

## BIOLOGY OF *POLYGONIA PROGNE NIGROZEPHYRUS* AND RELATED TAXA (NYMPHALIDAE)

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**ABSTRACT.** The life history of *Polygonia progne nigrozephyrus* is compared with that of *P. gracilis zephyrus*, *P. faunus hylas*, and *P. satyrus* in Colorado. Adult predator deterrent behaviors occur: adults resemble leaves as they rest on twigs showing leaflike undersides, roost with forewings drawn forward with antennae resting between them, and feign death when handled. Larvae also have predator-avoidance strategies: scoli presumably act as a physical deterrence, small larvae can drop using a silk thread, a ventral neck gland possibly repels predators, larvae vomit on an attacker, older larvae resemble twigs as they rest in a three-dimensional twisted-S shape, pupae resemble a dried curled leaf or short twig. Larval host plants differ between species, with some overlap. Identification features for the four species are presented for each stage. Despite adult similarity of *P. progne nigrozephyrus* and *P. gracilis zephyrus*, *P. g. zephyrus* larvae most resemble those of *P. faunus*.

**Additional key words:** *Polygonia gracilis*, *P. faunus*, *P. satyrus*, predator deterrence, chaetotaxy.

Scott (1984) described *P. progne nigrozephyrus* which occurs in Colorado-S Wyoming-Utah-SE Idaho-NE Nevada. It resembles *P. gracilis zephyrus* (Edw.) on the upperside, *P. p. progne* (Cram.) on the underside and in male abdominal structure, and was long confused with *zephyrus*. *Polygonia p. nigrozephyrus* is certainly the same species as *oreas* (Edw.), but some may question whether it and *oreas* belong to *P. progne*. Early stages of *nigrozephyrus* are similar to those of *oreas* and *progne*, and are distinct from *zephyrus* and other *Polygonia*; wing undersides and abdominal structures resemble those of *progne*. Therefore, *nigrozephyrus* does seem to be a subspecies of *progne*.

Since 1984, minor differences between populations of *nigrozephyrus* in Colorado have been found. Adults from the E slope of the continental divide in the Front Range usually have the dorsal hindwing darker because the submarginal spots are the same size as those of *P. g. zephyrus*, whereas adults from the W slope usually have the spots larger like those of *P. satyrus* (Edw.). However, the difference is not great enough to warrant a new name for W slope populations, and some adults from each area resemble those from the other. The Front Range populations may have slightly darker dorsal hindwings because of occasional immigration of subspecies *progne*, which has a very dark dorsal hindwing margin.

An additional difference not mentioned by Scott (1984) between some *P. p. progne* adults and other *Polygonia*, first noticed by W. H. Edwards, involves one of the dark stripes in the ventral forewing discal cell: in most *P. p. progne* the anterior stripe is unbroken, whereas in some of

them and in other subspecies and species the stripe is broken into two parts.

For oviposition and larval rearing, cut host-plant sprigs were put into water-filled vials, cotton-plugged so the water would not drain when vials were on their sides. For older larvae, large host branches were cut and placed in wet sand.

#### Adult Stage

Adults bask with wings spread (dorsal basking). In the laboratory, some *nigrozephyrus* females closed the wings above the thorax and vibrated them rapidly (up to 2 mm apart at the tips) when lights were turned on in the morning; this is shivering behavior to raise the thorax temperature prior to flight.

Adults of *nigrozephyrus*, *zephyrus*, and *faunus* (Edw.), as well as *Nymphalis milberti* (God.), roost on twigs with wings closed, forewings drawn far forward (nearly out of hindwings) and covering the head and antennae which rest between the forewings. This posture perfects the resemblance to a leaf on the twig by elongating the "leaf", breaking up its margin, and hiding antennae to avoid predation during fall, winter, and spring. Adults frequently feign death when handled, which would also signal a predator that the butterfly is a dead leaf.

There is evidently a circadian rhythm of oviposition, because females laid eggs in the laboratory only during daytime, and even when lights remained lit females began roosting in late afternoon. For obtaining oviposition, fluorescent bulbs were superior to incandescent bulbs, probably because the former produce a greater and more natural amount of ultraviolet light.

#### Immature Stages

**Host plants.** *Polygonia progne nigrozephyrus* feeds on gooseberry: *Ribes inerme* Rydb., in Delta and Douglas counties, Colorado, *R. leptanthum* Gray at Williams Canyon, El Paso Co., Colorado. In the laboratory, *nigrozephyrus* larvae accepted leaves of *Ribes inerme*, but refused wax currant, *R. cereum* Dougl., and ate very little golden currant, *R. aureum* Pursh. They ate only leaves. Additional host records for *P. p. progne*, based on preserved larvae in the Smithsonian, are gooseberry (St. Albans, West Virginia, Monticello, New York) and currant (Centreville, Rhode Island).

