

THE GENETICS AND REPRODUCTIVE ISOLATING
MECHANISMS OF THE *PIERIS NAPI* - *BRYONIAE* GROUP (cont.)

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III. GENITAL ARMATURE

One of the most important reasons why *bryoniae* and *napi* have been considered to be conspecific is that no structural characters have ever been detected between the genitalia of the two forms in either sex. But this lack of differences need not be a decisive proof for their specific identity, since good species are known without any remarkable distinction in the genitalia. The structural identity of copulatory organs is also evident from the fact that the pairing between *bryoniae* and *napi* takes place without mechanical hindrance. The other possible sexual isolating mechanisms will be discussed below.

IV. THE KARYOTYPE

The chromosome complexes of *napi* and *bryoniae* are identical in haploid chromosome count in the spermatocytes, with $n = 25$. The chromosomes are too small to show qualitative differences if standard cytological methods are used. An indirect indication for the qualitative differences could be given by the disturbance in the chromosome pairing during meiosis of the hybrids. Unfortunately a lot of fixed hybrid testes were accidentally lost on the occasion of a laboratory remodeling, but new testis material is in preparation and will be reported later.

V. PHYSIOLOGICAL AND ECOLOGICAL CHARACTERS

It has been impossible to carry out genetical analyses of the physiological features of the two forms owing to technical difficulties in our laboratory some 13 years ago. But since these physiological traits are as significant for their ecological interrelations as for their distribution, the most obvious gross differences are listed in Table 5.

Among the characteristics listed in the table, the number of annual generations and very likely also temperature tolerance are heritable. Both traits are modifiable to a certain extent through environmental influences, and should therefore be looked into more thoroughly.

We do not know to what extent foodplant preferences are hereditary or due to microclimatically conditioned behavior of the insects. No

Table 5. The Physiological and Ecological Differences between *bryoniæ* and *napi*.

Feature	<i>bryoniæ</i>	<i>napi</i>
Activity dependence on laboratory temperature	Above 28°C; in sunshine the ♂♂ sit exhausted in the shade, in ♀♀ no or slight egg-laying.	Above 28°C ♂♂ and ♀♀ fly in sunshine without sign of fatigue, egg-laying good.
Copulation	At 23°C and when cloudy, copulation frequent (P = 0.857); in sunshine infrequent (P = 0.162) (Petersen 1954).	At 23°C and when cloudy, copulation P = 0.143; in sunshine P = 0.838 (Petersen 1954).
Egg-laying flight	In the lowland populations ♀♀ fly from the wood to the meadow when cloudy, but return immediately to the wood when sun appears (Petersen 1954).	No striking behavior. The ♀♀ will lay the eggs in the open, though mostly in thin wood or at the border of the wood.
Food plants	In all investigated biotopes <i>Biscutella lævigata</i> is either the only food plant of the single-brooded populations or the preferred food plant in addition to <i>Thlaspi</i> and <i>Arabis</i> in low regions (according to the writer's observations as well as to Kautz 1939 and Petersen 1954). Only on Monte Mottarone near Lago Maggiore <i>Arabis halleri</i> is the exclusive food plant, since <i>Biscutella</i> is absent there (Petersen 1954).	No particular preference for a certain food plant, Foods are as follows: <i>Brassica</i> , <i>Rapa</i> , <i>Erysimum officinale</i> , <i>Raphanus raphanistrum</i> , <i>Cardamine amara</i> and <i>pratensis</i> , <i>Diplotaxis tenuifolia</i> and <i>Reseda</i> (Verity 1944); <i>Armoracia</i> , <i>Barbarea</i> , <i>Sinapis</i> , <i>Sisymbrium</i> , <i>Alliaria</i> (Kautz 1939); <i>Roripa silvestris</i> near Zagreb, <i>Cardamine trifolia</i> in the Julian Alps, <i>Biscutella lævigata</i> in the Julian Alps and in Montenegro.
Habitat preference	In the Alps between 1000-2200 m. only one generation. In the southern valleys down to 200 m. completely or partially 2-3-brooded. The single-brood of the highland populations modifiable through high temperature in which a certain percentage of pupæ develop without hibernation (diapause).	Everywhere 2-4 brooded. Where the single-brooded <i>bryoniæ</i> population borders with the two-brooded <i>napi</i> the flying time of the <i>bryoniæ</i> falls between the two generations of <i>napi</i> . Where multiple-brooded populations of both forms occur together, <i>napi</i> imagos seem to appear prior to <i>bryoniæ</i> (Kautz 1939).
Number of generations and pupal diapause	Mainly regions of <i>Pinus mughus</i> between 1100-2200 m. altitude. Below 1000 m. altitude, localities with <i>P. mughus</i> removed to the valley by torrents, if lower down localities with Black-pines (<i>Pinus silvestris</i>).	In the plain as well as in the mountains up to 1500 m. altitude, thin woods and borders of woods, less frequently open meadows, since the egg-laying occurs mostly in shady spots.

preference of *bryoniæ* for *Biscutella* over other Cruciferæ (as claimed by PETERSEN for his samples) was noted in captive populations by various breeders or by me. This applies not only to *bryoniæ*, but in general more or less for other closely related pierid species that I have investigated in laboratory tests (*P. rapæ*, *manni*, *Anthocharis cardamines*, *belia*, *Pontia daplidice*, *Synchloë protodice*, etc.). Notwithstanding, it is significant that *Biscutella* was found as the food plant of lowland *bryoniæ* too, for example in Posavje near Ljubljana at the eastern part of the Karavanke Alps (Petersen 1954). However, near Hrastnik on the extreme limit of *bryoniæ* range in Posavje, I found a small *Arabis* sp. on which a white *bryoniæ* female laid eggs. *Vice versa* I have also seen *napi* females laying on *Biscutella* in the Julian Alps as well as at Durmitor in Montenegro at 1400 m. altitude. Slight differences of behavior toward foodplant species are difficult or impossible to detect in laboratory tests, and various cruciferous species known to be foodplants for *bryoniæ* and *napi* should be transplanted to the natural biotopes of the two butterflies in order to test subtle differences in the strength of attraction of different plants to egg-laying females. Unfortunately, in this Atomic Age, funds are not available for such a harmless project.

In short, in the ecology of the two forms, especially in their physiological ecology, much remains to be resolved.

RELATIONS BETWEEN MORPHOLOGICAL VERSUS COLOR CHARACTERS AND PHYSIOLOGICAL-ECOLOGICAL ONES. We have not been able to discover whether and how far a relationship may exist between any morphological features and any physiological (*i. e.*, ecological) ones; that is, we can say very little about possible pleiotropy of the color genes for which the Mendelian behavior is known.

We have obtained some results for the allele pair *B*, *b*. Through ten generations, in which *bryoniæ* × *napi* hybrids have been either crossed to each other or back-crossed with *napi*, the phenotypic manifestation of *B* has been maintained, but no remarkable differences in behavior, vitality or number of generations between *Bb* and *bb* individuals have been observed. After these many crossings, the allele *Y*, which controls the brownish yellow color, was completely lost, since the presence of this highly sex-controlled gene was not manifested in the males, so that one could never know what a male carried. Thus, no one of the physiological traits considered seems to be related to the gene *B*. Such characters, however, could be perhaps related to *Y*, since yellow strains will not hold out for more than a few generations.

