

It may be conjectured that PPMs found in the pupae of other families of Lepidoptera will exhibit results similar to those indicated in the present and previous papers.

ACKNOWLEDGMENTS

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CERCYONIS PEGALA BLANCA, A "MISSING TYPE" IN THE EVOLUTION OF THE GENUS *CERCYONIS* (SATYRIDAE)

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Each of the smaller three species of the nearctic *Cercyonis* has a very distinctive whitish race which is adapted to the arid alkaline flats of the western deserts of the United States. *Cercyonis meadi alamosa* Emmel & Emmel occurs in salt flats of the isolated San Luis Valley of south-central Colorado at 8,500 feet elevation (Emmel & Emmel, 1969). *Cercyonis sthenele paulus* Edwards is a white-marked form occurring in extensive populations throughout the western portions of the Great Basin between the Rockies and the Sierra Nevada. *Cercyonis oetus pallescens* Emmel &

Emmel, an extraordinary form with whitish ventral surface, inhabits the dry alkaline meadows of the Reese Valley in Nevada (Emmel & Emmel, 1971). At the time of this last-mentioned publication, it was thought that the closest analogous phenotype in the large *Cercyonis pegala* complex was *C. pegala gabbi* Edwards from Utah, which has light undersurfaces.

However, in a remote part of Nevada in late summer 1970, one of us (SOM) discovered a heretofore-unsuspected form of *Cercyonis pegala* Fabricius, which matches for dramatic adaptation of ventral white coloration the previously mentioned smaller *Cercyonis*. The purpose of this paper is to formally describe the new set of populations and to report the unique life history of this subspecies.

***Cercyonis pegala blanca* Emmel & Mattoon, new subspecies**

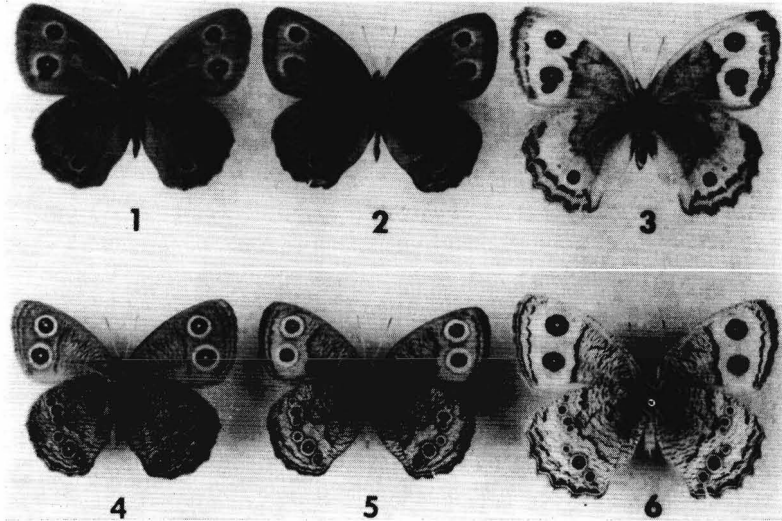
Holotype, male: Expanse, 47.8 mm. Forewing length, 16.6 mm. *Forewings, superior surface:* Identical to pattern and coloration of *C. pegala gabbi*, being dark brown with a faint yellow ring around each of two major ocelli. Both major ocelli pupilled with white scales. Occasionally one or two additional minor ocelli, lacking pupils. *Hindwings, superior surface:* Dark brown, with two or more (as many as five) well-marked submarginal ocelli. Large ocellus in cell Cu_1 is almost always pupilled with white scales. *Forewings, inferior surface:* Brown areas (except dark brown striations) present in other *pegala* subspecies are here covered with whitish or light tan scaling. Yellowish rings around major ocelli are broad but not joined as in *C. pegala ariane* f. *stephensi* [♀] Wright (see Emmel, 1969). *Hindwings, inferior surface:* Entire wing except for dark brown striations is heavily suffused with silvery white scaling. Six marginal ocelli present in all males collected. *Head, thorax, and abdomen:* Dark brown on dorsal surfaces, whitish on ventral surfaces. *Genitalia:* As in other *C. pegala* (Emmel, in prep.).