*Polygonia gracilis zephyrus* usually eats *Ribes cereum* in Colorado. However, I found an egg on *R. inerme* at Tinytown, Jefferson Co., on 2 June 1984, and reared it to a mature larva; and a larva under a *R. inerme* leaf 5 km W Idledale, Jefferson Co., on 12 June 1984, which I reared to an adult. In the laboratory, *zephyrus* larvae eat *R. cereum*,

and do not move off its leaves to eat adjacent *R. inermis* leaves, although larvae will also accept *inermis*. Additional host plants of *zephyrus* are *Ribes sanguineum* (Jones 1951), and *Rhododendron occidentale* (larvae reared to adults, Big Trees Park, Calaveras Co., California, 4 June 1983, J. F. Emmel & S. O. Mattoon).

*Polygonia faunus hylas* (Edw.) usually eats *Salix*, but I found three first-stage larvae and five eggshells under leaves of *Ribes inermis* at Tintown on 26 May 1984, and an adult emerged 20 June. In the laboratory, *faunus* larvae refused *Ribes aureum* leaves, but ate *R. inermis* and preferred it to *R. cereum*.

Thus all three *Polygonia* will eat *Ribes inermis* occasionally.

The only known Colorado host of *P. satyrus* is *Urtica dioica gracilis* (Ait.) Sel., though *Humulus lupulus* L. is eaten elsewhere. In the laboratory, *satyrus* larvae accepted *Humulus* and *Urtica* leaves equally well.

### Life Cycle

Five larval instars have the following approximate head widths, respectively: 0.4, 0.7, 1.2, 1.7, 2.6 mm. Stage 1 is easily recognized by its black head without scoli; stage 2 has head scoli but is still black; stage 3 has head scoli but is black usually with an ochre pattern tending toward the pattern of stages 4–5. Usual laboratory durations of *nigrozephyrus* stages at 19°C were: egg, 5–6 days; larval stages, 3, 2.5, 2, 2, 4 days, respectively; and pupa, 9–10 days; totalling 27–30 days. In the cooler and more variable temperatures of nature, these periods are probably nearly doubled, so that adults should appear by late July–early August, although eggs laid in late April might produce the few fresh late-June adults known in nature. A *faunus* stage 1 larva found 26 May emerged as an adult 20 June in the laboratory, even though *faunus* emerges in nature only in late July and August. The laboratory life cycle of *P. p. progne* is 31–32 days (Edwards 1880), of *P. interrogationis* 28–40 days (Edwards 1882b), and of *P. comma* 27–33 days (Edwards 1882a). Thus all *Polygonia* have similar developmental rates indoors, and all have five larval stages. However, in Colorado *P. faunus* and *P. progne nigrozephyrus* have only one generation per year, while *P. satyrus* and *P. gracilis zephyrus* have two generations at low altitude and one at high altitude; and *P. interrogationis* has two or three generations.

### Predator-Avoidance Structures and Behavior

Stinkbugs and ants were found on *R. inermis* host plants and may prey on immatures.

The scoli of stage 2–5 larvae presumably physically deter predators.

They slightly hurt the human skin when touched, evidently a physical puncturing rather than an urticating chemical.

A ventral neck gland occurs on stage 2–5 larvae of all 4 *Polygonia* species; it contains 2 internal transverse dark secretory pads which perhaps produce repellent chemicals.

When grasped, the larva often bends its head around and vomits green fluid onto the attacker.

Fourth- and fifth-stage larvae of *nigrozephyrus* grasp a twig with the prolegs, bend the front part of the body right or left, and raise the end of the abdomen. This “corkscrew” posture may make the larva resemble a dead leaf or twisted twig, perhaps lessening predation by birds. This posture also occurs in ssp. *progne* (Edwards 1880) and in *satyrus* (C. F. Gillette pers. comm.).

Young larvae of all four species rest on the underside of a leaf, and when older may also rest on a twig. Only older larvae of *P. satyrus*, also *P. comma*, live in a nest. It is made by chewing the base of the leaf on each side, thus making it droop, and silking *Urtica* leaf edges down and together below the enclosed larva, which rests on the leaf underside.

Disturbed young larvae can extrude a silk thread as they fall, then crawl up the thread to return to the plant.

Pupae are constricted in the middle where silver spots also visually break up the outline, making the pupa resemble a dead, shriveled leaf or twig.

Gooseberry hosts are armed with sharp spines which act as physical protection against vertebrates. A punctured pupa recovered completely.

### Descriptions of Early Stages

Colors are based on live individuals. Immatures have been deposited in the Smithsonian Institution. Many dozen individuals of *Polygonia p. nigrozephyrus* were reared from eggs laid by females from NE of Cedaredge, Delta Co., and Nighthawk, Douglas Co. Each stage is described, and is followed by comparisons with the other three *Polygonia* species and subspecies, each of which were represented by less than 10 individuals. Segments are named T1 for prothorax, A3 for abdominal segment 3, etc. (Fig. 3). Scoli are named with the letter B followed by name of nearest primary seta. They are not preceded by S because of confusion with primary seta SD1, etc.; sp is spiracle; VNG is ventral neck gland on older larvae. Names of setae are from Hinton (1946) and Scott (1986), with slight modifications (Scott 1988) that improve homology and make head and body setal nomenclature different to avoid confusion.

