A Compilation of Data on Wing Homoeosis in Lepidoptera

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Abstract. On the basis of published records and unpublished material in various collections, 302 examples of fore/hindwing homoeosis and 31 examples of dorsal/ventral wing-surface homoeosis have been assembled from 16 families of Lepidoptera. In addition to the compilation of these records, individual cases have been characterized and the homoeotic mosaics have been mapped in a schematic format. Further, quantitative and statistical analyses of the various modes of appearance of homoeosis have been carried out as a basis for further studies on the mechanism of pattern formation in lepidopteron ontogeny.

Introduction

A survey of wing homoeosis in Lepidoptera was published (Sibatani, 1980) in order to introduce to developmental biologists—with their rising interest in homoeosis—the wealth of reported data on this type of aberration. In that survey 161 cases already reported in the literature and three unrecorded cases of wing homoeosis in butterflies and moths were recorded.

Homoeosis is a morphological aberration of the animal body in which one part of the body is converted into another part. The examples of wing homoeosis I dealt with in that paper involve (a) the conversion of either a whole wing or part of the wing pattern on either surface of a wing into the corresponding structure of the wing on another thoracic segment, such as the conversion from fore to hindwing on one side of the host (F/H homoeosis), or (b) the conversion of part of the wing pattern on one surface of a wing into the corresponding part of the other surface of the same wing, such as occurs between the dorsal and ventral surfaces of either a fore or hindwing (D/V homoeosis).

In a continuation of this survey, data from more than 330 cases of wing homoeosis in Lepidoptera have been compiled, and are presented here in order that this information, hitherto recorded only in part be brought to the attention of lepidopterists. It is stressed that the principal aim of the communication is to gain more information into the nature of D/V homoeosis, to which Drosophila, the central subject of current studies on
homoiosis, has so far contributed very little, but to which the Lepidoptera have contributed a sizable number of interesting examples (Sibatani, 1980).

Materials and Methods

The cases of wing homoiosis dealt with in the previous report (Sibatani, 1980) included those compiled by Cockayne (1922, 1926, 1930) and Robertson (1969, 1977), recent reports of a lesser nature, and a few unrecorded specimens. In addition, I have now assembled more material, unrecorded and undescribed, from public and private collections, together with some recorded cases. The unrecorded material largely comes from the United Kingdom, the main source being the British Museum (Natural History) (BMNH) and the L. Christie collections.

The homoecotic specimens in the BMNH were in two sections, one the general collection of Lepidoptera from all over the world curated by Richard I. Vane-Wright, and the other, the collection of the British Lepidoptera, now under the curatorship of David J. Carter. Many of these specimens, all butterflies, had been set aside, as I understand by T. Graham Howarth, one of the disciples of the late Edward A. Cockayne and now retired from his service to the BMNH. Thus, in the collection of the British butterflies all the homoecotic specimens were grouped together and placed at the end of each species. This enabled me to work through them very efficiently within a relatively short period of time. The situation with moths was not so simple. Because of the sheer number of moths species from even the United Kingdom alone, and the apparent absence of a special cabinet for assembled homoecotic moths from other parts of the world, it has so far been impossible for me to assess all the homoecotic moths in the BMNH. I have therefore concentrated on only a few selected taxa of British moths.

L. Christie of London is a dedicated collector of homoecotic Lepidoptera, and his large collection, mostly butterflies, contains many good examples of wing homoiosis from the United Kingdom as well as from other parts of the world. Another remarkable source of material is an unpublished compilation of homoecotic specimens of Luehdorfia species (Papilionidae), all having bred in one year and mostly having arisen from a single local population in Japan (Masatoshi Nishimura, in litt.).

Altogether more than 330 cases were assembled. Most of the new material, as well as a significant fraction of the specimens reported in the literature, have now been examined directly or from good quality photographic records. Data were recorded and scored as in the previous report (Sibatani, 1980). Some of the descriptions made by Cockayne (1926, 1930) contain apparent inconsistencies in assignment of spaces between the veins: in some cases the space was called by the numeral used for the vein caudal to it (see *Papilio machaon* and "*Hyponephele*" lycaon—
Cockayne, 1926: pp. 216-217 and 222-223, respectively), but in other cases it was named according to the vein rostral to the space (see *Coenonympha pamphilus*—Cockayne, 1926: p. 222 and "Peiris" *davidis*—Cockayne, 1930: p. 219). I documented his descriptions with this point in mind, and was able to confirm my interpretation upon later examination of some of the specimens he described. Many cases reported by Cockayne, however, were not examined directly, as indicated in the following list which compiles the whole material used in this paper.

