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PACIFIC NORTHWEST POPULATION OF *LOPHOCAMPA MACULATA* HARRIS 1841: EVIDENCE OF A POSSIBLE HYBRID ORIGIN

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ABSTRACT. The different geographic populations of *Lophocampa maculata* Harris 1841 are characterized by a variety of phenotypic differences, of which larval color is the most obvious. Individuals of the Pacific Northwest (PNW) populations display significant variation in late instar coloration, arising from variation in setae pigmentation. Such variation is not found in other populations of *Lophocampa maculata*, including the western Interior population (WI) and California Coastal population (CAC). Analysis of the pattern of pigmentation of the PNW population suggests it represents a combination of features of the CAC and WI populations. A simple scheme that accounts for all of the color variations seen in the different geographic populations of *L. maculata* is presented. A laboratory mating experiment involving WI and CAC individuals resulted in viable offspring displaying the range of larval coloration seen in the wild PNW populations. The F1 hybrids were fertile and produced an F2 generation also exhibiting the PNW larval color patterns. Taken together, these results suggest that the PNW populations arose via hybridization between the adjacent WI and CAC populations. Evidence from laboratory-raised broods of wild-caught females suggests there can be significant individual variation in pigmentation even within a single brood. The present day PNW populations demonstrate features of a hybrid swarm resulting from relatively recent hybridization. A model for this process since the last glacial maximum is presented.

Additional key words: setae pigmentation, hybrid swarm, mosaicism, rare allele phenomenon, ecological speciation

The Spotted Tussock Moth, *Lophocampa maculata* Harris 1841, (Erebidae, Arctiinae (Lafontaine 2010)) is found across a wide expanse of North America, where it exists as several distinct populations defined primarily by last instar coloration (Strothkamp 2015). Each of these populations is characterized by one, or at most two, last instar color patterns, which are constant over a large geographic range. The one exception is the Pacific Northwest (PNW) population. This population extends from roughly the California/Oregon border to southwestern British Columbia, Canada and from the Pacific coast to the west slope of the Cascade Mountains (Strothkamp 2015). Within this region, last instar coloration is extremely variable in several respects.

The PNW population is bordered on the south along the Pacific coast by the California Coastal (CAC) population and on the east by the Western Interior (WI) population (Strothkamp 2015). These adjacent populations are characterized by a number of phenotypic distinctions from the PNW population, with larval coloration being the most obvious. Adults of the CAC and WI populations differ somewhat in wing patterns, as previously described (Strothkamp 2015). At present, the CAC and WI populations in California are kept isolated by the central valley of California.

This paper details both fieldwork defining the PNW population and a laboratory hybridization study. Together, these suggest the PNW population is derived from hybridization of WI and CAC individuals. A model for this process, in the context of the northward migration of both the CAC and WI varieties shortly after the last glacial maximum (LGM) is presented.

MATERIALS AND METHODS

Field data were collected with the aid of many individuals, who provided observations, photographs and specimens. Without their assistance this work could not have been carried out and they are listed alphabetically in the Acknowledgements section. Their efforts are a wonderful example of citizen science in action.

Detailed study of the offspring from wild females forms a major part of this work. Eggs and larvae were kept at 18–24° C and a light: dark cycle of 16:8 hours in glass petri dishes or, as they grew larger, in polyethylene plastic boxes covered with fine nylon mesh. Mating experiments on moths were conducted in nylon mesh cages under ambient summer conditions. Females were allowed to deposit eggs on the mesh walls. Newly hatched larvae were then transferred to leaves kept in petri dishes. Larvae were fed either pacific willow (*Salix lasiandra*) or vine maple (*Acer circinatum*). Previous work had shown that choice of food plant did not alter larval appearance (Strothkamp 2015). The CAC population showed a strong preference for willow as a food source, while PNW and WI larvae did well on either tree species.

