

## The Androconial Scales and Their Bearing on the Question of Speciation in the Genus *Pieris*.<sup>1</sup> (Lepidoptera)

By

B. C. S. WARREN

For many years the question of the affinity of *Pieris napi* and *P. bryoniae* has been debated. Many have sought enlightenment by crossbreeding experiments, but different workers have attached different values to the results they obtained. After much work Bowden concludes (1958), that *P. napi* and *P. bryoniae* are "biologically almost entirely distinct in the central Alps", but that hybridization has been going on elsewhere and there is no reason for drawing a firm line in one place rather than another. Previously (1957), he noted that although *adalwinda* belonged, biologically, at the present time to *napi*, it seemed to have much in common with Alpine *bryoniae*, and Petersen also held this view. Further, Bowden states the race *falvescens* "is almost certainly hybrid in origin, . . . but that *bryoniae* preponderates in its make-up". Present knowledge of distribution supports the idea of two distinct species, as it is known *napi* and *bryoniae* fly in proximity in several places. Verity recorded one such case above Bex in the Rhone Valley (1934); I have found the two at Kandersteg, and *napi* and *neobryoniae* in the eastern Hohe Tauern in Carinthia; Moucha has recorded them in the Tatra and also in several localities in the Carpathians (1957), and there are the known records in the Austrian Alps. Other workers hold the two insects as one species simply disregarding the distributional data. To most taxonomic workers the fact that the two can exist together in some places and in proximity in many, is a natural demonstration that two distinct species are present, and consequently have remained separate throughout what must in many cases have been a period covering thousands of generations. Compared with this the results derived from a few generations of crossbreeding seem transient occurrences, while their lack of constancy suggests more the susceptibility of the individual to the abnormal than the mingling of two established racial constitutions. But these fluctuating results are worthy of note, for they suggest that they may arise from causes other than those to which they are attributed. It is scarcely possible to identify the males of the two species

<sup>1</sup> This paper is given in the chronological order in which it was written. The systematic description of the scales was completed a year before the facts given in Appendix A were known. Later Appendix B was added. The facts revealed by the structural characters of the androconia are therefore seen to be confirmed by data derived from distinct sources at subsequent dates.

with certainty, but it is less known that it is often as difficult to distinguish the females. Much that has been written on such breeding experiments, especially on races in the south-eastern Alps, points to mistakes having been made in the initial identification of the material used; as for example when we are told that the same cross gives totally different results to the same worker on different occasions. Some accurate means of identification (i.e. anatomical), was obviously the first essential. The genitalia in this genus are very uniform (see Drosihn 1933; Okano 1951), and though they would probably give the needed information the dissection of specimens of each of the very numerous races already described would be necessary before the value attaching to the various developments could be estimated. The necessary material would be very difficult to get, and the distinctions observable not of a very marked type and consequently liable to be disregarded when the work was done. I therefore turned to the androconial scales which have given valuable data in other genera of the Pieridae. To test their value in *Pieris* I selected *P. rapae* and *P. manni*, species closely related but known to be biologically distinct (Powell 1909; Reverdin 1909); they are also known to occur on common ground over most of their geographical range. To these species I added *P. ergane*, also biologically distinct; and *P. brassicae* to get an idea of the extent to which scale development could vary in more remote species. Reverdin had already shown the scales in *P. rapae* and *P. manni* to be slightly but obviously different in shape (1909), and a few observations confirmed this; the degree of difference that separated *P. ergane* from *P. rapae* came as a complete surprise, remembering that in the past the two had been united, and even still are placed side by side in all reference works.

---

Plate 1. Androconial scales in *Pieris* species. Magnification of photographs 450 times, reduced on plate to about 300.

1. (*P.*) *brassicae*. Basal half of scale.
2. *P. rapae*, Lyndhurst, Hampshire. 2nd. generation.
3. *P. leucosoma*, Tehran, Persia. 2nd. generation.
4. *P. napi adalwinda*, Oslo, 2nd. generation.
5. *P. napi napi*, Grange-over-sands, Lancashire. 1st. generation.
6. *P. napi napi*, St. Triphon, Vaud. 2nd. generation.
7. *P. manni*, Martigny, Valais. 2nd. generation.
8. *P. manni*, Martigny, Valais. 2nd. generation.
9. *P. canidia*, Hong-Kong. (? 2nd. generation).
10. *P. krueperi*, Sliven, Bulgaria. 2nd. generation.
11. *P. napi adalwinda*, Maalselven, Lapland. Single generation.
12. *P. napi kamtschadalis*, Kamchatka. (? 2nd. generation.)
13. *P. napi napi*, Kandersteg, Bernese Oberland. 1st. (or single) generation.
14. *P. napi*, (dwarf). Vernayaz, Valais. 1st. generation.
15. *P. bryoniae flavescens*, Meiringen, Bernese Oberland. 1st. generation, bred specimen.
16. *P. bryoniae flavescens*, (data as No: 15).
17. *P. bryoniae flavescens*, (data as No: 15).
18. *P. ergane*, Delphi, Greece. 1st. generation.
19. *P. higginsii* Warren, Haji Omran, Kurdistan, Iraq. 1st. generation.
20. *P. pseudorapae*, Salahuddin, Kurdistan, Iraq. 3400 feet. 2nd. generation.
21. *P. pseudorapae*, (dwarf). Shaglaw, Kurdistan, Iraq. 1st. generation.
22. *P. pseudorapae*, Nahr ul Kalb. (R. E. Ellison, February 22, 1931). 1st. generation.
23. *P. higginsii*, Rayat, Kurdistan, Iraq. 2nd. generation, primitive type.
24. *P. higginsii*, Rayat, Kurdistan, Iraq. 2nd. generation.

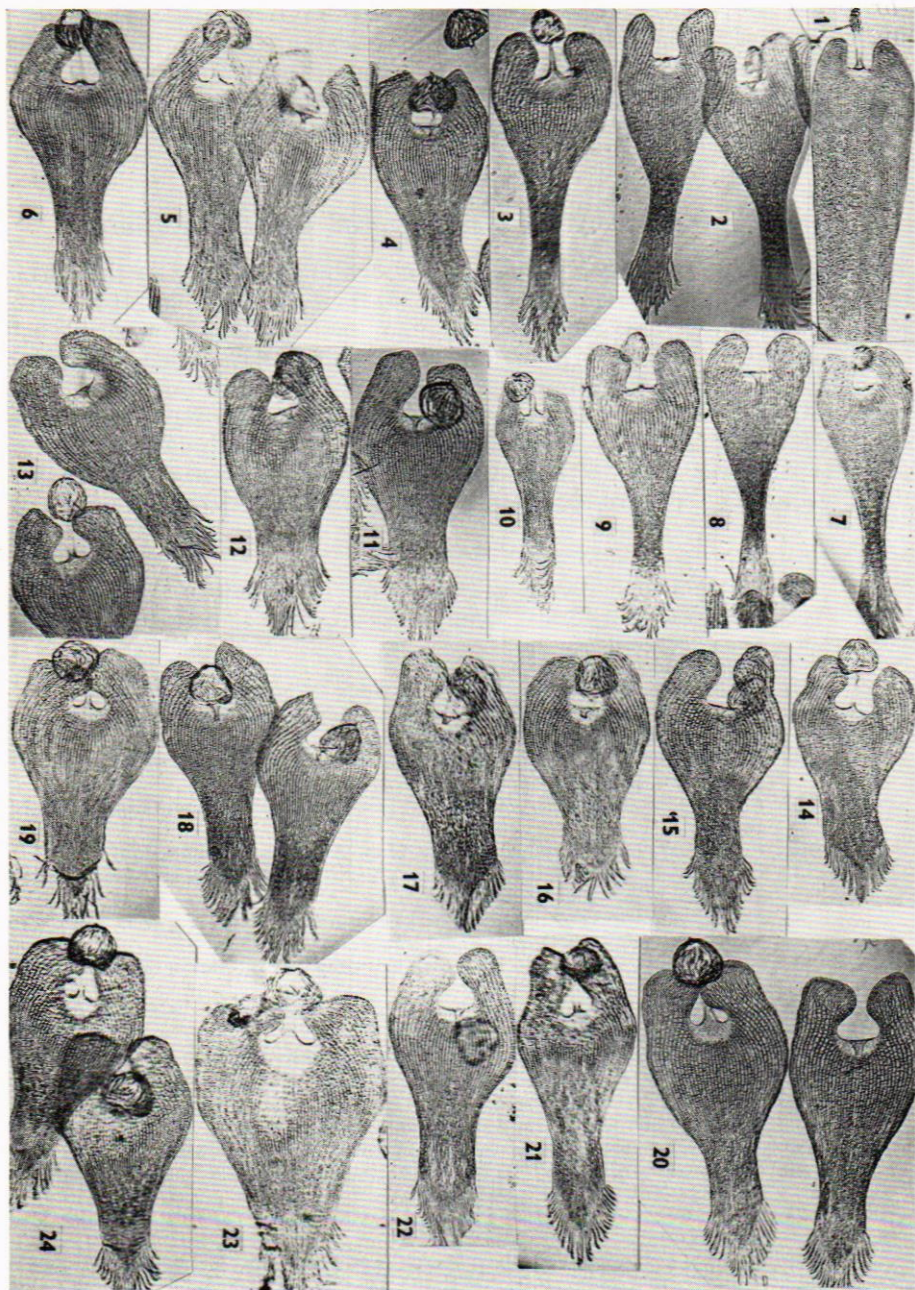


Plate 1.

*P. brassicae* proved to be of such a totally different type that doubts of its being congeneric with the other species were at once raised. (Some authors have already removed it from the genus). These results showed that in the androconia one could expect to find a clear guide to the relationship of species in the genus; expectations which proved fully justified by subsequent work.

### General Notes on the Androconial Scales in *Pieris*

The scale is small for such scales, in proportion to the size of the species; it is short and stout, sometimes angular in outline. In all species of the genus a scent cell which is roundish or rectangular in shape is connected with the scale. In *brassicae* the scale is extremely long and thin, tapering regularly and continuously from base to tip, and the scent cell is minute and tubular in form (fig. 1). This type of scale is so specialized that the species should not be included in *Pieris* so I follow those who have excluded it and make no further reference to it in this paper. The species of *Pieris* fall into three distinct groups. 1) The *rapae*-group: scale slender, neck narrow and cent

---

Plate 2. Androconial scales in *Pieris* species. Magnification as plate 1.

