

PUPIFORM LARVAE IN THE PHYLLOXERIDAE (HOMOPTERA: APHIDOIDEA)

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Abstract.—The existence of an unusual developmental form, here named a pupiform larva, in the life cycle of sexual males and females (sexuales) of the Phylloxeridae (Homoptera: Aphidoidea) is demonstrated for the first time to occur in five species of phylloxerans and is confirmed in a sixth species. Attention is called to erroneous reports on the development of the sexuales in the Phylloxeridae and to the total lack of information in textbooks on the existence of this unusual developmental form.

The Phylloxeridae, Aphididae, and Adelgidae constitute the superfamily Aphidoidea (Homoptera). In the Phylloxeridae the characteristic development of stem mothers (fundatrices) and apterous and alate females is hemimetabolous with progression through five instars, all of which feed and move about. The development of the sexual males and females (sexuales), however, is holometabolous rather than hemimetabolous; but they also go through five instars. Unusual development in the larval instars of the sexuales was reported in 1875 by Balbiani who worked on the grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), in Europe; and Maillet (1957) gave an excellent review of the early publications on the sexuales of the grape phylloxera. Nevertheless, the report of this unusual developmental form subsequently has gone unnoticed in texts on morphology, physiology, and phylogeny. Detailed studies of the biological development of phylloxerans have been conducted in the United States by Pergande (1904), Whitehead and Eastep (1937), and Caldwell and Schuder (1979); however, they have all incorrectly stated that the sexually mature males and females hatch directly from eggs. This report is being presented to demonstrate for the first time the occurrence of holometabolous development in sexuales of five species in the Phylloxeridae and to confirm the occurrence in a sixth species.

In 1978 I began a detailed study of the biology and morphology of the species of *Phylloxera* on pecan, *Carya illinoensis* (Wangenheim) C. Koch (Stoetzel, 1981). This study was soon expanded to include observations on field populations of six species of gall-forming *Phylloxera* (*P. caryaecaulis* Fitch, *P. caryaevenae* (Fitch), *P. deplanata* Pergande, *P. devastatrix* Pergande, *P. notabilis* Pergande, and *P. russellae* Stoetzel). I noticed the unusual larval development while observing molts of the various stages within the galls. Sexuparae were collected and isolated in small stender dishes where most readily laid eggs. The color (white, yellow, or yellowish green) and number (up to 25) of eggs depended on the species involved.

