

OBSERVATIONS ON THE BIOLOGY OF *PARNASSIUS CLODIUS* (PAPILIONIDAE) IN THE PACIFIC NORTHWEST

DAVID V. McCORKLE

Division of Math and Science, Western Oregon State College,
Monmouth, Oregon 97361

AND

PAUL C. HAMMOND

2435 E. Applegate, Philomath, Oregon 97370

ABSTRACT. This paper examines the biology and life history of *Parnassius clodius* Menetries in the Pacific Northwest. Habitats used by the species include subalpine meadows high in the mountains and lowland rain-forests west of the Cascade Range. The primary larval foodplants belong to the genera *Dicentra* and *Corydalis* of the family Fumariaceae. Larvae in alpine habitats often display a gray-brown camouflage pattern that blends with the rocks of the habitat. However, larvae in lowland rain-forests display a conspicuous black and yellow-spotted pattern that appears to mimic the warning colors of polydesmid millipedes. Larval development in lowland habitats is completed within a single year, and pupation takes place inside a strong, well-formed silken cocoon. Male butterflies display a "rape" type of mating, with no evidence of courtship behavior or sexual pheromones. Tough, tear-resistant wings and a large female sphragis may be related to this sexual behavior.

Parnassius clodius Menetries belongs to a genus that is considered to be relatively primitive within the Papilionidae (Tyler, 1975). These are the only butterflies that have a moth-like pupa enclosed within a silken cocoon. Because of the putatively "primitive" nature of these butterflies, their life history and ecology is of considerable interest. Of the three species of *Parnassius* found in North America, only *P. clodius* is uniquely endemic to this continent and is widely distributed in the western mountains from southern Alaska to central California, western Wyoming, and northern Utah (Ferris, 1976). Some details of the life history and ecology of this species are outlined by Edwards (1885), Tyler (1975), and Dornfeld (1980). During the past twenty years, the present authors have studied various aspects of *P. clodius* biology in Oregon, Washington, and western Wyoming, resulting in much additional information.

Ecology and Life History

In terms of ecology, *P. clodius* occupies two distinctly different types of habitat. One consists of open subalpine meadows and rocky slopes above timberline at high elevations in the mountains. We have observed the species in subalpine meadows throughout western Oregon and Washington, and in Yellowstone National Park of Wyoming. We

also observed the species on alpine talus slopes above timberline at Harts Pass, Okanogan County, Washington.

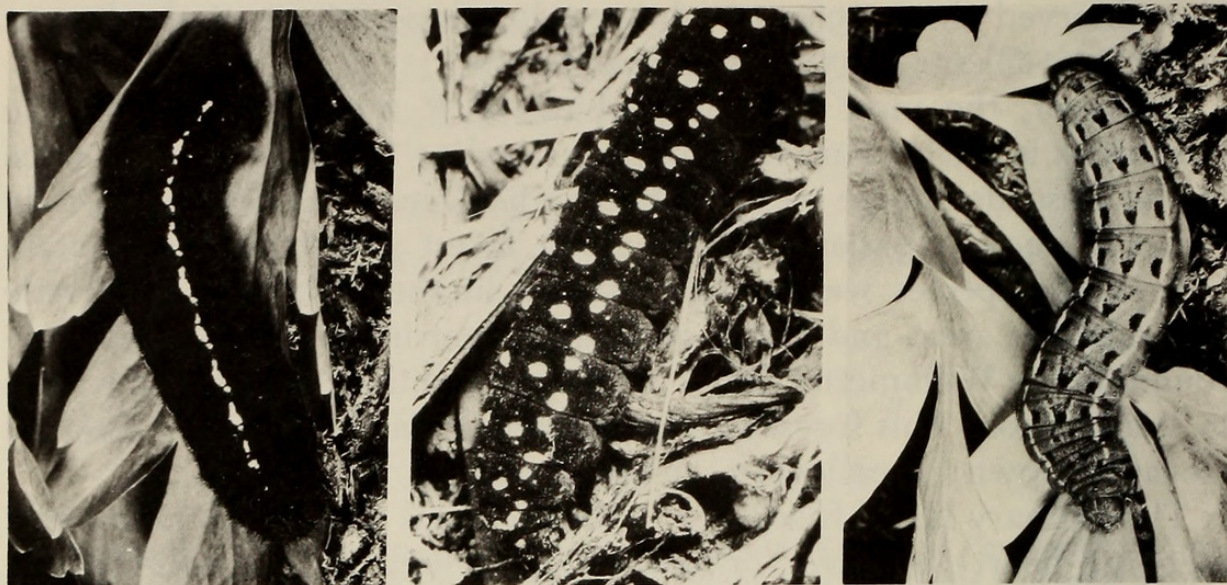
However, the most frequent habitat of *P. clodius* in the Pacific Northwest is the lowland rain-forests extending from the western slope of the Cascade Range west to the Pacific Ocean. Although typically found in moist riparian habitats along forest streams and mountain valleys, the species was formerly found in the Portland and Seattle metropolitan areas and is still quite abundant in the low foothills surrounding the Willamette Valley in Oregon and the Puget Sound trough in Washington. This forest habitat extends from the 4000 ft. (1200 m) elevation down to sea level near the ocean.