Hybridization of WI and CA Individuals

Moths were obtained from pupa raised the previous year. The CAC pupae were from a larval brood of the black/yellow/black last instar color variety (see Strothkamp 2015) from Aptos, CA. This brood consisted of all black/yellow/black individuals as 5th instars. Two males were used in the hybridization

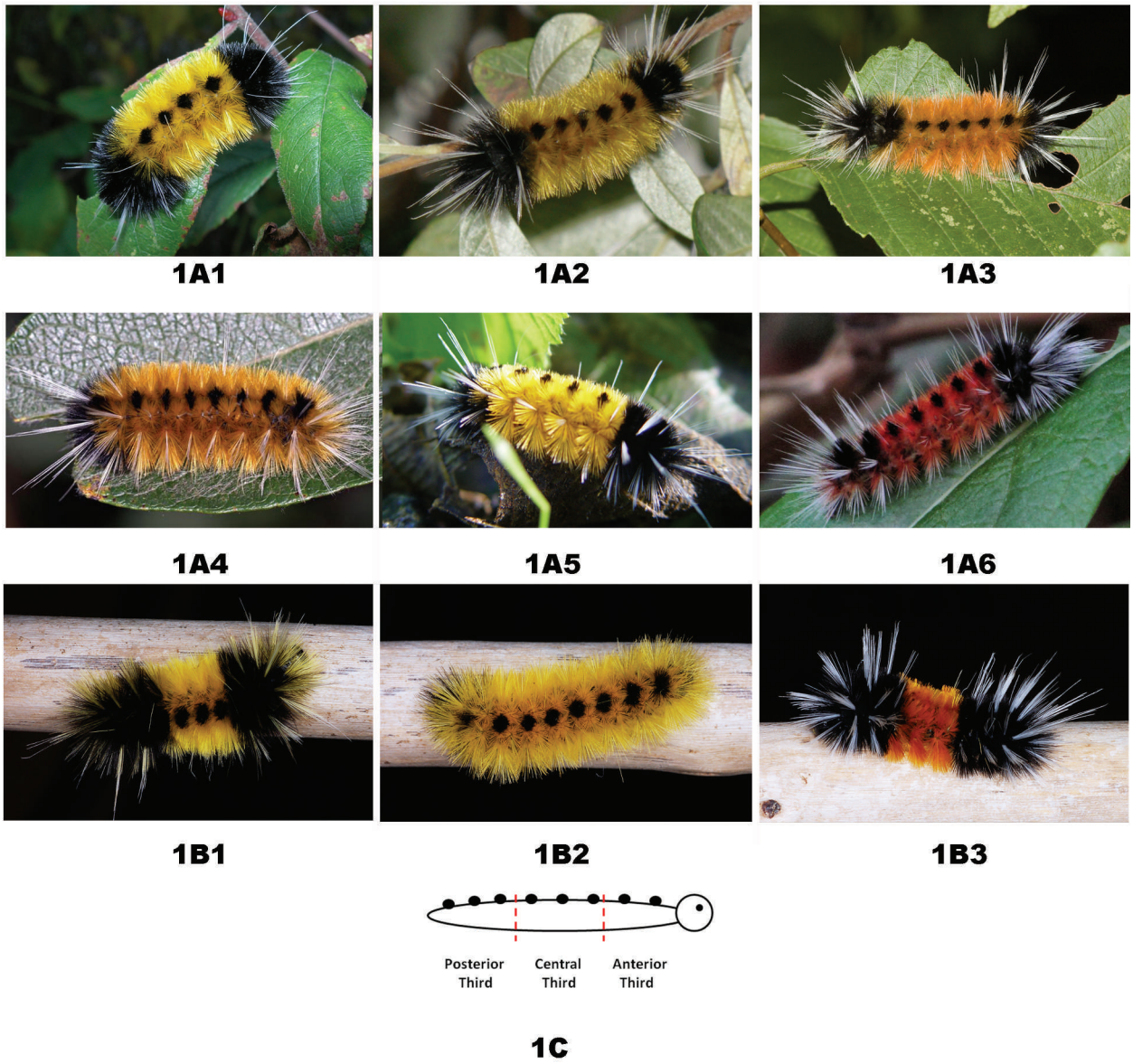

FIG. 1. Patterns of coloration in 5th instar *Lophocampa maculata*. All have long white setae clustered at both ends of the body. The shorter setae are pigmented. The Pacific Northwest (PNW) population is characterized by great variability in coloration (**A 1-6**). The Eastern and California Coastal (CAC) populations consist of two color phenotypes (**B 1,2**), while the Western Interior (WI) populations have only one (**B 3**). The color patterns of all 5th instar *Lophocampa maculata* can be explained by the diagram in (**C**). The red dashed lines divide the body into anterior, central and posterior regions. See text for the details of the pigmentation scheme.

experiment. The WI pupae were from a typical black/orange brood from the Sierra Nevada Mountains near Bishop, California. Three females from this brood were used in the hybridization experiment. Pupae were kept in individual containers prior to eclosure, insuring that mating did not occur prior to placement of the moths in the same cage for the experiment.

All five moths were placed in a mesh cage and maintained outdoors under ambient late summer conditions. They were provided with a dilute maple syrup solution on a banana slice. Oviposting began on the third night and continued for an additional two nights. Eggs were laid in clusters on the mesh top and upper sides of the cage, as is typical for this species when bred in captivity. Eggs were misted lightly with water to prevent desiccation. The eggs hatched over a one-week period and the newly hatched larvae were transferred to leaves of pacific willow (*Salix lasiandra*)

in glass petri dishes. They ate avidly and development throughout the larval stage was typical for this species. Cocoon formation and pupation occurred in late summer/early autumn.

Pupae of the hybrids were kept together in a mesh cage. They eclosed the following year and mated, producing fertile eggs. These F2 hybrid larvae were reared to the last instar as previously described.

RESULTS

Data on the larvae of the PNW population were obtained from Oregon, Washington and southwest British Columbia. Data on last instars are the most readily available because of their size, bright coloration and activity. Figure 1A shows examples of the great variety of last instar color patterns found throughout the Pacific Northwest. Figure 1B shows the two color varieties of the CAC population and the single color pattern that is found in the WI population.