**Egg.** Green, averaging 8.6 vertical ribs (Table 1), each rib steep-walled, increasing in height to maximum at top, then disappearing; 40–50 horizontal ribs forming ladder between adjacent vertical ribs; the day before hatching turning blackish with transparent silvery-reflecting shell as larva becomes partly visible.

**Comparison.** All *Polygonia* eggs green. *Polygonia p. progne* has 8–9 ribs, *P. g. zephyrus* averages 9.8, other *Polygonia* average 10.4–11.5 (Table 1).

**First-stage larva** (Figs. 1, 4, 5, 9, 11, 12, 16). Head black without pattern or horns. Body dark brown with long black setae, bumlike bases of which are chitin brown; with

TABLE 1. Number of vertical ribs on eggs.

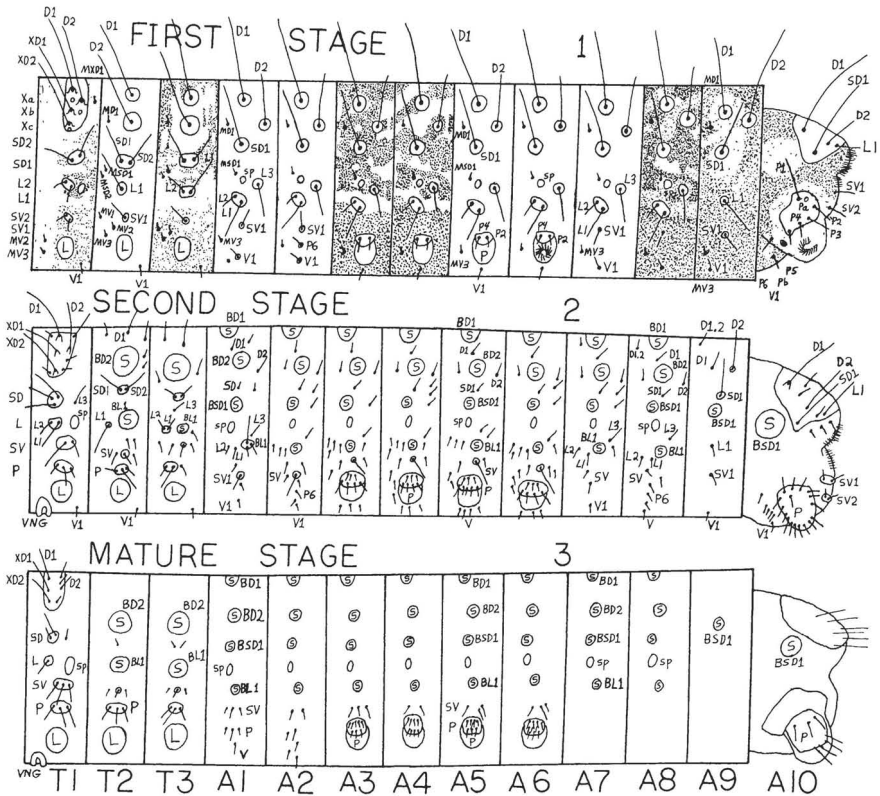
Taxon	Mean	SD	Range	N	Source
<i>Polygonia p. nigrozephyrus</i>	8.6	0.55	8-10	40	this paper
<i>P. p. progne</i>	—	—	8-9	—	Edwards (1880)
<i>P. g. zephyrus</i>	9.8	0.59	9-11	27	this paper
<i>P. satyrus</i>	10.4	0.54	10-12	43	this paper
<i>P. faunus</i>	10.5	0.63	10-12	31	this paper
<i>P. interrogationis</i>	—	—	8-10	—	Edwards (1882b), Pyle (1981)
<i>P. comma</i> (Colo.)	11.5	0.50	11-12	58	this paper
<i>P. comma</i> (Minn.)	10.6	0.54	10-12	38	this paper
<i>Nymphalis vau-album</i> (D. & S.)	11.0	—	9-12	—	C. F. Gillette, pers. comm.

cream spots (Fig. 1) as follows: front half of T1 cream except for small supralateral brown patch on some larvae; T1 cream in front of, behind, just beside black prothoracic shield; rest of T1 brown except for 2 cream dashes extending rearward above, below spiracle. T2-3 brown, large yellow-cream patch around D2, smaller cream patch around L1-2. A2, A4, A6 brown, with 4 pale patches: broad cream mid-dorsal V aimed posteriorly on anterior part of each segment; broad yellow-cream patch below D1; narrow supralateral light brown dash; long cream sublateral dash. A1, A3, A5, A7 brown, with 4 light brown patches on each side corresponding to pale patches on A2, A4, A6; sublateral dash cream on A3, A5, A7, A8. A8 same as A7 but 3 upper patches slightly creamier. A9 brown, subdorsal cream patch twice as long vertically as horizontally. A10 brown, suranal plate black, proleg cream, proleg plate brown, large circular cream supralateral patch.