**List of Specimens with Wing Homoeosis in Lepidoptera**

In this list edited versions of label data are given only when necessary for identification of individual specimens; they are given in full for so far unrecorded specimens, but only to a point needed to avoid an ambiguity arising from the nature of the reference to published data. In making this list, I have adopted the following policy and rules:

Usually, subspecies names are omitted. Personal collections are indicated by italicizing the collector’s name in brackets. The following abbreviations are used throughout: A, P: anterior and posterior compartments; D, V, R, L, F, H: homoeotic mosaic(s) on dorsal, ventral surfaces; right, left wings; fore, hindwings respectively. Some data, of course, are insufficient and are only partially characterized in these terms. W: whole wing (or surface) homoeosis; BMNH: British Museum (Natural History), London; JSM: Japan Science Museum, Tokyo.*: illustrated; (▽): reference to an illustration is given; †: the specimen was examined by me; (†): original photographic reproduction of the specimen was examined. Years of the twentieth century for data (but not references) are given, wherever practicable, by the last two digits; years before 1900 are given in full.

1. **Fore-/hindwing Homoeosis**

**Adelidae**

B1 *Adela viridella* Scopoli, Austria (?); Cockayne 1922: 13 WRH

**Zygaenidae**

B2 *Zygaena occitanica* de Villers, France (?); Cockayne 1922: 13 (*) WRH

B3 *Zygaena exulans* Reiner & Hochanwarth, Europe (?); Cockayne 1922: 13 (*) WLH

B4 *Zygaena carniolica* Scopoli ♂ Austria; Cockayne 1922: 13 WLH

B5 *Zygaena filipendulae* Linnaeus, UK(?) (No. 2 of 2) WLF
B6  [UK]; Cockayne 1926: 208 (Grosvenor) WRH
B7  [UK]; Cockayne 1922: 13 (Capper No. 1 of 2) WH
B8  Zygaena loniceræ Esper (or Z. trifoli?) UK; Cockayne 1922: 13; 1926: 208 WLH
B9  Zygaena trifolii Esper, UK(?); Cockayne 1922: 13 WLH

Lasiocampidae
B10  Dendrolimus pini Linnaeus ♀ Germany(?); Cockayne 1930: 218 DRLH
B11  Malacosoma castrensis Linnaeus ♀ UK(?); Cockayne 1930: 218 DRH

Hesperiidae
B12  Hasora taminatus Huebner, Philippines: Palawan iv.-v. 79 (Sibatani); Sibatani 1980: 3† VRLF

Papilionidae
B13  Parnassius apollo Linnaeus ♂ Austria; Cockayne 1922: 14 DRH
B14  ♂ Austria; Cockayne 1922: 14 DLH
B15  Pachliopta aristolochiae Fabricius ♀ Burma: Maymyo 18 vii 71 Kinju Ikeda; Sibatani 1980: 3* JSM† VLF
B16  Atrophaneura febanus Fruhstorfer ♀ Taiwan ex pupa 6 viii 67 (Shirozu) (†) VRLF
B17  Atrophaneura horishanus Matsumura ♀ [Taiwan]; Cockayne 1923: 3 VLF
B18  Papilio machaon Linnaeus ♀ UK(?); Cockayne 1926: 216* DLF
B19  ♂ [Russia]; Cockayne 1930: 213(*) DRF
B20  ♂ Austria; Cockayne 1930: 213(*) DRF
B21  ♀ UK: Norfolk Broads vi 36 L. W. Newman BMNH† DLH
B22  Papilio polytes Linnaeus ♀ Taiwan; Hayashi 1961: 97† VRLF
B23  Papilio memnon Linnaeus ♀ Japan: Fukuoka (Shirozu) (†) DRF
B24  Papilio maackii Menetries ♀ Japan: Fukuoka ex pupa 23 vi 68 (Shirozu)(†) DLH
B25  ♂ Japan; Hayashi 1961: 94* VRF
B26  Papilio dialis Leech ♀ Taiwan; Hama 1965* VLF
B27  Papilio bianor Cramer, China; Cockayne 1922: 14 VRH
B28  ♀ Japan; Nishiyama & Hiuga 1975: 196* VLF
B29  Papilio hoppo Matsumura ♀ Taiwan; Ishizaki 1977*(†) VRH
B30  Eurytides glaucoalaus Bates ♂ Columbia; Cockayne 1922: 14(*) VLF
B284-B302  vide infra