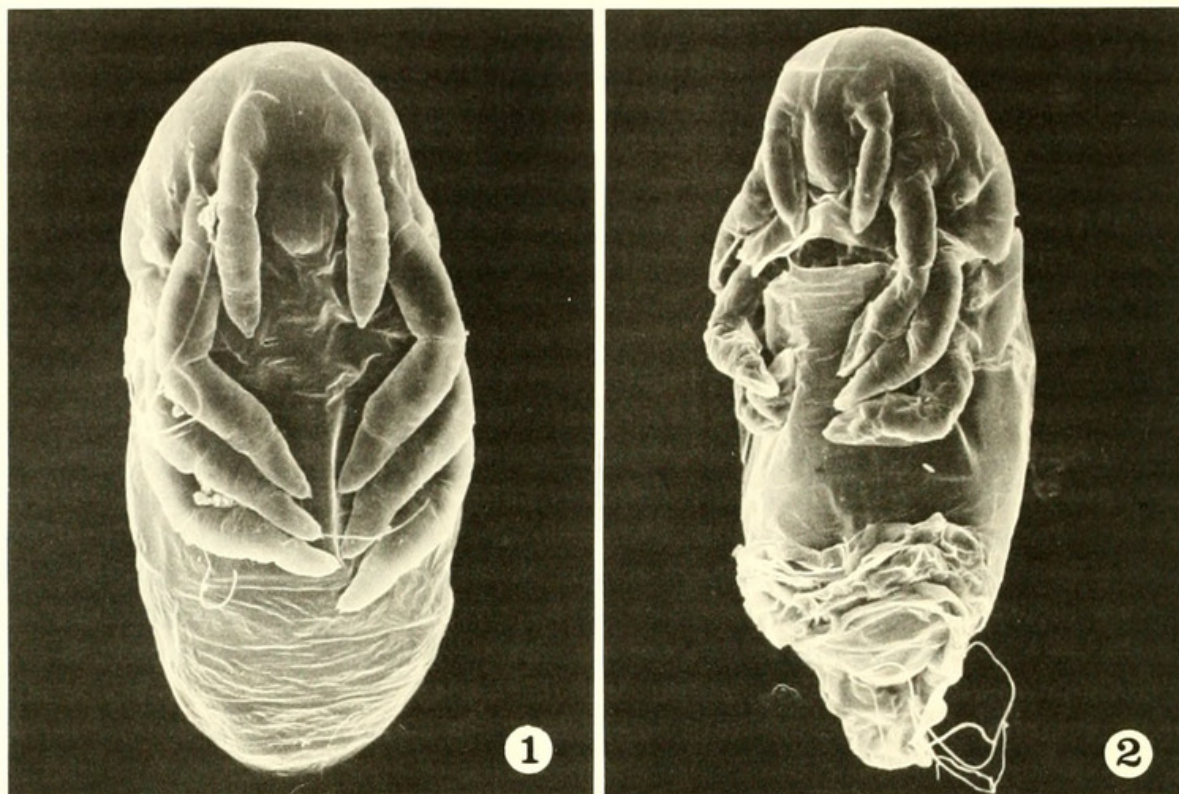


Fig. 1. Scanning electronmicrograph of a pupiform larva (*Phylloxera notabilis*) that has just hatched.

Fig. 2. Scanning electronmicrograph showing the layered exuviae that have accumulated at the posterior end of the pupiform larva (*Phylloxera notabilis*). The specimen has molted three times while remaining in place and "standing on end."

In three to four days a dark eclosion line between the two red eye spots was visible through the chorion. Pergande (1904), Whitehead and Eastep (1937), Maillet (1957), and Caldwell and Schuder (1979) all reported that the eggs were of two sizes with the larger eggs producing sexual females and the smaller eggs producing sexual males. However, all but Maillet reported that larger sexuparae lay only large eggs and therefore produce only females while the smaller sexuparae lay only smaller eggs and therefore produce only males. While larger sexuparae did lay more eggs than smaller sexuparae, in all of the six species studied, both sexual males and sexual females were produced by both the larger and the smaller sexuparae. By the fourth or fifth day after the eggs had been laid, they hatched into developmental forms which I call pupiform larvae (Fig. 1). They lacked mouthparts, often stood vertically on the substrate, and moved in undulating motions as they molted. Each pupiform larva molted four times, and the exuviae piled up in circular layers at the posterior end of the insect (Fig. 2). Between molts, the pupiform larvae do not feed, since they have no mouthparts; and they do not exhibit any apparent change in size or shape. At the final molt the sexuales are produced. Adult sexuales are larviform, without any indication of wingpads, and lack a rostrum; but they are quite active.

After mating, each sexual female (ovipara) produces only one overwintering egg that fills her abdominal cavity but is usually laid (*P. caryaecaulis*, *P. caryaevenae*, *P. deplanata*, and *P. notabilis*). Occasionally, the overwintering egg is only partially laid and the female's body remains attached to the egg (*P. russellae*) or

the overwintering egg is retained within the female's body (*P. devastatrix*) which then shrivels around the egg. Development from an egg to a sexual male or female averages 7 to 10 days. Developmental time from the hatching of an overwintering egg to the deposition of an overwintering egg is approximately 50–60 days for those species developing in galls on species of *Carya*.

I believe that these pupiform larvae will be found in the development of the sexuales of all species in the Phylloxeridae.

In the Aphidoidea most of the sexual females (oviparae) are wingless. Sexuales of the Pemphiginae (Aphidoidea) resemble those of the Phylloxeridae in that both females and males are very small, are active, have no functional mouthparts; and the oviparae lay only one overwintering egg. But the Pemphiginae do not have pupiform larvae as far as is known. Only in the Phylloxeridae have these pupiform larvae been found, but their existence usually is unrecorded in biological studies and in texts on morphology, physiology, and phylogeny.

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