The primary larval foodplant in these coastal rain-forests is the wild bleeding heart *Dicentra formosa* Andr., which is very abundant in moist forest habitats along the West Coast. A second probable foodplant is *Corydalis scouleri* Hook., a relatively uncommon species. We have not yet observed *P. clodius* larvae on this plant in the field, but they accept it readily in the laboratory. At high elevations in the alpine habitat and east of the Cascades, *Dicentra uniflora* Kell. is a likely foodplant. This species is a known foodplant of *P. clodius* in northern California (John F. Emmel, pers. comm.). All of these plants belong to the family Fumariaceae, and it is probable that related species such as *Dicentra cucullaria* L. and *Corydalis aurea* Willd. would also provide acceptable foodplants.

The female butterflies oviposit on and near the *Dicentra* plants. However, we have also observed females ovipositing on shrubs up to four feet above the *Dicentra* beds. Evidently a specific chemical emanating from the foodplant is sufficient to induce oviposition anywhere in the general vicinity of the foodplant. The larvae develop within the egg shell but do not emerge from the egg until the following spring. Eggs deposited on shrubs usually reach the *Dicentra* beds when the shrubs drop their leaves in the fall. Foodplant records such as *Viola* and *Rubus* mentioned by Ackery (1975) are almost certainly in error and may be due to this indiscriminate oviposition by the females.

Early instar larvae have small tubercles, but later instars are mostly smooth with fine hairs. The larvae stay hidden in debris at the base of the foodplant most of the time. Feeding takes place very rapidly, so the larvae are exposed from cover only briefly. Nevertheless, *P. clodius* is frequently parasitized by tachinid flies in many localities. Osmeteria are poorly developed in *Parnassius* larvae and are not as important for defense against predators compared to *Papilio* larvae.

Parnassius clodius larvae display two very distinct color morphs. One form is black with a lateral row of bright yellow spots on each side of the body (Fig. 1). The form of these spots is highly variable,



FIGS. 1-3. **Left (1)**, larva of *P. clodius*, black form, Benton Co., Ore. **Middle (2)**, larva of *P. phoebus*, Yakima Co., Wash. **Right (3)**, larva of *P. clodius*, gray-brown form, Castle Lake, Siskiyou Co., Calif.



FIGS. 4-6. **Left (4)**, *Harpaphe haydeniana*, Polk Co., Ore. **Middle (5)**, open net cocoon and pupa of *P. phoebus* (behind thick *Sedum* stems in lower center). **Right (6)**, well-formed cocoon of *P. clodius* cut open to reveal pupa ready to eclose.

ranging from large round spots to long slender bars, or may be divided into several smaller spots. This color pattern is very similar to that of *P. phoebus* Fabr. (Fig. 2) and the Eurasian *P. apollo* L. (illustrated by Stanek, 1969). However, *P. phoebus* differs in having a second, more dorsal row of yellow spots on each side of the body. The second color form in *P. clodius* is gray-brown or pinkish gray with creamy yellow lateral spots and dorsal rows of narrow chevron markings equivalent to the dorsal row of spots seen in *P. phoebus* (Fig. 3). In our experience,

TABLE 1. Sequence of experiment testing the mimicry-model system of *Parnassius clodius* larvae and the millipede *Harpaphe haydeniana* as protection against the grasshopper mouse *Onychomys leucogaster*.