The pattern of coloration in all *Lophocampa maculata*, is dependent on the spatial arrangement of the variously pigmented setae, which densely cover the body of 5th instar larvae. A hallmark of the species is the long setae at both ends of the body. These are invariably lacking in any pigment and thus white in color. All the shorter setae contain an exogenous xanthophyll pigment, which gives them a bright yellow color. In some cases, they contain black or orange pigment in addition (Strothkamp 2015). In the latter cases, the color of the setae is determined by the black or orange pigment. The diagram in Figure 1C accounts for the observed patterns of coloration of the Eastern, CAC and WI populations of *L. maculata*. The body is divided into three regions, anterior, posterior and central regions, each comprising about 1/3 of the body length. There is a uniform yellow coloration of all the short setae and, in addition, a row of eight black dorsal tufts in all populations except the WI. In all WI, the central region is overlaid with orange pigment, which obscures the yellow color. In addition, the anterior and posterior regions have black pigment, which also obscures the yellow. The Eastern and CAC populations can be simply all yellow with black dorsal tufts or can have black pigment on the setae of the anterior and posterior thirds of the body. The extent of these black colored regions is variable, which results in variation in the number of observable black dorsal tufts. The greater the extent of the anterior and posterior black regions, the fewer the number of visible black dorsal tufts. The PNW populations have variable amounts of orange and, perhaps, traces of black pigment overlying the yellow background color. This produces a wide range of background coloration, which can vary from bright yellow to golden yellow to orange to red-orange. PNW populations also have variable extents of anterior and posterior black pigmentation, which can range from none to roughly the anterior and posterior thirds of the body. The PNW populations always have the black dorsal tufts, which can vary in number as described above. The combination of orange central region and black dorsal tufts is a feature unique to the PNW population

The realization that the great variety of last instar coloration in the PNW population could be understood as an admixture of CAC and WI color determinants, along with the geographic proximity of the WI and CAC populations to the PNW population, suggested that the PNW varieties could be explained by hybridization of CAC and WI individuals. As a way to explore this possibility, a mating experiment utilizing CAC males and WI females was attempted. The two CAC males came from a brood raised in captivity from a wild gravid female caught in Aptos, CA. This brood was entirely the B/Y/B color variety as last instars and adults had the low contrast wing pattern (Strothkamp 2015). The three WI females were from the Sierra Nevada mountains (Bishop, CA) and had the standard WI color pattern as last instars. As moths they had the high contrast wing pattern.