25. *P. segonzaci*, Tachdirt, South Atlas Mts. July 3, 1933. 7400—8200 feet. Single generation.
26. *P. segonzaci*, (data as No: 25).
27. *P. bryoniae bryoniae*, Caux, Vaud. June. Single generation.
28. *P. bryoniae bryoniae*, Ueschinen Tal, Kandersteg, Bernese Oberland. June, single generation, primitive type.
29. *P. bryoniae flavescens*, Meiringen, Bernese Oberland, 2000 feet. 2nd. generation, primitive type.
30. *P. bryoniae bryoniae*, Pontresina, Grisons, single generation, primitive type.
31. *P. bryoniae neobryoniae*, Karawanken Alps. 2nd. generation.
32. *P. bryoniae pseudobryoniae*, mile 102, Steese Highway, Alaska, 2500 feet, June 23, 1955; single generation.
33. *P. bryoniae pseudobryoniae*, Mackenzie delta, N. W. T., June 1955, about 68° N. L., primitive type; single generation.
34. *P. bryoniae flavescens*, Hauenstein Forest, Seis, Dolomites; single generation.
35. *P. bryoniae oleracea*, Grande La Cloche Island, N. W. Georgian Bay, Ontario; May 15; 1st. generation.
36. *P. bryoniae oleracea*, data as No: 35; primitive type.
37. *P. ochsenheimeri*, Mountains near Namangen, Ferghana, Turkestan; normal scale, advanced type.
38. *P. ochsenheimeri*, normal scale; data as No: 37.
39. *P. venosa venosa*, Santa Cruz, California; 1st. generation.
40. *P. venosa virginensis*, Grande La Cloche Island, N. W. Georgian Bay, Ontario; May 17., 1st. generation.
41. *P. venosa* (? race), Lake Louise, Alberta; 6000 feet, July 14, 1939; single generation.
42. *P. japonica japonica*, Lake Towada, Aoneori Prof., Japan; 2nd. generation.
43. *P. bryoniae frigida*, Fort Smith, N. W. T.; May 27, 1955; probably single generation.
44. *P. bryoniae frigida*, primitive type; data as No: 43.
45. *P. narina*, Naryn, Turkestan; (? generation).
46. *P. narina*, primitive type; data as No: 45.
47. *P. bryoniae pallidissima*, Rocky Mt. National Park, Colorado; (? generation).

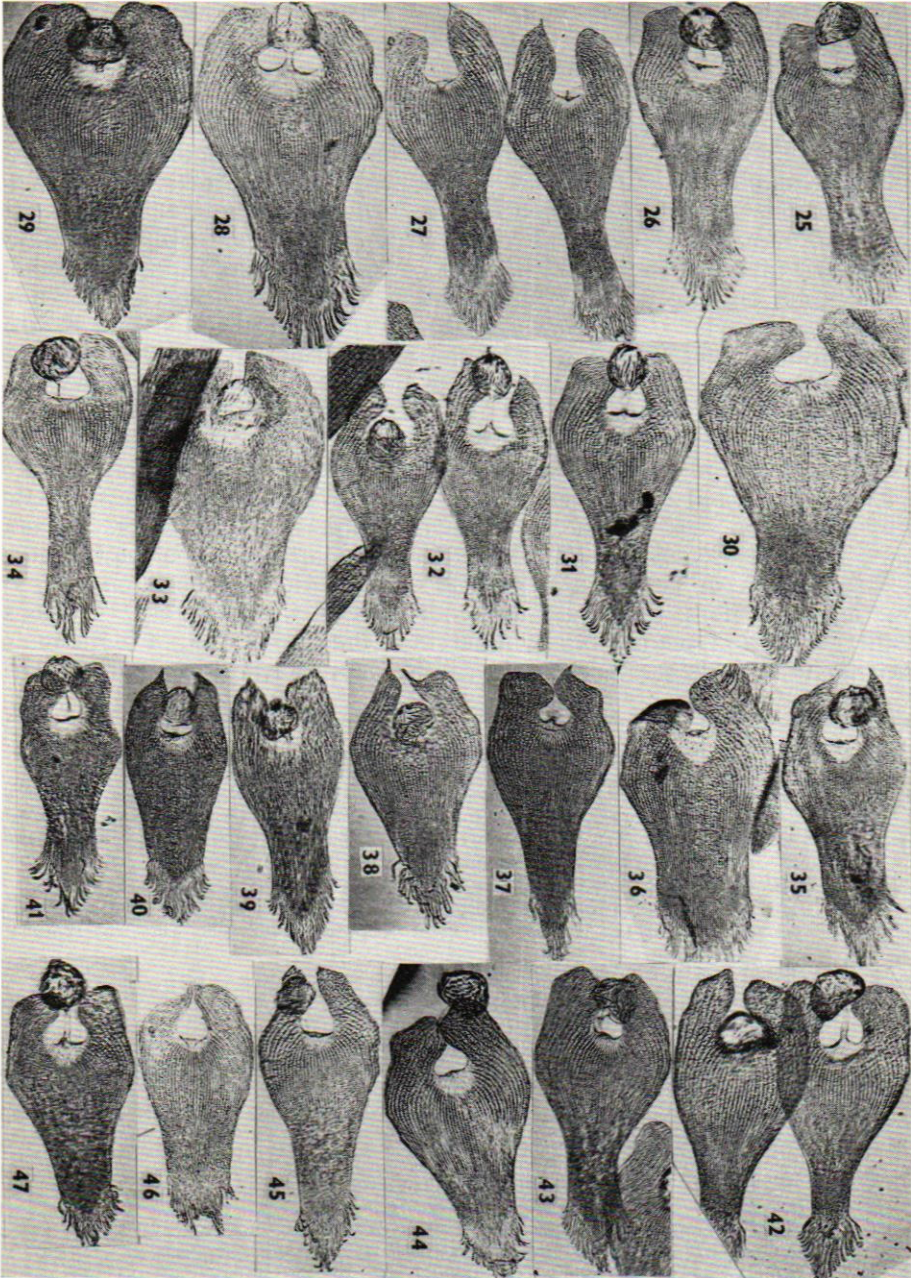


Plate 2.

cell small and roundish (figs. 2, 3, 7—10). 2) The *napi*-group: scale body and neck stout, scent cell almost twice the size of that in the *rapae*-group (figs. 4—6, 11—47, 57—59). 3) The *melete*-group: scale more angular in outline, scent cell much distended, rectangular, oval or rounded (figs. 48—56). As a rule there is no difficulty in recognizing the group to which a given insect belongs by a glance at the scale. The drawbacks to the use of the scales are their very small size and vitreous appearance. Their refractive index is too high to enable them to be mounted in any of the ordinary oils or resinous media. But mounting is essential for accurate comparison or illustration; and this is best done in air. There is also considerable variation, and though this does not obscure the type of formation peculiar to a species, it renders comparison difficult. The scales are true morphological units; that is structures "intimate with function" as Snodgrass defines it (1935, p. 1); to be distinguished from the pigment with which many become charged when developed, which of course is not in itself a structure any more than the resulting patterns produced on the wing of the insect. The use of the term "morphological" to cover such pigmentary patterns may be convenient in a general sense, but is quite misleading when employed, as it unfortunately is, by some who seek to give the inconstant superficial characters the taxonomic value of the anatomical. The existence of an element of variability in all structure is of course an essential in evolutionary development, and affecting as it does all species under all conditions, must as I previously postulated, be a perpetual activity inherent in the constitution of living matter (Warren 1937, p. 320). Recently, in calling attention to asymmetrical varia-

Plate 3. Androconial scales in *Pieris* species; magnification as plate 1.

48. *P. melete melete*, Unzen, Kiushiu, Japan; July 30, 1907; 2nd. generation.
  49. *P. melete* form *aglaope*, Yokohama, April; primitive type, 1st. generation.
  50. *P. melaina*, Trulung, S. E. Thibet; 6800 feet, July 6, 1913; (? generation).
  51. *P. nesis*, Hokkaido; (? generation).
  52. *P. orientis orientis*, Isle of Askold; 1st. generation.
  53. *P. ajaka* form *ajanta*, Pahalgam, N. E. Kashmir; July 1956, 1st. generation.
  54. *P. ajaka ajaka*, Pahalgam, N. E. Kashmir; 7400 feet, July 25, 1956. 2nd. generation.
  55. *P. ajaka ajaka*, data as No: 54.
  56. *P. extensa extensa*, China; (? generation).
  57. *P. dulcinea*, ? N. Korea. (? generation).
  58. *P. dulcinea* form *aestiva*, Kamuikotan, Hokkaido; 2nd. generation.
  59. *P. bryoniae flavescens*, Meiringen, Bernese Oberland; normal scales and primitive type, 2nd. generation.
- Androconial scales from cross-bred *Pieris*; all from specimens bred by S. R. Bowden. Magnification as plate 1.
60. *P. napi adalwinda* × *P. napi napi*.
  61. *P. napi napi* × *P. bryoniae neobryoniae*.
  62. *P. napi napi* × *P. bryoniae neobryoniae*.
  63. *P. bryoniae neobryoniae* × *P. napi adalwinda*.
  - 65, 66, 67 and 68. *P. napi adalwinda* × *P. bryoniae bryoniae*.
- Pieris higginsii* Warren. (2/3 natural size).
69. Male, allotype. Rayat, Kurdistan, Iraq. 2nd. generation.
  70. Under side of No: 69.
  71. Female, holotype. Haji Omran, Kurdistan, Iraq. 2nd. generation.
  72. Under side of No: 71.

Specimens of figs: 69—72, in the Wiltshire collection.

All photographs by B. C. S. Warren.