Allotype, female: Expanse, 55.5 mm. Forewing length, 31.1 mm. *Superior surface:* Generally similar to the variable dorsal phenotype found in *C. pegala ariane* f. *stephensi* [♀], with a broad yellow submarginal band always found on the forewing and usually present on the secondaries also. The ground color usually quite tannish rather than a dark brown as in the male. Forewing ocellation varying from two to five ocelli, but usually only two major ones and these are always pupilled. Hindwing ocellation very well developed, with as many as six black ocelli (M_3 and Cu_1 ocelli pupilled). *Inferior surface:* Both forewings and hindwings heavily suffused with whitish or silvery white scaling, obscuring all brown areas except principal striations. Forewing-band area is light tan on most specimens. *Head, thorax, and abdomen:* As in male, though lighter on dorsal surface corresponding to lighter color of wings.

Holotype male: Nevada, Hwy. 140 at Dufurrena Ranch—Chas. Sheldon Antelope Range, T45N, R26E, Humboldt County, August 21, 1970, S. O. Mattoon, collector.

Allotype female: Nevada, Hwy. 140 at Dufurrena Ranch—Chas. Sheldon Antelope Range, T45N, R26E, Humboldt County, August 11, 1970, S. O. Mattoon, collector. Paratypes: 20 ♂♂, 10 ♀♀, same locality and date as holotype, S. O. Mattoon, collector; 8 ♂♂, 20 ♀♀, same locality and date as allotype, S. O. Mattoon, collector.

The holotype and allotype will be deposited in the Florida State Collection at the University of Florida. Pairs of paratypes will be deposited in the following institutions: American Museum of Natural History, Allyn Museum of Entomology, Cali-



Figs. 1-6. (1) *Cercyonis pegala gabbii* male, dorsal surface, from Salt Lake City, Salt Lake Co., Utah, 3 July 1965, Kenneth B. Tidwell, collector; (2) *Cercyonis pegala blanca* Emmel & Mattoon, dorsal surface of holotype male, from the type locality, Humboldt Co., Nevada; (3) *Cercyonis pegala blanca* Emmel & Mattoon, dorsal surface of allotype female; (4-6) ventral surfaces of the above specimens, respectively.

fornia Academy of Sciences, and the Los Angeles County Museum of Natural History. The remainder of the paratypes are being retained by the authors for further study. The subspecific name, *blanca*, is Spanish for "white."

This subspecies differs from previously described forms of *Cercyonis pegala* primarily in its extraordinary white scaling on the undersides of both wings. It is of special evolutionary interest because its development of white scaling matching its unusual white alkaline-flat environment parallels the phenetic changes that have occurred in *Cercyonis meadi*, *sthenele*, and *oetus* under similar environmental regimes. Each represents a terminal point as offshoots of the main stocks of the respective species, and while the existence of *C. pegala blanca* was previously unsuspected it is gratifying to find such a development to complete that particular picture of adaptive phenetic change in the genus *Cercyonis*.

Description of the Habitat

This butterfly inhabits the swampy alkaline area around the Dufurrena Ranch sub-headquarters of the Charles Sheldon Antelope Range in Humboldt County, northern Nevada. Thousand Creek Spring feeds this area in a former lake basin surrounded by lava flows. The wet area

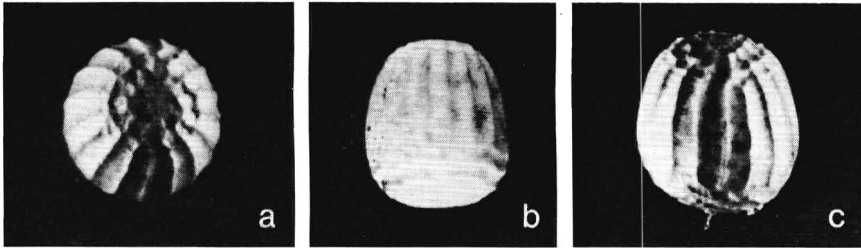


Fig. 7. The egg of *Cercyonis pegala blanca* Emmel & Mattoon: (a) dorsal end, showing micropylar region; (b) ventrolateral view; (c) dorsolateral view.

vegetation is dominated by lush grasses and willows, while wild rye, *Elymus cinereus*, dominates the slightly drier adjacent terrain. The latter species of tall bunch grass is used as a roosting site for *Cercyonis pegala blanca*, while one or more of the shorter grasses and sedges in the wet areas are apparently used for oviposition. These latter grasses include *Eleocharis palustris*, *Juncus balticus*, *J. lescurii*, and *Beckmannia syzigachne*, and the sedge *Carex nebrascensis*. Aside from the springs area the vegetation dominating this arid basin is sagebrush (*Artemisia confertifolia* and *A. truncata*).