**Comparison.** Other *Polygonia* larvae very similar, with black hornless head and similar body pattern. *Polygonia satyrus* same as *nigrozephyrus*, pale bumps cream-white, a few creamy sublateral dashes. *Polygonia g. zephyrus* same as *nigrozephyrus*, except pale bumps cream-white instead of yellow-white, seta D1 on T3 on whiter bump as is seta D2, no supralateral brown patch on front of T1 though it appears on some second-stage larvae so may be individual trait, supralateral dash on A2, A4, A6 cream, A1, A3, A5, A7, A8 all brown except for lateral cream dash. *Polygonia interrogationis* similar (Edwards 1882b), but *P. comma* "whitish-green" (Edwards 1882a). *Polygonia faunus* larvae differ from all other *Polygonia* in having white areas expanded away from bumps: for instance, white patch on T2, T3 includes both D1, D2 setae; on A2, A4, A6 white V lengthened anteriorly, subdorsal white patches below D1 extend posteriorly.

**Second-stage larva** (Figs. 2, 6-8, 17). Head black with 2 short black spiny horns (BPA2 scoli) each with 1 long seta on tip, 5 setae on crown just below, no setae on long stalks; bases of PA1, AG3, LH1, O2 pale, membranous; very narrow short pale line along middorsal groove. Body reddish brown, brownish orange toward rear, similar to 1st stage in pattern, prothorax mostly orangish yellow; orange V's on top of A2, A4, A6, yellow-cream areas of first stage now orange, scoli present with bases orangish. Scoli BD2 on A2, A4, A6 ochre on some larvae, mostly brown on most, other scoli black. BD2 scoli on T2, T3, A2, A4, A6 rest on large orange bumps making segments conspicuously paler, other scoli rest on small orangish bumps. Body has weak cream mid-dorsal, subdorsal spots which help form abdominal V's; remaining segments have thin wavy lateral cream line between BL1 scoli, thin wavy supralateral cream line between BSD1 scoli. Tiny pale subdorsal transverse dashes present. Ventral neck gland present.

**Comparison.** *Polygonia g. zephyrus* has slightly shorter horns, body undergoes less color change from first stage: color pattern the same, pale patches still white, though BD2 on A2, A4, A6 yellow-cream, in some larvae blackish, making segments still paler on top, other scoli black. Only BD2 on T2-3, A2, A4, A6 rest on yellow-cream bumps; other scoli rest on small whitish bumps. Tiny cream transverse dashes occur behind, before BD2 on A2, A4, A6 to help form V's as in *P. satyrus*; middorsal, subdorsal, supralateral, lateral

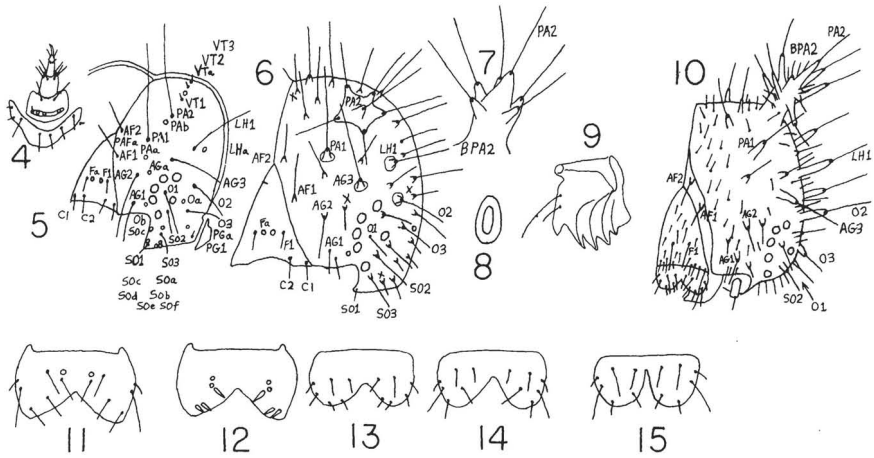


FIGS. 1-3. Setal maps of *Polygonia progne nigrozephyrus* larvae. **1**, First stage. Color pattern shown on some segments, except that plates at base of setae, including prothoracic shield and suranal plate, are dark brown; T2 and T3 patterns similar; A1, A3, A5, A7 patterns similar; A2, A4, A6, A8 patterns similar except that A8 darker; **2**, Second stage; **3**, Fifth (mature) stage. L inside circle is true leg; P inside circle is proleg; S inside circle is scoli. Hundreds of small setae not shown. See text for further explanation.

white spots present. *Polygonia satyrus* resembles 1st-stage *zephyrus*, thus head black, T1 mostly white except for black prothoracic shield. BD2 on A2, A4, A6 also yellow-cream; other scoli black, except BD1 on A6 whitish, BD1 on A4 partly whitish, BL1 on A4, A6, A7, A8 mostly white. BD2 on T2, T3, A2, A4, A6 rest on large yellow-cream bumps; other scoli rest on small tan hills, though BD1 on A2, A4, A6, BL1's rest on fairly white bumps. *Polygonia faunus* has enlarged white areas compared to other species, on at least 1 larva BD1 and BD2 on A2, A4, A6 pale. Ventral neck gland occurs in all 3 *Polygonia*.