The F1 larvae were uniform in appearance for the first three instars but beginning with the 4th instar, considerable individual variation was observed, which was even more pronounced in the final instar (Fig. 2A). Because the matings were done under communal conditions, the assignment of color varieties to broods produced by specific parents was not possible. However, the range of color patterns found in the hybrids matches well with the variety found in wild PNW individuals (compare Figs. 1A and 2A).

As adults, the hybrids showed the high contrast wing pattern (Strothkamp 2015), characteristic of the WI population. The adults resulting from this hybridization experiment were allowed to breed and produced a second generation of hybrid larvae. These larvae, as last instars, showed the same variety of color patterns as their parents (Fig. 2B). The F2 hybrids are evidence of several important points. First, the 1st generation hybrids were obviously fertile. Second, the variability of last instar coloration was passed on from 1st to 2nd generation larvae.

An interesting feature of the laboratory hybrids were two individuals, one a 5th instar, and the other a 4th, which had small regions of the body with a mixture of yellow and orange setae, found on the same pinaculum (Fig. 2C 1,3 (dorsal view)). I have never observed this in CAC or WI individuals, either raised in captivity or

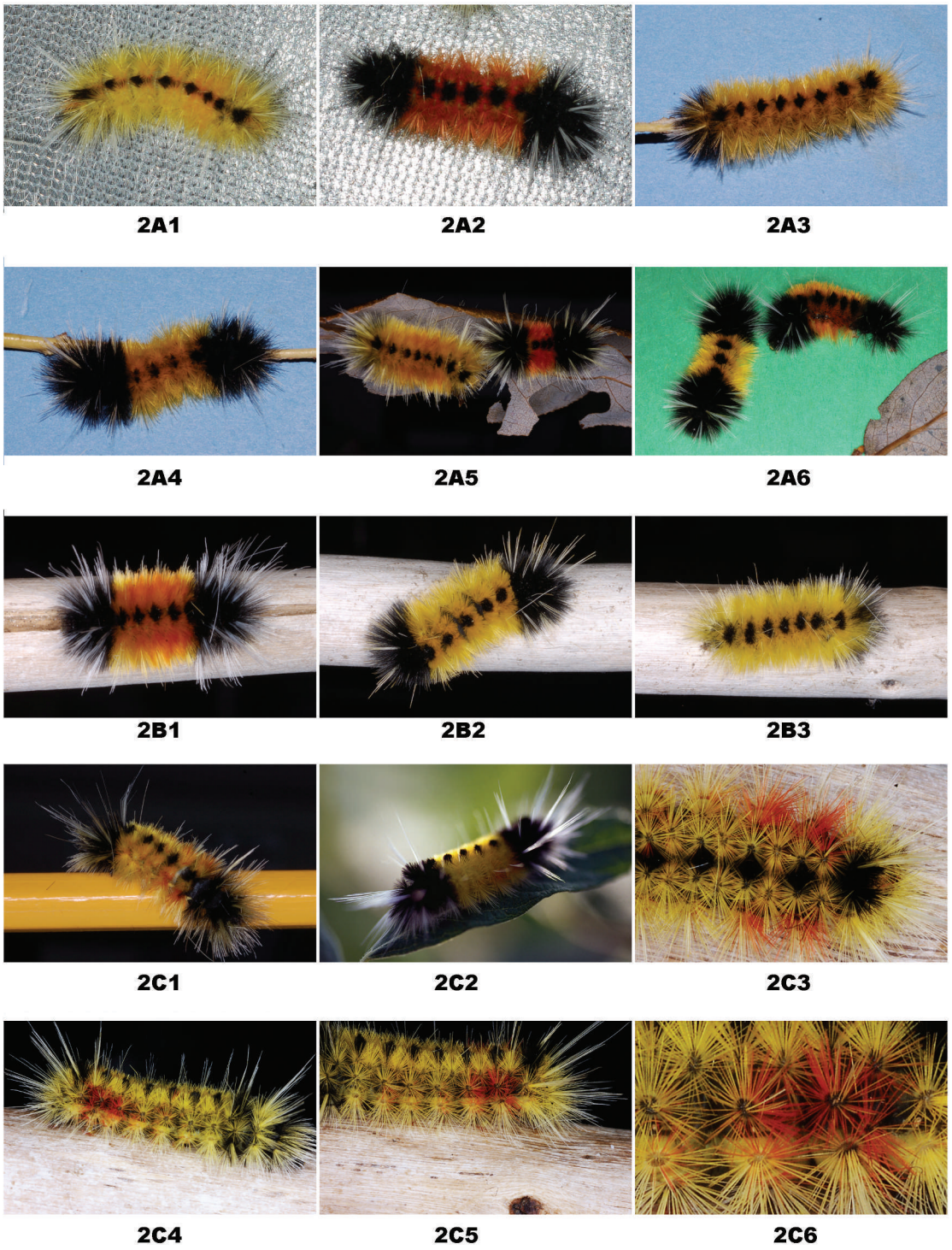

FIG. 2. Coloration in 5th instar laboratory hybrids resulting from mating of CAC and WI individuals. The F1 generation is shown in (**A**), and is characterized by a wide range of coloration (compare with wild PNW individuals (Figure 1A). The F2 generation (**B**) shows a similar variety of color patterns. Individuals showing a mosaic pattern of small orange regions on a yellow background are shown in (**C**). Figure **C 1** shows an F1 5th instar laboratory hybrid. Note the symmetrical location of the orange setae. Figure **C 2** shows a wild PNW 5th instar from Vancouver Island, British Columbia, Canada, which also show a mosaic