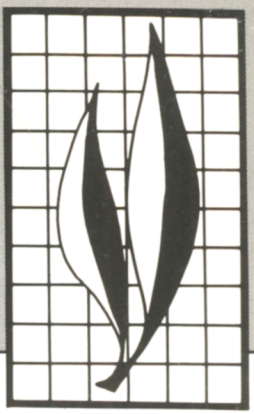

Life History of the Incense Cedar Scale, *Xylococculus macrocarpae* (Homoptera: Margarodidae), on Incense Cedar in California With a Description of the Larvae of One of Its Common Predators, *Eronyxa expansus* Van Dyke (Coleoptera: Trogositidae)

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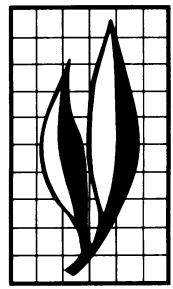

ABSTRACT

Xylococculus macrocarpae (Coleman) had one generation a year on incense cedar (*Calocedrus decurrens* (Torr.) Florin) at Blodgett Forest, El Dorado County, California, at 1200 to 1550 m elevation. There were four female stages and five male stages. On small incense cedar, adult females laid eggs on the foliage in spring. Crawlers then settled on branches and middle and upper boles, where they molted to legless stages in summer. Females overwintered as legless second and third stages, and males as legless second stages and legged prepupae. In spring, male prepupae and pupae migrated lower on the bole while female adults moved to the foliage.

X. macrocarpae was the most common prey under incense cedar bark during the winter months when insectivorous birds forage on the tree; the insect was especially abundant on branches and the upper and middle boles. Two hymenopterous parasitoids were reared from *X. macrocarpae*, the previously undescribed *Parechtrodryinus xylococculi* Beardsley and Gordh (Encyrtidae), and *Mesopolobus* sp. (Pteromalidae). The trogositid beetle *Eronyxa expansus* Van Dyke was a common predator, possibly restricted to the scales.

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Life History of the Incense Cedar Scale, *Xylococculus macrocarpae* (Homoptera: Margarodidae), on Incense Cedar in California With a Description of the Larvae of One of Its Common Predators, *Eronyxa expansus* Van Dyke (Coleoptera: Trogositidae)[1]

INTRODUCTION

XYLOCOCCULUS MACROCARPAE (Coleman) (Homoptera: Margarodidae) is a common insect on incense cedar (*Calocedrus decurrens* (Torr.) Florin) in California's Sierra Nevada. It was first described as *Xylococcus macrocarpae* from Monterey cypress (*Cupressus macrocarpa* Hartw.) (Coleman 1908). Florence (1917) described its life history in more detail on that host. Morrison (1927,1928) placed the North American species of *Xylococcus* in the new genus *Xylococculus* based on the presence of legs and antennae in the adult female. Ehrhorn (1911) noted infestations on incense cedar in Yosemite and the Shasta area.

The insect is widely distributed within the range of incense cedar, which grows from Baja California to Mount Hood near Portland, Oregon (Griffin and Critchfield 1972). In California, the scale is found from San Diego County on the southern border (Ferris 1919) to Modoc County on the northern border.

The scale lives under the flaky bark of incense cedar, mostly on the boles of small trees, the upper boles of larger trees, and on branches. Small suppressed trees are especially likely to have heavy infestations (Ehrhorn 1911). The feeding stages emit honeydew through threadlike white wax anal tubes that often protrude from the bark, as Florence (1917) reported for the insect on Monterey cypress. On heavily infested trees, a prominent black deposit of sooty mold often gives a scorched appearance to the boles and branches (Salman 1933).

In California's Sierra Nevada, incense cedar is abundant in the mixed conifer forest (Griffin and Critchfield 1972). Two early accounts (Ehrhorn 1911, Salman 1933) reported that the scale killed young trees, especially in dense new stands. Since then, the insect apparently has not caused economic damage (Furniss and Carolin 1977). However, it appears to be important as winter food for some insectivorous birds in the Sierra Nevada (Morrison et al. 1985, 1989; Dahlsten et al. 1986).

Several bird species increase their use of incense cedar in winter compared to summer, spending up to about 50% of their winter foraging time on cedar (Morrison

[1]Portions from a thesis submitted by the senior author, S. M. Tait, to the University of California, Berkeley, in partial fulfillment of the M.S. degree, December 1986.

et al. 1985). Birds move along the trunk and branches of the trees, flaking off the bark and eating the insects beneath. Winter bird abundance was associated with abundance of incense cedar (Morrison et al. 1989). Winter exclosure studies (Dahlsten et al. 1986, Morrison et al. 1989) indicate that bird predation may be an important scale mortality factor.

The objective of this work was to study the life history of *Xylococculus macrocarpae* on incense cedar by examining the characteristics, phenology, and location of its stages. The study answered questions about the importance of the scale for insectivorous birds by providing information on the availability of *X. macrocarpae* in winter when other prey may not be abundant, its density compared with that of other prey available beneath the bark, and its within-tree distribution compared with bird foraging patterns. Knowledge of scale biology is also necessary to determine how tree and stand characteristics affect scale populations, and thus is a basis for forest management decisions (Morrison et al. 1990). Another objective of this study was to compare the biology of *X. macrocarpae* on incense cedar with its biology on Monterey cypress.

MATERIALS AND METHODS

Study site. Material from incense cedar was collected at the Blodgett Forest Research Station of the University of California Berkeley. The forest is located on the western slope of the Sierra Nevada, El Dorado County, California, between 1200 and 1550 m. Principal tree species are incense cedar, white fir (*Abies concolor* [Gord. & Glend.] Lindl.), sugar pine (*Pinus lambertiana* Dougl.), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), California black oak (*Quercus kelloggii* Newb.), ponderosa pine (*Pinus ponderosa* Laws), and tan-oak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.) (Airola and Barrett 1985).

Fecundity and egg hatch. Eggs were counted from 25 dead adult females, that had completed egg laying. Crawlers hatching from eggs of 10 other dead adult females were counted at 1- to 5-day intervals.

Life history samples. Because preliminary observations indicated that different scale stages occurred on different parts of the trees, samples to determine the annual history of the scale were taken throughout the tree. Life history samples on which most of the analysis was done were taken from small trees, 6 to 10 cm diameter at breast height (dbh). Sample units within those trees consisted of 80-cm sections centered on the lower, middle, and upper boles; at least 240 cm of branches (on two early dates the sample was less than 240 cm); and, after it was discovered that adult females occur on foliage, foliage from at least 10 linear meters of branches. Only those portions of branches with foliage-bearing twigs were collected for the foliage sample units; for these samples, branches were measured from the beginning of the foliage to the branch tip. Samples were collected from February 1985 to June 1986, approximately once per month, except from late May to early August when samples were collected every 2 weeks. (Once 2 months elapsed between winter collections.)