Great difficulty attended the attempts to maintain the *W* factor, which was never obtained in the homozygous condition. More detailed experi-

ments should of course be carried out, but it is evident that the typical physiological characters of *bryoniæ* cannot be related to the *W* gene simply because there is only such a slight concentration of this gene in certain typical *bryoniæ* populations.

If the three allele pairs of *bryoniæ* and *napi* have no correlation with the physiological and ecological characteristics of these two forms, then these genes are bound to have a direct selective advantage. It may be that the dark and yellow-brown pigments act to capture radiant heat, which would be an advantage for animals of colder areas and would explain the distribution of the two forms in relation to climate. The adaptive correlation of *W* is unknown, but it could conceivably be investigated by comparing habitats of the populations with various concentrations of this allele.

VI. RECOMBINATION IN NATURE

We come now to our main subject: to what extent may the amount of gene flow or, in other words, the frequency of crosses between *bryoniæ* and *napi* in nature be deduced from the frequency of recombination in nature? In standard taxonomic practice, the amount of recombination is usually judged by the presence and proportions of intergrading morphological types found where two populations are in geographical contact. If intergrades are absent or very rare, the two populations are judged as species; if intergrades are common, judgement is usually for subspecific status of the populations.

Curiously enough the recombination situation in the *napi* - *bryoniæ* complex differs strikingly on the northern and southern sides of the Alps. Though both forms occur on both sides of the Alps, their recombinations are very rare on the northern side, while at the southern approaches there exist all the recombinations described above.

Tables 6A to 6C and Figures 4 and 5 (from Petersen 1954) show variation classes of two characters, the dark markings and ground color. In these tables, *napi* is represented by the horizontal classes 1-3 and vertical 1 - 2, *bryoniæ* by horizontal classes 5 - 9 and vertical 2 - 6. Table 6A illustrates clearly how in the Allgäuer (northern) Alps, *napi* and *bryoniæ* are sharply distinct from each other, the intermediates numbering only one out of 174 samples. But in the south, for instance in Carinthia, as shown in Table 6B, there is no distinctly concordant gap between the variations of the two forms. Class 4 (horizontal), contrary to its rarity in the northern Alps, is in Carinthia even more common than the typical *napi* class 2 (horizontal). The most frequent combinations (bold face

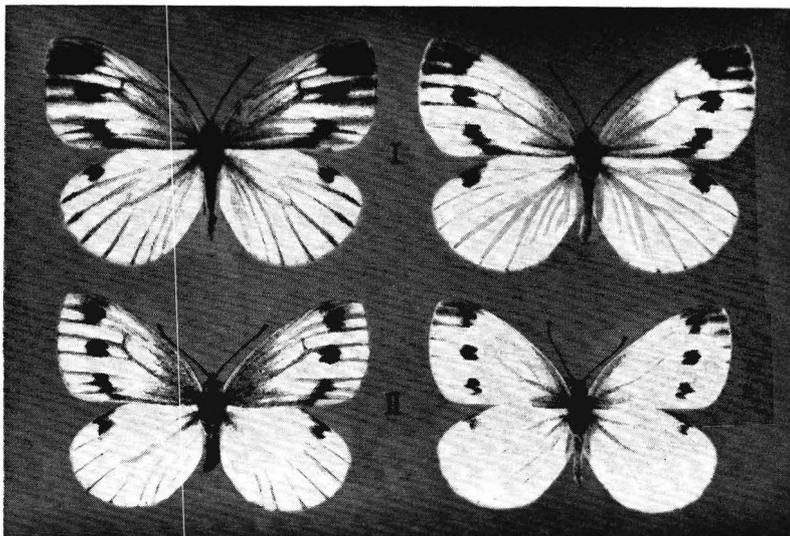


Fig. 3. Segregation in *bryoniæ* and *napi* females in two backcrosses resulting from the mating of two similar heterozygous *bryoniæ* sisters and two differently marked *napi* fathers: The father of brood I (upper level) had the melanic pattern very extended and dark, whereas the father of brood II (bottom) had the pattern very reduced and pale. At left are heterozygous *bryoniæ* ♀♀, *Bb*, at right *napi* ♀♀ homozygous for *bb*.

numbers in the tables) are much closer together in Table 6B than they are in Table 6A. The discontinuity in the Vienna area (Mödling) appears to be nearly or quite completely lost (Table 6C). Since Tables 6B and 6C are based on museum specimens, *napi* may be under-represented, as PETERSEN has rightly pointed out. This suspicion was confirmed by his investigations near Mödling, through which he learned that *napi* is really more frequently present than as noted in Table 6C. My investigations in the Yugoslavian section of the southeastern Alps (Karawanke and Steiner Alps) are in substantial agreement with those of PETERSEN, but from here we also have breeding and crossing studies.

So at Fala in the Drava valley (about 300 m. altitude) near Maribor (Marburg) a mixed *bryoniæ* (*flavescens*) and *napi* population occurs (Table 6D). Both forms are double or even triple brooded. In the offspring of one of two wild yellow *bryoniæ* females captured between 7 and 9 July 1931 (brood "Fala 1") were one *bryoniæ* male and one *napi* female. (At that time my rearing methods were still very imperfect, and a great number of caterpillars died of diseases. Later on, this obstacle was entirely removed.) They paired and yielded four imagoes: 1 white

Table 6. Frequency of variation classes of dark markings and yellow color in five localities (see text).

		Dark markings									
		1	2	3	4	5	6	7	8	9	
Yellow color	1	4	12	8	-	-	-	-	-	-	24
	2	-	3	1	-	-	-	-	-	-	5
	3	-	-	-	1	-	1	3	12	1	54
	4	-	-	-	-	1	3	16	28	6	18
	5	-	-	-	-	-	5	21	42	5	73
	6	-	-	-	-	-	1	2	2	-	5
		4	15	9	1	1	10	42	85	12	179

A. Allgäuer Alps (northern Alps).

		1	2	3	4	5	6	7	8	9	
Yellow color	1	1	2	3	1	-	-	-	-	-	7
	2	-	3	6	2	2	3	4	2	1	23
	3	-	-	2	2	2	2	3	1	1	13
	4	-	-	-	1	4	6	2	2	2	17
	5	-	-	-	-	2	-	2	1	-	5
	6	-	-	-	-	-	-	-	2	-	2
		1	5	11	6	10	11	11	8	4	67

B. Carinthia (southern Alps).

		1	2	3	4	5	6	7	8	9	
Yellow color	1	1	2	-	-	-	-	-	-	-	3
	2	1	1	1	6	3	2	-	-	-	14
	3	-	3	3	3	3	1	-	-	-	13
	4	-	1	1	1	4	-	-	-	-	7
	5	-	1	2	1	2	1	-	1	-	8
	6	-	-	-	-	-	-	-	-	-	0
		2	8	7	11	12	4	0	1	0	45