**Third-stage larva** (Figs. 8, 13, 18). Head black with black scoli, following structures ochre: Mid-dorsal notch, adfrontal cleavage line (lateral to frontoclypeus), lower frontoclypeus, head just above antennae, bases of all major setae except black horns; but some individuals have head mostly black, nearly devoid of pattern. Head setae AG3, PA1, LH1, O2 on long ochre stalks. Body dark brown, with long mostly orange scoli: BL1, BSD1 mostly black; BD2 mostly orange; BD2 on T3, A2, A4, A6 strongly orange; scoli on T2, A10 mostly black. Body pattern similar to stages 4-5.

**Comparison.** *Polygonia g. zephyrus* larvae have BD1, BD2 more whitish cream on abdomen. *Polygonia satyrus* differs greatly: head black with cream notch on top running



FIGS. 4-15. Leg and cranial setae of *Polygonia prognegrozephyrus*. 4, Ventral-medial view of first-stage larval thoracic leg, showing setae typical of butterflies; 5, Setae and olfactory pores of first-stage larval head; 6, Head of second-stage larva. Head horn derived from, or incorporates, seta PA2. Setae PA1, AG3, LH1, O2 arise from small cones on transparent circles of exoskeleton. X's show positions of setae present on some larvae; 7, Head horn of second-stage larva, includes PA2 seta of first stage; 8, Ventral neck gland of larval stages 2-5 partly everted. It appears slitlike when retracted, is fully everted in some preserved larvae; 9, Mandible of first-stage larva; 10, Head setae of fifth-stage (mature) larva with primary setae whose origin is traceable to first-stage larval seta lettered; 11, Labrum of first-stage larval head, anterior view showing one olfactory pore; 12, Labrum of first-stage larval head, posterior view showing two olfactory pores, three spatulate setae; 13, Labrum of third-stage larval head, anterior view; 14, Labrum of fourth-stage larval head, anterior view; 15, Labrum of fifth-stage (mature) larval head, anterior view.

forward to inverted cream V on face, head horns, setae mostly black, some setae on sides and lower face white; body has lateral cream band with cream BL1; top of body cream with cream scoli, black dashes in shape of V without point angling forward from each BD1.

**Fourth-stage larva** (Figs. 8, 14). Head as in mature larva. Body similar to mature larva, but scoli more orangish, BD1, BD2 on A3, A5, A7 with dark brown ring around each above base, whereas other scoli and all scoli on mature larva, lack brown ring.

**Comparison.** The other species also resemble mature larva.

**Mature larva** (Figs. 3, 8, 10, 15, 19, 20, color photo on pl. 3 of Scott 1986). Head black, horns dark brown, orangish cream notch on top, orange-red W on front consisting of streak along upper part of each adfrontal cleavage line plus streak angling down from base of each horn, lower 3rd of frontoclypeus orange-brown, orange-red patch surrounding eye cluster, orangish mottling beside neck. Some setae everywhere on head including AG3, PA1, LH1, O2 orange-red, on long orange stalks; AG2, some dorsal setae beside neck, about 3 lateral setae beside neck on smaller orange stalks. Body scoli ochre, only needle tips orange, except: BD2, BSD1 on T2 black with some orange branches; BD2 on T3 mostly black, orangish on basal 5th, BSD1 ochre; BD2 on A8 partly black, BSD1 mostly black, BD1, BL1 ochre; BD2 on A9 partly black; BD2 on A10 black. Body blackish brown in ground color, with complex pattern. T1 brown with mid-dorsal, subdorsal, supraspiracular, subspiracular orangish lines, some small mostly orange spinelike setae; mid-dorsal ochre band extending from head to T1, narrowing on T2, very narrow on T3. A few ochre transverse dorsal lines between T1, T2, between A8-10. Body joints between