Life History

Living females collected in August 1970 were induced to oviposit in the laboratory of S. O. Mattoon at Chico, California, and the eggs were maintained and larvae reared on commercial-brand blue grass in an outdoor greenhouse there. Techniques were as described by Emmel (1969) in general. All measurements and descriptions of the stages are by the second author.

It is particularly noteworthy that the life history of this Nevadan *Cercyonis pegala* subspecies has only five larval instars (at least under our experimental conditions), whereas Colorado and coastal California *Cercyonis pegala boopis* exhibited six larval instars under constant-temperature conditions (Emmel, 1969). We plan to investigate further this variation in instar number. As in all other *Cercyonis*, this new subspecies diapauses and overwinters in the first larval instar; when the larvae hatch several weeks after oviposition, they crawl to the base of a grass clump and enter diapause without feeding.

EGG. SHAPE: Egg 1.1 mm in height, 1.0 mm maximum width; somewhat conical, broader and flatter at base with top more rounded. Adorned laterally by numerous vertical ridges (approximately 19) which intersect and traverse approximately four progressively smaller ridges approaching the top of egg, producing a somewhat scalloped appearance. The vertical ridges terminate basally just below the widest

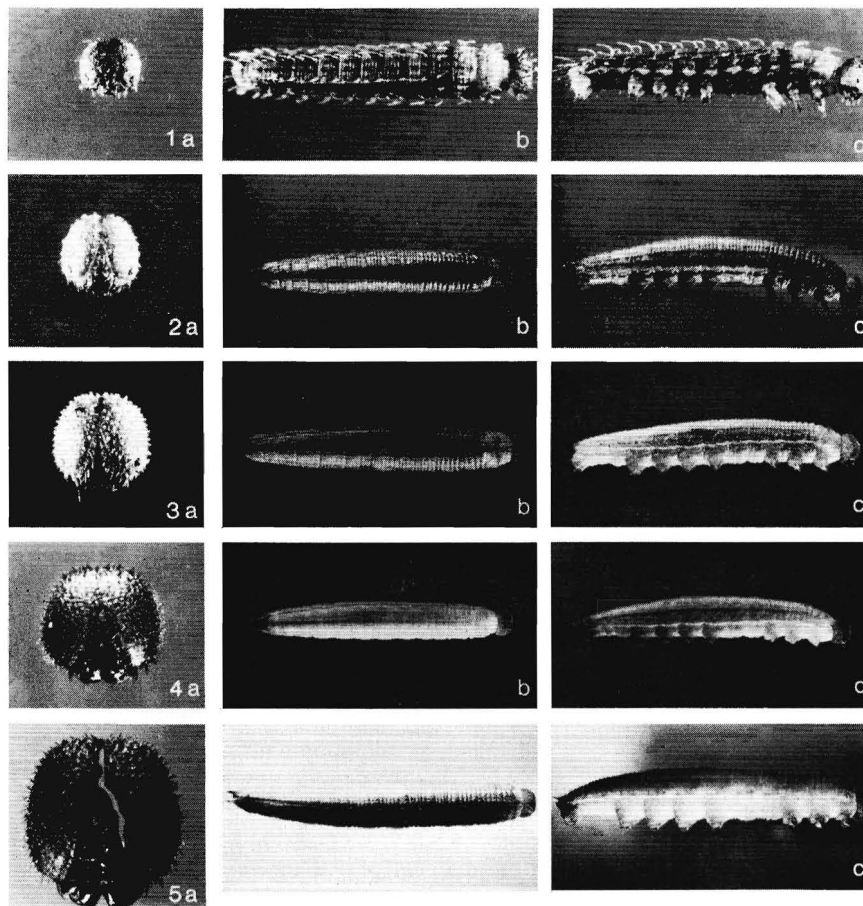


Fig. 8. The five larval instars of *Cercyonis pegala blanca*: (1) first, (2) second, (3) third, (4) fourth, and (5) fifth instars. Head capsule (a), dorsal view of larva (b), and lateral view of larva (c).

portion of the egg and do not traverse another series of similar but more numerous basal concentric ridges. COLOR: White at oviposition, turning tan within three days, and lightly marked between the ridges by a sparse mottling of irregularly sized orange-brown spots and splotches during later development.