C. Mödling and the environs of Vienna.

		1	2	3	4	5	6	7	8	9	
Yellow color	1	1	1	-	-	-	-	-	-	-	2
	2	-	1	-	1	1	-	-	-	-	3
	3	-	-	1	1	1	-	-	-	-	3
	4	-	-	-	-	1	2	-	-	-	3
	5	-	-	1	-	-	-	1	-	-	2
	6	-	-	-	-	-	-	-	-	-	0
		1	2	2	2	3	2	1	0	0	13

D. Fala (Drava Valley).

	1	2	3	4	5	6	7	8	9	
1	-	1	-	-	1	-	-	-	-	2
2	-	-	-	-	-	1	-	-	-	1
3	-	-	1	1	1	1	1	-	-	5
4	-	-	-	-	2	-	-	-	-	2
5	-	-	-	-	-	1	-	-	-	1
6	-	-	-	-	-	-	-	-	-	0
	-	1	1	1	4	3	1	0	0	11

E. Rogovilec (Savinja Valley).

Variability of the dark markings of *P.(n.) bryoniae* and the hybrid populations

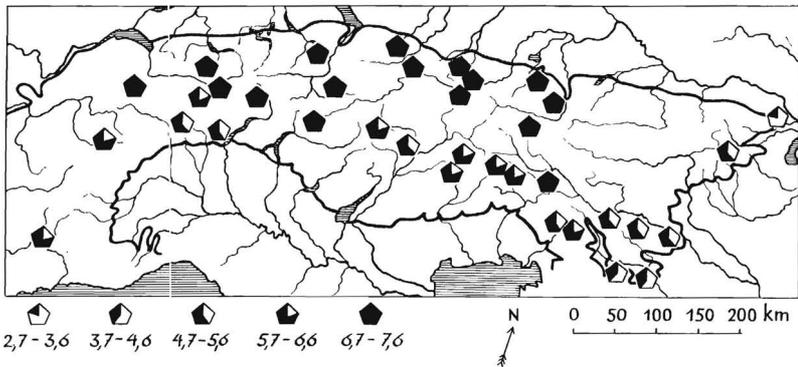


Fig. 4. Variability of the dark markings in the Alps (modified from Petersen, 1955).

bryoniae female, 1 white *bryoniae* mosaic intersex, 1 *napi* male, and 1 *napi* female, a back-cross ratio as would be expected. From the other female ("Fala 2") three generations were obtained and from two sib matings reared together, 44 *bryoniae* and 3 *napi* females emerged, one of the latter having been yellowish. One of these two matings was probably $BB \times Bb$, the other $Bb \times Bb$. Thus it has been proved that among the offspring of *bryoniae* females from this locality specimens with *napi* traits segregate which cannot be distinguished by their phenotype from pure lowland *napi*. Thus it seems likely that the population of Fala has some similarity to that of Mödling.

Another *bryoniae* population from which some broods were also reared has been found in the upper Savinja valley on the eastern end of the

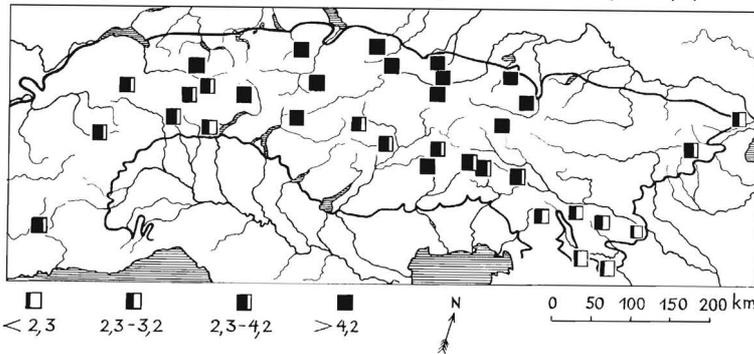
Variability of the yellow ground colour of *P. napi bryoniae* and the hybrid populations

Fig. 5. Variability of yellow ground color in the Alps (modified from Petersen, 1955).

Karawanken Alps (Table 6E). Here all three pairs of *bryoniae* alleles are still present, since among five males one “rubtalba” *napi* was found. Among 11 females taken here at Rogovilec (about 650 m. altitude) during 10 to 17 August 1931, 2 show *napi* pattern on the yellowish versus white ground color. From the eggs of one female 3 imagos were reared the next spring. One of these, a deep yellow “radiata” female, already mentioned (brood “R × P - 1932”), mated with a *napi* male from Podsused near Zagreb, where no other than homozygous *napi* occur. The 58 female descendants segregated in a dihybrid back-cross ratio, *i.e.* 14 yellow “radiata”, 14 white or whitish “radiata”, 16 yellow or yellowish *napi*, and 15 white *napi*. Accordingly, the “radiata” mother of this brood had been heterozygous for both the *Bb* and *Yy* alleles. It has also to be noted that a cross between one male of the three specimens reared from Rogovilec and a *bryoniae* female reared from Fala gave 11 *bryoniae* and 12 *napi*, both more or less yellowish, but among them were also three white *napi* which did not differ from any pure *napi*.

Properly speaking, not one of about ten *bryoniae* broods from these two localities was true-breeding. If we add that the most characteristic wild *bryoniae* females were selected for the breeding experiments, one can easily imagine how highly mixed must be the genetic constitution of both the Fala and Savinja populations.

On the strength of these breeding results, supported by PETERSEN’S analysis of the colonies at Mödling and Carinthia, the conclusion must follow that the *bryoniae* populations of the south-eastern Alps cannot

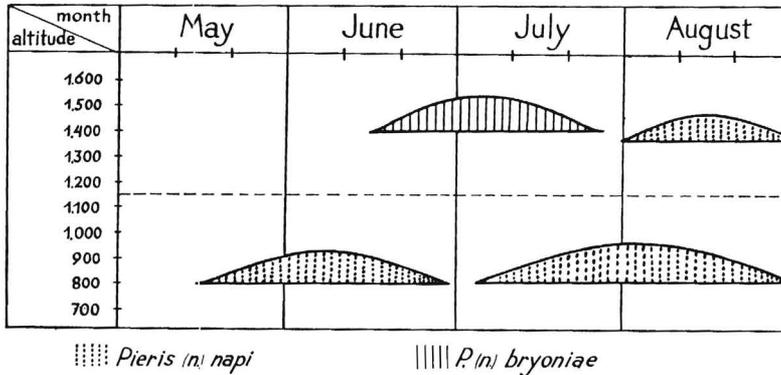
Annual generations of *P.(n) bryoniae* and *P.(n) napi* in the northern Alps (after Petersen)

Fig. 6. Seasonal and altitudinal distribution of *Pieris bryoniae* (univoltine) and *napi* (uni- or bi-voltine) in the northern Alps.

be considered as a closed genetic entity reproductively separated from *P. napi*, because all these populations carry a more or less large amount of *napi* genes. The excellent Table 8 in the Müller-Kautz work shows at a glance that what is true for the Falla and the Savinja valley is not less applicable to the more western parts of the Karawanken slopes, especially for the Singerberg district southward of Klagenfurt. This table likewise represents a clear dihybrid segregation, and if the undersides of the hindwings had been visible too, a tri-hybrid segregation would appear.