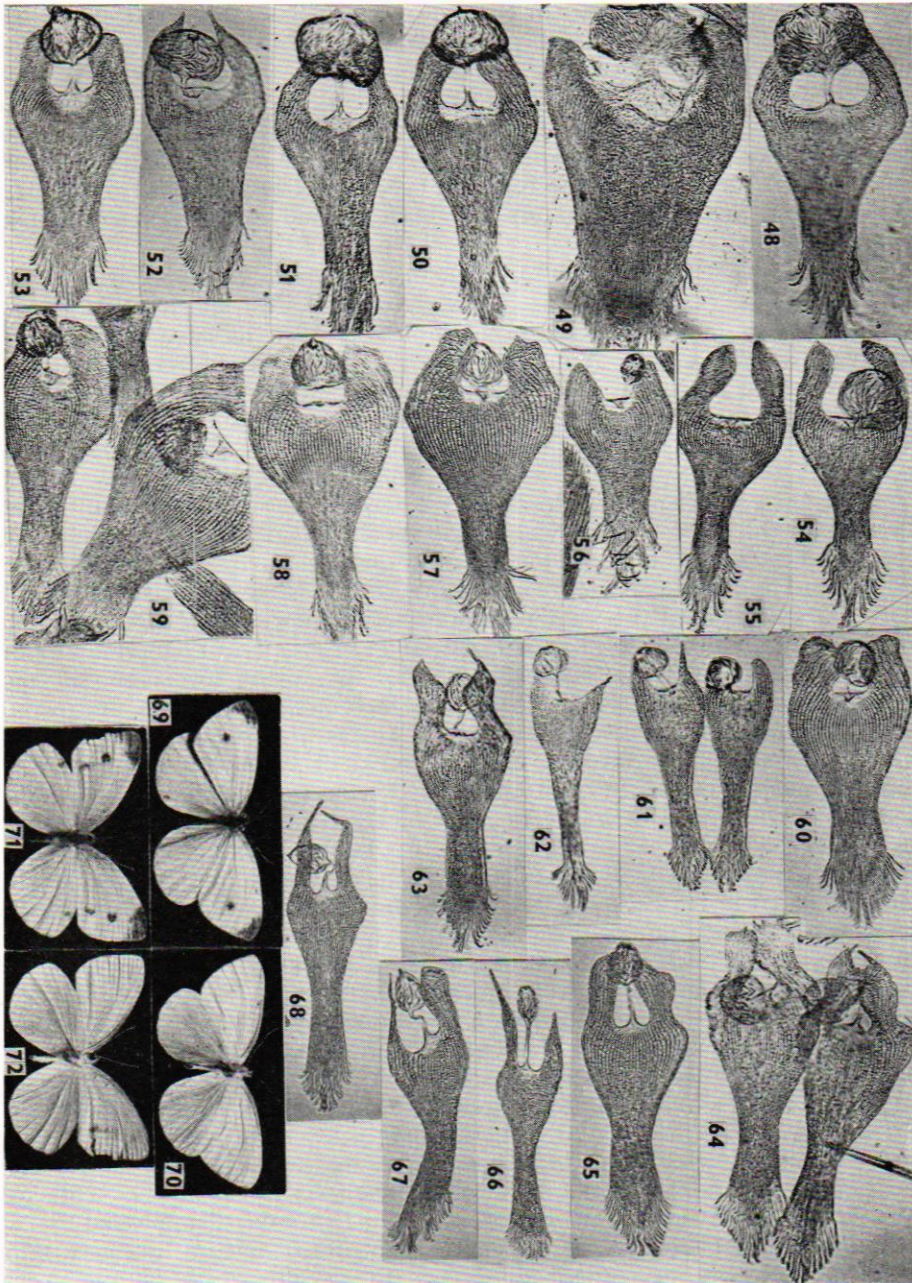


Plate 3.

tion, Jordan has been forced to the same conclusion, that "variability is a primary attribute of life" (1958, p. 59). The degree of variability that effects the scales sometimes increases the difficulty of recognition of the types. With such small objects, requiring a magnification of between 400 and 500 diameters, to obtain certainty in comparison it is necessary to make extremely accurate drawings of each; I doubt if it is possible to do this simply by using a micrometer grid in the microscope eyepiece. Photographs to an exact magnification are unquestionably the best method, and in many respects the easiest also.

The scales are not affected by the size of the individual insect, though they can vary in size racially; nor is it always the smallest species that has the smallest scales. This is remarkably demonstrated in the case of *P. extensa*, the largest species in the genus. As will be seen in fig. 56, the scale is one of the smallest, and the scent cell quite the smallest of the round type. Another very important feature is the existence of seasonal dimorphism in these scales. Chapman was the first to discover this phenomenon in the androconia of some Lycaenids (1914). The degree to which this seasonal change makes itself apparent in *Pieris* varies in different species, but usually the neck of the scale is narrower in the second generation; broader, or less specialized, in the first. From his observations Chapman concluded that the spring generation was the more ancestral form. The seasonal scale development in *Pieris*, as will be shown, supports this view. Verity also has noted that the similarity of the spring females of *P. ergane* and *P. manni* supports the hypothesis that in the Palaearctic *Pieris* the spring forms are the most ancestral types (1908, p. 154). Most *Pieris* have a single type of androconia, but a few produce a restricted number of scales of a second type, which is twice the width of the normal scale. From their limited numbers and the almost complete obliteration of the neck in these distended scales, I hold them to be a survival of an early form of scale, and will refer to them as the "primitive" type. In some species the 1st. generation scale differs so markedly from those of the 2nd. generation, that they may be said to be a transitional stage between the latter and the primitive type scales. Even so the seasonal change does not obliterate the specific characters of the scales; nor do the 1st. generation scales assume the dimensions characteristic of the primitive type scales. The latter are most frequent in *P. bryoniae* in all its races; but also occur in one or two other Asiatic species. There is no means of estimating the number of the androconial scales, the normal types can be present in incredible masses in some species (*brassicae* for example), or only appear as a sparse sprinkling in others. The primitive type is always rare, seldom more than 2 or 3 in any one sample of scales examined. Apart from those species in which the primitive scales are normally present, I have found a single example in *P. napi*, which suggests the primitive scale may still occur in other species from which it seems to have disappeared.

Of equal importance to the seasonal dimorphism existing in these scales is the development of recognisable types by various races of one species. In *P. napi* this phenomenon takes the form of two types, each of which exists in a number of races. That these two types did not indicate two distinct species, but were developments of a single type, was proved by the occurrence of transitional types and the fact that under certain conditions the more advanced type of scale reverted to the more primitive. The charac-



teristics of the scale and the scent cell are constant, and provide an accurate means of identification of species in all generations; where other data are available, biological, ecological or genetical, they have been found to concur.

### Nomenclature

The species of the genus *Pieris* have suffered from excessive race naming which has been further complicated by the addition of names for most seasonal forms. This has resulted in a position where it has become almost impossible to gather what many of the names stand for. As an example, some 14 or more western Palaearctic "races" (i.e. subspecies), of *P. napi* have been named; but most of these "racial" names are used for various generations in other "races". Sometimes one has even been used for generations in two or more of the other "races". The position of the Asiatic and American species is equally confused. To this it must be added that many of these names are synonyms or homonyms or both. It is obvious that a majority of the western Palaearctic "races" are forms of one subspecies that produces a number of local seasonal forms. To establish the true value of these names would necessitate a very large material and be a work quite outside the scope of the present paper, which is an effort to establish a more generally correct view on speciation within the genus. I follow Müller and Kautz (1939), in using the name *P. napi* (L.), for the wide-spread central European race of the insect. The effort to restrict it to the Scandinavian race on the strength of the specimen in the Linnean collection has caused endless trouble. Verity in his "Revision of the Linnean types" accepted "*napi* L." as the insect to which he had given the name "*arctica*". Later (1922), he attached "*arctica*" to the "single generation of N. Norway", and *napi* to the "race" of S. Sweden. Still later (1935), he placed "*napi* L." as the 1st. generation of the race of central Europe, as at Martigny in Switzerland, at the same time stating it was racial in central Scandinavia but occurs "mixed with race *septentrionalis*" at Scania in Italy. These conflicting essays have been followed by other writers in slightly varying ways, all of which shows that a single specimen from one locality can resemble those from a number of other widely-separated localities; which makes the solitary Linnean specimen completely inadequate as a guide to the race it may really represent. The Scandinavian race is now usually referred to as "*adalwinda* Frhst." or "*arctica* Vty." This race in slightly varying forms spreads all across the northern area of the Palaearctic Region from Scandinavia and Finland to Kamchatka. The name *kamtschadalis* Röber (1907), would seem to be the first valid name for it; the Scandinavian insect can however, be separated under the name *adalwinda* Frhst. The name *arctica* is invalid. Verity described it (1911, p. 334), as the "arctic race of Europe"; at the same time he marked an arctic European specimen from Finmark, that he had previously figured (Verity 1908, pl. 32 fig. 37), as type of a North American race "*pseudobryoniae* Vty." Fruhstorfer (1909), had already given the name *adalwinda* to the same figure of Verity's, so *adalwinda* had two years priority. The name *arctica* cannot apply to any North American race either, for none of these so far as I know, are conspecific with the "arctic race of Europe". The selection of a specimen from Finmark as type of

*pseudobryoniae* by Verity, might invalidate that name also, but on the strength of fruhstorfer's work restricting *pseudobryoniae* to the Alaskan specimen Verity figured (Verity 1908, pl. 32, fig. 36), I continue to use it. These instances are typical of the confusion surrounding many names in use in the genus.

## Specific Characteristics of the Androconial Scales in *Pieris* Species

### A. *Rapae*-group

*P. rapae* (L.). The scale in *P. rapae* (fig. 2), is essentially asymmetrical especially in the basal parts. It shows closer affinity with that of *P. canidia* (see fig. 9), than any other species. The seasonal change is slight, the scale in the 1st. generation is a little heavier. The distinctive feature of the *rapae* scale is the irregularity of outline of the basal area which is also more extended. In the other species the outline is perfectly symmetrical.

*P. leucosoma* Schaw. Fig. 3. This species has always been referred to as a race of *P. rapae*. The scale however, is very distinctive. The base is much rounder in outline, as broad as in *P. rapae* but shorter and beautifully symmetrical. The neck is much longer than in the *rapae* scale. The specimen illustrated is from the 2nd. generation, I have not seen the first, but even if the neck is somewhat broader the scale could not be mistaken for that of any other species. One may note that the species is the smallest in the group but the scale is the longest. As well as this distinctive scale the geographical distribution of *P. leucosoma* points to its being distinct from *P. rapae*. In addition to the wide range of the species in the eastern Mediterranean area (see Graves 1925), *P. leucosoma* occurs both in Iraq and Persia. The race *iranica* of *P. rapae* is said by Wiltshire (1957), to be "one of the most universally distributed butterflies in Iraq", and specimens of *P. leucosoma* from Bagdad are in the Wiltshire collection. Higgins (1958), records *P. rapae* from Bagdad, so it seems certain the two species must exist in proximity in that country, if not in Persia also. The yellowish streak at the base of the costa on the underside of the fore wings is said to be one of the most striking characteristics of *P. leucosoma* both by Graves (1925), and by Schawerda in his original description (1905). It was strongly-marked in every specimen I have seen, and the very pale, almost white, unicolorous underside of the hind wing is another striking characteristic of the species. Verity (1908), figured on pl. 33, fig. 37, a male upperside from Forte dei Marmi, and a male underside (fig. 39), from Florence as "*P. rapae*", but these figures look extremely like *P. leucosoma*, so the latter may actually be an Italian species. If this should prove to be so its occurrence in proximity to *P. rapae* in the localities mentioned may be taken as a certainty.