The small-tree samples were supplemented with less frequent collections from larger trees, 15 to 25 cm dbh, from which the same sample units were taken as from the small trees. The third type of sample, also collected less frequently, consisted only of lower-crown branches and foliage of trees over 30 cm dbh. As only one of each sample

type was collected per date, heavily infested trees, and branches within trees, were selected nonrandomly for sampling.

Insects were removed from the samples in the laboratory, usually after cold storage at 5°C. For each sample unit (for example, upper bole), 50 scales were collected if available, plus extras to allow for losses in making slide mounts. Actual area examined, up to the whole unit when density was low, was recorded. When crawlers and second-stage larvae were present, samples were examined with a dissecting microscope, and the maximum area searched was reduced to 5 cm of bole and 25 cm of branch length. Because of the resulting variation in area sampled, and because only one nonrandom sample was taken per date for each sample unit, no statistical analysis was done on scale and associate density. However, mean density and its range were calculated for the winter months (November–March), for scales and for total nonscale arthropods, excepting mites, to examine the abundance of *X. macrocarpae* relative to other prey available for birds.

Scale stages. Specimens of each stage, except for adult males, were stained for study and mounted in balsam on permanent microscope slides, using a technique developed and refined by systematists of the U.S. Department of Agriculture and the California Department of Food and Agriculture. An incision was made on each specimen on one side of the abdomen. Specimens were placed in 10% potassium hydroxide (KOH) at room temperature for 1 to 1½ hours. (Heating or longer soaking produced a viscous substance difficult to eliminate.) Body contents were teased out as much as possible while the specimens were still in KOH. Specimens were then placed in 75% ethanol for at least 5 minutes to remove KOH. They were then heated in 10 ml beakers at 40° to 60°C in 2 to 5 ml of Essig's aphid fluid (Wilkey 1962), with one or two drops of 0.5% acid fuchsin stain added. About 6 hours of heating was necessary to obtain well stained and cleared specimens.

Remaining body contents were teased out in warm clear Essig's solution. Specimens were then dehydrated in cellosolve (ethylene glycol monoethyl ether) for at least 1 hour. Specimens were mounted in balsam thinned with xylene. For slides of larger specimens (late third stages and succeeding stages), cover slips were propped with small pieces of nylon filament fishing line (12-pound test).

Temporary slides were made to distinguish larger numbers of specimens, using a technique developed by Quednau (1964). Specimens were punctured and soaked in chloralphenol until cleared, 3 days to 3 weeks depending on size. Body contents were then pumped out and the specimens mounted in a modified Faure solution. Features were sufficiently discernable without the addition of iodine to the mounting medium.

Permanent or temporary slides were made of all legless stages from the small-tree samples. Specimens in the process of molting were used to help determine the number and sequence of legless stages for each sex. As a further aid in distinguishing stages, anal tubes (length and width) and body length were measured on a number of legless specimens, using a compound microscope with a micrometer. Anal tube measurements were also compared between newly hatched crawlers and settled male crawlers eclosing to second instars, using the Student's *t*-test, to detect any differences that would indicate that the crawlers included two stages.

Scales from the larger trees were not slide mounted. These scales were classified only by stages distinguishable with a dissecting microscope in order to compare general patterns of movement and phenology to those on the smaller trees.

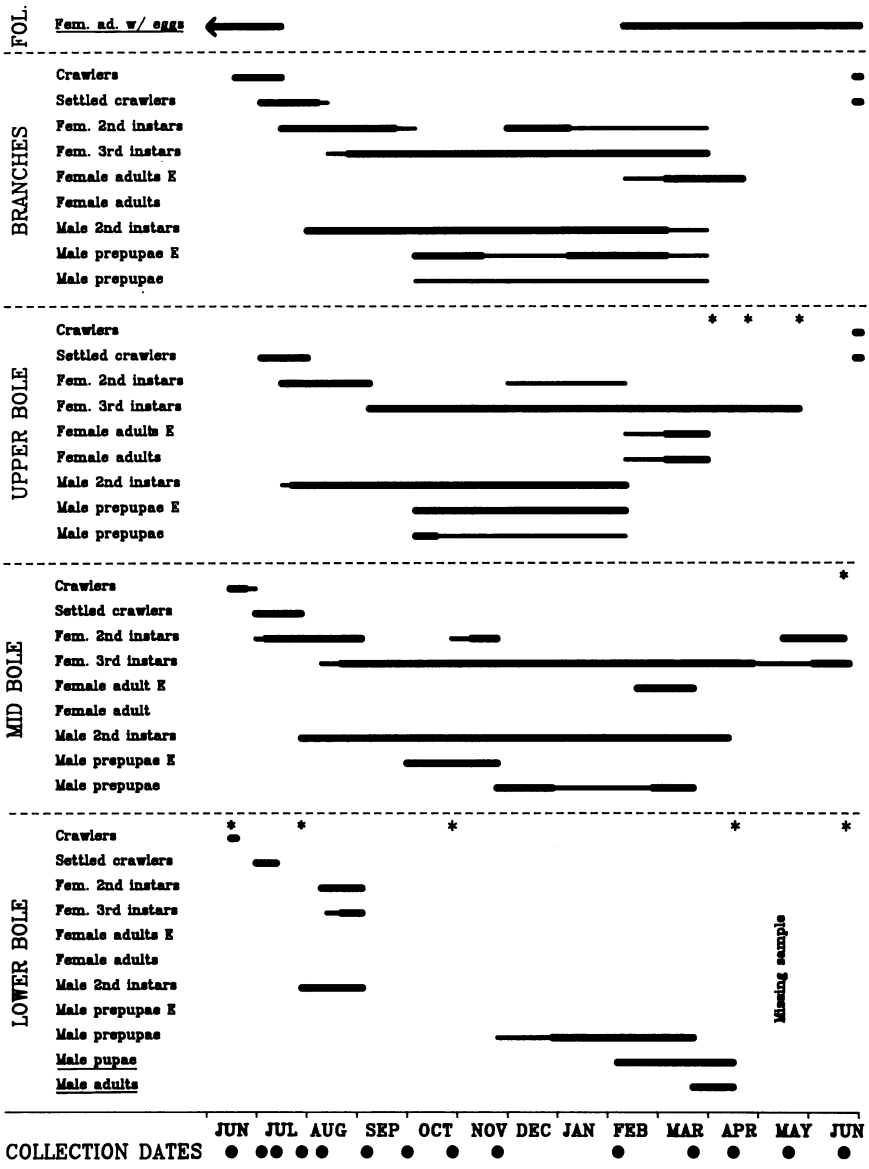


Fig. 1. Phenology and within-tree distribution of *Xylococculus macrocarpae* on small incense cedar at Blodgett Forest, El Dorado Co., Calif., 1985–86. One 6- to 10-cm dbh tree sampled per date. Female adults with eggs appear only on foliage; male pupae and adults appear only on lower bole (these stages underlined):

Heavy lines: stage ≥ 5% of sample for that tree part

Light lines: stage < 5% of sample for that tree part

E: legged stage emerging from previous stage, not yet mobile

Arrow: stage present before this date

*: < 10 scales in sample for that tree part

Life history. For the small-tree samples, the percentage of each stage was calculated for each part of the tree (sample unit) on each date, and diagrammed for the year from June 1985 to June 1986 (fig. 1). When a stage was found on one date but not the preceding or following dates, it was not diagrammed for that part of the tree on that date.