But once we have established the great difference in recombination frequency between the northern and southern Alps, how do we explain this unexpected situation? Part of the answer lies in a comparison of the ecological and temporal isolation between the two forms in the two regions. In the northern Alps, *bryoniae* and *napi* are sharply spatially and temporally isolated. There, *bryoniae* is almost exclusively single-brooded, and lives between 1350 and 1750 m. altitude. Its flight period lasts from mid-June until the end of July, with the greatest activity from the end of June to mid-July (Fig.6). *P. napi*, on the other hand, does not occur above 1150 during its first generation, and here flies from mid-May to mid-July, although at the end of the flight period, in mid-July, it does in rare cases fly up nearly to 1700 m. The second brood of *napi* flies after mid-July, but mainly in August, at a time when *bryoniae* ♂♂ are finished and all of the *bryoniae* ♀♀ have already been fertilized. There is only a slight chance of the two forms meeting during their

mating periods. The exceptions are so infrequent as to be insignificant, but we shall mention them again later.

On the southern side of the Alps, *bryoniae* lives at altitudes above 1100 m. and there has only one generation, as in the northern Alps. But it also occurs at lower elevations. On the slopes of the Karawanke Alps its range extends in the Sava Valley down to 200 m. Below 1100 m. *bryoniae* is two-brooded, and in the lowlands partially even three-brooded. It therefore overlaps *napi* spatially and temporally in adult breeding condition, so that one would expect to find all Mendelian combinations possible between the two forms. Indeed, this is just what was found, and summarized in Tables 6B-6E.

Despite the fact that conditions are favorable for a mixture of the two forms, their blending is still not total. PETERSEN (1954) argued as highly probable that in the populations from Mödling and Posavje (Sava Valley) the hybrid populations would be slightly less well represented than either "pure" form ($\chi^2 = 11.80$, $P < 0.001$). Hybrids do appear to be much rarer at higher elevations in the southern alpine valleys than they are in the lowlands. In Krnica Valley at the base of Prisojnik Peak in the Julian Alps, there lives at 1100 m. in a thin, low beech wood a pure *napi* population, while outside this wood in the vicinity of the torrents, where *Pinus mughus* forms the main cover, *bryoniae* (partially two-brooded) are seen flying. The caterpillars of *napi* live in the beech forest on *Cardamine trifolia*, while those of *bryoniae* feed on the plants of *Biscutella laevigata* that fringe the low pine cover. Both butterflies remain faithful to their habitat and food-plant preferences. In conditions of frequent hybridization, these physiological characters should be expected to form recombinations with the morphological ones. Proof that crossing is probably rather limited in Krnica Valley is the lack of the *W* gene in the *napi* individuals, while in *bryoniae* this gene is present in almost half of the individuals. Furthermore, yellow *napi* ♀♀ (*Yy bb*), which segregate only in the F_2 and the back-crosses, are here much rarer than in the Sava Valley or at Mödling. Thus we see that in the higher parts of the southern Alps circumstances are much as in the northern Alps; that is, crossing appears to be considerably less frequent than in the lowlands. In the vicinity of the Vršič pass between 1400 and 1700 m., almost fresh *bryoniae* of the first brood were found late in June and only one old *napi* female at 1400 m. More fresh *napi* females were found here in the first half of August when only the last few worn *bryoniae* were on the wing. This fact corresponds well with the lack of phenotypically detectable recombinations which carry the recessive allele *b*, since the recombination yellow *napi* females (*Yy bb*) were not yet

observed at these elevations in the Julian Alps. Thus one might get the impression that *bryoniæ* and *napi* of the Julian Alps are as strictly reproductively isolated as they are in the northern Alps. This conclusion revealed itself as incorrect after some breeding and crossing experiments that led to a quite unexpected result.

In the biotope of the "pure" *bryoniæ* just mentioned, caterpillars of *bryoniæ* were collected on *Biscutella* late in July 1947, and these were bred through to butterflies. These adults were partly paired among each other and partly with *napi*. Of seven such butterflies that paired and produced progeny, at least three (2 ♂♂, 1 ♀) were heterozygous for the *B* gene (broods 2 b, 4 b, 5₂). Two matings with *napi* yielded half *bryoniæ* and half *napi*, while pairing with *bryoniæ* yielded partly heterozygous animals, a fact manifesting itself only in their progeny, since in none of these four insects was it recognizable that they were of mixed type.

It follows from this that the apparently pure highland single-brooded *bryoniæ* population of the Julian Alps is far more heterozygous, *i.e.* mixed with *napi*, than could be expected from its morphological features. This "unexpectedness", however, surprises only those who claim *bryoniæ* to be a separate species, whereas in the view of the others the remarkable percentage of white *bryoniæ* females in this district points to a considerable flow of *napi* genes into this *bryoniæ* population. With such a situation in highland populations, how large must be the inflow of *napi* genes in lowland *bryoniæ* populations like those from Mödling near Vienna, where the appearance of obvious hybrids nobody can deny. The circumstances remain as yet somewhat obscure only in the many *bryoniæ* "races" from lowland districts of the Carpathian Mountains in Czecho-slovakia, as described by MOUCHA (1956, 1957, 1959).

It does seem that the relatively large number of heterozygous insects captured in the larval stage in the higher elevations of the Julian Alps is fortuitously somewhat exaggerated, since the offspring of the *bryoniæ* females captured as imagos in the same region and already fecundated there consisted of *bryoniæ* as a rule. This may be explained by the fact that on the biotope of *bryoniæ*, heterozygous insects pair predominantly with homozygous ones where the latter are in the majority, or perhaps the inbreeding F₁ hybrids show a decreased fertility that would put a strict limit to recombinations. Regardless of the explanation, this situation demonstrates with force how easily we may be mistaken about the genetic constitution of a population if it be considered only from the morphological point of view.

Crossing between *bryoniae* and *napi* is not restricted to the southern Alps, since hybrids have occasionally been found in the northern Alps. PETERSEN (1954b) discovered a *bryoniae* ♂ × *napi* ♀ copulation in the Allgäuer Alps, and there is a similar report by another writer. If we consider the fact that copulation in butterflies is rarely seen, even under the best conditions, then these two observations signify a relatively frequent occurrence of cross-pairing, conforming to the discovery of heterozygous *bryoniae*. Though we have established that the single-brooded high-altitude *bryoniae* populations are genetically not so pure as has been supposed, it is nevertheless evident that the crossing of two forms is not unlimited. Two factors seem worth further consideration: (1) sexual isolation and (2) the biotope preference.