*P. manni* Mayer. Figs. 7 and 8. Reverdin (1909), has pointed out the difference between the scales of this species and *P. rapae*. The *manni* scale is more slender all over but not quite so long, and much more symmetrical, even if not as perfect in this respect as the scale in *P. leucosoma*. In many *Pieris* species (? all), occasional dwarf specimens occur among the normal ones. These minute specimens are not merely unusually small examples, but actual dwarfs, less than half the normal size. They occur in any generation, and as they must have lived under the same conditions in every respect as

the other individuals with which they fly, their stunted development can only be attributed to chance-compelled, abnormal food supply or some pathological cause. In *P. manni* a dwarf specimen of the 1st. generation from Switzerland, gave an androconial scale that was an exact miniature in every respect of the scale in the normal specimens that were flying with it. This might seem what would be expected, but the fact as will be seen later, is of great importance when contrasted with the scale development in other species under similar circumstances. The two normal scales figured show differences of outline such as are frequently to be seen, but though in fig. 8, there is a tendency to asymmetrical development, suggesting that habitual in *P. rapae*, this does not obscure the slender form of neck and body and the regularity of outline that is so characteristic of the *P. manni* scale.

*P. canidia* Sparrm. Fig. 9. As previously noted the scale in this species is closer to that of *P. rapae* than any other species. The body is however, perfectly symmetrical, equalling the scale of *P. leucosoma* in this respect though different in formation, and the neck is much shorter. The latter feature more resembles the *rapae* scale, but the regularity of the body curvature is more as in the *manni* scale. It is one of those scales that is difficult to distinguish when seen alone under the microscope, but when comparison is possible, as in the photographs, it is easily recognized. The scent cell in the four species dealt with is similar in size and shape; it is slightly larger in *P. leucosoma*.

*P. krueperi* Stg. Fig. 10. The small size of the scale in this species is unmistakable. The photograph speaks for itself. The insect is fully as large as the others in the group, which emphasises the fact that the size of the scale is in no way related to the size of the insect.

#### B. *Napi*-group

*P. napi* (L.). This species shows the phenomenon of racial dimorphism in the androconial scales in marked degree. The species, so far as I at present have been able to establish, is restricted to the Palaearctic Region, but it produces two very distinct types of scales; one, in those races located in the north of Europe and Asia, the other in the races of the more southern areas. The dividing line between these groups of races is approximately the 60th parallel, though the northern strain comes a good way south of this in Sweden and Kamchatka; possibly also in central Siberia, but I have no exact data from that region. The scales of the races *kamtschadalis* and *adalwinda* are illustrated as typical examples of the northern strain (figs. 4, 11, 12). I use the name *adalwinda* to cover all north European insects; it is to be noted that the females of this strain are dimorphic everywhere, in varying degree, ranging from white *napi*-like examples to heavily suffused dark examples of the "*bryoniae*" type. The northern scale is a little shorter than the southern one, but the neck is very broad and short. Fig. 4, shows an example of the more advanced scale of the 2nd. gen. in which the neck is obviously better developed and narrower though still of heavy proportions. Figs. 11 and 12 are examples of the 1st., or single generation scale. The scent cells seen in fig. 4, are typical of the form of this cell; owing to its fragile nature it is most often compressed in mounting which more or less distorts it. This scale is so markedly different from the southern one and so completely constant

that it might well be thought to be a specific development, the differences of formation being as marked as those distinguishing such species as *P. rapae*, *P. manni*, *P. leucosoma* and *P. canidia*. On turning to the southern type however, one finds proof that both are developments of one specific type. The southern races from central Europe and North Africa produce a longer scale, basally broader, but with a strong restriction to the neck which is markedly narrower. This type is illustrated from a number of races. Of *P. napi napi* fig. 5, shows the 1st. generation from England, fig. 6, the 2nd. generation from Switzerland, and fig. 13, the 1st. or perhaps single generation, from somewhat over 4000 feet in the Kandersteg district. The slightly narrower neck in the 2nd. generation scale (fig. 6), can be contrasted with the somewhat broader neck in the Alpine 1st. (or single), generation scale and the English 1st. generation one. The alpine race in that district flies with *P. bryoniae*, yet the scale makes no approach either to the formation or length of the scale of the latter (fig. 27), but rather a very slight contraction in length causing the scale to come closer in length to the northern scale than to that of the 1st. generation *napi*. This very slight change is the only effect resulting from the considerable increase in altitude. It is however, sufficient to show that the Central European race as it attains alpine conditions ceases to draw away from the northern type of scale as it has been doing, and tends to a slight reversion towards it again. Had *P. bryoniae* and its races been evolved from *P. napi* this would not have been the case. *P. napi* has in fact attained its most specialized and advanced formation (i.e. furthest removed from the primitive northern scale), in its summer generations in Central and Southern Europe; and in this stage the scale makes its nearest approach to the *bryoniae* type. But also in these regions the occasional dwarf specimens occur, which have been mentioned previously in connection with *P. manni*. It will be recalled that the effect of this phenomenon in that species was to produce a miniature scale otherwise similar in every detail to the normal scale. In *P. napi napi* such dwarfs develop scales that are slightly shorter than the normal ones, but this change is not just the result of stunted development for it is accompanied by a marked increase in the width of the neck. The scale has in fact reverted to the more primitive northern scale (fig. 14). This takes place whether the dwarf specimen is of the first or second generation, proving the racial *napi* and *kamtschadalis* scales to be extremes of one type. The northern scale is obviously less remote from the primitive type scale, such as persists in the *bryoniae* races, than is the *napi* scale, and as the latter when affected by some abnormal occurrence restricting the growth of the individual but not that of the scale, reverts to the northern type, it seems certain that *napi* is just a more advanced race of *adalwinda*. This also suggests that in a remote past *adalwinda* originated from a *bryoniae*-like ancestor; which accords with Bowden's and Petersen's results and demonstrates why *napi* is more definitely distinct from *bryoniae* than *adalwinda* appears to be, although the latter and *napi* are conspecific. The dimorphic females in *adalwinda* are but an indication of its ancestry not of any close specific affinity with *bryoniae*, for this phenomenon frequently appears elsewhere, as in the *melete*-group species. In the south *napi* produces several races. Of these *persis* Vty. (1922, p. 140), is the only *napi* race I have seen from Iraq or Persia. Verity figured it as "*pseudorapae*" (1908, pl. 49, figs. 3, 4, 5), the figures do not quite support the description

but do differ from true *pseudorapae*. Race *persis* resembles a summer generation of *P. rapae* more than *P. napi*. The underside of the hind wings however, resemble *pseudorapae* of the 2nd. generation, but the black, discal spots on the underside of the fore wings distinguish race *persis* as does its general shape and the reduced extent of black scaling at the base of the wings on the upperside. One specimen, from the Wiltshire collection, was labelled as having been captured "above 8200 feet"; this must represent a race that only has a single generation. The scale however, is of a very advanced type, the neck is more reduced in width than it is in any central European district: actually making some approach to the *bryoniae flavescens* scale (fig. 34). One finds a similar type of scale in the North African race *atlantis* which also flies at a considerable altitude; 7500 feet; but it would seem that it is conditions engendered by latitude rather than altitude, a combination of heat and dryness, that stimulates this advance in the scale development of *P. napi*, for it is seen to progress continuously as one passes from the extreme north to the sub-tropical south. That this indicates a totally different constitution from that which has produced the *bryoniae flavescens* scale seems irrefutable. Moucha records (1957), that in the Carpathians typical *P. napi* often ascends to altitudes over 6000 feet, and that in all the localities where he has collected in those mountains both *P. napi* and *P. bryoniae* fly together at lower levels. From the Vihorlat Mountains in eastern Czechoslovakia he has described a beautiful race of *P. bryoniae* as *vihorlatensis*, which is abundant at levels between 800 and 1300 feet, in two generations. In the same locality there also flies a race of *P. napi*, very slightly smaller than the usual central European insect. The scale of this race can only be described as a transitional stage between the advanced *napi* scale and the northern one; closest to the 2nd. gen. *adalwinda* scale (fig. 4), but a little more slender. Although this race flies with *P. bryoniae* at an altitude unusually low for the latter, the change in the *napi* scale is away from *bryoniae* which retains its normal scale. This remarkable transitional scale also appears in some individuals of *napi* of the spring generation in other localities, such as southern England, it is an obvious link between the primitive and advanced types of scale in the species. In Spain and the Mediterranean islands, a superficially very distinctive race is found: *P. napi dubiosa*. This race has a look of *P. krueperi* and it has been suggested that it may be a distinct species. The scale however, shows it is a true *napi* race. I have not examined race *maura* Vty., from North Africa, of which *bladana* Holl and *atlantica* Rths. seem to be synonyms. Race *maura* seems to have much in common with race *atlantis*. The facts given in connection with these *napi* races leave little doubt that *P. napi* and *P. bryoniae* are distinct species; and study of the latter further emphasizes the fact.

A number of races attributed to *P. napi* have been described from eastern Asia. So far however, the subsp. *kamtschadalis* is the only *napi* race I have seen from that region. Two of these supposed *napi* may be dealt with here, for though they constitute a link between the western *napi*-group species and the eastern *melete*-group, they are perhaps closer to the former.

*P. dulcinea* Butler. Fig. 57. This Korean insect has usually been referred to *P. melete*. Shirôzu pointed out (1953), that this was impossible as the two fly together in North and Central Korea; he therefore accepted it as a race of *P. napi*. The scale shows that *P. dulcinea* is clearly distinct from

either of these species. It perhaps most resembles the scale of *P. napi napi* (fig. 5), but differs from it by the squarer base, the more abrupt neck restriction and its much reduced width, which makes a marked contrast with the body development and is suggestive of the *melete*-group species. In these features the *dulcinea* scale especially resembles the formations of the neck in *P. ajaka* and even *P. japonica*, but the body and cell distinguish it from these species.

The Japanese insect named *aestiva* by Verity and placed by him as a race of his *pseudomelete*, proves to be a race of *P. dulcinea*. The *aestiva* scale (fig. 58), shows obviously that it has no connection with *P. nesis* Frhst. (= *pseudomelete* Vty. in part), a *melete*-group species (fig. 51). The slight differences observable in the scales of *dulcinea* (fig. 57), and *aestiva* (fig. 58), may be racial, but they might also be the result of the specimens coming from different generations, for I do not know which generation the specimen of *dulcinea* is. It may be noted that Verity's *pseudomelete* was described from specimens from Usuri in the Maritime Province, it was only at a later date that he selected one of his types from Hokkaido (Verity 1911, p. 167, fig. 9, male). It may be that the Usuri *pseudomelete* actually is *dulcinea*. The name *aestiva* is a homonym of *P. canidia aestiva* Rühl.