T2, A8 have 5 ochre joint lines, line 2 grayish, lines 1, 3 widest, separated by 4 black joint lines, most posterior very narrow. Segments T2, T3 ochre on top, with paired short black grooves on either side of black mid-dorsal line. Segments A1, A2 similar but paired dark grooves form brown transverse streak behind BD1. A1, especially A2, begin to show dorsal black rearward-aimed V's characteristic of all *Polygonia* on A3-8. Tip of V blunt, wide, corresponding to brown transverse streak on A1-2 just behind BD1, each arm of V thickest in middle anterodorsal to BD2 where V becomes orangish black, outlined by ochre bands as thick as V itself. Three more black spots posterior to point of each V that continue point: black transverse mid-dorsal dash formed by 2 interruptions in 1st black joint line circling segment, narrower dash formed by narrower interruptions in next joint line, mid-dorsal black triangular spot on anterior edge of posterior segment. Ochre joint lines stop at 2 wavy lateral lines characteristic of all *Polygonia*. Upper wavy lateral line orange, on each segment obliquely extending from BSD1, which is ochre with orange base, up, forward then down; behind BSD1 obliquely extending down, backward then down, forward, resembling orange staple aimed down, forward, centered on BSD1. Upper line interrupted between segments by last 3 ochre joint lines which splinter into about 5 ochre wavy narrow lines that stop just above lower wavy lateral line. Lower wavy lateral line ochre, extending from each BL1 obliquely up, forward, then straight forward, then angling down toward BL1 of preceding segment. Beneath this line a vague ochre line above prolegs. Prolegs, underside blackish brown, ochre ventral bands running along abdomen on each side of mid-ventral line. Ventral neck gland present.

Of more than 50 larvae, a few slightly paler (dorsal areas yellow anteriorly, cream behind). Early 5th stage slightly more pinkish violet as orange-red scoli of 4th stage change to ochre.

**Comparison.** California *P. p. oreas*, based on preserved larvae, photos, same as *nigrozephyrus*, except that top front of former orange, yellowish orange vs. orangish yellow on top of thorax, A1-2; BSD1 on orange upper wavy lateral band more orangish than *nigrozephyrus*, ochre in latter with only base orangish. Based on 50-year-old preserved larvae in Smithsonian, ssp. *progne* similar to *nigrozephyrus* in structures, all pattern elements seem present, though impossible to discern true colors; dorsal V-marks, transverse lines between segments present. Edwards (1880) described *progne* color as buff (ochre), dorsal area "reddish" (probably orangish ochre) around black V's; he described T2-3, A9-10 scoli as black, others ochre as in *nigrozephyrus*; described BSD1 as black, but contradicted on the preserved larvae, these being pale also. T1 collar described as yellow in *progne*, and is pale in the preserved larvae, whereas it is black except for mid-dorsal line in *nigrozephyrus*, other 3 species. Head seems to have larger black areas in *nigrozephyrus* than ssp. *progne*. Evidently ssp. *progne* larva does not change color from front to rear as much as western subspecies, and dark brown areas of former are smaller.

Mature larvae of other *Polygonia* species differ greatly. All 3 have black V's on top of abdomen slightly narrower than *nigrozephyrus*, point of each V less strongly connected. All 3 have wavy lower lateral lines as in *nigrozephyrus*, but these are slightly reddish cream in *zephyrus*, red-orange in *faunus*, orangish cream in *satyrus*. *Polygonia g. zephyrus* (Fig. 27, color photo on pl. 2 of Scott 1986) much more 2-toned, top of segments T2-3, A1-2 red-orange, especially T3, A2); top of A3-8 whitish, especially A4, A6 which are yellowish white. Basic pattern elements of *zephyrus* same as in *nigrozephyrus*, but wavy lateral lines weak, slightly reddish, scoli black except BL1 along lower wavy line whitish in some larvae, BD1 orange within orange areas, white within white areas. Head of *zephyrus* also mostly black, except for white mid-dorsal notch, sometimes thin orange inverted V on front, scattered small white seta bases. Some *zephyrus* larvae have T3, A2 orangest on top, A4, A6 whitest, whereas in others T2-3, A1-2 equally red-orange on top, A3-8 equally white on top. Latter characteristic of *P. faunus*, which has top of body orange in front, white behind as in photo 14 of *faunus* (= *silvius*) in Pyle (1981). *Polygonia faunus* has both wavy lateral lines red-orange, BL1 on lower line white, head black with some cream setae, cream dorsal notch, orange W on front. Thus mature larvae of *P. g. zephyrus*, *P. faunus* are similar. *Polygonia c-album* L. larvae resemble *faunus* closely (photos in Pyle 1981, Whalley 1979:19, Brooks & Knight 1985:79).

*Polygonia satyrus* mature larvae differ greatly from other *Polygonia* (Fig. 25, color



photo on pl. 2 of Scott 1986). Top near-uniform yellow, same pattern elements present: head black, inverted cream V on front, mid-dorsal cream notch, some small cream setae; middorsal line cream on thorax, transverse rings between segments, dorsal V's present. However, entire top of body greenish yellow, T2-3, A1-2 ochre-yellow in some larvae, lower wavy line thick, pale yellow, orangish between segments in some larvae, yellow BL1's; upper wavy line nearly absent, with black BSD1's or line thin, orange, with cream BSD1's in some larvae.

*Polygonia interrogationis* (Fab.) mature larvae are also very different from other *Polygonia* (Pyle 1981:photo 15, Edwards 1882b). *Polygonia comma* (Harr.) mature larvae vary (Edwards 1882a).

Ventral neck gland present in stages 2-5 of *P. g. zephyrus*, *P. faunus*, *P. satyrus*.