**Pieridae**

B31  *Delias hyparete* Linnaeus ♀ Burma: Maymyo vi 24 (Christie)† VRF

B32  ♂ India(?): K. Hills BMNH† VRF

B33  *Delias belisama* Cramer ♂ Indonesia: Java, Goekaboemi iv 26 G. Overdijkink BMNH† VRF

B34  *Aporia davidis* Oberthur (as *Pieris*) ♂ China; Cockayne 1930: 219* BMNH† VRF

B35  *Pieris brassicae* Linnaeus ♀ UK; Frohawk 1938: 156* BMNH† VRF

B36  ♂ UK; Cockayne 1922: 14 VRF

B37  *Pieris rapae* Linnaeus ♀ UK: Kent, Bexley bred Lot 78 L. W. Newman BMNH† VRF

B38  ♂ UK: 3rd brood bred 1. week x 31 Sutton *(Frohawk)* BMNH† VRF

B39  *Pieris napi* Linnaeus ♀ UK; F. Green Lush 10 iv 32 (R. C. L. Perkins) BMNH† VRF

B40  ♂ Japan; Kuzuya 1969: 37* VRF

B41  ♀ UK: mixed parentage England × Ireland Anthony Thompson strain bred vii 49 *(Naomi Storer)* BMNH† VLH

B42  ♂ UK: Derry 1898 BMNH† VRLH

B43  ♀ UK: Dorset, Holcombe Wd. 16 vii 44 R. Troup *(Christie)*† VRF

B44  ♂ UK: Surrey, Hinchley Wood 21 iv 45 (Christie)† VRF

B45  *Pieris melete* Menetries ♀ Japan; Kuzuya 1969: 38* DVRH

B46  *Pontia daplidice* Linnaeus ♀ UK: Folkestone 11 viii 02 (H. K. Smith) BMNH† VLH

B47  *Euchloe crameri romana* Calberla ♀ Italy: Ceri 30 km NWW of Rome 20 iv 80 *(Nakamura)(†)* VRF


B49  ♂ UK: Sandley 10 iv 45 *(H. B. Williams)* BMNH† VRF

B50  ♂ UK: Grassington (Grass Woods) W. Feather BMNH† VRF

B51  ♂ UK: Kent, Bexley v 41 L. T. Ford BMNH† VRF

B52  ♀ UK: Sussex, Loxwood bred ex ovo 27 iv 73 R. M. Craske BMNH† VLF

B53  ♂ UK: Herts., Tring 25 v 42 Goodson BMNH† VRF

B54  ♂ UK: Sussex, Loxwood bred ex ovo 23 iv 73 R. M. Craske BMNH† VRLF

B55  ♂ Japan; Fujisawa 1980* VLH
Lycaenidae

*B66* *Eumaeus atala* Poey ♀ USA; Cockayne 1926: 220 VRF

*B63* *Thecla betulae* Linnaeus ♀ UK: Newton Abbot bred ex ovo vii 29 Perkins (Christie) † VLF