LARVAL STAGES. First Instar. HEAD CAPSULE: Average width, 0.64 mm, height, 0.65 mm (20 larvae). Ground color purplish brown (light brown after ecdysis). Surface retiform, depressions between ridges more darkly pigmented. Antennae (in all instars) light amber, basal area green, distal extremity becoming darkened. Labial and maxillary palpi translucent, darkened distally. Mandibles translucent, cutting edge with broad margin of black. Labrum translucent, notch black. Facial suture margins darkened. Ocelli black. Head capsule setae sparse, spiniform, all oriented anteriorly then most curving slightly ventrally (in all instars),

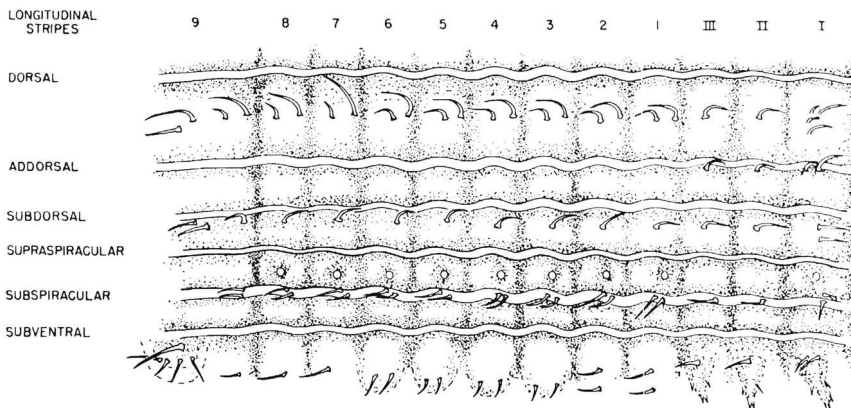


Fig. 9. Map of setal arrangement and pigmented stripes described in text for first-instar larva of *Cercyonis pegala blanca*.

setae long (averaging three times the width of large ocelli), translucent, granular (in all instars), darkened at juncture with head with minute purplish brown chalazae, and in a constant bilaterally paired arrangement. TRUNK: Average length 5.0 mm. First abdominal proleg segment width, 0.85 mm (20 larvae). Ground color of diapausing larva light tan to light brown, turning grass green within 24 hours after feeding. Body segments annulated, five annuli per thoracic and six per abdominal segments, marked by dorsal, addorsal, subdorsal, supraspiracular, and subventral purplish brown longitudinal stripes, and laterally by a prominent greenish white subspiracular stripe. Randomly distributed whitish green pigment spots showing through integument are more concentrated bordering stripes. Thoracic legs faint purplish brown, darkened distally. Claw darkened at juncture with tarsus. A pair of spinose, opposed setae extend beyond claw in all instars. Abdominal prolegs grass green; crochets in a uniordinal uniserial latero-series, colored brownish black. The anal prolegs with purplish brown pigment patch (sometimes obscure) on lateral aspect. Spiracular openings on distal extremity of rusty orange, globe-tipped stalks. Globe with minute transverse ridges running from opening to stalk. Body armed bilaterally by five longitudinal rows of long spiniform setae, some knob-tipped on cephalic margin of first abdominal segment. Setae barely discernible without magnification. Setal arrangement (Fig. 9) is as follows. *Row I*: Located dorsal of the addorsal stripe. Comprised of posteriorly-oriented, horizontally-aligned pairs on each abdominal segment and one seta anteriorly oriented on each thoracic segment, except headed by a group of four (sometimes knob tipped) on cephalic margin of first thoracic segment. *Row II*: Single, anteriorly oriented, spiniform, except paired and sometimes knob tipped on first thoracic segment (row restricted to thoracic segments only), located on addorsal line. *Row III*: Ventrad of subdorsal line. All spiniform, single, anteriorly oriented except posteriorly oriented on abdominal segments nine and ten, and paired on caudal and first thoracic segments. *Row IV*: In subspiracular line, all spiniform (except sometimes knob tipped on first thoracic segments), paired, and posteriorly oriented except on thoracic segments two and three. *Row V*: Located subventrally at leg bases. All posteriorly oriented and paired, except singular on thoracic segments two and three and abdominal segments seven, eight, and nine. Five long, spiniform, ventrally or posteriorly oriented setae arise from within the perimeter of anal proleg color patch. Caudal segment blunt. Long, spiniform, posteriorly oriented, bilaterally paired setae project from conical purplish

brown chalazae on the posterior of caudal segment. The longest pair arise dorso-laterally and appear to extend caudally the tapering body line.