pattern (photo courtesy of David Droppers). Figure **C 3, 4, 5** show the symmetrical location of orange pigment regions in an F2 4th instar laboratory hybrid from a dorsal view (C3) and lateral views from the right (**C4**) and left (**C5**) sides.. Figure **C6** show a close-up of an orange region. Note that within a pinaculum there are both yellow and orange setae.

found in the wild. However, a wild PNW individual, as a 5th instar, had a similar pattern (Fig. 2C 2). This appears to be a form of mosaicism. Figure 2C 4–5 show right side lateral and left side lateral views of the 4th instar individual. Figure 2C 6 is a close-up of the 4th instar individual. Note in Figure 2C 1,3,4,5 the symmetrical location of the orange regions. Within a pinaculum there are both yellow and orange colored setae, most clearly seen in Figure 2C 6, with the two most posterior pinacula on either side having the greatest number of orange setae. The number of orange setae in a pinaculum decreases as you move anteriorly or above or below the lateral row of pinacula.

Because all matings were carried out under communal conditions, and larvae were raised together from multiple egg masses, it is not possible to know whether a single brood of the hybrids, resulting from a mating between a female and a single male, would produce uniform coloration of larvae within the brood or a random mixture of coloration among individuals of the same brood. A small egg cluster obtained from Port Alberni, British Columbia, Canada, which consisted of five eggs, all produced by the same female, provides a partial answer to this question. The five individuals, as forth and fifth (final) instars, show marked variation in coloration (Fig. 3). Other broods from single females, also from Port Alberni, were highly variable in coloration as 4th instars but uniformly colored as 5th instars. Thus, while PNW populations can show considerable intrabrood heterogeneity in instar coloration, that is not always the case and variability in one instar does not predict variability in a subsequent instar.