*B64* *Favonius cognatus* Staudinger ♀ Japan; Ishizaki 1976*(†) VLF

*B65* *Favonius orientalis* Murray ♀ Japan; Fujioka 1975: 54 (No. 37)* VLF

*B66* *Lycanena phaeneas* Linnaeus ♂ UK; Newman, 1959: 65* VLF

*B67* ♀ UK; Robertson 1969: 88 (No. 11)* BMNH † VLF

*B68* ♂ UK; Robertson 1969: 88 (No. 18)* VRH

*B69* ♀ UK; Robertson 1977 (No. 3)* VRLH

*B70* ♀ UK: Isle of Wight, Ventnor 1965 D. H. Tress BMNH † VLF

*B71* ♀ UK; Robertson 1969: 88 (No. 27)* VRLH

*B72* ♂ UK; Near Devon 1881 (Leech) BMNH † VRH

*B73* ♂ UK; Robertson 1969: 88 (No. 26)* VRLH

*B74* ♂ UK; Robertson 1969: 88 (No. 24)* BMNH † VRLH

*B75* ♀ UK; Robertson 1969: 87 (No. 2)* (Christie) † VRLH

*B76* ♀ UK: Hunts., Abbots Ripton vii 28 W. Quibell (Christie) † VRH

*B77* ♂ Eire: Cork viii 33 (Christie) † VLF

*B78* ♂ UK; Robertson 1969: 88 (No. 20)* BMNH † VRLH

*B79* ♀ [UK?]: Haar (or Haan?) 25 v 18 (Christie) † VRLH

*B80* ♀ UK; Robertson 1969: 88 (No. 25)* VRLH

*B81* ♂ UK; Robertson 1977 (No. 2)* VLF

*B82* ♂ UK; Robertson 1977 (No. 1)* VRH

*B83* ♀ UK; Robertson 1969: 88 (No. 17)* VRH

*B84* ♀ UK; Robertson 1969: 88 (No. 19)* (Christie) † VRLH

*B85* ♀ UK; Robertson 1969: 87 (No. 10)* VLF

*B86* ♀ UK; Robertson 1969: 87 (No. 6)* VLF

*B87* ♂ UK; Robertson 1969: 88 (No. 11)* VRH

*B88* ♂ UK; Robertson 1969: 87 (No. 8)* VLF
B89  ♂ UK; Robertson 1969: 87 (No. 9)* VLH
B90  ♂ UK; Robertson 1969: 88 (No. 14)* VRH
B91  ♂ UK; Robertson 1969: 87 (No. 7)* VLH
B92  ♂ UK; Robertson 1969: 88 (No. 13)* VRH
B93  ♂ UK; Robertson 1969: 88 (No. 16)* VRH
B94  ♂ UK; Robertson 1969: 88 (No. 15)* VRH
B95  ♂ UK; Robertson 1969: 88 (No. 21)* VRLH
B96  ♂ UK; Robertson 1969: 88 (No. 23)* VRLH
B97  ♂ Eire: Cork vii 33 (Christie)† VRLH
B98  ♂ UK; Robertson 1969: 87 (No. 1)* VLH
B99  ♂ UK; Robertson 1969: 87 (No. 4)* VLH
B100 ♂ UK; Robertson 1969: 87 (No. 3)* VLH
B101 ♂ UK; Robertson 1969: 88 (No. 5)* VLH
B102 ♂ UK; Robertson 1969: 88 (No. 22)* VRLH
B103 ♂ UK; Robertson 1969: 88 (No. 28)* DRH
B104 ♂ UK(?); (H. Symes) bought 1970 (Christie)† VLF
B105 Lysandra coridon Poda ♂ UK; Right & Leeds 1938: 86 (No. 131)* VRF
B106 (as Agriades) ♂ UK; Cockayne 1926: 219* BMNH‡ VRF