VII. SEXUAL ISOLATION

In the discussion of the physiological traits of our two forms, the question of sexual isolation has purposely been set to one side, so as to allow unbiased evaluation of the degree of reproductive isolation from data on recombination. In captivity, crosses between *bryoniae* and *napi* are rather readily carried out although not always, a result quite at variance with the usual difficulty in crossing fully distinct species of pierid butterflies (Lorković 1928, 1957). But it has been noticed in the crossing tests that mating between *bryoniae* and *napi* is not absolutely free, either. PETERSEN (1952) and I have discovered independently that *napi* males are only slightly or not at all attracted by the yellow females. PETERSEN made experiments with dummies, in which he was able to demonstrate that yellow dummies only rarely attracted *napi* males. But the dark melanic *bryoniae* coloration has no influence on the attraction of *napi* ♂♂; dark ♀♀ with a white ground color have the same attractive effect as the pure ones. In my experiments, the white or whitish homozygous *bryoniae* females, however dark they may be, are immediately pursued by *napi* males as soon as noticed, and in a few seconds pairing occurs.

An unexpected result of PETERSEN's experiments showed that *bryoniae* males also were much less attracted by the yellow *bryoniae* females than by the white *napi* females. This certainly complicates the matter, since it would seem to speak in favor of hybridization in at least one direction. This finding also agrees with PETERSEN's observation of a *bryoniae* ♂ × *napi* ♀ pairing in the northern Alps, as well as with the fact that he also obtained *bryoniae* offspring from one *napi* ♀ from Mödling. Conversely, two *napi* ♀♀ captured in Krnica Valley yielded only *napi*

offspring (*bb*), and several caterpillars collected on *Cardamine trifolia* yielded only *napi* progeny. The attraction of *bryoniæ* males by yellow *bryoniæ* females must be largely a matter of the flight activity of the females. I have succeeded also in gaining attractiveness of the yellow females for *napi* males when the wings of the resting female were fastened in a folded position in such a way that the greenish-yellow *underside* of the hindwings (it should be not confused with the brownish-yellow color of the upperside) and the whitish underside of the forewings became visible.

Since even the *bryoniæ* males are not as strongly attracted by their own yellow females as by the white, the negative attitude of *napi* males in relation to the yellow females cannot furnish compelling evidence of strong sexual isolation between *napi* and *bryoniæ*. Sexual isolation by visual sense between the two forms is only a half-effective one, since in one direction (*napi* ♂ × *bryoniæ* ♀) hybridization is prevented, but not the reciprocal direction. Accordingly, the index of sexual isolation (ISI) calculated by the simplest way (*i.e.* the number of intraspecific minus the number of inter-specific matings divided by the total number observed [Smith, 1953]) would be + 0.33, a rather low value; the index of complete isolation being 1.0, and that of no isolation zero.

However, the visual attraction by color is not by itself decisive in promoting or preventing hybridization, since it represents an orientation factor for males at distance, as is evident from the well known fact that the males frequently approach other males as well as other white or whitish butterfly species. It is obvious that this distance-orientation behavior would sometimes lead to pairing errors if other isolating mechanisms did not act preventively. Among such more effective isolating factors the specific odoriferous substances come especially into play by stimulating particularly the females to render the copulation possible. In pierid butterflies such readiness for mating may be recognized by a special behavior: a flying female, when approached by the male, alights and puts her wings upward (as in the resting position), which enables the male to land by the female, and copulation can take place. A non-stimulated female spreads the wings down, while its abdomen protrudes upwards, a position which makes copulation impossible. The same behavior follows after mating. There seems to be little or even no difference between the sexual odors of *bryoniæ* and *napi*, since such a defensive posture of females against males of the other form was only exceptionally observed. However, a striking resistance of captive females to both the males, *bryoniæ* and *napi*, is not rare, but it seems to have nothing to do with sexual differences between the species.

VIII. HYBRID VIABILITY

Reared F_1 hybrids develop well and show normal vigor. However, this applies perhaps only to the summer brood with the subitan development, since PETERSEN and TENOW (1952, 1954) found a rather great degree of mortality of the hibernating pupæ, especially in females. PETERSEN considers this female mortality as the most important isolating factor. In my crossings I had not the occasion to confirm this finding because in our broods the hybrids always developed as the summer brood in the same season without diapause. BOWDEN (1953) and BOWDEN and EASTON (1955) in their breeding in England obtained no significant mortality of F_1 hybrids, but stated that in certain broods, particularly when *bryoniæ* was the mother, "many females seem to complete their diapause abnormally early, even before the winter, and in consequence emerge before the usual time". As the males of butterflies under normal conditions emerge always a week or so before the females, BOWDEN held that just this "separation in time of emergences of the sexes provided an interspecific barrier of importance". If this separation applies for the hybrids in nature, I do not see why this early emergence of females would be a reproductive barrier, since *bryoniæ* emerge somewhat later than *napi* and so the backcrosses with *napi* males would be preferred, decreasing by this way the important infertility of the F_1 hybrids. The latter will be discussed in the following section.

IX. HYBRID STERILITY OR INFERTILITY

The most obscure point in these investigations has been the question of the degree of hybrid sterility or infertility, although this is one of the two most important aspects of the relationship between the two forms. Unfortunately, the climate of Zagreb is badly suited during summer for the rearing of alpine butterflies, and the fertility of the animals in the laboratory is affected adversely by the heat (Table 7, Broods 2b and 4b). The results obtained will all therefore bear checking under more natural conditions.

In spite of the normal vigor of the F_1 hybrids as well as their apparently normal gonads and germ cells, the fertility of the hybrids is obviously decreased but in a variable extent. In Table 7 is indicated the total of the offspring of the individual broods in the F_1 pairings, also of backcrosses and of pure *bryoniæ* pairings for different strains. Brood 1 b n represents 11 inbred pairings of F_1 hybrids of one single *napi* × *bryoniæ* cross which had produced 59 sound, vigorous hybrids. Series III shows 14 F_1 inbred pairings and 7 F_1 pairings among the progeny of various

Table 7. Fecundity of *napi* × *bryoniæ* hybrids, backcrosses and pure *bryoniæ* in laboratory breeding.

	Brood	Number of broods	Frequency of broods with respect to the number of offsprings						Total number of offsprings	Average number of offsprings per brood	χ^2	
			0	1-9	10-19	20-29	30-39	40-49				60-69
I bn	F ₁ -inbred	10	5	4	1					16	1.60	3.76) $\chi^2=4.9583$ 10.86) $0.02 < P > 0.05$
III	F ₁ -inbred	14	7	5	2					62	3.75	
III	F ₁ -crossbred	7	1	4		1	1			76	10.86	
	Total	31	13	13	3	1	1	0	0	144	4.65	
III	R-inbred	5	1	2	1			1		66	13.20	4.65) $\chi^2=7.8719$ 15.05) $P < 0.01$
III	R-crossbred	5		2	2		1			81	16.20	
III	R-wild	10	2	4	1	2			1	154	14.40	
	Total	20	3	8	4	2	1	1	1	301	15.05	
2 b	P-bryoniæ May, June	4		2	2	1				63	15.70	
4 b	P-bryoniæ July, August	5	2	1	1					18	3.60	
	Total	9	2	3	3	1	0	0	0	81	9.0	

parents, as well as 20 back-crosses (R) from 7 broods in which the F_1 hybrids were crossed either with wild *napi* or with *napi* from the F_2 generation. In the last case we are concerned with not entirely true back-crosses, since the Bb heterozygotes mate with the bb homozygotes of the same brood. As to the controllable Bb pair of alleles, this is of no importance, but for the other invisible characters, it is.