*P. japonica* Shirôzu. Fig. 42. This is the second species linking the eastern and western species as already noted. Shirôzu (1952), separated *P. japonica* from *P. melete* and placed *japonica* as a race of *P. napi*; it has been referred to that species by all writers since. Shirôzu pointed out (l.c. p. 18), that *japonica* flies mingled with *P. melete* in Honshu, Shikoku and Kyushu, and the scale corroborates this for it is not of the *melete*-group type. It also distinctly separates *P. japonica* from *P. napi*, the neck formation being very specialized, much more restricted compared with the very extended basal development, than in any other species of the *napi*-group. The scent cell is also remarkable being larger than in any other advanced scale in this group of species. I have not been able to examine the 1st. gen. of *P. japonica*, which was described by Murayama (1953).

*P. pseudorapae* Vty. Figs. 20, 21, 22. This species has been held to be a race of *P. napi*, but the scale is very distinct. Its greater size is obvious as is the formation of the body, which is more suggestive of *P. bryoniae*, but distinctly heavier in build all over (compare fig. 27). Fig. 20, is a 2nd. gen. scale, the 1st. gen. one (fig. 22), is a little smaller but even so the neck is slightly broader. The 1st. gen. scale is somewhat like that of *P. segonzaci* (figs. 25, 26), but does not develop the remarkable terminal expansion peculiar to the latter. A further distinctive feature of the *pseudorapae* scale is given by a dwarf specimen of the 1st. gen., which I was fortunate enough to be able to examine. This scale (fig. 21), is slightly restricted in width but otherwise scarcely differs from the normal 1st. gen. scale, though the scent cell is slightly reduced. It displays no tendency to revert to the northern type *napi* scale, as certainly would have been the case if *pseudorapae* had been a race of the latter. Finally, the existence of a true *napi* race in Persia shows that the development of the *pseudorapae* scale cannot be attributed to the conditions prevailing in that region. In the first generation of *P. pseudorapae* the general appearance and extent of the markings on the underside of the hind wings distinguish it from *P. napi persis*. In the 2nd. generation the underside of the hind wings is much less strongly marked, and therefore more like

*persis*, but this generation is without the black spots on the underside of the fore wings as in *persis*, though such spots are occasionally present, or partly so, in specimens of the 1st. generation.

*P. segonzaci* Le Cerf. Figs. 25, 26. This species has always been connected with *P. napi*, but the scale is obviously distinctive. The remarkable terminal expansion at once catches the eye, in other species the neck retains its normal width to the end. Some scales in the *bryoniae* races show a tendency to expand slightly towards the termination, but this is an aberrational rather than a racial character. The great width of the neck in *P. segonzaci* is also very different from the more slender type prevailing in *P. bryoniae*.

*P. ergane*, Hb. Fig. 18. This species has always been considered very closely related to *P. rapae* and even at one time was placed as a race of the latter. The fact that the two species fly together in many districts has long been known and their specific standing accepted: biologically they are also distinct. Higgins has recently made a valuable record (1958 a). At Malka in Macedonia he took *P. krueperi*, *P. ergane*, *P. rapae*, *P. manni* and *P. napi* all flying in the same locality. This record emphasizes how little importance attaches to the enforced production of hybrids as a test of speciation. Experiments have shown that any cross between such congeneric species could be produced if desired. Natural hybrids are always a great rarity, but if found in company with the parent species are a proof that these are specifically distinct and have therefore remained unchanged. I have shown that the presence of natural hybrids in such cases is probably the result of mistaken identity between the insects concerned (Warren 1958). In this collection of similar-looking *Pieris* species noted by Higgins, hybrids may well have occurred some time in the past; but they continue to live side by side, unaffected. It is interesting to note that *P. ergane* occurs as far north as the South Tirol (Daniel, Wolfsberger & Pröse, 1957).

The point of greatest interest about the *P. ergane* scale is of course that it shows the species to be a member of the *napi*-group, with no close affinity with *P. rapae*. The scale shown in fig. 18, is a 1st. gen. one, with perhaps more resemblance to the *bryoniae* scale than the *napi* one. In the 2nd. gen. the neck is longer and to a very slight extent narrower, but in either generation it is easily recognized.

#### *P. higginsi* N. Sp.

Synonymy: *P. napi* 1st. gen. Higgins, 1958, p. 40. *P. ergane* Wiltshire, 1957, p. 21, (? in part).

This species resembles several others to a certain extent, especially *P. leucosoma*, *P. pseudorapae* and *P. ergane*. The 1st. gen. is smaller than *P. pseudorapae*, both sexes measuring 24 mm. from the centre of the thorax to the tip of the fore wing; as compared with 27—28 mm. in the latter. The apex of the fore wing and the two discal spots in *higginsi* are a pale gray and very diffused in the female; the male is without any discal spot. The underside of the hind wings in both sexes is a pale yellow and there is a broad but very thin superscaling of black; neither sex has a discal spot on the underside of the fore wings. The 2nd. generation (figs. 69, 70, 71, 72), is slightly larger, the gray markings pale but more pronounced and the male has a discal spot on the upperside of the fore wings. The underside in both

sexes is almost unicolorous and consequently resembles *P. leucosoma*, but of course the latter has two strongly-marked discal spots on the fore wings underside which *higginsi* has not. The underside also suggests *P. ergane*, but the hind wings in the latter are a deep yellow. In fact the very striking, pale, unicolorous underside, can be relied on to distinguish *P. higginsi* in both generations.

The holotype and allotype are in the Wiltshire collection; and a male and female paratype of the 1st. generation in the Higgins collection. I dedicate this curious species to Dr. Higgins who first drew my attention to it, and sent me specimens he had taken at Haji Omran in Iraq. This district is the only one from which I have seen the species as yet. It flies there between 5000 and 5500 feet. Rayat, from where Wiltshire's specimen came, is only a mile or so from Haji Omran and about 4500 feet. The scales are very remarkable, fig. 19, shows the 1st. generation, figs. 23 and 24, the second. The heavy basal development and extremely short neck in the 1st. generation do not suggest close affinity with any known species. The advanced formation and distinct though still very short neck in the second is surprising; especially as it is accompanied by the large primitive type. The most primitive type of 1st. generation scale in *P. ergane* bears some resemblance to the 2nd. generation scale of *P. higginsi*, but the neck in the *ergane* scale is distinctly longer and the entire scale narrower. The resemblance is lost in the 2nd. generation scale of *ergane* in which the contrast between the neck and body is greater.

*P. bryoniae* subsp. *bryoniae* O. Figs. 27, 28, 30. The typical scale of this race differs from that of *P. napi* by the less expanded, more oval, base and longer neck, very clearly seen in the photographs. In addition to this the hairs which spring from the distal extremity in all these androconial scales have a distinctive character. They are stouter than in most species and more evenly dispersed, tending to be waved, and ending hooked rather than pointed. Owing to their extremely fine nature this characteristic appearance is often obscured in mounting, but it is observable in the photographs of all the *bryoniae* races. In *napi* these hairs are spaced irregularly, finer and curved at the tip, less hooked. In *P. segonzaci* and *P. pseudorapae* these hairs are somewhat similar to the *bryoniae* hairs, in their even dispersal, but they are less waved and not bluntly hooked. As well as these normal (advanced type), scales, which are present in great numbers, a few primitive scales will often be found (figs. 28, 30). They exist in both generations (when there are two generations), at all altitudes. Fig. 30, came from a specimen taken at over 6500 feet, fig. 28, from about 4000 feet, in a locality where *P. napi* was also flying. I have noted that I found one solitary example of these primitive scales in *P. napi napi*, and as I have examined a far larger number of specimens of the latter owing to its wide range, there is little doubt that the evolution of the scales in *P. bryoniae* has followed a different course from that which has led to the present *napi* scale, which suggests a separate line of ancestry in the two species.

*P. bryoniae flavescens* Wagner. Fig. 34. The scale in this race has the long, narrow neck, so typical of many *bryoniae* races. Fig. 34 is a good example, and though the neck can be slightly broader in some cases, this variation is not at all frequent. The race flies at lower levels than subsp.



*bryoniae* and has two generations in the Eastern Alps. Further to the west in the Bavarian Alps and neighbouring mountains it is supposed to have only a single generation. Wolfsberger (1951), dealt with this question in detail, stating that only very exceptionally do 2nd. generation examples appear; he also quotes the experience of several other collectors supporting this view. The race of the Dolomites, from which fig. 34 was taken, may possibly also only have a single generation, such dates of captures as I have seen support this idea. Meyer-Dür (1852), recorded "*bryoniae*" specimens from Meiringen in the Hasli Tal, Switzerland, flying in late May. Müller states the race from Meiringen is the same as that from Mödling, therefore presumably *flavescens* (Müller & Kautz 1939, p. 8). This race must have two generations for in the Meiringen district in late August I found a race differing slightly from *P. napi* in the markings on the underside of the hind wings, which are stronger than is usual in the 2nd. generation of the latter, and the uppersides, which are entirely white in the females, also unusually heavily marked for the Central European summer race. In the males the inner edge of the apical and marginal black markings on the upperside of the fore wings is regularly curved and even, as is most usual in *flavescens*. On examining the scales I found they agreed with those of subsp. *flavescens* quite unmistakably. A considerable number of the primitive type scales were also present (figs. 29, 59). The long, narrow neck of the ordinary scales which are visible in fig. 59, are remarkable in contrast to the expanded neck of the primitive scale touching them. The exact agreement between these scales, 2nd. generation from a lowland locality, and those from the Dolomite locality at 3800 feet (probably single generation), is remarkable. This constancy of scale development over a range of at least 2000 feet of altitude, gives no support to the idea that race *flavescens* is the outcome of hybridization between *P. napi* and *P. bryoniae*. This white generation is not so abnormal as might be thought, for on the rare occasions when a 2nd. generation specimen of the high-level race *bryoniae* does appear, it is always a much paler yellow than the 1st. generation, and at times can be pure white and no more suffused with dark scaling on the upperside than normal *P. napi*. I have taken such a white female above 6000 feet in the Engadin, among worn dark specimens of the 1st. generation *bryoniae*. Further, it is interesting to note that a bigenerational change of colour occurs in the race *marani* in the Tatra. Here the females of the 1st. generation are white, and those of the second, yellow (Moucha 1959). It is possible then that in the Bavarian Alps a 2nd. generation of *flavescens* exists, but has white females. (See appendix B.)

*P. bryoniae neobryoniae*. Shelj. Fig. 31. The scale in this race is a little shorter and broader than that of race *bryoniae*; it is suggestive of the scale of *P. segonzaci*, but the development of the terminal hairs and the narrower neck and more oval body, show affinity with the *bryoniae* races. A very similar scale is found in race *frigida* (fig. 43); the shorter broader neck in these two races makes one wonder if they may not represent a transitional stage between the primitive scale (figs. 28, 29, 30), and the more advanced normal one (figs. 27, 32).