Nymphalidae

B107 Mellicta athalia Rottemburg ♂ UK: 19 P. M. Bright (Stevens/Webb/Cockayne-Kettlewell) BMNH† VLF
B108 ♂ UK; Cockayne 1926: 219 (No. 2 of W. Crocker) VRF
B109 ♂ UK: Essex 23 vi 37 B. J. L. (Christie)† VRF
B110 ♂ UK: Abbots Wood vi 1890 J. Slenny (Christie)† VRF
B111 ♂ UK: Belfairs Wood Southend 1936 C. P. Pickett, BMNH† VLF
B112 ♂ UK: Belfairs Wood 1936 C. P. Pickett, BMNH† VLF
B113 ♂ UK: Kent, Blean vi 22 Lyon (Christie)† RLF
B114 ♂ UK: Blean 5 vii 31 BMNH† VRLF
B115 ♂ UK: Kent, Blean Woods vi 25 W. Crocker BMNH† VRLF
B116 ♂ UK: Blean Wood 24 vi 42 J. Shepherd (Christie)† VRF
B117 ♂ France: Gorge du Tarn 25 N. Malis (Christie)† VRLF
B118 ♂ UK; East Kent vi 21 L. W. Newman BMNH† VLF
B119 ♂ UK: near Canterbury 7 vii 33 H. Wood BMNH† VRF
B120 ♂ UK; Cockayne 1926: 219 (No. 2 of ♂♂) BMNH† VRF
B122 ♂ UK: Sussex 01 BMNH† VRF
B123 ♂ (as Melitaea) ♂ UK; Cockayne 1926: 218 (No. 3 of 2♂♂)∗
BMNH† VRF
B124 ♀ UK: Canterbury bred vi 34 A & LB BMNH† VLF
B125 ♀ UK: Essex Hadleigh bred vi 33 A. F. Bowden
BMNH† VRF
B126 ♂ UK: East Kent vi 19 BMNH† VLF
B127 ♂ UK: Blean Wood vii 35 Shepherd BMNH† (cf.
B133) VLF
B128 ♂ UK: East Kent 17 vi 19 Willoughby Ellis BMNH†
VRLF
B129 ♀ UK (H. B. Williams) BMNH† VLF
B130 ♂ UK: East Kent vii 31 (Ellis) BMNH† VLF
B131 ♂ UK: East Kent 27 vi 24 H. Wood (Ellis) BMNH†
VRLF
BMNH† VRLF
B133 ♂ UK: Blean Wood vii 35 Shepherd (cf. B127)
BMNH† VLF
B134 ♀ UK: (Christie)† VLF
B135 ♂ (as Melitaea) ♂ UK; Cockayne 1926: 218 (No. 1 of
3♂♂)∗ BMNH† VRLF
B136 ♂ (as Melitaea) ♀ UK; Cockayne 1930: 215∗ VRF
B137 ♂ (as Melitaea) ♀ UK; Cockayne 1930: 216 VLF
B138 ♂ UK: Kent, Blean Wood 26 vi 24 A. R. (Christie)†
VRF
B139 ♂ UK: Kent, Blean vii 25 C. R. Verling-Brown
(Christie)† VLF
B140 ♂ UK: Blean vi 34 P. A. Cardew (Christie)† VRF
B141 ♂ UK: Blean Wood vii 38 Shepherd BMNH† VLF
B142 ♂ UK: East Kent vii 1893 BMNH† VLF
B143 ♂ (as Melitaea) ♀ UK; Cockayne 1926: 219∗ BMNH†
VRF
B144 ♀ UK: East Kent 21 L. W. Newman BMNH† VLF
B145 ♂ (as Melitaea) ♂ UK; Cockayne 1930: 216 (No. 1 of 3♂♂)
VRF
B146 ♂ (as Melitaea) ♂ UK; Cockayne 1930: 216 (No. 2 of 3♂♂)
VRF
B147 ♂ (as Melitaea) ♂ UK; Cockayne 1930: 216 (No. 3 of 3♂♂)
VRF
B148 ♀ UK: Blean Wood 6 vii 36 J. N. Marcon BMNH†
VRLF
B149 ♀ UK: Essex Hadleigh bred vi 33 A. F. Bowden
BMNH† VLF
B150  ♂ UK: Kent, Blean Wood vi 22 W. G. Nash BMNH† VLF
B151  ♂ UK: East Kent 23 vi 37 H. Wood BMNH† VLF
B152  (as Melitaea) ♂ UK; Cockayne 1930: 217 VRF
B153  Melitaea varia Meyer-Duer (as Melitaea) ♀ Switzerland; Cockayne 1930: 217* BMNH† VRLF