Comparison with Xylococculus from other hosts. Adult female *Xylococculus* from incense cedar were compared to specimens from Monterey cypress collected at Pebble Beach, Monterey County, California, and from Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) near Kolob Arch in Zion National Park, Washington County, Utah. Additional specimens collected by others previous to this study from various sites in California were also examined.

Parasitoid rearing. Parasitized scales were placed in small petri dishes with tight-fitting lids. Usually, the scales were collected on a small chip of bark, but if they detached from the bark they were placed in the dishes without it. Dishes were checked weekly or biweekly for emergence of adults.

RESULTS AND DISCUSSION

Life history synopsis. Female adult *X. macrocarpae* laid eggs on the foliage in spring (figs. 1-3). Hatched crawlers moved to branches and the upper and middle bole where they settled, and molted in summer to legless feeding stages (fig. 4). Females overwintered as legless stages and males as legless stages and legged prepupae (fig. 5). In early spring, legged female adults emerged and moved to foliage while male legged stages moved lower on the bole where they molted to winged adults (fig. 6).

Fecundity and egg hatch. The mean number of eggs per intact settled female was 136.5 (SD = 27.8, n = 25), with a range of 90 to 205 eggs. Mean number of crawlers hatched per female (different females than those from which eggs were counted), was 121.3 (SD = 38.3, n = 10), with a range of 69 to 184. At laboratory temperatures, eggs hatched over a period of 3 to 16 days, except for a single crawler that hatched at 18 days.

Scale stages. Four female and five male stages of *X. macrocarpae* were observed (fig. 2). The legged crawlers changed appearance considerably as they fed after settling. There was a continuum from the elongate shape of newly hatched crawlers with coiled mouthparts to plumper crawlers, with extended mouthparts, that had started to feed. Crawlers were observed with robust legs, with shrivelled legs, and with some legs missing. Usually, settled crawlers had lost the legs except for coxae and trochanters. The legs may have been lost in processing the specimens; it is not known if legs are shed in nature.

The stages of *X. macrocarpae* can be distinguished without detailed examination if microscope slides are made of the legless stages. The following characteristics are sufficient to distinguish stages (see also fig. 2). Second stage males sometimes resemble early third stage females. Anal tube size may be used to help classify ambiguous specimens of these two stages. Body-length measurements are from at least 10 specimens, except that only five adult females were measured.

Crawler (females and males): Length 0.7 to 0.8 mm; legs, six-segmented antennae, and mouthparts present. Oblong body.

Settled crawler (females and males; same stage as crawler): Like crawler but plumper, oval. Legs usually lost except coxae and trochanters.

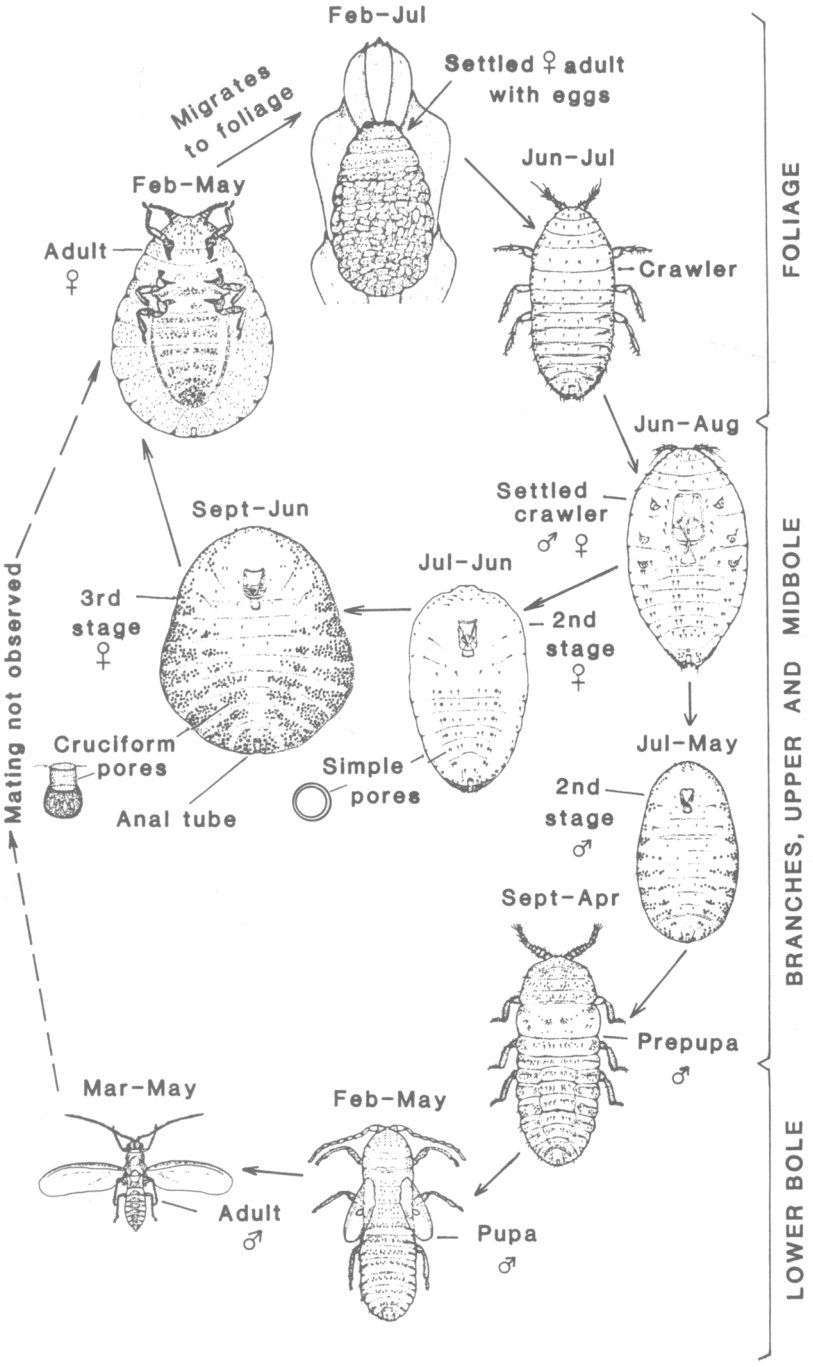


Fig. 2. Life history of *Xylococculus macrocarpae* on 6- to 25-cm dbh incense cedar at Blodgett Forest, El Dorado Co., Calif.