*P. bryoniae pseudobryoniae* Vty. Figs. 32, 33. For the North American races I use the names as in most modern works. They may not be correct, as for example *pseudobryoniae* is probably invalid, but a very extensive material would be essential to work out the correct ones. However, the north

Canadian and Alaskan insects have been mostly referred to as "*pseudobryoniae*", so I continue to use that name as separate names for the various races are essential.

In race *pseudobryoniae* the scale is very similar to that of subsp. *bryoniae* in shape, though slightly shorter (compare figs. 32 and 27). The primitive scale is also quite similar. This race is said to have but one generation in the season, which of course is also the case in subsp. *bryoniae* (with rare exceptions). The colour of the underside of the hind wing is pale yellow, the nervures broadly marked in a brownish colour without any white line showing along the nervure, as in other North American races.

*P. bryoniae frigida* Scudder, Figs. 43, 44. The insect I take to be this race I have only seen from the Fort Smith district in Mackenzie. It is somewhat like race *oleracea*, the male completely white on the upperside with just a trace of gray scales at the apex of the fore wings. The underside of the hind wing is tinged with pale yellow, the nervures sharply marked with dark brown, which is both broader and darker than in race *oleracea*. The figures given by Verity (1908, pl. 32, figs. 33 male, 36 female), both from Nulato, Alaska, are good likenesses of this insect. The female has a look of subsp. *neobryoniae*, which is remarkable for the scales in these two races are somewhat similar, as already noted. There is considerable variation in the *frigida* scale, some examples (as fig. 44), approaching the formation in the 1st. generation of race *oleracea*.

*P. bryoniae oleracea* Harrison, Figs. 35, 36. The 1st. generation scale of this race is distinctive, and shows the race to be in a somewhat less advanced stage than race *frigida*. I have only seen the 1st. generation of *oleracea*, the 2nd. generation scale would probably show more pronounced restriction of the neck. The primitive type scale (fig. 36), is characteristic of this type of *bryoniae* scale. Superficially *oleracea* and *frigida* are very similar, and in spite of the specialized 1st. generation scale of *oleracea*, it seems best to retain both as races of *P. bryoniae*.

*P. bryoniae pallidissima* B. & Mc. D. Fig. 47. The scale in this race is apparently more advanced than the 1st. generation scale of race *oleracea*, but the example figured may be either 1st. or 2nd. generation. Data was lacking. The considerable size of the scent cell however, points to affinity with race *oleracea*, for the cell is much smaller in such other North American races as I have examined, which are all obviously connected with *P. venosa*.

*P. venosa* Scudder, Fig. 39. This species includes several races confined to North America. The scale suggests that its development has been checked (which would account for the small size of the scent cell), being small and uniformly narrow, yet each race of the species that I have examined so far, has a distinctive racial type of scale. In subsp. *venosa* (fig. 39), the scale though the largest, has only a slight restriction representing the neck; in race *virginiensis* Edw. there is no neck, the scale tapering in the most primitive manner (fig. 40); I have not seen a 2nd. generation specimen, but the scale in it would probably be more developed.

A race from the Rocky Mountains of Alberta (fig. 41), has quite a marked neck development, though the scale is the narrowest of the three and the race is said only to have a single generation. There are a number of other races connected with this species which may give other transitional stages of scale development when they can be examined. It is interesting to note

that *P. venosa virginensis* occurs in proximity to *P. bryoniae oleracea* on Grande La Cloche Island, Ontario, which proves that these two insects are distinct species, as the scales so clearly demonstrate. Superficially these three *P. venosa* races show the same characteristic markings of the underside of the hind wings. These wings are very broadly marked with brownish scaling, while the actual nervure is marked by a sharp, fine, white line. There is no doubt that a really representative material of North American *Pieris* races in all their generations would give most interesting results if they could be examined.

*P. ochsenheimeri* Stg. Figs. 37, 38. The scales show this species is indeed a very primitive one as Staudinger supposed long ago. Only occasionally is a somewhat advanced type of scale found (fig. 37). The normal type, (fig. 38), a little resembles the normal scale in *P. higginsii*, but has even less neck development, the body tapering without restriction after the manner of the most primitive scales in *P. bryoniae* and *P. higginsii*. The species is said only to have one generation; the scales illustrated all came from the same specimen. This species and *P. narina* are usually united as one species; the latter is however more advanced in the scales and the two show a remarkable reversal of characters, which excludes the possibility of their being conspecific.

*P. narina* Vty. Figs. 45, 46. This small insect was described by Verity from Naryn in Turkestan. It seems to have been a puzzle to many authors. Its area of distribution is not much removed from that of *P. ochsenheimeri*, but the full range of either is far from known. Both insects are minute; the male *narina* has little marking on the upperside and is without a discal spot on the fore wings, the female is very dark and like *P. bryoniae*. *P. ochsenheimeri* has a heavily marked male and a much less strongly marked female. In those specimens that I have seen, the underside of the hind wings in the male *narina* is deep yellow, the nervures very broadly suffused and the ground colour reduced to narrow, internural streaks; there is a poorly-marked discal spot on the fore wings. In *P. ochsenheimeri* the underside of the hind wings is less heavily suffused, and much paler in colour, and there are two distinct discal spots on the fore wings. This reversal of characteristics, if the two occur in proximity anywhere, as they well may, would point to their being distinct species. Strangely enough, the scales also display an exact reversal of characters. The *ochsenheimeri* type, as noted, is a primitive one, with which an occasional scale of more advanced forms occurs. The *narina* type is an advanced one (fig. 45), with which an occasional primitive form (fig. 46), occurs. The latter differs from the usual type in *P. ochsenheimeri* by terminating more bluntly, more like the formation seen in the *P. bryoniae* primitive scales. This reversal of scale types suggests an independent ancestry of these two insects. *P. narina* shows some affinity with certain North American races (*pallidissima* and *frigida*), but differs markedly in the much smaller scent cell, and the curious fact that the primitive-type scale (fig. 46), is actually smaller than the normal type (fig. 45). In all other species which produce these two types of scales, the reverse is the case. Even in *P. ochsenheimeri* in which the two types of scale are very similar and seem to be in a transitional stage of development, they are approximately the same size. This is another point in which these two species stand apart.

C. *Melete*-group

There are a large number of races in this group, but only some of the best-known can be dealt with at present. However, this enables some very distinct species to be recognized.

*P. melete* Mén. Fig. 48, 2nd. generation, and Fig. 49, 1st. generation, primitive type. A glance at fig. 48, will enable the characters of the scale in this group of species to be recognized: the angular formation, length of basal extensions and great size of the scent cell. In *melete* the cell is rectangular and larger than in any other species. The great width of the base of the primitive scale is also remarkable (fig. 49), the cell too increasing in size more than is usual. The normal width of the neck in the 1st. gen. scale is only a little broader than in that of the 2nd. generation.

*P. melaina* Röber. Fig. 50. The scale of this species is easily recognized by the somewhat smaller size of the scent cell and its more oval shape. It is very typical of the group and looks like a small specimen of *P. melete*, but the shape of the cell is unmistakable. The distribution of this species may well be wider than is supposed.

*P. nesis* Frhst. Fig. 51. This species was described by Fruhstorfer in 1909 from Hokkaido as a race of *P. napi*. It has always since been referred to the latter species. The name *pseudomelete* Vty. (1908), was described as a race of *P. napi* from Usuri in the Maritime Province, but may be referable to any of several species from this eastern area. Verity later cited the female he had figured from Usuri (Nov. 1908, pl. 49, fig. 10), and a male of *nesis* from Hokkaido (1911, pl. 67, fig. 9), as types of *pseudomelete*. As *nesis* was the first name given to the Japanese species it must be retained. What *pseudomelete* represents can only be determined when all the races from the Maritime Province are available for examination. The scale of *P. nesis* shows the species has not the least connection with *P. napi*, but has considerable affinity with *P. melaina*. The scale differs from that of the latter by its slender basal formation and longer neck, and the larger scent cell suggestive of that of *P. melete*. These characters distinguish *P. nesis* very clearly, but there is no doubt that the two species are closely related. Unfortunately I have not been able to examine the various generations of these two species. Anyone wishing to identify *P. nesis* should consult the very excellent illustrations and descriptions of this species, *P. japonica* and *P. melete* given by Shirôzu (1952).

*P. orientis* Obth. Fig. 52. This species has always been connected with *P. melete*, but the scale shows there is no real affinity between the two, indeed *P. orientis* seems to be rather an isolated species. The formation of the scale suggests a rather primitive type, somewhat like the primitive scale of *P. narina*, but the scent cell is closest to the type seen in *P. melaina*, a combination of characters that is quite unmistakable. The example figured is from a 1st. gen. specimen; I have not seen the second.

*P. ajaka* Moore. Figs. 53, 54, 55. The scale in this species is very characteristic of the group; but is distinguished by its smaller size. It develops very marked seasonal dimorphism. In the 1st. gen. the neck of the scale is so broad that it somewhat resembles the scale of *P. segonzaci* (compare fig. 53 with 25 and 26); but the great size of the scent cell clearly separates the *ajaka* scale, and shows its connection with the species of the *melete*-group.

There is considerable variation in the form of the cell, which can be roundish or oval. The neck varies in width the specimen shown in fig. 53 being about the broadest seen in the normal type, but occasional examples of the large primitive type scale appear in which it is of course much broader. The 2nd. gen. scale is no less variable in neck development, the specimens illustrated (figs. 54, 55), show about the extreme in reduction of width, and though these are on the whole the most normal, others can approach the dimensions of neck development found in the first generation scales, very closely. The range of cell formation is about the same in both generations. It is interesting to note that in spite of the very small size of the first generation specimens, the scale is slightly larger than that of the second generation specimens. The great difference in size, as well as in markings, between the two generations of *P. ajaka* has probably helped to cause uncertainty about the identity of the species in the past. *P. ajaka* seems to have a considerable range in altitude, and in some localities in Kashmir late specimens of the first generation have been taken flying among numbers of the second. The under side of the second generation is much less heavily marked than that of the first, especially the scaling along the nervures on the hindwing which is reduced to thin lines confined to the actual nervures. In all the male specimens of *P. ajaka* that I have seen there is only one black discoidal spot on the upper side of the forewings, though the second one nearer the inner margin is inclined to show through from the under side. This effect is slightly increased if the specimens are a little worn.

