

# Apparent Parthenogenesis in *Pityophthorus puberulus* (Coleoptera: Scolytidae)<sup>1</sup>

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**ABSTRACT** No males were found among 559 specimens of *Pityophthorus puberulus* (LeConte) from several localities. No sperm was found in the spermatheca of 10 females taken from recently established galleries containing eggs and young larvae. This is the third record of thelytoky in a scolytid. The known distribution and environment of parthenogenetic populations of *P. puberulus* does not fit the usual patterns of distribution and environmental situations associated with parthenogenetic animals.

Few scolytid lineages have completely eliminated sexual reproduction. It is known or suspected that males result from unfertilized eggs (arrhenotoky) in species belonging to the distantly related inbreeding genera *Coccotrypes* (Herfs 1959), *Xylosandrus* (Entwhistle 1964) and *Araptus* (Wood 1978). In several *Ips* spp., females are produced asexually (thelytoky), but insemination is necessary to stimulate oviposition and embryo development (gynogenesis) (Hopping 1964, Lanier and Oliver 1966, Bakke 1968). Some females in an Israeli population of *Scolytus rugulosus* Ratzeburg (= *S. mediterraneanus* Eggers) reproduce asexually without the presence of males; breeding these with or without males yields broods composed entirely of asexually-reproducing female offspring (Gurevitz 1975).

We report here a probable third known instance of a thelytoky in the Scolytidae and the only known case in which the condition seems to be widespread.

*Pityophthorus puberulus* (LeConte) is a small (1.2 to 1.6 mm long) bark beetle inhabiting eastern North America from New Brunswick south to North Carolina and west to Minnesota and Kansas (Bright 1981). In our collecting sites in Indiana, Michigan, and Maine, we found this species to be the most common scolytid in dead twigs of native and exotic pines. *P. puberulus* also breeds successfully in spruces and firs (Bright 1981). The galleries are usually in small, damaged or broken leaders and terminal twigs, but also occur in branches up to 2 cm in diameter. Blackman (1919) observed occasional attacks in apparently healthy white pine twigs.

## Materials and Methods

Most of the gallery systems we examined were from Michigan or Indiana, but collections were also made in Maine and Massachusetts (Table 1). Numerous galleries in all stages of development were studied in twigs of *Pinus resinosa* Ait., *P. strobus* L., *P. banksiana* Lamb., and *P. virginiana* Mill. The outer bark was removed with a scalpel, and the gallery systems examined under a binocular microscope.

Adult beetles were sexed, either by dissection of specimens preserved in alcohol, or by examination of individuals cleared with lactophenol. Male internal genitalic

structures are sclerotized and easily seen in scolytids treated in either fashion.

The spermathecal pump and sac of females with offspring were examined for the presence of sperm. Ten females, taken from galleries containing both eggs and young larvae, were dissected under water. The spermathecae were removed, placed in a drop of water on a slide, squashed with a coverslip, and observed at 1000× magnification. Spermatozoa were visible in similar spermathecal squashes from breeding females of *Pityophthorus lautus* Eichhoff, *Hylesinus pruinosis* Eichhoff, *Xyleborus sayi* (Hopkins), and *Ips acuminatus* (Gyllenhal).

We attempted to induce breeding in females taken from their pupal cells, but these teneral individuals failed to bore into the white pine twigs presented to them.

## Results and Discussion

No males were found among 559 specimens examined (Table 1). The spermathecae of the 10 females with offspring were empty.

The absence of males in a collection of scolytid adults is not necessarily proof of thelytoky. For example, males may be absent from collections of parent beetles of those species in which males stay with females for only a short time (e.g., *Hylesinus*, *Phloeosinus*, and *Scolytus*.) Only females of species of *Xyleborus*, *Xylosandrus*, or *Hy-pothenemus* are taken in flight traps or found initiating galleries because males in these groups are wingless and remain in their natal galleries. Examination of progeny of only a few mothers in species with gynogenetic forms might also provide a long series of females.