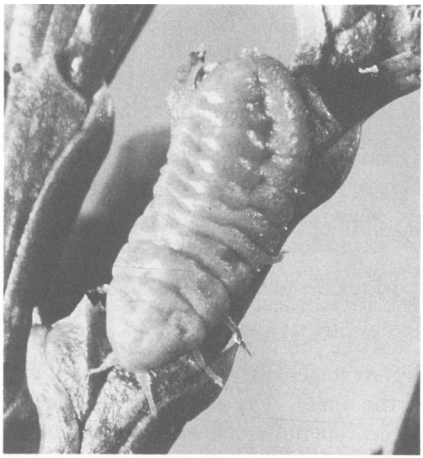


Fig. 3. *Xylococculus macrocarpae* adult female.

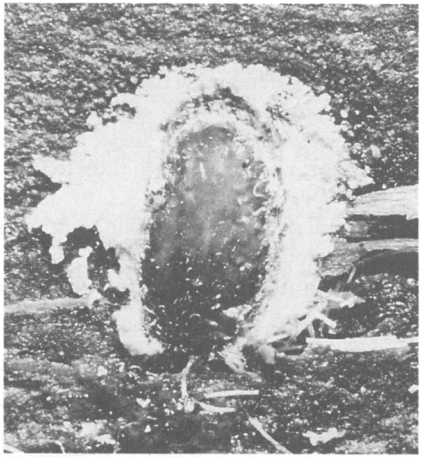


Fig. 4. Legless stage of *Xylococculus macrocarpae* with wax deposit. Outer bark of incense cedar has been removed.

Fig. 5. *Xylococculus macrocarpae* male prepupa with surrounding filamentous wax removed.

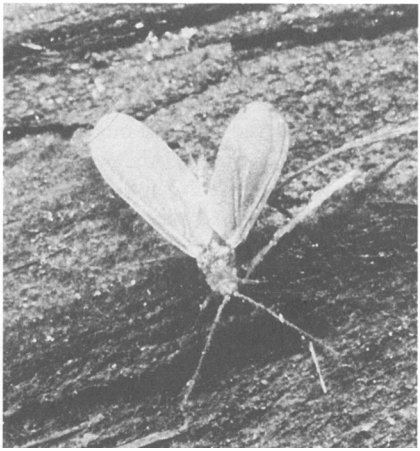


Fig. 6. *Xylococculus macrocarpae* adult male.

Female second stage: Length 1 to 2.1 mm; no legs; antennae indicated only by small lobes bearing a cluster of setae; mouthparts present; few or no cruciform pores; pores all lateral except two longitudinal rows of simple pores on abdomen.

Female third stage: Length 1.5 to 4.5 mm; similar to second stage, but with many cruciform pores laterally and extending in rows, usually more than one pore deep, across abdomen; anal tube length 0.15 to 0.25 mm (see fig. 7, pg. 9).

Female adult: Length 4.4 to 5.3 mm (actual range probably greater); legs; nine-segmented antennae present; stout. Abdomen infolded ventrally. No filamentous wax surrounding this stage. When settled on foliage, thorax shrinks, abdomen forms sac around eggs, often with dark brown lines laterally.

Male second stage: Length 1 to 3 mm; no legs; antennae indicated only by lobes bearing a cluster of setae. Some specimens similar to early female third stage; cruciform pores extending across abdomen, but rows less dense than in the female, often only one pore deep. More elongate shape than female. Last three abdominal segments usually sclerotized late in stage; anal tube and spiracles smaller than those of female third stage; anal tube length 0.09 to 0.15 mm.

Male prepupae: Length 3.1 to 3.8 mm; legs; nine-segmented antennae present. Body more slender than female adult; with longer, finer setae; often covered with mass of filamentous wax.

Male pupae: Length 2.8 to 3.4 mm; legs; 10-segmented antennae, and wing pads present.

Male adult: Legs; 10-segmented antennae, and one pair of wings present.

Circular, flat wax deposits surrounded the legless stages laterally, and often remained prominent in areas where birds had removed the scales. Wax associated with legged male prepupae, pupae, and adults was a mass of delicate fluffy filaments over the scales.

The four female and five male stages observed here for *X. macrocarpae* contrast with five stages for each sex observed by Florence (1917), and with five female and six male stages reported for *X. betulae* by Hubbard and Pergande (1898). No second-stage legged male like that described by Hubbard and Pergande was found between the crawler and the legless male stage in *X. macrocarpae*. For females, only two legless stages were observed in this study, compared to three in the life histories described by Florence (1917) for *X. macrocarpae,* and by Hubbard and Pergande (1898) for *X. betulae*.

Molts observed in slide-mounted specimens helped determine the sequence of *X. macrocarpae* stages. All molts were observed except that between male prepupa and pupa, and between pupa and adult. These molts were probably not seen on slides because fewer legged stages were mounted, as they could be distinguished without mounting. No other molts were seen in examining the more than 3300 specimens slide mounted in this study, about 2300 of them legless stages.

Anal tube measurements (length and width) were made to confirm that there are only four female and five male stages in *X. macrocarpae* collected from incense cedar. Unlike most scales, *Xylococculus* possesses an indented and sclerotized anal tube (fig. 2). In molts observed before shedding of the exuvium, the anal tube of the new stage could be clearly seen inside the previous stage, forming around the old anal tube. Thus, anal tubes are larger in successive stages, and, like head capsules in other insects, are less variable in each instar than overall body size of these soft-bodied insects. (For use of head capsules to determine instars in other insects, see Fox et al. 1972, Parker and Moyer 1972, Hoxie and Wellso 1974, VanDerwerker and Kulman 1974; but for cautions on this method see Kishi 1971 and Schmidt et al. 1977.) Anal tubes should fall into a single size group for scales of one instar, with differences between succeeding instars.

For males, anal tube dimensions of slide-mounted just-hatched crawlers were compared to those of settled crawlers eclosing to male legless stages. These would have to be separate stages if there are two male legged stages before the legless stage as described by Hubbard and Pergande (1898). Mean anal tube measurements for recently hatched crawlers ($\bar{x}$ length = 0.036 mm, SD = 0.002; $\bar{x}$ width = 0.025, SD = 0.001, n = 17) were not significantly different from those of crawlers molting to legless males ($\bar{x}$ length = 0.036, SD = 0.002; $\bar{x}$ width = 0.026, SD = 0.001, n = 5).

Since only a few crawlers were found in the molting process, the numbers are too low to provide conclusive evidence, but suggest that these scales are all one stage. Hubbard and Pergande described the crawler of *X. betulae* with six antennal segments and the next stage with seven. *X. macrocarpae* specimens examined all had six segments (counts were made on 11 crawlers and the four molting settled crawlers available with intact antennae). From this evidence, the presence of a second male legged stage following the crawler is unlikely.