B154  Melitaea cinxia Linnaeus ♂ UK: Isle of Wight bred ex larva vi 45 E. W. Classey BMNH† VLF
B155  ♂ UK: Isle of Wight, St. Catherines 19 vii 24 C. R. Verling-Brown (Christie)† VRLF
B156  ♀ UK: Isle of Wight bred v 26 G. Watkinson BMNH† VRLF
B157  ♂ UK; Cockayne 1930: 217 (No. 1 of 2♂♂) VLF
B158  ♀ UK: Isle of Wight 10 BMNH† VRF
B159  ♂ UK: Niton 15 vi 10 BMNH† VRF
B160  ♀ UK; Cockayne 1930: 217 VRLF
B161  ♂ UK; Cockayne 1930: 217 (No. 2 of 2♂♂) VLF
B162  ♂ UK: Ventnor 24 vi 29 BMNH† VRLF
B163  Clossiana seleae Schiffermueller ♂ UK; Nevin 14 vi 30 W. Buckley BMNH† VLF
B164  (as Brehnis) ♂ Germany; Cockayne 1930: 215 VWRNF
B165-167 (as Brehnis) ♀ Germany; Cockayne 1930: 215(*) VWRNF
B168  ♂ UK: near Folkestone v 28 D. G. Marsh (Christie)† VLF
B169  Clossiana euphorosyne Linnaeus ♂ UK: Braemar 5 vi 31 E. A. Cockayne BMNH† VLF
B170  (as Brehnis) ♀ UK; Cockayne 1930: 214* VWRF
B171  Argyris paphia Linnaeus ♂ UK: New Forest 14 vii 29 A. R. Hayward (Christie)† VRLF
B172  ♂ UK: near Tring 25 vii 42 A. T. Goodson BMNH† VRLF
B173  ♂ UK: New Forest 17 vii 19 D. C. Johnstone (Christie)† VRLF
B174  ♀ UK: Herts., near Tring 27 vii 41 A. L. Godson BMNH† VRLF
B175  ♀ UK: Somerset 17 vii 29 A. R. Hayward (Christie)† VRLF
B176  Fabriciana adippe Schiffermueller ♀ UK: New Forestr bred vii 09 Ellis (R. E. Ford) BMNH† VRF
B177  Mesoscidalia aglaia Linnaeus ♀ UK: Isle of Wight, Freshwater 27 vii 47 Goodson BMNH† VRF
B178  Inachis io Linnaeus ♀ UK: Bexley bred 1937 (Cockayne-Kettlewell) BMNH† DLF
B179 Aglais urticae Linnaeus ♀ UK; Ford 1945: 229*; Sibatani 1981* BMNH† VLH
B180 ♂ UK; Cockayne 1930: 218* DRH
B181 ♀ UK: North Kent bred vii 14 L. W. Newman (Ellis/Ford) BMNH† VLH
B182 ♂ UK: North Kent ix 73 L. W. Newman BMNH† VRH
B183 ♀ UK: W-D 1 ii 54 (T. C. B. Craske/F. W. Frohawk) (Christie)† VLH
B184 Polygonia c-album Linnaeus ♂ UK; Herts., Tring 14 ix 46 Goodson BMNH† VLF
B185 Vanessa cardui Linnaeus ♀ (Christie)† VRH
B186 ♂ (as Pyrameis) ♂ India; Cockayne 1926 223* VLH
B187 Vanessa indica Herbst ♂ Japan; Hayashi 1961: 92* JSM† DLH
B188 Vanessa atalanta Linnaeus (as Pyrameis) ♂ UK; Cockayne 1926: 223* VLH
B189 Precis orithya Linnaeus ♀ Japan; Yayeyama ex pupa 3 viii 78 (Shirozu)(†) DLH
B190 Precis oenone Linnaeus (labelled as Junonia delta) ♂ Zimbabwe: Mashonaland, Umfuli R., Gadzema 4200 ft. BMNH† DLH
B191 Nepipt sappho Pallas (as N. aceris) ♂ Japan; Hayashi 1961: 90 JSM† VLH
B192 Benaustis pogei Dewitz (labelled as f. nelsoni) ♀ [Africa] BMNH† VRH
B193 Acræa eponina Cramer (labelled as A. terpsichore butsoni) ♀ South Africa: Umlali [Umhlali], Vumba ii 32; Sibatani 1980: 4* BMNH† VRH