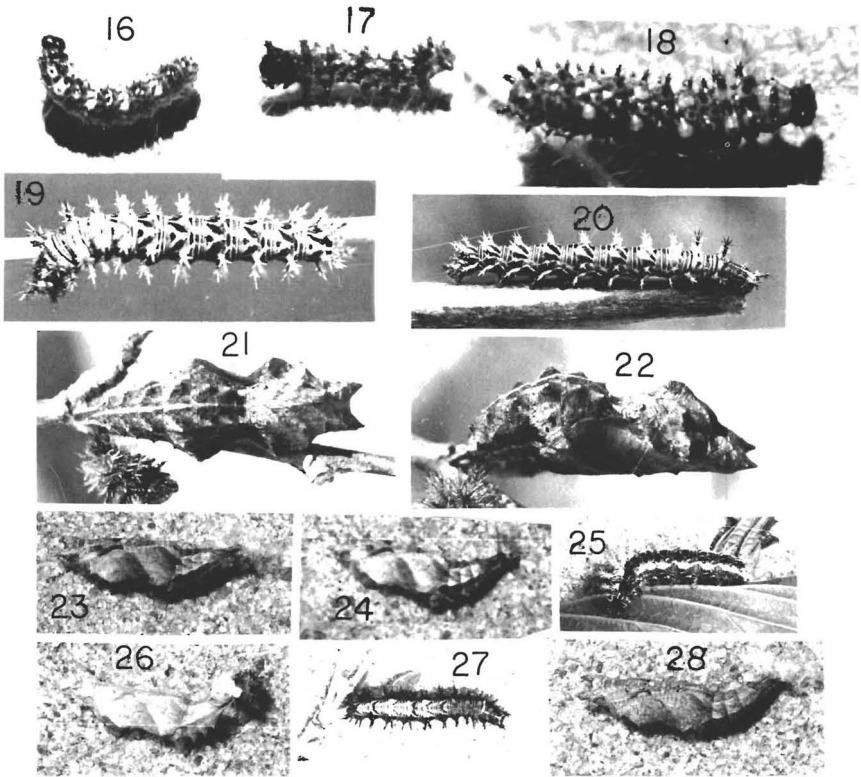
**Chaetotaxy** (Figs. 1-7, 9-15). Head of 1st-stage larva has only primary setae. Second-stage head has many secondary setae, scoli BPA2; each horn incorporates seta PA2 of 1st stage because scoli in same position as 1st-stage PA2, other dorsal primary setae recognizable on 2nd-stage head by large size, position. Each 2nd-stage horn has long PA2 seta on tip, 5 setae on crown below tip. Head setae, horns on stages 3-5 like those of stage 2 except for proliferation of small setae, primary setae recognizable on mature larval head by larger size, horn still including only 1 primary seta, PA2. Setae on labrum constant at 6 on each side, 3 spatulate setae on posterior oral surface, during larval stages 1-5, setae on other mouthparts also constant, except mandible setae which rise from 2 on each stage 1 mandible to about 10 on stage 5.

Proprioceptor setae, those that detect cuticular folds telescoping over, on head, body same as present in other Lepidoptera.

Body of 1st-stage larvae has mainly primary setae, also some secondary L2 setae, present on all individuals examined, on T3, A1-8; on A3-6 of some larvae 4th L seta present near L2. On 2nd-stage body, many secondary setae, scoli appear. Body scoli of 2nd-stage larva not homologous with 1st-stage larval primary setae because primary setae of 1st stage occur on 2nd stage, sometimes slightly moved in position, with scoli. Thus A10 of 1st stage has paler spot where BSD1 appears on 2nd stage, yet both stages have same dorsal primary setae on A10; on T2-3, 2nd stage retains same SD, L setae of stage 1 adds BL1; on A8, 2nd stage retains same D1-2, SD1 setae of stage 1, adds BD1, BD2. Body scoli add small setae between stages 2-5, otherwise change little. Small SD plate on T2-3 of stage 2 disappears, only 1 or 2 setae remain on stage 5. Body setae multiply between stages, hundreds of which are not shown on stage 5 setal map (Fig. 3). Crochets typical of butterflies: 14 of anterior 8 prolegs forming circle in stage 1, medial crescent in mature larvae; 12 anal crochets form anteromedial crescent in all stages. Each true leg has 5, 2, 6, 2 tactile setae plus 3, 1, 0, 2 proprioceptor setae on 1st 4 leg segments of stage 1, the usual number in 1st-stage butterflies, additional setae joining these on mature larvae, 1st segment having about 8 setae, for instance, on mature larvae. No anal comb present on any stage.

**Comparison.** Setae, scoli of all larval stages same in 4 *Polygonia* compared, also in mature *P. interrogationis* larvae based on preserved specimens, Petersen (1965) showing drawing of mature *interrogationis* larva: thus secondary 1st-stage L2 seta occurs in all species, L1 on A3-6 in some *zephyrus* individuals splitting into 3 instead of 2 setae, making 4 L's instead of the normal 3, head horn on stages 2-5 incorporating primary seta PA2, consisting of 1 terminal setae, crown of 5 main setae below. Secondary L2 seta on 1st-stage T3-A8 distinguishes *Polygonia* from *Nymphalis*, *Vanessa*.