The most straightforward evidence of thelytoky in *P. puberulus* is the lack of sperm in the spermatheca of reproducing females; this indicates that neither fertilization nor gynogenesis is occurring. The series of females we collected becomes equally convincing evidence of thelytoky when it is considered that 1) brood size is small (usually less than 10) and thus the beetles collected must have come from many different families, and 2) most of the individuals examined had not yet emerged (many were still teneral) and therefore should accurately represent the sex ratio of progeny.

The habits of *P. puberulus* contrast with those of most scolytids and may have a bearing on the origin of parthenogenesis in this species. Most *Pityophthorus* are harem polygynous. Gallery systems are begun by males,

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Table 1. Collecting data for *P. puberulus*

Locality	Date	Host	Females	Situation
MI: Washtenaw Co.	28 June 1978	<i>Pinus strobus</i>	7	Beginning galleries, ovipositing
MI: Livingston Co.	29 Aug. 1979	<i>P. resinosa</i>	1	Ovipositing
MI: Livingston Co.	29 May 1980	<i>P. resinosa</i>	4	Beginning galleries
MI: Livingston Co.	29 May 1980	<i>P. resinosa</i>	22	Beginning oviposition
MI: Gratiot Co.	23 Sept. 1980	<i>P. strobus</i>	10	Unemerged progeny
MI: Livingston Co.	11 Oct. 1980	<i>P. resinosa</i>	20	Unemerged progeny
MI: Livingston Co.	12 Oct. 1980	<i>P. resinosa</i>	5	Unemerged progeny
IN: Tippecanoe Co.	22 Feb. 1981	<i>P. strobus</i>	42	Unemerged progeny
IN: Tippecanoe Co.	11 Mar. 1981	<i>P. strobus</i>	84	Unemerged progeny
MI: Livingston Co.	12 Apr. 1981	<i>P. resinosa</i>	6	Unemerged progeny
IN: Clark Co.	17 June 1981	<i>P. virginiana</i>	46	Unemerged progeny
IN: Clark Co.	17 June 1981	<i>P. strobus</i>	9	Unemerged progeny
IN: Porter Co.	13 July 1981	<i>P. banksiana</i>	31	Ovipositing, some progeny
IN: Tippecanoe Co.	20 July 1981	<i>P. strobus</i>	14	Ovipositing
ME: Kennebec Co.	4 Aug. 1981	<i>P. strobus</i>	16	Unemerged progeny
ME: Kennebec Co.	4 Aug. 1981	<i>P. resinosa</i>	76	Unemerged progeny
ME: Kennebec Co.	9 Aug. 1981	<i>P. strobus</i>	127	Unemerged progeny
MA: Hampden Co.	3 Aug. 1981	<i>P. strobus</i>	39	Parents and unemerged progeny

and males may accumulate as many as 15 females in one gallery system (Bright 1981). In contrast, the galleries examined during the present study all contained solitary females. Bright (1981) also found that galleries of *P. puberulus* were occupied by only one individual, sometimes a male, more frequently a female. The galleries (Fig. 1) are irregular, quite unlike the galleries of polygynous species.

Among other Nearctic *Pityophthorus* harem polygyny is absent in some, but not all twig-nesting species. The species formerly placed in the genus *Myleborus*, such as *P. ramiperda* Swaine (Blackman 1928) are not harem polygynous, nor is the species *P. orarius* Bright. Females of the latter species lay only one or two eggs per twig, and males are only occasionally found accompanying reproducing females (Hedlin and Ruth 1970). In

the allied genus *Conophthorus* females initiate galleries in pine cones and often work unaccompanied (Lyons 1956, Ruckes 1958, Kinzer et al. 1970). It would seem that fine twigs may lead in some cases to the loss of polygyny in *Pityophthorus* and consequently to major alterations in male behavior. These changes probably occurred in *P. puberulus* before the acquisition of thelytoky.