Second Instar. HEAD CAPSULE: Average width 1.01 mm, height 0.90 mm (20 larvae). Ground color grass green with faint purplish brown cast (light brown after ecdysis). Capsule surface features as in first instar, except surface reticulations more irregular, the depressions not darkened. Facial sutures only faintly darkened with two dark spots on attachment margin of labrum. Head capsule setae more numerous, minute, strongly knob tipped in cephalic region, averaging one-half the width of large ocellus, becoming more spiniform and longer around frontal portion. Setae not darkened at juncture with chalazae as in first instar. Chalazae white (slightly larger than in first instar) and more bulbous. TRUNK: Average length, 7.8 mm; first abdominal proleg segment width, 1.13 mm. Ground color grass green. In second through fifth instars, integument surface textured with a multitude of minute circular smooth convex areas producing translucent frosted appearance, more pronounced early in instar and lessening as skin tightens. The longitudinal dorsal, addorsal, subdorsal, and supraspiracular solid purplish-brown stripes more obscure than in first instar. Subventral stripe dashed and purplish brown dorsad of leg bases. Subspiracular stripe along the somewhat protruding extreme lateral aspect of trunk well defined and solid white. Body segments more noticeably annulated. Thoracic legs brownish green, tarsal claw and distal half of tarsus darkened. Tibia, femur, and proximal half of tarsus amber brown, coxae green. Abdominal prolegs green, crochets more numerous. Setae on all leg bases strongly knob tipped from minute green chalazae, becoming progressively more numerous and spiniform from smaller chalazae distally. The more distal setae sometimes darkened at attachment with chalazae. Spiracles with stalk much reduced to absent; often, globe incomplete distally, exposing hollow interior with spiracular opening at base. Body setae now numerous, minute (much shorter than first instar, not discernable without magnification in second through fourth instar), irregular but in somewhat poorly defined longitudinal rows. Most strongly knob tipped and posteriorly arching from minute green chalazae except some anteriorly arching; setae longer, spiniform, darkened at juncture with chalazae along cephalic margin of first thoracic segment and along lateral aspect of all thoracic segments. Caudal segment now divided into two posteriorly-projecting, fleshy-rose-colored, short, conical forks, each covered with posteriorly-oriented, short, strongly knob-tipped, slightly rose colored setae.

Third Instar. HEAD CAPSULE: Average width, 1.47 mm; height, 1.42 mm (20 larvae). Ground color grass green with very slight brownish cast (brown after ecdysis). Head capsule very similar to second instar, except setae more numerous, chalazae more prominent, bulbous, and white. TRUNK: Average length, 13.5 mm; width at first abdominal proleg segment, 2.00 mm. Ground color grass green, modified especially on dorsal and lateral surfaces between longitudinal stripes by whitish pigmented chalazae of next instar showing through integument. Annulae more strongly pronounced, giving the appearance of minute whitish transverse rings. Longitudinal striping limited to dorsal, subdorsal, and subspiracular lines. Dorsal stripe faint purplish green, central portion almost obscured. Subdorsal stripe area lacks underlying pigment spots, thus appearing translucent grass green with faint yellowish white stripe along dorsal margin. Subspiracular stripe solid white, well defined on the less pronounced lateral aspect of body. Thoracic and abdominal legs grass green, setae as in second instar, thoracic legs darkening distally with tarsus and claw amber brown. Crochets basically biordinal uniserial lateroseries (an apparent biserial condition sometimes results from approximately three of the shorter central crochets being slightly offset from uniserial line, but not enough to be considered biserial). Crochets amber brown, anal proleg series in a biordinal uniserial mesal semicircle. Spiracles rusty orange and each comprised of a prominent circular peritreme raised along central caudal margin into fleshy incurving nipple-like conical projection. Peritreme larger, transverse, and elliptical on first thoracic and eighth