For females, legless second stage specimens were homogeneous in appearance. However, third stage specimens exhibited considerable variation in body size and in number of cruciform pores extending across the abdomen; an undetected legless stage would most likely have been classified with that stage. Anal tube length was plotted against body length to illustrate the difference in overall size of the two stages as well as the difference in anal tube size (fig. 7). Anal tube measurements fell into two groups, with no evidence of a third stage.

The number of stages of *X. macrocarpae* found in this study falls within a range reported for other members of the subfamily Xylococcini. From three to five female stages and four to six male stages have been reported, with males having from one to three more stages than females (references in Tait 1986). At least some of this reported variation may be due to the difficulty in accurately determining the number and sexes of stages (Morrison 1928).

For *Xylococculus*, what Hubbard and Pergande (1898) described as a second male legged stage for *X. betulae* may have been the settled crawler. Florence (1917) did

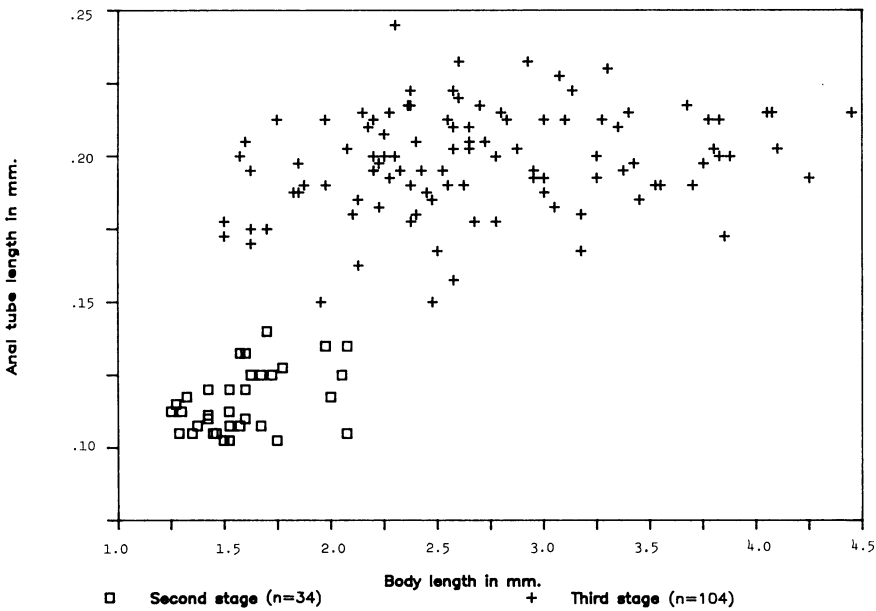


Fig. 7. Anal tube (AT) length of *Xylococculus macrocarpae* legless females (second and third stages), plotted against body length. Second stage AT length: $\bar{x}$ = .12 mm, SD = .01, range .10-.14, n = 44. Third stage AT length: $\bar{x}$ = .20 mm, SD = .02, range .15-.25, n = 112. AT means are based on more specimens than appear in the graph.

not find this stage in *X. macrocarpae, X. quercus, or X. alni.* Differences among the three legless female stages described by these authors are small and mostly of degree. Thus, it is not certain that the number of stages differs between *X. macrocarpae* on incense cedar and the *Xylococculus* species studied by Hubbard and Pergande (1898) and Florence (1917).

Scale phenology and within-tree distribution of stages. Distribution and phenology were similar on the small and large trees, so they were only diagrammed for the small tree, on which all stages were distinguished. Adult females were found on the foliage from early spring until early summer (fig. 1). They laid eggs beneath the abdomen, which formed a protective cover over the eggs after the adult died. The thorax shrivelled and became inconspicuous.

Crawlers were present in spring and early summer, and settled mostly on branches and the upper and middle boles, where they molted to legless stages. Females overwintered as second and third stages, and males as second stages and prepupae. Eclosed female adults were found in substantial numbers on bole and branches for only a short time, as they evidently migrated to the foliage soon after eclosion in spring. Similarly, male prepupae evidently moved lower on the bole once they emerged. Male pupae and adults were found only on the middle and lower boles. (These two male stages were found on the middle bole on only two dates and do not appear in the life history diagram on midbole since those were isolated collection dates.) Irregularities in the life history diagram, such as the disappearance and reappearance of second stage females, are probably due to between-tree variation in phenology and distribution of stages in these single-tree samples.

Lower crown branches from the over 30 cm dbh tree fit the pattern observed on the other trees, with adult females moving to the foliage and relatively few male legged stages present. Observations of trees this size indicate that larger diameter boles, where the bark is ridged rather than flaky, are unsuitable for the scale.

X. macrocarpae phenology could be related to physiological time, measured in degree-days, after further years of field sampling (Arnold 1959, Gordon and Potter 1988, Potter et al. 1989), with samples taken weekly during periods of interest.

New-generation female adults and male pupae first appeared in samples in early February 1986; the previous collection was in late November 1985 (fig. 1). The early appearance of these stages suggests that the scale may not diapause during winter. Most insects probably enter diapause where winters are too cold for development (Chapman 1969), but for some scale insects development continues where winters are mild (Beardsley and Gonzalez 1975). Host tree activity may also continue in winter. Photosynthesis, dry weight increases, and cambial activity have been recorded in conifers during winter (references in Savidge and Wareing 1982). Observations suggest that in Utah the black pineleaf scale (*Nuculaspis californica*) feeds during late winter and early spring when daytime temperatures rise above freezing. However, no increase in size of that overwintering scale was found before mid-April (Edmunds 1973).

Winters are mild at Blodgett Forest. During the coldest months of December through March, daily minimum temperatures average 0° to 1°C per month, with below freezing temperatures some nights. In 1985-86, daily minimums averaged 1° to 4°C by month from November to March; below-freezing temperatures occurred on some nights each month from October through May (unpublished climatological data, Blodgett Forest). More frequent sampling would be necessary to determine whether *X. macrocarpae* feeds and develops during these mild winters. Local temperature

effects on scales can be strongly influenced by topography and even small elevation differences (Edmunds 1973), so winter activity and survival of *X. macrocarpae* may be site-specific.

Comparison with Xylococculus collected from other hosts. In this study, a small number of specimens were collected from Monterey cypress and Rocky Mountain juniper. Apparently *X. macrocarpae* has not been reported from Rocky Mountain juniper before. Additional specimens were examined that were previously collected by others at various sites in California from Monterey cypress, incense cedar, hosts described only as cedar, and *Cupressus sargentii* Jeps. Some adult females had multilocular pores ventrolaterally, on the nonindented area of the abdomen, while others lacked these pores. Specimens lacking such pores included three adult females collected from incense cedar in this study and seven collected in other areas within the main range of incense cedar with host recorded as incense cedar (five specimens) or cedar (two specimens).