If we compare the mean values of the total offspring of all $F_1 \times F_1$ matings (144) with the total of the progeny of the back-crosses (301), the difference is striking ($\chi^2 = 7.8719$, $P < 0.01$), with the offspring of the $F_1 \times F_1$ pairings being almost three times less than in the back-crosses. But a more detailed comparison has revealed that the fertility of the F_1 broods varies considerably according to whether we are concerned with 1) inbred pairings from one single pair of parents, 2) inbred pairings in various F_1 strains, or 3) pairings among F_1 individuals of several different strains. The difference between the last and the back-crosses is less than that between the inbred and non-inbred F_1 matings. We may conclude that the decreased fertility of our F_1 hybrids is only partially due to the known reduction in fertility of inbred broods in general, since the inbred back-crosses show a fertility only slightly lower (13.20) than that of the non-inbred back-crosses (16.20 and 14.40).

Pure *napi* can be bred through three of four generations without an important decrease in fertility. This applies also to other species of Pieridæ: *P. rapæ*, *P. manni*, *P. ergane*, *P. daplidice*.

We have therefore to assume that the F_1 hybrids of *bryoniæ* and *napi* in the inbred matings have considerably decreased fertility, since a very small number of eggs is laid, and of these up to 90%, or even 100% remain either unfertilized or undeveloped. On the other hand, the matings of F_1 individuals from different strains are noticeably more fertile, and the back-crosses show a nearly normal fertility. It is to be recalled that some larvæ of *bryoniæ* were captured as natural heterozygotes; these have turned out to be normally fertile as reared adults. One of these *bryoniæ* ♀♀ yielded abundant offspring, even when crossed with a (*napi* × *bryoniæ*) ♂, indicating that neither the wild ♀ nor the F_1 of the laboratory brood would be very highly sterile. Two other wild heterozygous *bryoniæ* ♂♂, paired with two homozygous *bryoniæ* ♀♀ and one *napi* ♀, have also been established as normally fertile.

Our results, indicating a greatly decreased fertility of the F_1 hybrids, are in rather astonishing contrast to the facility with which BOWDEN obtained the F_2 generation by pairing F_1 individuals. On the contrary, in his crossings the difficulties arose with the third generation, which could not be obtained when F_2 individuals were mated *inter se*, so that

only the back-crosses were successful. The cause for this unexpected difference remains still obscure. BOWDEN inclines to the explanation that the difference between English subspecies of *napi* and the Continental one could be responsible for this hybridization difference in the sense "that the reproductive barrier between *bryoniæ* and the adjacent subspecies of *napi* would be rather greater than that separating the more distant British subspecies" which is in no contact with *bryoniæ*, an opinion expressed in a general sense by HUXLEY (1942). However, STEBBINS (1958: p.195) emphasized that "the available data do not indicate that those strains of the two species which occur sympatrically are more likely to form inviable or sterile hybrids than strains of the same two species which occur in different regions". In fact, it would be just as reasonable to suppose the English climate more suitable than that of southeastern Europe for the breeding of such alpine butterflies as *bryoniæ* and their hybrids. The breakdown with the F₃ generation could be accounted for as an effect of laboratory or breeding infertility.

In any case, the considerable degree of decreased fertility of F₁ and/or F₂ *bryoniæ* × *napi* hybrids remains somewhat puzzling.

X. ON THE DEGREE OF REPRODUCTIVE ISOLATION AND THE TAXONOMIC STATUS OF *Pieris napi* AND *bryoniæ*

Having established the genetical and reproductive relation between *bryoniæ* and *napi* we can try to relate the degree of reproductive isolation between them to the various stages in the process of speciation, *i.e.* are they subspecies or full species. Such an attempt turns out to be by no means so easy to perform as one could imagine. In spite of the well defined species concept of to-day, established by the comprehensive works of RENSCH (1929), DOBZHANSKY (1935, 1951), HUXLEY (1942), and MAYR (1942) as well as some other authors, it is clear only for sympatric populations; only in such cases may the existence of reproductive isolation be deduced without experimenting. In allopatric populations (forms, races, species, borderline cases), however, such a consideration of the degree of reproductive isolation is impossible; it always remains more or less subjective or arbitrary. Therefore, in this field of taxonomy great unconformity or even disagreement prevails. Especially difficult and apparently without any final criteria remains the designation for intermediate stages between geographic races and species, which is left to one's own judgment. MAYR (1931) attempted to alleviate the difficult situation by introducing the new category "superspecies", but in fact the subjectivity was not removed, since the superspecies is com-

posed mainly of allopatric “species” whose real isolation status remained uncertain. This began to be more and more important owing to the increasing experimental research on the innate reproductive isolating mechanisms in both animals and plants, often revealing incomplete stages of speciation. The lack of an appropriate taxonomic name or category for such an intermediary stage leads mostly the taxonomically uninterested workers to assign the uncertain cases either to subspecies or to species. Taxonomists, however, tend to promote such borderline cases to the species level, because of their unconscious desire to increase the actual number of species of the group they are dealing with. Clearly, such a situation cannot lead to a satisfactory knowledge of the actual occurrence of the borderline cases in nature, apparently highly underestimated so far. Moreover, an important difficulty for the establishment of objective limits between the subspecies and the species are the differences in the number and degree of isolating mechanisms between species in different groups, of both animals and plants (Stebbins 1958).

If we also add that the subspecies concept itself is seriously attacked or even denied (Wilson & Brown 1953, Gillham 1956, Burt 1954), it is clear that taxonomy at the infraspecific level is not in a satisfactory state.

In regard to these considerations we are now going to compare the relation between *napi* and *bryoniæ* with the circumstances in related pierid species known from my interspecific crosses carried out many years ago, although only a very limited part of this research has been published as yet (Lorković 1928, 1953, 1957). Of course, we shall try to account also for the generally accepted line in this matter and, finally, to formulate the characteristics of the intermediary stages between subspecies and the true species.

1) The first comparison which must be made concerns the morphological differences between *napi* and *bryoniæ*. There are only two, in some populations also three, imaginal color differences; no visible differences exist in the larval stage and some slight and inconstant ones are present in the pupal stage. This is a far lower number of distinguishing characters than usually found between sympatric species, including Pieridæ; e.g. the closely related and very similar species *P. rapæ* and *P. manni* differ in as many as 24 structural and color-pattern characters. (Of course, this does not mean that there are as many different genes controlling these characters.) In contrast to the minute differences between *manni* and *rapæ* the differences between *napi* and *bryoniæ* are very conspicuous. If the two or three characters in *napi* and *bryoniæ* were so inconspicuous as those between *rapæ* and *manni* the former two forms would never be recognized even as two subspecies.