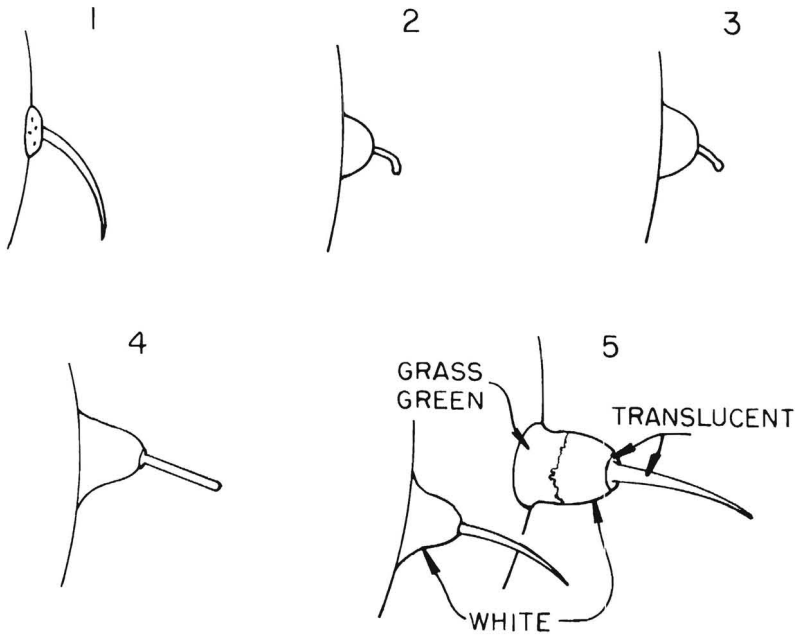


Fig. 10. Details of shape of head capsule chalazae and setae on (1) first instar, (2) second instar, (3) third instar, (4) fourth instar, and (5) fifth instar larvae. Stippled area in (1) is light purplish brown; white areas are pearly white unless otherwise indicated.

abdominal segments. Structure of first thoracic spiracle reversed with raised projection on cephalic margin. Body setae as in second instar except more numerous and randomly distributed, darkened setal bases not as extensive except ventrally where spiniform setae arise from more bulbous white chalazae along leg bases and in groups on corresponding segments lacking legs. Caudal segment as in second instar.

Fourth Instar. HEAD CAPSULE: Average width, 2.21 mm; height, 2.27 mm (20 larvae). Ground color grass green (green after ecdysis). Surface with reticulation of ridges connecting chalazae. Ridges less pronounced ventrally. Setae more numerous than in third instar; blunt and spiniform to knob tipped dorsally, becoming predominantly knob tipped ventrally, all arising from slightly more conical, white chalazae. Facial sutures more heavily margined brown, otherwise head capsule as in third instar. TRUNK: Average length, 21.9 mm; first abdominal proleg segment width, 2.94 mm (20 larvae). Ground color grass green. Body setae mostly blunt and spiniform dorsally, knob tipped laterally becoming shorter and strongly knobbed ventrally, all from minute conical green chalazae. Annulations strongly pronounced, integument and setae producing whitish pubescence. Ground color modified late in instar dorsally and laterally, appearing yellowish white due to coloration of developing chalazae beneath integument. Longitudinal striping as in third instar, except dorsal stripe grass green, sometimes faintly bordered yellowish white. Subdorsal stripe lightly defined yellow to greenish white, sometimes bordered dorsad with grass green. Legs as in third instar, except setae are knob tipped on leg bases, becoming progressively more spiniform terminally and in corresponding areas on segments without legs. Some chalazae mostly on lateral aspect of thoracic leg bases darkened