All other adult female specimens examined had multilocular pores ventrolaterally. These included six specimens from Monterey cypress (one from this study, five from other collectors), two from *Cupressus sargentii*, the two specimens from Rocky Mountain juniper, and three specimens collected at the southernmost part of the main range of incense cedar. Piute cypress, *Cupressus nevadensis* Abrams, is found in the last area (Griffin and Critchfield 1972), so those specimens were not necessarily from incense cedar.

The specimens examined suggest possible differences between *Xylococculus* from incense cedar and from *Cupressus* and *Juniperus*. Such differences may be genetic or host induced (Miller and Kostarab 1979). However a larger number of specimens from the different hosts would have to be examined to clarify the distribution of this and other characteristics of *Xylococculus,* and to determine if more than one species is involved.

Parasitoids. Parasitoids were observed only in *X. macrocarpae* legless stages. Parasitized scales first became sclerotized laterally, the sides of their bodies forming a darkened ring. Later, up to six larvae per scale became visible inside (fig. 8). Two species of Hymenoptera were reared from parasitized scales. *Parechtrodryinus xylococculi*

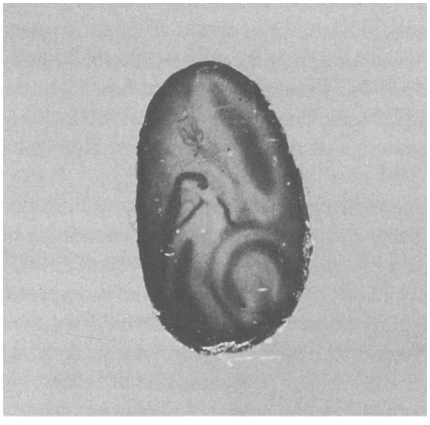


Fig. 8. Parasitized *Xylococculus macrocarpae.*

Beardsley and Gordh (Encyrtidae) was previously undescribed, although it had been collected before (Beardsley and Gordh 1988). A pteromalid, *Mesopolobus* sp., may be a hyperparasite.

The earliest parasitoid larvae observed were found in three early second stage scales, not visibly parasitized without magnification, when they were examined microscopically as slide mounts. Because the process of making the slides involved making an incision and pumping out body contents, many more such larvae may have been lost. Two of the larvae were found in July and August, one in a second stage scale still inside the intact crawler exuvium. Thus, the scales may be attacked in summer as early second stages or even as crawlers.

No parasitoids were visible without magnification in November, but by February, 31% of the legless scales collected were visibly parasitized (Tait 1986). Unparasitized scales molted to mobile stages and moved off the bole and branches in spring and early summer; parasitized scales evidently did not molt to legged stages and remained behind. Thus, percent parasitization of the old generation legless stages tended towards 100% in early summer (Tait 1986).

The largest number of parasitized scales was collected on May 27, 1985. Peak emergence in the laboratory of *Mesopolobus* sp. from that collection occurred at least 1 week before peak emergence of *P. xylococculi.* From 231 parasitized scales collected on that date, 78 *Mesopolobus* and 134 *P. xylococculi* emerged.

Hymenopterous parasitoids are rare in the Margarodidae (Rosen and DeBach 1978). The superfamily Coccoidea is divided into two groups. The Archaeococcoidea, composed of Margarodidae and Ortheziidae, have abdominal spiracles and are considered the more primitive group. All other families lack abdominal spiracles and are classified as Neococcoidea (Howell and Williams 1976).

Although the Neococcoidea contain many primary parasitic hosts, few hosts are reliably recorded from the Archaeococcoidea, and it is thought that the Hymenoptera/scale association developed after the two groups separated (Rosen and DeBach 1978). Encyrtidae have a broad host range; however, only a few have been reported from archeococcids and these have been associated with the relatively specialized Monophlebinae. The occurrence of an encyrtid attacking the Xylococcinae, one of the most primitive coccid groups, is therefore of interest (Beardsley and Gordh 1988).

Density of scales and associates. The density of scales and other arthropods was examined from November to March, the period when Morrison et al. (1985) found that insectivorous birds increase foraging on incense cedar boles and branches. Our interest was where *X. macrocarpae* was most available, and how its numbers compared to other prey. During these months, scale density was less on the lower bole than on the middle and upper boles and branches of the small trees sampled (table 1). The pattern was similar all year.

The three winter samples from larger trees (15 to 25 cm dbh), indicated that scale density also decreased going down the bole, but the decrease tended to occur higher on the larger trees. As trees get larger, the area of flaky bark suitable for scales is confined to progressively higher portions of the bole, so it is to be expected that lower areas have fewer scales than they do on smaller trees. On all trees, scale density also decreased to almost zero where the bark of the upper bole became smooth, with few flakes except at branch nodes. However, most upper bole samples fell below this area.

The most common other insects, probably predators, found under the bark were a Coleoptera larva, *Eronyxa expansus* Van Dyke (Trogossitidae), and snakefly larvae,

TABLE 1. WINTER (NOVEMBER TO MARCH) DENSITY OF *XYLOCOCCULUS MACROCARPAE* AND ARTHROPOD ASSOCIATES COLLECTED ON 6-10 CM DBH INCENSE CEDAR AT BLODGETT FOREST, EL DORADO CO., CALIF. MEANS OF DENSITY PER DM^2, WITH RANGE IN PARENTHESES, ARE OF SIX DATES, WITH ONE TREE SAMPLED PER DATE

	X. macrocarpae	Associates*
Branches	18.2 (4.7-40.7)	0.06 (0-0.33)
Upper bole	19.0 (0.7-62.1)	0.15 (0-0.73)
Mid-bole	20.5 (1.1-37.7)	1.0 (0-2.5)
Lower bole	3.8 (1.1-6.9)	1.2 (0.3-2.2)

*Mostly Trogositids and Raphidids.

Agulla sp. and *Inocella* sp. (Neuroptera: Rhaphidiodea). Since the larva of *Eronyxa* has not previously been associated but is of taxonomic importance to the higher classification of Cleroidea, it is characterized below. Samples were not handled in a way to ensure that insects loose on the bark surface were captured, so other arthropods may have been lost.