**Pupa** (Figs. 21-24, color photo on pl. 5 of Scott 1986). Usually pinkish tan, sometimes paler, rarely blackish gray. Segments T3, A1, A2 have silver or gold subdorsal spot, usually silver on T3, A1, often gold on A2 because of reddish tan A2 top, making 6 in all, mid-dorsal silver streak sometimes on A1. Segment A2, to lesser extent A3, reddish tan on top. Four abdominal bands: lateral tan-edged brown band, mid-ventral tan-edged brown band, mid-dorsal brown-edged tan line. Basal half of each tibia brown. Sliver of hindwing just above forewing brown. Light-brown V's on A4-7, weakly on A3, on both sides of tan mid-dorsal line, 1 arm of each V ending at each subdorsal cone. Broad brown, often greenish brown, band crosses wing from tornus to mid-costa, short brown subapical band parallel to it. Many cones, bumps usually at larval scoli positions: very small mid-dorsal



FIGS. 16-28. *Polygonia* larvae and pupae. 16-24 *P. progne nigrozephyrus* from Delta Co., Colorado; 25-28 other taxa as noted from Jefferson Co., Colorado. 16, First-stage larva, dorsal view; 17, Second-stage larva, dorsolateral view; 18, Third-stage larva, dorsal view; 19, Fifth-stage larva, dorsal view; 20, Fifth-stage larva, lateral view; 21, Pupa, dorsal view; 22, Pupa, lateral view; 23, 24, Pupae, lateral views showing variation; 25, *P. satyrus* mature larva, lateral view; 26, *P. satyrus* pupa, lateral view; 27, *P. gracilis zephyrus* mature larva, dorsal view; 28, *P. faunus hylas* pupa, lateral view.

bump on A2-8; large subdorsal cone on T2-3, A1-8; supralateral bump on A3-7; lateral bump on A4-8, lateral bump on each head horn; large bump on wing base; bump on lower basal corner of wing; subventral bump on A5-6, another on head, 1 on each tibia; 2 stout cones (horns) projecting forward from each side of head; mid-dorsal keel on T2.

Silk pad spun by pupating larva bright pink.

**Comparison.** All *Polygonia* pupae have similar silver or gold spots in saddle, similar cones, keels, horns, dark bands on abdomen. Species differ in overall color, shape, size of cones, horns. *Polygonia p. oreas* resembles *nigrozephyrus*, but 2 *oreas* pupae seen were brown, not pinkish tan. *Polygonia p. progne* pupa (Edwards 1880) also pinkish brown like *nigrozephyrus*, with similar markings; head, thorax sometimes greenish brown. *Polygonia g. zephyrus* like *nigrozephyrus* in shape, but most individuals light brown, some creamy gray or tinged with green, rarely blackish gray, abdomen more mottled, subdorsal area on A4 lighter than on other segments, on A5-A7 a paler streak angling forward, down from each subdorsal cone. Few *zephyrus* pupae resemble *nigrozephyrus* in overall color, yet reddish tan top of A2 of *nigrozephyrus* identifies most. *P. faunus* pupa (Fig. 28, color photo 14 of Pyle 1981, as *silotus*) light brown (often with reddish

flush on top of A2-3 as in *nigrozephyrus*) or dark gray, easily identified by elongate shape, >10% longer, long head horns, twice as long as other *Polygonia*. *P. satyrus* pupa (Fig. 26, color photo on pl. 5 of Scott 1986) paler, tan or straw, sometimes yellowish dorsally, rarely brown all over, easily identified by mid-dorsal T2 keel being twice as high as other species, subdorsal abdomen cones about twice as large. *P. interrogationis* similar in color to some *nigrozephyrus*, *faunus*, with similar sized bumps, but its T2 keel very large (color photo 15 of Pyle 1981, Edwards 1882b). *P. comma* pupa quite variable (Edwards 1882a). *Polygonia c-album* pupa brown, resembling *nigrozephyrus* in shape but T2 keel larger as in *satyrus* (Brooks & Knight 1985:79).

Oddly, silk cremaster pad spun by pupating larvae colored differently in other species: bright pink in *nigrozephyrus*, also *interrogationis* (photo in Pyle 1981); pale pink in *zephyrus*, *faunus*; yellowish white, rarely faintly pink, in *satyrus*.

#### ACKNOWLEDGMENTS

I thank J. R. Heitzman for larvae of *P. interrogationis*, R. K. Robbins for loans of *Polygonia* immatures from the Smithsonian Institution, P. A. Opler for photos of *P. progne oreas* immatures, and C. F. Gillette for reviewing the manuscript.

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Received for publication 22 April 1987; accepted 2 October 1987.