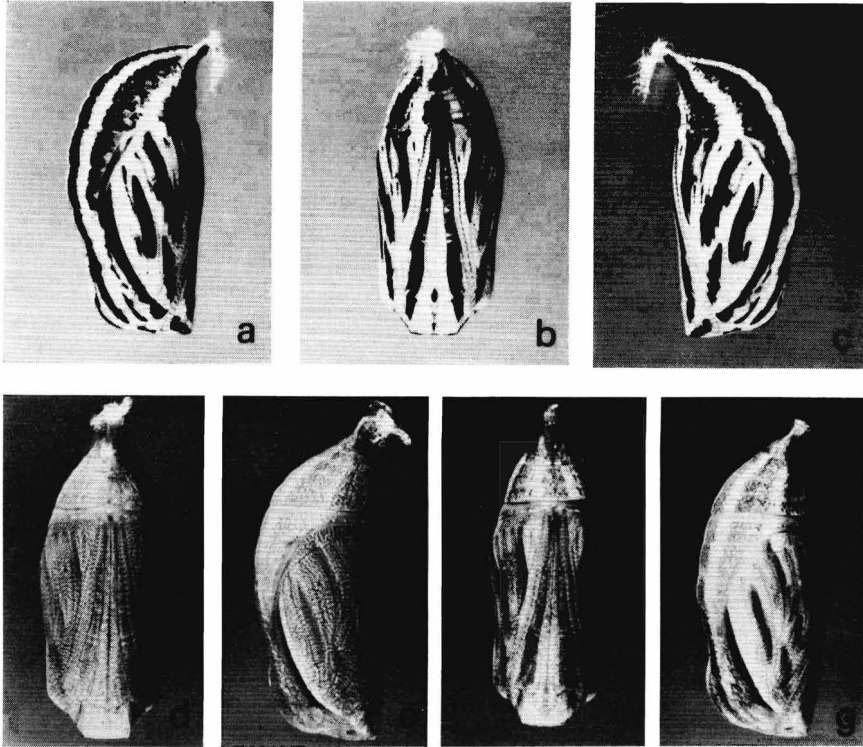


Fig. 11. Dorsal and ventral views of the three pupal color phases of *Cercyonis pegala blanca*: (a-c) black-and-white form (d-e) green form; (f-g) intermediate form.

terminally. Abdominal proleg crochets a uniordinal biserial lateroseries; crochets on anal proleg a uniordinal biserial penellipse opened caudally. Spiracles as in fourth instar except larger with raised projection smaller in proportion to diameter of peritreme. Caudal segment as in third instar except extreme posterior extremity of segment between forks adorned with small patch of purplish brown microspines.

Fifth Instar. HEAD CAPSULE: Average width, 3.21 mm; height, 3.35 mm (20 larvae). Ground color grass green (splitting along frontal suture with cast skin remaining attached, brown after ecdysis). Surface and setae as in fourth instar, except setae slightly longer, spiniform along dorsal cephalic margin. Chalazae large and bulbous, pearly white, sometimes becoming green basally. Most longer setae have bases expanded into a collar at attachment with chalazae. Mandibles with blackish brown color of cutting edge margin comprising one-third of mandible, central one-third cream colored, outer one-third translucent. Labrum translucent to cream colored distally, notch usually darkened. Bases of maxillary and labial palpi green, otherwise amber brown. Facial sutures heavily margined amber brown with brownish curved line connecting bases of in line ocelli. TRUNK: Average length, 33.2 mm (20 larvae; from 29.5 to 38.0 mm). Average width at first abdominal proleg segment, 4.65 mm. Ground color grass green modified by strongly defined segment annulations and frosted integument surface, and by pubescence of the predominantly spini-

form setae (barely discernible without magnification), to give trunk a whitish overcast, transversely ringed appearance. Chalazae greenish white and conical. Dorsal and lateral areas of trunk between longitudinal striping sometimes yellowish green, resulting from yellowish pigment spots under integument. Longitudinal striping as in fourth instar, except white of subdorsal and subspiracular stripes more pronounced. Abdominal prolegs as in fourth instar, except setae all long and spiniform arising from conical chalazae. Chalazae darkened distally along lateral aspects of legs. Crochets uniordinal and triserial (third row sometimes very limited). Anal proleg crochets form uniordinal triserial penellipse opened caudally. Spiracles all larger, transverse, and elliptical, otherwise as in fourth instar. Caudal segment setae on forks spiniform and a translucent rose color. Chalazae have distinct rose colored collar at juncture with setae. Amber brown microspines cover most of caudal extremity between forks.

PUPA. GREEN FORM: Entirely grass green, unmarked by any trace of black and white pattern. BLACK AND WHITE FORM: Pupal case totally marked by black and white longitudinal stripes. Around abdomen, striping evenly spaced and widest at thorax tapering to cremaster. The stripe located addorsally continued anteriorly adjacent to the dorsal meson white stripe terminating at the head. The subdorsal black stripe follows the dorsal margin of wing case to head, and the ventral meson black stripe divides at juncture of wing cases following the inner margin of antennae; they are nearly reconnected by a transverse black mark which crosses the head anterior to the crest of the eyes. Wing cases marked with irregular black dashes oriented obliquely to, and some appearing as extensions of, the longitudinal abdominal striping. INTERMEDIATE FORMS: Ground color of all pupae green. The extent to which black and white markings overlay the green highly variable, the green often being incompletely masked; thus all gradations of black, white, and green occur between the two extreme color forms. Black and white, however, modified simultaneously in that both tend to increase and decrease together. Occasionally, black pigment totally absent, exposing the green ground color which is still silhouetted by a remaining trace of white.

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