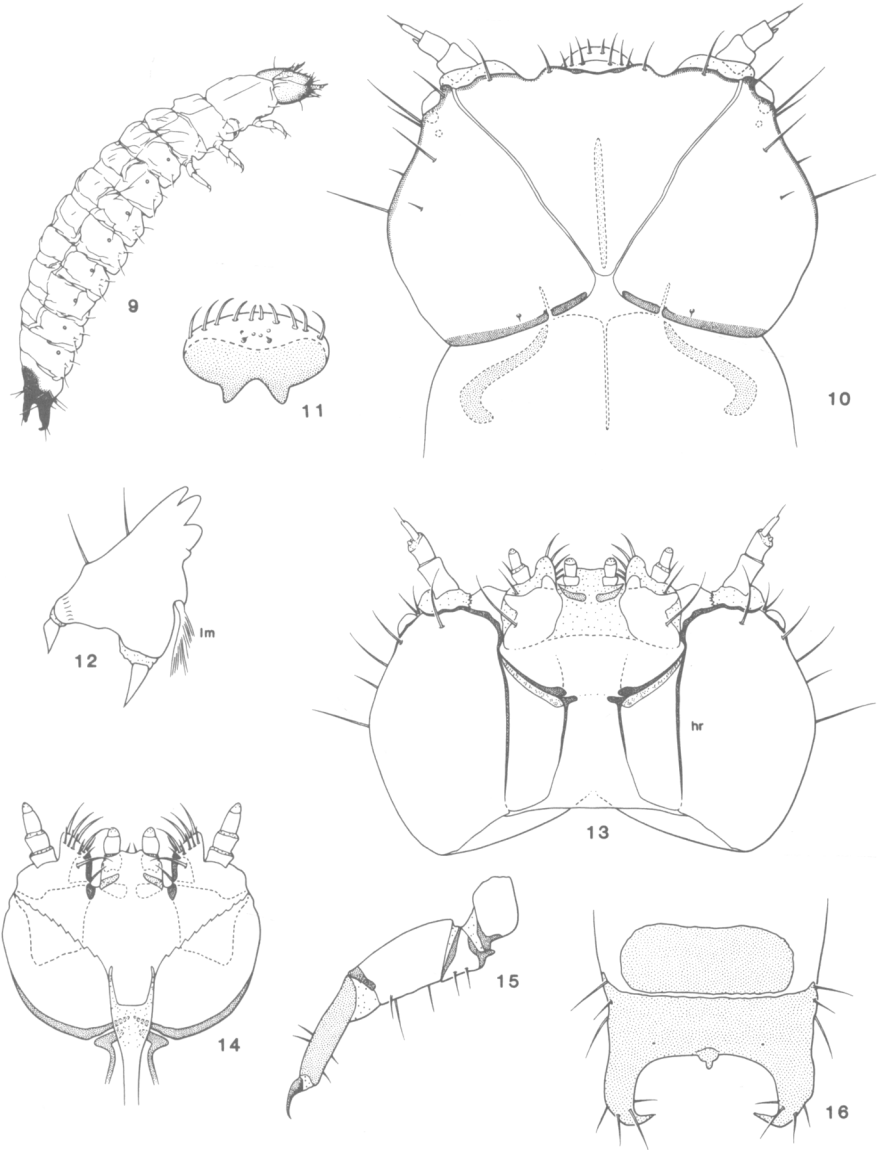
For the small-tree samples, nonscale arthropods beneath the bark were few on branches and upper bole in winter (table 1). Their density increased on the middle and lower bole, but was on average still considerably lower than that of *X. macrocarpae*. This pattern was similar year round. However, for some nonwinter samples, mostly from the lower bole, the number of associated arthropods equalled or exceeded that of scales. For the large tree, numbers of associates were also low all year.

The figures in table 1 give only a general indication of density patterns. However, they suggest that *X. macrocarpae* is the chief prey under bark, at least on the middle and upper boles and branches of 6- to 25-cm dbh trees. Morrison et al. (1985) observed that birds preferred small incense cedar (less than 30 cm dbh) for winter foraging at Blodgett Forest. Smaller cedar were used in winter than in summer. The authors suggested that smaller trees have thin bark, which is easily scraped off by small billed birds in winter, when prey on the bark surface are less available. Our data indicate that prey may be less available beneath the bark of larger diameter boles, as well as harder to reach.

Description of the larva of Eronyxa expansus Van Dyke (figs. 9 to 16). Late instar larva (fig. 9). Length 8.5 to 11.2 mm. Body flattened, gradually broadened to about abdominal segment six or seven; head, protergum, and parts of legs pale yellow to tan, weakly to moderately sclerotized; ninth tergum dark brown, strongly sclerotized; remainder white, membranous.

Head (figs. 10 and 13) strongly flattened, prognathous; smooth, pale tan except for dark-brown or black mandibles, margins of anterior foramen, gular and paragular sutures, and dorsal rim of occipital foramen. Head capsule almost twice as broad as long; lateral margins strongly rounded. Epicranial stem absent, frontal arms V-shaped, extending to anterior foramen just above antennae; median endocarina extending about three-fifths from occipital foramen to labrum. Lateral stemmata 2; larger anterior stemma with domed lens, smaller posterior one without lens. Antenna with three segments of subequal length, retractable (shown extended in figures); appendage of segment two conical, about one-fourth length of segment 3.

Frontoclypeal suture absent; labrum free with three pairs dorsal setae; epipharynx



Figs. 9 to 16. Eronyxa expansus larval features. 9, Last instar larva. 10, Head and anterior prothorax, dorsal; endocarina (medial) and internal comma-shaped sclerites are shown dashed and densely stippled; heavily sclerotized anterior and anterolateral cranial margins are densely stippled, membrane lightly stippled. 11, Epipharynx; stippled area is sclerotized. 12, Right mandible, ventral; lm indicates lacinia mobilis. 13, Head, ventral; dense stipple indicates baculi and other heavily sclerotized regions; light stipple indicates membrane; hr indicates hypostomal rod. 14, Maxillolabial complex, dorsal; serrate lines indicate sectioned cuticle, other conventions as before. 15, Right metathoracic leg, anterior. 16, Abdominal segments 9 and 10, dorsal.

Scale line as follows: fig. 9: 2.2 mm; figs. 10, 13: 0.36 mm; figs. 11, 12, 14: 0.25 mm; figs. 15, 16: 0.7 mm.

(fig. 11) sclerotized, pigmented posteriorly, membranous anteriorly, with five pairs hairlike setae, four annular sensilla, and two very small conical sensilla. Mandibles (fig. 12) with two apical teeth, one large and one small subapical tooth, two lateral setae and plumose, posteriorly directed lacinia mobilis; mola absent. Maxillolabial complex (figs. 13 and 14) about as long as gula; cardo and stipes poorly differentiated; maxillary articulating area absent. Stipes and mala with irregular ventral sclerite extending medially as two dark, strongly sclerotized plates (fig. 14); mala rounded with medial row of about five long, stout setae, dorsal row of four shorter setae, and single stout seta near basal plate; palp 2 segmented. Labium submembranous with segmentation indistinct; labial palps 2 segmented with crescentic palpiger sclerite extending onto dorsal surface (fig. 14); ligula with pair of minute setae anteriorly. Gular sutures diverging posteriorly, expanded anteriorly as condoyles for maxillolabium; hypostomal rods parallel, briefly curved near occipital foramen.

Protergum with sclerotized plate with medial suture; paired, apostrophe-shaped plates situated anterolaterally just beneath tergum and articulated with posterior rim of head capsule (fig. 10). Prosternum with longitudinal, weakly sclerotized plate extending posteriorly from gula, becoming indistinct posteriorly. Mesothorax and metathorax membranous. Legs (fig. 15) similar; coxa globular, trochanter subtriangular with two setae, femur and tibia subcylindrical with few scattered setae; femur and trochanter whitish except for articulatory areas, tibia pale tan; claw simple, darkly pigmented.