The extent of the geographic range of parthenogenetic *P. puberulus* remains unknown. Aside from Bright's information (1981) on males occurring on spruce in Canada, there is no mention of males in discussions of the habitats of *P. puberulus* (Blatchley and Leng 1916, Blackman 1919, 1928, Dodge 1938, Chamberlin 1939, Beal and Massey 1945). This could be attributed either to the absence of males among the specimens observed

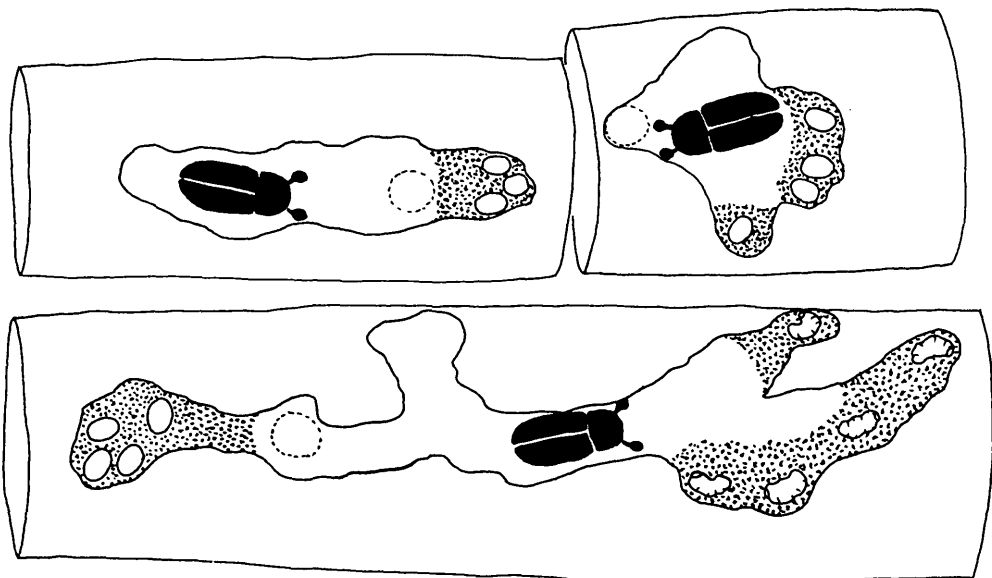


FIG. 1. Diagram of recently initiated gallery of *P. puberulus* in pine twig.

or failure to distinguish between the similar appearing sexes (Bright 1981).

Even with the limited information available, it appears that *P. puberulus* does not fit the geographic patterns of parthenogenetic groups. Glesener and Tilman (1978) note that asexual lineages frequently occur at the edge of the range of sexual progenitors or in populations introduced to new regions. They suggest that escape from parasites and predators in such geographic circumstances could allow the loss of genetic recombination; Jaenike (1978), Hamilton (1980), and Bremermann (1980) present rigorous models for the maintenance of sexuality via gene-for-gene interactions between parasites and hosts. A number of widespread Palearctic thelytokous weevils (*Otiorrhynchus*) and moths (*Solenobia*) are represented by relict, supposedly ancestral bisexual populations in unglaciated areas (White 1978). The wide distribution of the thelytokous forms is ascribed to their ability to rapidly colonize areas made available by the retreat of the Wurm glaciation (White 1978). The applicability of these hypotheses to *P. puberulus* cannot be judged without further information on the ecology of this species and its nearest relatives, but the following points can be made: 1) *P. puberulus* is not an introduced species, and there is no evidence that all the collecting sites are within recent range extensions. Pines were recently introduced into central Indiana, but the same is not true of the sites in Michigan, Maine, northern Indiana, and southern Indiana. 2) There is no obvious lack of natural enemies attacking *P. puberulus*. Four parasitoids (two pteromalids, one braconid, one bethylid), and one parasitic nematode were found attacking the bark beetle. However, too little is known to say whether or not these natural enemies are reasonable candidates for testing a biotic interaction model for the maintenance of sexuality. 3) Responses to genetic variability in hosts are not likely to be important in selecting against the parthenogenetic form as this species is basically a polyphagous scavenger. *Pityophthorus puberulus* seems to be one of the rare exceptions to the geographic trends for parthenogenesis reviewed by Glesener and Tilman (1978).

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