DISCUSSION

Lophocampa maculata consists of several populations characterized by a number of phenotypic distinctions, of which last instar larval coloration is the most obvious (Strothkamp 2015). Within each geographic region, except for the Pacific Northwest populations, there is uniformity of last instar coloration, with a single phenotype in the WI populations and two phenotypes in the Eastern and CAC populations. The diversity of the Pacific Northwest populations was discovered based on random observations of individuals from across the region. The methods by which this variation was discovered raised the question of whether it resulted from intrabrood variability or interbrood variation, with, in the latter case, all individuals of a single brood being uniform in coloration. The data from captive rearing of egg clusters from wild-caught females (Fig. 3) indicate that a single brood can exhibit great variability in ultimate or penultimate instar coloration, although that does not necessarily have to be the case. Thus, the accumulated data on PNW color variation indicate it is the result of both intra and interbrood variability, both of which exhibit a much greater range than in other *L. maculata* populations.

The resulting limited color variations, found in all populations of *L. maculata*, could be accounted for by a small number of "patterning genes," which control expression of pigmentation in the different regions of setae. The color variation found in the central region of the PNW populations is in contrast to the uniform orange or yellow pigmentation of the WI, Eastern and CAC populations respectively. This may reflect variation in the amount of black and orange pigment, which overlies the yellow color. Similar striking patterns of coloration are found in the fur pigmentation of many mammals, such as many of the large felines. The main difference is the addition of black or orange to the yellow base color of the setae, as opposed to the white base color of unpigmented mammalian fur.

The data presented in this paper suggest that the PNW population of *L. maculata* shares characteristics of both the WI and CAC populations. In particular, larval coloration appears to be a mixture of features characteristic of the WI and CAC populations. All of this suggests that the PNW population resulted from hybridization between the WI and CAC populations. The laboratory hybridization experiment, which produced viable F1 and F2 generations, both having larval coloration similar in variety to wild PNW individuals, is consistent with that interpretation. The different populations of *L. maculata* suggest an evolutionary history in which the organism has recently experienced both divergent evolution into several distinct populations, as the result of range expansion since the last glacial maximum (LGM), and hybridization between the distinct CAC and WI populations giving rise to the PNW population.

The hybridization experiment leads to several conclusions. First the successful mating of CAC and WI individuals supports the argument that all *Lophocampa maculata* populations should, at least based on ability to reproduce successfully, be considered the same species, although clearly significant diversification has occurred in the different geographic regions. Hybrids produced from the CAC and WI populations were fertile and produced a second generation of individuals exhibiting similar variation in last instar coloration. The color variability of the hybrids thus appears to be stably transmitted from one generation to another. In addition, these varieties of coloration match well with those seen in