Abdominal segments 1 to 8 membranous, with one pair of setae dorsally near posterior margin, one pair posterodorsad of spiracles, three pairs on lateral prominence posteroventrad of spiracles, and three pairs ventrally near posterior margin. Segment 9 (figs. 9 and 16) with tergum consisting of strongly sclerotized anterior ovoid plate and stout, incurved urogomphi with sharply attenuate apices; urogomphal plate with median tubercule with papillate apex. Spiracles annular, nearly equal in size.

Material examined. Numerous larvae, probably of ultimate and penultimate instar, from California, El Dorado County, Blodgett Experimental Forest (near Georgetown), collected between March 2, 1985, and July 12, 1986. One adult was reared from field-collected larvae. As described, all larvae were found on *Calocedrus decurrens*, in association with *Xylococculus macrocarpae*, upon which they apparently feed.

Crowson (1964, 1966, 1970) included *Eronyxa* in Peltidae (= Peltinae of Lawrence 1982) on the basis of adult characteristics. Placement in Peltidae is supported by the distinct mandibular mola, as well as several other features, such as form of the antennal club, maxilla, and procoxa, and the presence of two tibial spurs on the forelegs. However, most of these features are subject to exceptions, which is clear from Crowson's (1964, 1970) keys, and subfamily membership is based primarily on mandibular configuration. Furthermore, examination of various species of *Eronyxa* shows that the foretibiae possess a single apical spur. Fixed spines on the tibial rim often appear to be a second spur.

Eronyxa (= *Ostomodes*) was further classified in Crowson's (1964, 1966) peltid subfamily Decamerinae, which was characterized by the coarsely tuberculate mandibular mola and the presence of a spine on the inner edge of the lacinia (rather than on its apex). Most of the other genera included in Decamerinae are South American, and differ from *Eronyxa* in several features, such as the bifid tarsal claws (simple in *Eronyxa*), and the asymmetrical antennal club (symmetrical in *Eronyxa*). Lawrence (1989) questions the placement of *Eronyxa* in Decamerinae, but without specifying reasons.

Crowson (1964) briefly described a larva that he attributed (without positive association) to the Chilean decamerine genus *Diontolobus*. This larva agrees with that of *Eronyxa* in having a plumose lacinia mobilis, but differs in many other features, including the gross shape of the mandibles, the form of the ninth tergum, and in having biforus spiracles (simple in *Eronyxa*).

Thus, both adult and larval characteristics suggest that *Eronyxa* does not belong in Decamerinae. Moreover, the features of its larva agree almost perfectly with those of known Trogossitidae–Lophocaterinae (characterized by Crowson 1970, and separated as the family Lophocaterinae). The following similarities appear to be synapomorphies: (1) head with a larger anterior and smaller posterior stemmata on each side; (2) antennae retractile, with sensory appendage of segment 2 small, conical; (3) mandibles with two, subequal apical teeth and backwardly projecting, plumose lacinia mobilis; and (4) tergum of segment 9 divided transversely into an anterior oval portion, and a strongly sclerotized posterior portion bearing large urogomphi and medial tubercule.

A number of features listed as diagnostic for Lophocaterinae apparently do not occur in *Eronyxa*. These are: (1) tubular, coiled glands opening posteromesad of spiracles on abdominal segments 1 to 8; (2) meso- and metatergal sclerotizations (only the protergum of *Eronyxa* is sclerotized); and (3) bicameral spiracles. The spiracles of *Eronyxa* appear to be simple annuli. However, the abdominal glands are very difficult to detect and annular spiracles apparently occur in some other Trogossitidae (sensu lato) (Lawrence 1989).

Without commenting on the limits or relationships of Decamerinae, it seems certain, based on larval characters, that *Eronyxa* properly belongs in Lophocaterinae. This transfer requires practically no changes in Crowson's (1970) diagnosis of adults. Only the few changes discussed above are required in the diagnosis of larvae.

Adults of most species of *Eronyxa* are commonly found on flowers of shrubs such as *Ceanothus* and *Prunus*. where, judging from gut contents, they feed on pollen. *Eronyxa expansus*, however, is very uncommon in collections, being known from only 11 specimens at the time of Barron's (1971) revision. The only ecological information available from these and seven additional adults that we have examined includes three collections from beneath bark of *Calocedrus decurrens*, a single record "sweeping *Ranunculus*," and one from unspecified foliage. It therefore seems very unlikely that *E. expansus* is floricolus as an adult. No gut content examinations were made.

Nearly all collection records of *E. expansus* are from within the range of *Calocedrus decurrens*. This suggests that this species is restricted to feeding on *Xylococculus*. The single exception is labeled Panamint Mountains, Inyo County, which could indicate either an error or an additional host. Other species of *Eronyxa* have geographic ranges broader than that of *Calocedrus*, and may have different larval feeding habits.

CONCLUSIONS

The number of stages observed for *X. macrocarpae* on incense cedar, based on the large number of specimens collected in this study, differed from the number of stages reported for the insect on Monterey cypress, and fell within a wide range reported for related scales (references in Tait 1986). Further study of *X. macrocarpae* on Monterey cypress would be necessary to determine whether there is a difference in number of

stages in the two hosts. *X. macrocarpae* located under the loose flaky bark of incense cedar was less cryptic than on Monterey cypress, where it lies buried in layers of bark (Florence 1917). It may thus be more available as prey for insectivorous birds than it is on Monterey cypress. *X. macrocarpae* moved extensively within incense cedar trees seasonally; such movement was not reported for *X. macrocarpae* on Monterey cypress, and rarely reported for closely related margarodids (references in Tait 1986).

This study suggests that density of *Xylococculus macrocarpae* is high compared to the density of other arthropods living beneath incense cedar bark. In winter, when insectivorous birds forage intensively on small incense cedar (Morrison et al. 1985,1989), the scale was most dense on branches and middle and upper boles of the small (6 to 25 cm dbh) incense cedar sampled. More extensive sampling would be necessary to quantify density of *X. macrocarpae* and other arthropods beneath bark. Grouping legless stages by size would give an indication of biomass available for birds and eliminate the time-consuming process of making slide mounts.

This study suggests that there are differences in scale distribution patterns among trees of different sizes below 30 cm dbh, with scales concentrated on smaller diameter trunk areas regardless of tree size. Scale populations may also be dense on the upper bole of trees larger than those included in this study. Thus, future scale studies should quantify density on different tree sizes as well as in different areas within trees. Bird studies that examine foraging patterns within trees, as well as between trees of different sizes, would help correlate foraging patterns with prey density.

Scale density may be affected not only by incense cedar size but also by the characteristics of the surrounding forest; dense stands may favor high scale populations. Thus, scale density should be quantified in stands under different types of management, especially different stocking levels.

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