*P. extensa* Pouj. Fig. 56. The scale in this species is perhaps the most remarkable in any *Pieris*. The insect is far the largest species in the genus, the scale almost the smallest. It is a characteristic *melete*-type scale, but the scent cell more resembles that of the *rapae*-group species, and is even smaller than the normal size in the latter. The scale is one of the most easily recognized, and in spite of its connection with the *melete*-group species, the formation of the scent cell excludes any possibility that *extensa* could be a race of *P. melete*.

The range of variation in the development of the scent cell in the species of the *melete*-group emphasizes very strongly how widely separated this group is from the others; in spite of the considerable superficial resemblance which still remains suggestive of the *napi*-group species.

### Appendix A. Reaction of the Androconial Scale to Racial and Specific Cross-Breeding

In January 1960 Mr. S. R. Bowden kindly gave me a number of specimens he had bred, of which he knew the exact parentage. The material consisted of one mongrel (interracial cross), and four hybrids of differing parentage. Study of the scales emphasized their taxonomic value remarkably. *P. napi napi* × *P. napi adalwinda*. The normal scales of these races have already been described and illustrated, the *adalwinda* type, that of the northern races, (figs. 4, 11 and 12); the *napi* type, that of the southern races, (figs. 5 and 6). It was shown that the southern type in occasionally occurring dwarf specimens, reverts to the northern type (fig. 14). In the cross the scale produced is very close to the northern type, but the *napi* strain shows in the slightly

longer neck (fig. 60). The scale is beautifully formed, *absolutely symmetric and the scent cell normal*. There is no appearance of any malformation. The normal process of growth has obviously not been interfered with.

*P. napi adalwinda* × *P. bryoniae bryoniae*. In this case there is little if any more difference in the actual sizes and forms of the two types of scale evolved than in the *napi* × *adalwinda* cross. But the result is very different. Some *adalwinda*-like scales do appear, but the symmetry of formation is wanting and the scent cells mostly somewhat contracted. Other scales are closer to the *bryoniae* type (fig. 65), but there is an extremely high percentage of malformed scales and the scent cells of these are distorted and much restricted in size. A few examples are shown (figs. 66, 67 and 68), which give some idea of the chaotic results of this cross. In comparison with the intraspecific *napi* × *adalwinda* cross, it is obvious that in the *adalwinda* × *bryoniae* cross one sees the result of two distinct specific natures incapable of combining. The degree of parentage seems controlled by chance, so it is only when one predominates that an attempt at a more normal scale appears. This proves the androconial scales to be highly susceptible to any change in specific nature; a remarkable demonstration of their taxonomic importance.

*P. bryoniae bryoniae* × *P. napi napi*. In structure the two types of scale involved in this cross have more in common than in the last case, and consequently a type of scale appears that is so much a transition that did it come from a specimen of unknown parentage it would only be guesswork to attribute it to one species or the other. In spite of the degree of combination that is achieved there remains a high percentage of malformed scales; fig. 64 shows some of the marked basal deformities and also a lack of constancy of form in the widths of the necks. These abnormalities clearly show a disruption of development which indicates two contending specific natures. The scent cells remain practically normal, which suggests the development of the cell to be dependent on the full development of the scale, so far as size is concerned.

*P. bryoniae neobryoniae* × *P. napi adalwinda*. The normal *neobryoniae* scale is somewhat specialized (fig. 31), its broad base and neck are suggestive of the *adalwinda* scale, but in size and shape it is a *bryoniae* type, and the large, primitive scale of the latter also exists. The result of the cross with *adalwinda* is a general reduction in width of the scales; there is no approach to anything in the nature of a transitional type and the percentage of malformed scales is very high (fig. 63). A few examples of the primitive *neobryoniae* scale were found, which are also somewhat reduced in size as are the scent cells of all scales. *P. napi napi* × *P. bryoniae neobryoniae*. As in the case of the *napi napi* × *bryoniae bryoniae* cross, there is a certain extent of similarity between the scales crossed, yet the result reveals the complete antipathy of the two specific natures. All the hybrid scales are undersized to an astonishing extent, it is obvious that development has been checked at an early stage and malformation is almost invariably present (figs. 61 and 62). A comparison of these photographs and that showing the massive, perfectly developed type of scale resulting from the *napi* × *adalwinda* cross (fig. 60), is very striking. The inability to develop any approach to a transitional, or even a full sized scale, suggests that the race *neobryoniae* is a specialization of *bryoniae* that has become even more remote from *P. napi* than the former. These results confirm very definitely the specific relation-

ships of the *bryoniae* and *napi* races as established in the systematic part of this paper, on the strength of the structural characters of the androconia.

To summarize briefly: in the intraspecific cross, the *napi* scale gives place to a perfect, practically typical *adalwinda* scale. In the four interspecific crosses, that of *bryoniae* × *adalwinda* alone produces some individuals with an approximately natural scale formation (i.e. that of one of the parent species), but an extended range of intensely distorted formations appear in others. In the *napi* × *bryoniae* cross the scales are essentially transitional in formation, but much affected by malformation. The *neobryoniae* × *adalwinda* cross gives no recognizable approach to the scales of either species, but stunted scales of the primitive *neobryoniae* type occur; while the *neobryoniae* × *napi* cross results in malformed scales that can be said to be little more than rudimentary. These facts clearly accord with our suggestion (ante), that *napi* is a comparatively recent, southern offshoot of *adalwinda*, and that the latter has originated from a *bryoniae*-like ancestor at some remote time, when, presumably, the primitive type scale was still the normal one. Since then *bryoniae* and *adalwinda* have developed on divergent lines, which has led to the advanced type of scale now normal to the 2nd. generation, or single generation, of the former. The *neobryoniae*—*flavescens* races are a continued specialization of the *bryoniae* line; they are consequently still more remote from the *adalwinda*—*napi* line of development. These facts, as previously noted in connection with *P. napi*, accord with Bowden's and Petersen's findings relative to the nature of *adalwinda* and *bryoniae*; but they seem to oppose the theory that in origin *neobryoniae* or *flavescens* are hybrid races.

### Appendix B. The Identity of the *Napi*-Like, Lowland Race of *P. Bryoniae* Established by Breeding

When referring to the summer (2nd. generation), *bryoniae* race of the Hasli Tal (ante), I used the name "*flavescens*", following Müller and Kautz who say this race is the same as the Mödling race (1939, p. 8). It is remarkable for its white females and the low altitude at which it flies. It was only on examination of the scales I realized that it was a *bryoniae* race. This suggested that the "*bryoniae*" females recorded in spring from this locality (Meyer-Dür 1852), must have been the offspring of this *napi*-like summer generation. Müller noted that in *flavescens* the white females predominate in all areas north of the Alps (1939, p. 46), and Kautz states that "all" the *bryoniae* females in the Tatra are white (l.c. p. 153), which must refer to the 1st. generation only (see ante, Moucha's record 1959), but it is known that a *bryoniae* race with white females exists in a certain district of the Caucasus. The females of the spring generation in the Hasli Tal might therefore be either white, coloured, or both. In 1959 I obtained some eggs laid at Meiringen on August 23rd and 24th. The larvae hatched in a few days, and though some died, eleven had pupated by late September. Between May 6th. and June 12th. 1960, 3 males and 4 females emerged, followed by one male on July 12th., the remaining three pupae are apparently going to pass a second winter in that stage.

The females of the summer generation resemble the figure in Müller and

Kautz (1939, pl. 7, fig. 1). They are like some white female *bryoniae* I have taken at high altitudes, and very similar to many *napi*. The males are very close to Müller and Kautz's figure (pl. 6, fig. 1), but the discoidal black spot on the fore wings is usually larger; the evenly curved inner edge of the apical, black tip, is very characteristic. In the spring generation one male has a small discoidal spot; three are without it; especially noticeable however, is the curved inner edge of the apical patch. The four females are smaller than those of the 2nd. generation, with the same type of markings and no greater extent of black scaling. The ground colour of the upperside of the fore wings is white, that of the hind wings a pale lemon-yellow. The fringes of the hind wings in three are also yellow, and two have narrow but distinct, yellow streaks extending through the grey apical patch of the fore wings. There is no exact illustration of this form in Müller and Kautz's plates. As the four females are identical they must represent a usual form. Considering the range of colour-variation normal to *flavescens*, it would be natural if more strongly-marked *bryoniae* types occur from the same parentage as these pale-coloured forms; entirely white females might also be expected. But these four remarkable females are sufficient to confirm the evidence of the scales, for such specimens could not be held to be *P. napi*. In 1960 I visited the Kien Tal, about 1200 feet higher up. Here I got a few male and two normal female *bryoniae*, and with them two other females with white fore wings and pale yellow hind wings, similar to those bred from the Meiringen parents. This was unexpected confirmation that the lowland race was *bryoniae*.

The androconia of the spring generation are a typical 1st. generation type; distinctly shorter with a broader neck than the second generation scale. There is considerable variation in formation; figs. 15, 16 and 17, show characteristic examples. Some forms are somewhat similar to fig. 35, the 1st. generation scale of *bryoniae oleracea*, and fig. 15, approaches fig. 43, the scale of the monogenerational race *frigida*. This suggests the 2nd. generation of *oleracea* might develop a more advanced type of scale than would be supposed from our knowledge of the 1st. generation scales. In all three of these races the primitive type scales occur: *frigida* (fig. 44), *oleracea* (fig. 36), and the Hasli Tal *flavescens* (fig. 59; and a transitional, small form, 1st. generation, fig. 16). Some scales of *P. venosa* also approach this type, but as noted in my account of that species the small size of the scent cells as well as the reduced width of the scales in the *venosa* races, show them to be a highly specialized group.

Among the spring *flavescens* scales, some make an approach to the *adalwinda* type of scales, or more exactly are intermediate between their seasonal types, having the neck better defined and narrower than the 1st. (or single) generation type (figs. 11 and 12), but more massive than in the 2nd. generation type (fig. 4). The occurrence of such scales in *flavescens* is another indication of some past connection between the latter and *adalwinda*. An idea of how remote in time this connection must have been is given by the similarity of the other types of 1st. generation *flavescens* scales to those of the Nearctic *bryoniae* races, for these types do not appear in *adalwinda*; the latter must therefore have lost its connection with the common ancestor at an earlier period than the now geographically remote Nearctic forms did.

The normal 2nd. generation *flavescens* scale (seen with the primitive type



in fig. 59), is a distinctly advanced type, also present in the monogenerational *bryoniae* races (figs. 27, 32, 34). This suggests that it was the 2nd. generation that first attained, and became established at, really high altitudes, where conditions did not permit of the production of an earlier generation; for the occurrence of two generations whenever possible, points to the probability that all *bryoniae* originated from some bigenerational form.

The three examples of *P. venosa* scales figured on plate 2, suggest that the same phenomenon is inherent in that species also. Fig. 41, the monogenerational scale, probably indicates what the 2nd. generation scale of figs. 40 and 39, might be expected to look like.