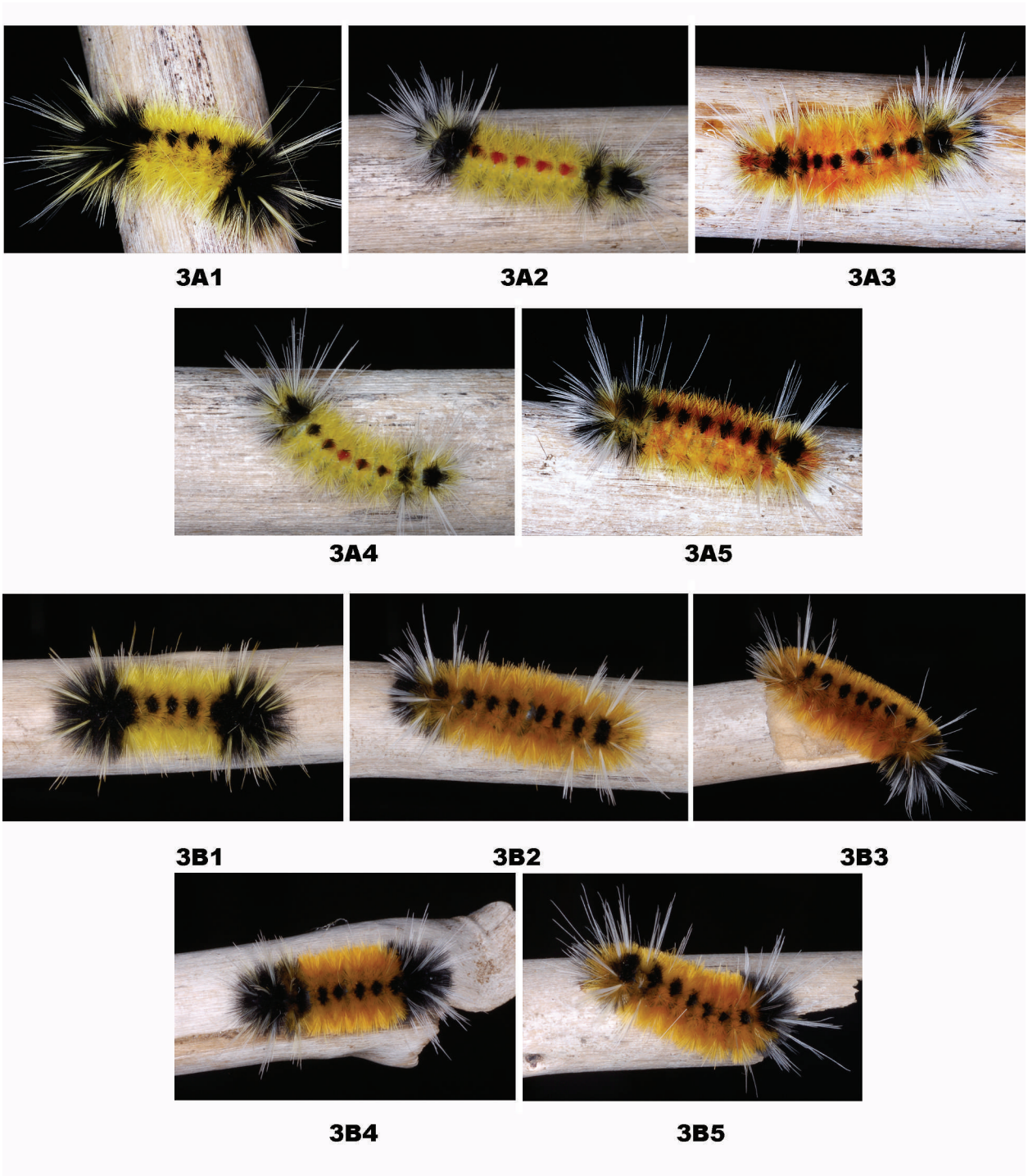

FIG. 3. The five individuals shown in this figure were obtained from a small egg cluster from a single wild-caught female. The individuals, numbered 1–5, which differ dramatically in coloration, are shown as 4th instars (**A**) and 5th instars (**B**).

PNW wild individuals (Figs. 1A and 2A). Thus, a reasonable scenario is that the present PNW populations resulted from hybridization of CAC and WI individuals.

Hybridization has been historically considered to be unimportant in evolution. However, more recently it has been recognized as a factor contributing to the origin of species (Arnold 1997; Mallet 2007), and several well-documented examples of homoploid hybridization between animal species have been discovered (Dowling 1997, Buerkle 2000, Abbott 2013), including Lepidoptera (Mavarez 2006, Gompert 2006). The entire *L. maculata* complex, consisting of several clearly defined populations, may be an example of speciation in progress, involving both divergent and hybridization speciation.

Geographic isolation of the present Eastern, WI and CAC populations is maintained by regions of unsuitable habitat: the Great Plains separate the Eastern and WI populations and the Central Valley of California separates the WI and CAC populations. *L. maculata* is not found in the Central Valley now (Strothkamp 2015) and paleoclimate data based on pollen records (Adam 1981, 1983; Davis 1988), sedimentary charcoal deposits (Brunelle 2003), geochemical data (Street 2012) and hydrologic data (Goman 2000, Malamud-Roam 2006) suggest it has been unfavorable habitat since LGM because of both climate and lack of suitable plant species for larval development. These three allopatric populations have diverged enough to have distinct phenotypes (Strothkamp 2015).