Satyrinae

B194 Maniola jurtina Linnaeus ♀ UK; Dover (P. M. Bright) Lot 30 at sale 3 xi 42 BMNH† VLF
B195 ♂ (as Epinephele) ♀ UK; Cockayne 1930: 220 (No. 1 of 2♀) VLH
B196 ♂ ♀ UK; Howarth 1973: pl. 4* VLH
B197 ♂ UK: Herts., Tring 10 viii 48 Goodson BMNH† VLH
B198 ♂ (as Epinephela) ♂ UK; Cockayne 1922: 15(*) VRH
B199 ♂ (as Epinephela) ♀ UK; Cockayne 1930: 220 (No. 2 of 2♀) VRH
B200 ♂ ♀ UK(?); “0/2/9/12” (J. Matheson) (Christie)† VLH
B201 Hyponephela bycan Rottemburg ♀ France(?); Cockayne 1926: 222*; Sibatani 1980: 4* BMNH† VLH
B202 Pyronia tithonus Linnaeus ♂ UK; Russwurm 1978: pl. 40, fig. 3* VRH
B203  *Erebia pandrose* Borkhausen (as *E. lappna*)♀ Europe;
     Cockayne 1926: 223 (30 vi 12)* BMNH † VRH
B204  ♂♀ Europe; Cockayne 1926: 223 (28 vi 12)* BMNH †
     VRH
B205  *Erebia aethiops* Esper (as ab. *derufata*)♀ UK(?); Cockayne
     1930: 220* VLH
B206  *Coenonympha pamphilus* Linnaeus ♂ UK; Cockayne 1926: 220
     (Hunts. 1891 or 1894)* VLH
B207  ♂♀ UK: Box Hill 10 vi 00 (Christie)† VLRLH
B208  ♂♂ UK: Surrey, Chipstead 36 D. G. Marsh (Christie)†
     VLRLH
B209  ♂♀ UK: Surrey 22 vi 20 T. Grosvenor (Cockayne-
     Kettlewell) BMNH † VRH
B210  ♂♂ UK; Cockayne 1926: 221 (Market Rasen No. 3)
     BMNH † VRH
B211  ♂♂ UK; Cockayne 1923: 2 (Kent) VLH
B212  ♂♂ UK: Sussex 12 vi 40 J. H. M. BMNH † VRH
B213  ♂♂ UK; Cockayne 1926: 221 (Market Rasen No. 1)
     BMNH † VRH
B214  ♂♀ UK; Cockayne 1926: 222 VRH
B215  ♂♂ UK; Cockayne 1926: 222 (Theydon Bois) VLH
B216  ♂♂ UK: Dorset, Hod Hill, Blandford vi 49 L. H. Newman
     BMNH † VRH
B217  ♂♂ UK; Cockayne 1926: 221 (Market Rasen No. 2)
     BMNH † VLRLH
B218  ♂♂ UK(?): Dondist 2 vi 49 (Christie)† VLH
B219  ♂♂ UK: Sussex, Eastbourne, Birling Gap 26 vi 47 L.
     Christie (Christie)† VRH
B220  ♂♂ UK: Bucks., Chiltern Hills 27 v 19 G. B. Oliver (H. B.
     Williams) BMNH † VLRLH
B221  ♂♀ UK: Belfairs Wood 23 vi 36 C. P. Pickett (H. B.
     Williams) BMNH † VLRLH
B222  ♂♂ UK: Sutton Colfield 17 vi 15 G. B. Oliver BMNH †
     VLH
B223  ♂♂ UK(?): Dondist 4 vi 49 (Christie)† VLRLH
B224  ♂♂ UK: Sussex, Chipstead 31 v 24 F. W. Forhawk
     BMNH † VRH
B225  ♂♂ UK: Lewes 28 viii 31 L. A. E. Sabine (H. B. Williams)
     BMNH † VLH
B226  ♂♂ UK: Co. Clare vi 26 A. E. Sabine BMNH † VRH
B227  ♂♂ UK(?): (Christie)† VRH
B228  ♂♀ UK: New Forest 14 vi 31 C. King Smith BMNH †
     VLRLH
B229  ♂♂ UK: Lincoln vi 27 W. Sperring BMNH † VLH
B230  ♂ UK; Cockayne 1923: 1 BMNH (but 17 vii 22)† VRH
B231  ♂ UK: Kent 18 vii 22 H. A. Leeds BMNH† VRH
B232  ♂ UK; Cockayne 1926: 221 (Grayshott v 15) BMNH† VRH
B233  ♀ UK: Bucks., Chilterns 19 G. B. Oliver (H. B. Williams) BMNH† VRH
B234  ♂ UK: Chiltern Hills vii 41 BMNH† VRH
B235  ♂ UK(?); Cockayne 1922: 15 (A. W. Mera)* VLH
B236  UK; Cockayne 1922: 14-15 (Trans. Lond. N. H. Soc. 1915) VLH
B237  UK; Cockayne 1922: 15 (Headley Common) VH
B238  UK; Cockayne 1922: 15 (Maddison) VLH
B239  ♂ UK; Gomshall S.G.C.R. 2 v 52 (Castle-Russell/E. A. Cockayne) BMNH† VRH
B240  ♀ UK: Herts. Royston 31 vii 30 BMNH† VLH
B241  ♂ UK: Kent(?), Lenham v 37 D. G. Marsh (Christie)† VRH
B242  ♂ UK: St. Osyth 13 vii 04 B. S. H. (Christie)† VRH
B243  ♀ UK: Surrey, Mitcham 5 ix 53 J. C. B. Craske (Christie)† VRF
B244  ♀ UK; Cockayne 1926: 220 BMNH† VRF
B245  ♂ UK; Cockayne 1923: 3 BMNH (but Monks Wood 7 v 22)† VRF
B246  ♀ UK: Somerset, Loxley Wood 15 vii 23 R. Troup (Christie)† VRF
B247  ♀ Eire: Sligo 20 vii 20 A. E. Sabine BMNH† VLF
B248  Coenonympha tulia Mueller ♂ UK: Shropshire 23 vi 35 G. Greenwood BMNH† VRH
B249  ♀ UK: Perthshire (Cockayne-Kettlewell) BMNH† VRH
B250  (as C. tiphon) ♂ UK; Cockayne 1930: 219 BMNH† VRH