The seasonal variation in the scales is much more extreme in the *bryoniae* races than is the case in *P. napi*, or possibly in *P. venosa* either. The high-level *napi* scale (fig. 13), approximates in width of the neck closely to the 1st. generation scale (fig. 5), and this is markedly the case in the *adalwinda* scales also; the opposite of what we have seen to be the case in *bryoniae*.

A somewhat similar degree of size-variation to that existing in the seasonal scales of the *bryoniae* races is found in *P. pseudorapae*. The 1st. generation scale of the latter (fig. 22), though only slightly shorter than the second (fig. 20), is greatly reduced in width, yet the neck is slightly heavier. If the 1st. generation scale was the only one known, the great development of the 2nd. generation scale would never have been anticipated.

The data given in Appendix A, prove the Hasli Tal *flavescens* cannot be a hybrid race. The bred 1st. generation specimens prove it to be *bryoniae*. The capture of the same remarkable form of female as those bred, flying with normal *bryoniae* females in the Kiental, is further proof of the fact.

Six characteristics connected with the development of the androconia contrast very markedly in *P. napi* and *P. bryoniae*.

- 1) The normal type of androconial scale differs in each.
- 2) The regular presence of a limited number of scales of the primitive type in every race of *bryoniae* in Europe and America: this type is practically nonexistent in *napi* races.
- 3) The marked seasonal change in formation, accompanied by extensive variation in the 1st. generation scales in *bryoniae*: the relatively slight seasonal change, and constancy of form in the scales of both generations in *napi*.
- 4) The monogenerational *bryoniae* race of high levels is shown by the androconia to be the equivalent of the 2nd. generation of levels where two generations are normal: in *napi* the high level race is shown by the androconia to be the equivalent of the 1st. generation of low levels.
- 5) The reaction of the androconia to cross-breeding between the European races; as recorded in Appendix A.
- 6) Slightly specialized types of androconia appear in each *bryoniae* race: in *napi* two very distinct types are developed, each of which is common to a number of races.

These facts are incompatible with any theory of specific unity between the *napi* and *bryoniae* groups of races; they clearly indicate two distinct lines of evolution.

Since the completion of the present paper further corroboration of the taxonomic value of the androconial scales has been revealed.

In their recent work on the chromosomes of North American Rhopalocera, published in December 1960, Maeki and Remington record the number of chromosomes in *P. nesis* and *P. virginiensis* as 26; while in *P. napi* and *P. bryoniae* it is 25. (Journ. Lepidopterists' Soc. **14**:37—57). This as well as corroborating the evidence of the scales in the case of *nesis* and *virginiensis*, emphasizes the value of their remarkable sensibility to any change in specific nature in other cases where the chromosomes give no guide.

### Acknowledgments

I am indebted for the loan of material to Mr. S. R. Bowden, the late Mr. R. E. Ellison, Dr. L. G. Higgins, Dr. E. Scott, Mr. E. P. Wiltshire, the Baron de Worms and Mr. C. W. Wyatt. Though abroad at the time Mr. Wiltshire gave me permission to borrow specimens from his collection, and I have to thank Mr. Goodson of the Tring Museum and Dr. Higgins for selecting those I needed. I have also to thank the Authorities of the British Museum for the loan of several little-known races, and Mr. T. G. Howarth for selecting them and searching for specimens from special localities. To Mr. J. Moucha of the National Museum in Prague, I owe specimens of some of the races he has described from the Tatra and the Carpathians. I am especially indebted to Mr. Bowden for much helpful information as well as the material dealt with in Appendix A; also to Dr. Higgins for the loan of some of his remarkable captures in Kurdistan, and to Mr. Wyatt for his from Kashmir and a wide selection of material from Asia and North America. The readiness of the late Mr. Ellison to lend any specimens I asked for, regardless of their rarity or the numbers he chanced to possess, was very helpful.

### List of Species and Races of *Pieris* Mentioned in this Paper

#### *Rapae*-Group

- P. rapae* (L.).
- \**P. leucosoma* Schaw.
- P. manni* Mayer.
- P. krueperi* Stg.
- P. canidia* Sparrm.

#### *Napi*-Group

- P. napi* (L.).
  - subsp. *napi* (L.).
    - » *kamtschadalís* Röber.
    - » *adalwinda* Frhst.
    - » *maura* Vty. (= *blidana* Holl; *atlantica* Rths.). (Scales not examined).
    - » *atlantis* Obth.
    - » *persis* Vty.
    - » *dubiosa* Röber.
- \**P. dulcinea* Butler.
  - subsp. *dulcinea* Butler.
    - » *aestiva* Vty. (Homonym of *P. canidia aestiva* Rühl, 1896).

- \**P. japonica* Shirôzu.  
 \**P. pseudorapae* Vty.  
 \**P. segonzaci* Le Cerf.  
*P. ergane* Hb.  
 \*\**P. higginsi* Warren.  
*P. bryoniae* O.  
   subsp. *bryoniae* O.  
     » *flavescens* Wagner. (? name invalid).  
     » *neobryoniae* Shelj.  
     » *marani* Moucha.  
     » *vihorlatensis* Moucha.  
     » *pseudobryoniae* Vty. (? name invalid).  
     » *frigida* Scudder.  
     » *oleracea* Harrison.  
     » *pallidissima* B. & McD.  
 \**P. venosa* Scudder.  
   subsp. *venosa* Scudder.  
     » *virginiensis* Edw.  
     » (?).  
*P. ochsenheimeri* Stg.  
 \**P. narina* Vty.

#### Melete-Group

- P. melete* Mén.  
   subsp. *melete* Mén. form *aglaope* Motsch.  
*P. melaina* Röber.  
 \**P. nesis* Frhst. (= *pseudomelete* Vty. in part).  
 \**P. orientis* Obth.  
*P. ajaka* Moore.  
   subsp. *ajaka* Moore. form *ajanta* Röber.  
*P. extensa* Pouj.  
 \*Species hitherto classed as races of other species.  
 \*\*Hitherto unnamed species.

#### References

- BOWDEN, S. R., 1957, Diapause in female Hybrids: *Pieris napi adalwinda* and related sub-species. *Entom.* **90**: 247—254; 273—281.  
 — 1958, Sexual Mosaics in *Pieris*. *Lepidopterists' News*. **12**: 7—13.  
 CHAPMAN, T. A., 1914, On a new form of seasonal (and heterogoneutic) dimorphism in *Agriades thersites* Cant. *Trans. ent. Soc. Lond.* 1914, 309—313.  
 DANIEL, F., WOLFSBERGER, J., and PRÖSE, H., 1957, Die Föhrenheidegebiete des Alpenraumes als Refugien wärmeliebender Insekten. *Mitt. Münch. ent. Gesl.* **47**: 21—121.  
 DROSIHN, J., 1933, Über Art- und Rassenunterschiede der männlichen Koppulationsapparate von Pieriden. *Ent. Rdsch.* **50**: 1—93.  
 GRAVES, P. P., 1925, The Rhopalocera and Grypocera of Palestine and Transjordan. *Trans. ent. Soc. Lond.* 1925, Pts. 1 & 2, 17—125.  
 HIGGINS, L. G., 1958, Butterflies in Kurdistan. *Entom.* **91**: 38—45.  
 — 1958 a, A holiday amongst Macedonian Butterflies. *Entom.* **91**: 225—228.  
 JORDAN, K., 1958, Reminiscences of an Entomologist. *Proc. Tenth Intr. Cong. Ent.* **1**: 59—60.  
 MEYER-DÜR, 1852, Verz. Schmett. Schweiz.

- MOUCHA, J., 1957, *Pieris napi* und *Pieris bryoniae* in der Karpaten. *Ent. Nachrichten Blatt*, **4**: 1—6.
- 1959, Neueste forschungsergebnisse über unsere Lepidopteren-fauna und deren bedeutung für die lösung zoogeographischer fragen in der Tschechoslowakei. *Acta Faun. ent. Mus. Nat. Pragae*, **4**: 3—81.
- MÜLLER, L., und KAUTZ, H., 1939, *Pieris bryoniae* O. und *Pieris napi* L. *Abhd. Oestr. ent. Ver.* **1**.
- MURAYAMA, S., 1953, Some new forms of Butterflies from Honshu. *New Entom.* **3**: 35—37.
- OKANO, M., 1951, Comparative Morphology of the male genitalia of Japanese Pieridae. *Ann. Report Gakugei Fac. Iwate Univ.* **2**: 38—46.
- PETERSEN, B., 1955, Geographische variation von *Pieris (napi) bryoniae*, durch Bastardierung mit *Pieris napi*. *Zoo. Bidrag Uppsala*, **30**: 355—397.
- POWELL, H., 1909, Notes on the early stages and habits of *Pieris manni* Mayer. *Ent. Rec.* **21**: 37—40; 66—72.
- REVERDIN, J., 1909, *Pieris rapae* L., and *P. manni* Mayer. *Ent. Rec.* **21**: 149—150.
- RÖBER, J., 1907, The genus *Pieris*. in Seitz, *Macrolep.* **1**.
- RÜHL, 1896, Palaerct. Gross Schmett.
- SHIRÓZU, T., 1952, New or little known Butterflies from north-eastern Asia, with some synonymic Notes. *Sieboldia*, **1**: 11—37.
- 1953, New or little known Butterflies from north-eastern Asia, with some synonymic Notes, Part 2. *Sieboldia*, **1**: 149—159.
- SNODGRASS, R. E., 1953, Principles of Insect Morphology.
- VERITY, R., 1905—1911, Rhopal. Palaearctica. Florence. (References to Verity's work at dates between the two mentioned here all apply to this book).
- 1922, Seasonal Polymorphism and Races of some European Grypocera and Rhopalocera. *Ent. Rec.* **34**: 124—142.
- 1934—1936, The Lowland Races of Butterflies of the Upper Rhone Valley. *Ent. Rec.* **46**: **47**: **48**: Supplements.
- WARREN, B. C. S., 1937, On the evolution of subspecies as demonstrated by the alternation of variability existing in the subspecies of the genus *Erebia*. *Journ. Linn. Soc. Zool.* **40**: 305—323.
- 1958, On the Recognition of the species. *Proc. Tenth Intr. Cong. Ent.* **1**: 111—123.
- WILTSHIRE, E. P., 1957, Lepidoptera of Iraq.
- WOLFSBERGER, J., 1951, Die zweite Generation von *Pieris bryoniae* O. subsp. *flavescens* Wagner, in den bayerischen und angrenzenden österreichischen Kalkalpen. *Ent. Nachrichtenblatt Östr. u. Schweizer Entomologen.* **3**: 137—139.