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1. *Clodius* larvae given to mouse—larvae eaten.
 2. Millipedes given to mouse—millipedes bitten, producing defense odor detectable to observer, mouse then rejected millipedes.
 3. Meal worms given to mouse—worms eaten.
 4. *Clodius* larvae given to mouse—larvae sniffed and rejected.
 5. Adult meal worm beetles given to mouse—beetles eaten.
 6. *Clodius* larvae given to mouse—larvae sniffed, handled, finally eaten after long delay.
 7. Millipedes given to mouse—millipedes sniffed and rejected.
 8. Meal worms given to mouse—worms eaten.
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the gray-brown form is dominant in alpine populations of *P. clodius*, for example at Harts Pass in Okanogan County, Washington and at Donner Pass in Nevada County, California. This morph appears to be a camouflage pattern that blends with the rocks in the alpine habitat. By sharp contrast, the black and yellow-spotted form is very conspicuous, is dominant in the lowland rain-forest populations of *P. clodius*, and appears to mimic the warning colors of polydesmid millipedes such as *Harpaphe haydeniana* Wood (Fig. 4). These millipedes are very abundant in the moist, riparian habitats used by *P. clodius* larvae.

Some populations of *P. clodius* are polymorphic for both larval color forms. For example, larvae sent to us by John F. Emmel from Castle Lake in Siskiyou County, California displayed both color forms. Likewise, an adult female butterfly collected at Chinook Pass near Mt. Rainier National Park, Washington produced ten larvae, five of the black form and five of the pinkish gray form. In these, the black larvae retained the narrow yellowish dorsal chevrons of the gray larvae, a trait absent in most lowland black larvae. This ratio between the black and gray forms is suggestive of a simple Mendelian inheritance for these color morphs. However, the chevron markings are apparently controlled by a separate set of gene loci.

In 1973, one of the present authors (McCorkle) conducted an experiment to test the predator protection of the mimicry-model system that apparently exists between lowland *P. clodius* larvae and the millipede *Harpaphe haydeniana*. Grasshopper mice (*Onychomys leucogaster* Max.) from eastern Oregon were used as predators in this experiment, since these insectivorous rodents do not occur within the ranges of the butterfly or millipede and would have no prior experience with these arthropods. The sequence of this experiment is shown in Table 1.

This experiment appears to demonstrate that the mimicry color pattern of lowland *P. clodius* larvae can give them a degree of protection

against predators, although predators may with sufficient experience learn to distinguish the larvae from millipedes. In nature, however, the millipedes are commonly exposed in the open, while *P. clodius* larvae are usually hidden and only briefly exposed during feeding. Thus, the mimicry may work quite well in nature, since predators would be expected to have abundant experience with the millipedes and little experience with the larvae.

In lowland populations of *P. clodius*, development is completed in a single year. The larvae emerge from the egg shells during March and start to feed on the young *Dicentra* plants. Full larval development is reached usually by late April or May, followed by pupal development of several weeks, and adult butterfly emergence in June and July depending upon elevation. The pupa is short and rounded, dark brown in color, and quite similar to a saturniid moth pupa. It is enclosed within a strong, well-formed silken cocoon (Fig. 6). By contrast, the cocoon of *P. phoebus* is very loose and poorly formed (Fig. 5). Wilson in Ehrlich and Ehrlich (1961) has suggested that this terrestrial cocoon may be an adaptation to the harsh, alpine climate, rather than a primitive trait. However, the above observations do not support this idea, since the lowland *P. clodius* has the best formed cocoon, and the more alpine *P. phoebus* has a poorly formed cocoon.