The fact that there are no known differences in the genital armature, nor in any other structural character, is very important, for this is a circumstance rarely lacking among specific distinctions.

2) The considerable ecological difference between *napi* and *bryoniæ* is greater than can usually be found between closely related species, so that in general it keeps apart the populations of both forms. However, the effect of the ecological distinctness varies greatly in its control over reproductive isolation, since it depends too much on environmental circumstances. This is shown by the great difference in the reproductive isolation between *napi* and *bryoniæ* populations of the northern and the southern Alps, since in the former district *napi* and *bryoniæ* behave as good species, in the latter, however, nearly as subspecies.

3) Sexual isolation is only half-way developed, because of the discrimination in the instinctive reaction of the *napi* males to the yellow female color stimulus. This must lead, along with the lack of spatial isolation, to frequent hybridization but not more than to about 33%. This percentage, however, surpasses manifold what is known about sexual isolation between perfectly distinct pierid species; even between such closely related species as *P. rapæ* – *P. manni*, *P. manni* – *ergane*, *P. ergane* – *P. napi* the females always obstinately refuse the assaults of strange males, making hybridization by natural ways impossible. The index of reproductive isolation between these species is approximately 1.0. Also, among about 470 individuals of *Leptidea sinapis* and *Leptidea morsei* originating from their sympatric range near Zagreb only one suspected individual could be considered as a possible hybrid, and another one perhaps also as somewhat alike; hence the index of reproductive isolation would be 0.9957 or = 1, i.e., the highest degree of isolation.

4) The incomplete sexual isolation between *napi* and *bryoniæ* conforms well with the great amount of hybrids in nature, especially in lowland populations where *napi* and *bryoniæ* overlap widely. Moreover, an unexpectedly high percentage of genotypically hidden hybrids were also found among the high alpine *bryoniæ*, mostly considered to be a pure-breeding population. All this surpasses by far the ordinary unremarkable share of the hybrids in populations even of very closely related sympatric species.

5) Although the F_3 hybrids of *bryoniæ* × *napi* are of a very good vigor and with apparently normal production of spermatozoa and eggs, their fecundity is greatly reduced or even gone when they mate together. Since the F_3 hybrid sterility is doubtless a characteristic of species

On November 17, 1961 at 4:40 a.m. I saw a female *Precis orithya* (Linnaeus) (Nymphalidæ) resting motionless on the floor of the front porch in New Delhi, about eight feet away — in a direct line — from the 150 watt light. It was easily caught and was not very active. Temperature 60°F.

While I drove through desert scrub at night with a spotlight, about 50 miles south-southwest of Pali, Rajasthan State (northwest India), on October 6, 1961, a *Precis orithya* flew into the open Jeep, where it was caught and identified. But this specimen had obviously been disturbed by the passing vehicle, and happened to fly inside. It is a very common species that has a strong preference for sun and desert or dry areas.

The greatest number of records I have for the nocturnal occurrence of a single species, however, is for *Melanitis leda* (Drury) (Satyridæ). On August 29, 1961 a very active *M. leda* (wet season form "determinata" Butler) was netted as it fluttered around our New Delhi porch light. On August 31, 1961 another specimen was seen on our porch, but it was too active to capture (it persisted in settling at the base of the ceiling fan, about 15 feet up). On September 24, 1961 a *M. leda* form "determinata" was seen on our New Delhi porch at 11:30 p.m. It was about one foot from a 60 watt bulb, hanging upside down from the ceiling. When I failed to catch it with my fingers it left its resting spot and flew around the bulb, then spiraled below the bulb, rapidly rising, falling, and circling just as a disturbed and confused moth would. It abruptly landed and I caught it. The temperature was 81°F., the moon full, and the night was damp and dewy (it had rained in the morning).

On November 2, 1961 two *M. leda* (wet season - dry season transition forms) were observed flying around our New Delhi porch at 5:47 p.m. (just 12 minutes after official sunset). I turned on the 60 watt light and one of the individuals immediately flew to the light. By 6:00 p.m. both individuals had settled near the light (both were about 50 inches away). The temperature was 67°F. at this time. Periodic observations were made until 12:45 a.m. the next morning, when the temperature had dropped to 64°F. One individual remained stationary in its original position throughout the period of observation. The other was inclined to change positions more frequently: at 6:21 p.m. it was 21 inches from the light, at 6:22 p.m. it moved to within 12 inches of the light, and at 11:42 p.m. it was about 14 inches from the light. By 10:00 a.m. the next morning both butterflies were gone.

Finally, on November 28, 1961 I collected a *M. leda* (dry season form "ismene" Cramer) at 9:50 p.m. at Karwar, Mysore State (west

hybridization, *bryoniæ* and *napi* should be considered as separate species. However, the high fertility of the F_3 hybrids in back-crosses does not agree with what commonly occurs in species hybridization. My pierid crosses between the well known species or genera: *Pieris rapæ* \times *P. napi*, *P. manni* \times *P. napi*, *Pontia daplidice* \times *Synchlöë protodice*, *Euchloë belia* \times *Anthocharis cardamines* yielded hybrids with degenerated gonads and germ cells, so that the hybrids were completely sterile in $F_1 \times F_1$ matings as well as in back-crosses. Nevertheless, the crosses between the closely related intrageneric species *Pieris rapæ* \times *P. manni*, *Leptidea sinapis* \times *L. morsei*, *Anthocharis cardamines* \times *A. euphenoides* are also completely infertile when mated with each other, although their production of gametes seems to be normal, except the disturbed chromosome pairing and distribution in meiosis. But it is significant that the back-crosses with the parental species were almost completely sterile too, as a rather great number of (*rapæ* \times *manni*) σ backcrosses gave rise to only one, two, or three offspring of reduced viability and no fecundity. The other two hybrids were also in the backcrosses entirely sterile. There is only one case as yet known from the pierid crosses, *Pieris ergane* ♀ \times *P. (napi \times bryoniæ)* σ which produced a F_2 generation – true for a few individuals only – and a successful backcross. However, although *napi* and *ergane* are in their anatomical structure extremely similar, their sexual isolation is complete.

This short comparison of the *bryoniæ* - *napi* case with other pierid crosses shows that the reproductive isolation between *bryoniæ* and *napi* is at such a low level that neither the partial sexual barrier, nor the decreased hybrid fertility and the ecological distinctness, may prevent a considerable gene flow, greatly surpassing any usually known to occur between species of this family. On the other hand the breeding is also far from being panmictic (with the isolation index = 0), so that the relation between *napi* and *bryoniæ* cannot be classified as a subspecific one, either. Strangely enough, experimental crosses between subspecies of Lepidoptera are rather scarce, so that we are not able to give a good comparison of our case with other crosses between subspecies of a single species. This is not surprising if the difficulties of getting breeding material from afar are taken into account. Therefore we must content ourselves with the well known assumption that there are usually no barriers, neither sexual nor those of hybrid sterility, to crossing among races. Of course, there are exceptions to this, but one wonders whether in those occurrences borderline cases are involved.