The Siskiyou Mountains, which form a high elevation, forested bridge between the Sierra Nevada/Cascade Mountains and the Pacific coast created a region of sympatry between the WI and CAC populations, allowing them to hybridize. Movement of the hybrids north into the Pacific Northwest climate zone, west of the Cascade Mountains, may have provided the reproductive isolation necessary for the hybrids to become established (Gross 2005). A similar hybridization involving hybrids occupying an "extreme" habitat not suited to either parental species has been proposed for Lycaeides butterflies (Gompert 2006, Gompert 2014).

The present day CAC population is bivoltine, while the WI and Eastern populations are univoltine. The PNW population appears to be universally univoltine. This raises the question of whether the timing of the adult stage would have allowed for mating between the CAC and WI populations. It is possible that the differences in voltinism between the WI and CAC populations result in phenological isolation. Phenological isolation has been reported for elevation-based differences in flight period for *Euphilotes enoptes* (Peterson 1995). Study of present day WI and CAC populations indicates that there would be overlap of the flight period of the WI populations with the spring CAC flight period and an even greater overlap with the late summer flight (compare Figure 6 a & c of Strothkamp 2015), thus allowing for hybridization to occur even if the CAC population was already bivoltine when the WI and CAC populations met.

Among the often-observed characteristics of a hybrid population are (1) considerable individual genetic variation, a "hybrid swarm," often detected by allozyme analysis (Seehausen 2004) and (2) an increased frequency of rare alleles that are found in the parental populations (Bradley 1993, Hoffman 1995, Schilthuizen 1999, Schilthuizen 2004). The *L. maculata* of the PNW appear to show both characteristics. The great variation in larval coloration may be a visual indication of a "hybrid swarm." This variation is found both in wild individuals, captive reared broods obtained from wild females and the laboratory hybridization experiment. All populations of *L. maculata* experience a rare phenomenon referred to as partial depigmentation (Strothkamp 2011, 2015), where an individual looses some, but not all, of its typical setae pigmentation as a third or forth instar but returns to normal coloration as a fifth instar and adult. This is thought to result from a rare allele or combination of alleles affecting the patterning genes, which control pigmentation of setae. While the specific coloration of these "white" individuals seems to be population specific, it occurs in all the geographic populations of *L. maculata*. It is impossible to quantify the frequency with which this form occurs in wild populations for a variety of reasons. However, over a five-year period of collecting reports on this variation, it appears to occur much more frequently in the PNW populations, especially on Vancouver Island, British Columbia, Canada. This appears to be an example of the "rare allele" effect in a hybrid population.

Another very rare feature of the wild PNW populations and the laboratory hybrids, is a mosaic pattern of coloration in which regions of yellow setae have small areas of setae with orange pigmentation (Fig 2C). Mosaics are individuals that consist of two genetically different cell types. There are many types of mosaics and they can arise in a variety of ways. In many cases the mosaic cells may be difficult to distinguish. However, if the mosaic cells are involved in the pigmentation of skin, fur or setae, obvious visible differences can occur. Variation in fur pigmentation in mammals (Robinson 1957), particularly the mouse

(Mus musculus) (Gruneberg 1966, Panthier 1990, Favor 1994), has been well documented.

The mosaic individuals seen in *Lophocampa maculata* have only been observed in the Pacific Northwest populations, and may be a consequence of their hybrid origin. The F1 generation of the hybrids has, of necessity, a genome in which the pairs of homologous chromosomes are derived from parents from the two different populations and are thus likely to differ at many loci, including those responsible for setae pigmentation. The same will be true of many individuals from succeeding generations. Thus, somatic cell mitotic crossing over could explain the observed color mosaics in *L. maculata* (Bateman 1967, Koopman 1999).

In summary, the phenotypic characteristics of the PNW populations of *Lophocampa maculata* suggest this population has evolved from a hybridization of the CAC and WI populations. Investigation of the molecular genetic characteristics of the population will undoubtedly shed more light on this possibility.

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