Sexual Behavior

The mating system of *P. clodius* adults is quite interesting, since these butterflies display virtually no evidence of courtship behavior. Indeed, the males display a "rape" type of mating in which the males engage the females and copulate by brute force. In dramatic contrast, most higher butterflies display elaborate courtship rituals in mating, often involving specialized sexual pheromones in both the male and female. For example, Brower, Brower and Cranston (1965) have outlined in detail the courtship patterns of *Danaus gilippus* Cramer. Likewise, *Speyeria* butterflies display a very elaborate courtship ritual in which the males flutter around the females, stimulating the females with a sweet, musky smelling pheromone that is easily detected by the human observer. In turn, the females release a second pheromone that stimulates the male to twist his abdomen towards the female for actual copulation. There is evidence that the female pheromone of *Speyeria* is often species specific and frequently serves as a reproductive isolating mechanism that prevents interspecific hybridizations (see Grey, Moeck & Evans, 1963).

However, *P. clodius* males, upon sighting a female, chase rapidly after her and literally attack her from behind. Upon grasping the female in mid-air, the male and female drop abruptly to the ground.

The female then lies limply on the ground, often with wings crumpled in the vegetation, while the male sits on top of her in copulation. *Parnassius* have extremely tough, tear-resistant wings, which may be an adaptation to this rough mating behavior. Otherwise, few females would survive mating with intact wings. Both of the present authors have independently observed this mating behavior in the field on several different occasions. Two additional anecdotal observations of mating behavior may also be mentioned here. On one occasion in the field, McCorkle captured a virgin female in the first swing of the net, followed shortly by capture of a male in a second swing. Before the two butterflies could be removed from the net, they were already in copulation. On a second occasion, a reared male was placed near a virgin female in a laboratory window. Upon seeing the female, the male immediately attacked and engaged her in copulation. We would suggest that the "rape" mating behavior observed in these butterflies may be a primitive trait, compared to the elaborate "courtship" mating behavior observed in most other groups of butterflies.

Moreover, females of many so-called "primitive" butterflies carry an external sphragis or internal genital plug following mating in order to prevent subsequent matings by additional males. Mated females of *P. clodius* carry one of the largest and best developed sphragis structures seen in butterflies. By contrast, the sphragis of *P. phoebus* is much smaller (see illustrations in Tyler, 1975 and Dornfeld, 1980). Presence of a sphragis may be typical of butterflies with a "rape" type of mating behavior, since older, mated females are often resistant or non-responsive to males in species with a "courtship" mating type.

Scott (1973) has made similar observations of the mating behavior in *P. phoebus*. He has suggested that virgin females of *Parnassius* may release a sexual pheromone attractive to the males, and that the females cease to produce this pheromone after mating and attachment of the sphragis. As a consequence, the males do not waste time and energy pursuing mated females. This possible pheromone system may well exist in *P. clodius*, but further studies are presently needed for confirmation. Such a pheromone system could be species specific and serve to prevent interspecific hybridization between *P. clodius* and *P. phoebus* when sympatric. However, females of *P. clodius* also differ from those of *P. phoebus* in having the dorsum of the abdomen completely naked, which may also be important for species recognition during mating.

In terms of relationships, it is quite possible that *P. clodius* represents a relatively generalized, primitive condition within the genus, considering the lowland habitat, well-formed cocoon, and large female sphragis. *Parnassius clodius* is closely related to a group of Eurasian *Coryda-*

lis-Dicentra feeders which include *P. eversmanni* Menetries, *P. mnemosyne* L., *P. stubbendorfi* Menetries, and *P. glacialis* Butler. It is interesting to note that these last two species are also reported to feed upon *Aristolochia* (Ackery, 1975), the same foodplant used by such related genera as *Archon* and *Parnalius* (= *Zerynthia*). In contrast, the *Sedum-Saxifraga* feeders such as *P. phoebus*, *P. apollo*, *P. bremeri* Bremer, and *P. nomion* Waldheim appear to be more specialized in habitat, foodplant, cocoon development, and female sphragis.

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