We must, therefore, conclude that our analysis gives us no strong support for the classification of the *napi* and *bryoniæ* as either two species

or as subspecies. They are at the typical transitional stage between the subspecies and the species. Such transitional stages in butterflies had been called "semispecies" independently by KIRIAKOFF (1948) and myself (1953, 1955, 1957). Each attempt to classify *bryoniæ* as a species or subspecies has not dealt with reality, but rather has tried to insert the different stages of speciation into a rigid system which cannot apply to refined taxonomy which fits adequately various evolutionary problems.

SUMMARY

1. *Pieris napi* L. and *bryoniæ* Ochs. differ morphologically in three groups of alleles of which the allele *B* for the melanic *bryoniæ* pattern is dominant over the allele *b* for *napi*, and the allele *W* for the white color of the underside of the hindwings is dominant over yellow, *w*. The brownish yellow color of *bryoniæ* females is not entirely dominant over the white one of *napi* and is probably multifactorial.

2. The restriction of *bryoniæ* to the Alps, Carpathians, and the northern parts of Europe, Asia, and North America is connected with genetic ecological preferences for low temperature and certain food plants as well as to univoltinism. This ecological distinction is the principal reproductive barrier between populations of *napi* and *bryoniæ*.

3. The effect of ecological distinction on reproductive isolation depends greatly upon the climatic conditions; these are more effective in the northern Alps than in the southern, and in the latter hybrid populations are the rule.

4. The partial breakdown of ecological isolation leads to extensive hybridization, the sexual isolation being restricted mainly to the *napi* males, which are less attracted by the yellow *bryoniæ* females.

5. The third partial isolating mechanism is the infertility of the F_1 hybrids which is particularly high in inbred F_1 matings, lesser in matings between different F_1 strains, and low in back-crosses.

6. Accordingly, a comparatively great amount of gene flow between the populations of *napi* and *bryoniæ* occurs in districts where the populations are not kept apart by the ecological barrier. This gene flow surpasses very greatly that between other closely related sympatric species of Pieridæ which have been studied in Europe.

7. Consequently, *bryoniæ* can by no means be considered as a true species but only as a transitional stage between subspecies and species; such incomplete stages of speciation can best be denoted as SEMISPECIES.

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4. *C. salapia* (Druce), NEW COMBINATION. Colombia.
Hasodima salapia Druce, 1900, *Annals & mag. nat. hist.*, ser. 7, vol.5: 522.
 5. *C. arana* (Dognin), NEW COMBINATION. Colombia, Peru, Bolivia, Argentina.
Caripeta arana Dognin, 1896, *Ann. soc. ent. Belgique* 39: 117.
Erilophodes arana (Dognin), Warren, 1909, *Nov. zool.* 16: 109.
Neodesmodes arana (Dognin), Covell, 1963.
 6. *C. muscosa* (Dognin), NEW COMBINATION. Colombia.
Neodesmodes muscosa Dognin, 1911, *Hétérocères nouv. Amér. Sud*, fasc.III: 38.
 7. *C. pruna* (Dognin), NEW COMBINATION. Colombia, Ecuador, Peru, Bolivia.
Bryoptera pruna Dognin, 1892, *Le Naturaliste*, 1 March 1892: p.59.
Hasodima puta Druce, 1900, *Annals & mag. nat. hist.*, ser. 7, vol.5: 522. NEW SYNONYMY.
 8. *C. dardania* (Druce), NEW COMBINATION. Colombia.
Hasodima dardania Druce, 1900, *Annals & mag. nat. hist.*, ser. 7, vol.5: 521.

In addition to these species, others from Latin America may belong in *Cargolia*. The author hopes to carry on more detailed investigation of this genus and others closely related to it, studying the biology and ecology of species as well as morphology.

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CORRIGENDA FOR VOLUMES 16 AND 17

Vol. 16:

- p. 106, left column — words in last two boxes should be reversed; thus, the lower left box should be "Habitat preference".

- p. 119, in 3rd horizontal data row — “62”, “3.75”, “3.76”, and “4.9583” should be “52”, “3.71”, “3.76”, and “4.9585”.
- p. 123, 1st and 4th lines from bottom, and p. 124, 2nd line from top — “F₃” should be “F₁”.
- Vol. 17:
- p. 109, bottom — line omitted just above mail address:
“9. *Adopaea lineola*: VI-10-59, Stevenson, Baltimore Co.”
- p. 168, 16th line from bottom — “♀ *P. protenor* × ♂ *P. helenus*” should be “♀ *P. polytes* × ♂ *P. helenus*”.
- p. 193, 3rd line from bottom — “Zucht *quercus*” should be “Zucht von *Marumba quercus*”.
- p. 195, 20th line from bottom — “524-629” should be “624-629”.
- p. 198, 20th line from bottom — “Yohrinori” should be “Yoshinori”.

A MEXICAN SATYRID AT LIGHT

In view of the recent increased interest in Rhopalocera being attracted to light it is appropriate to note an addition to the body of information on this subject.

A large lepidopteron was taken at some time very near 9:00 pm, Pacific Standard Time, 14 November 1952, at San Blas, Nayarit, Mexico. It was sitting on the ceiling of an outdoor corridor about two feet from a yellow light of the insect-repelling type. The location was a hotel there (the only modern one at that time) on the south edge of town. The place the specimen was taken faced jungle which was about three hundred feet away. The Pacific Ocean was about two hundred feet in the opposite direction.

This specimen was recently identified, with the aid of Dr. C. L. Remington, as *Taygetis mermeria* Cramer, probably form *excavata*. Identification was based on figures in Seitz' *Macrolepidoptera of the World*, Volume 5. The specimen has been placed in the Peabody Museum of Natural History at Yale University.

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BOOK NOTICE

The DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Edited by R. F. Morris. Canadian Entomologist, Memoir 31, 332 pp., numerous textfigs., graphs, & halftone plates. May 21, 1963. Paper and cloth.

The spruce budworm, *Choristoneura fumiferana* (Clem.) (Tortricidae) probably is the most intensively studied species of Lepidoptera in North America, if not in the world. Its tremendous outbreak capabilities and resultant economic importance to Canadian foresters precipitated a myriad of detailed studies on numerous aspects of its bionomics during the past 20 years.

This monograph is a series of closely related papers presenting the results of population studies on the spruce budworm. It is an attempt to ascertain and model mathematically where possible, the mode of action of the principal variables affecting density of the species. Major topics covered include general bionomics; development of outbreaks; analysis of survival and reproduction in both unsprayed and sprayed areas; a discussion of the major factors and processes affecting the bionomics, including dispersal, hosts and host conditions, parasites, predators, diseases, and insecticides. In all, twelve authors are contributors. — EDITOR