Danaidae

B251  Danaus chrysippus Linnaeus ♀ South Africa: Johannesburg on loan from A. M. Altson BMNH† VLF
B252  (as f. alcippus Fabricius) ♀ Cameroon; Cockayne 1930: 213 DRLF

Sphingidae

B253  Amorpha populii Linnaeus, Europe(?); Cockayne 1930: 214 DRLF

Geometridae

B254  Euthikis prunata Linnaeus (as Cidaria) ♂ UK; Cockayne 1923: 2 DRLF
B255  *Semiothisa (Macaria) notata* Linnaeus ♀ UK; Cockayne 1930: 218 DLH

**Saturniidae**

B256  *Philosamia cynthia* Drury ♂ Europe(?); Cockayne 1930: 219 DRH

**Noctuidae**

B257  *Bryoleuca domestica* Hufnagel (as *Bryophila perla*) UK; Cockayne 1930: 219(*) DLH

B258  *Mamestra thalassina* Hufnagel, Germany; Cockayne 1922: 18 DLH

B259  *Diarsia mendica* Fabricius (as *Noctua primulae*) ♂ UK; Cockayne 1926: 220 DLH

B260  *Diarsia rubi* Vieweg (as *Noctua*) ♀ UK; Cockayne 1926: 220* DLH

B261  *Noctua pronuba* Linnaeus ♀ UK: Sheringham 31 vii 57 P. R. Clarke BMNH† DRF

B262  *Orthosia angulipennis* Matsumura ♀ Japan; Nakamura & Kishida 1976* DLH

B263  *Orthosia gothica* Linnaeus (as *Taeniocampa*) ♂ UK; Cockayne 1922: 18* DLH

B264  *Graphiphora augur* Fabricius ♂ UK: Dorking MV vi 58 R. F. Haynes (*Christie*)† DRH

B265  *Tholera cespitis* Schiffermueller (as *Neuronia*) Europe(?); Cockayne 1922: 18(*) DRH

B266  *Mythimna conigera* Schiffermueller (as *Leucania*) UK; Cockayne 1922: 18 DLH

B267  *Xestia alpicola* Zetterstedt (as *Pachnobia hyperborea*) Europe(?); Cockayne 1922: 18 DLH

B268  *Catocala nupta* Linnaeus ♂ UK; Cockayne 1926: 217* DRF

B269  ♂ UK(?); Cockayne 1922: 18 DRLF

B270  ♀ UK: Aldwick 14 viii 50 W. Minnion (*Christie*)† DLF

**Arctiidae**

B271  *Arctia caja* Linnaeus UK; Cockayne 1922: 16 DLF

B272  ♀ UK; Cockayne 1922: 17 (No. 1 of 5 on p. 17) BMNH† DLH

B273  ♀ Europe (?); Cockayne 1922: 17 (No. 3 of 5) DRF

B274  ♂ Europe (?); Cockayne 1922: 17 (No. 4 of 5) DF

B275  ♀ UK; Cockayne 1922: 17(*) BMNH† DLF

B276  ♀ UK; Cockayne 1930: 214* BMNH† DRLF

B277  ♂ UK(?); Cockayne 1922: 17 (No. 2 of 5) BMNH† DRH

B278  ♂ UK: Bright (*Rothschild*) BMNH† DRLF
B279  ♂ French stock 15 iii 60 M. B. D. Nettlewell BMNH †
       DLF
B280  ♀ UK: Peterborough ex larva iv 31 F. W. Sharman
       BMNH † DVRH
B281  ♂ UK: Wicken 6 viii 37 W. H. A. Harris (Cockayne-
       Kettlewell) BMNH † DLH
B282  ♀ UK (Howarth) † DRLH
B283  Pericallis matronula Linnaeus, Europe(?); Cockayne 1922: 
       17*(†) DRH

Addenda

Papilionidae

B284  Luehdorfia japonica Leech ♂ Japan: Niigata-ken, Nishi-
       kambara-gun, Tsunodayama bred emrg. 4 iv 80 E. Yamazaki
       (Nishimura in litt. No. 4) (†) VRLF
B285  ♂ Japan: as above but 3 iv 80 (No. 3) (†) VRLF
B286  ♀ Japan: as above but 2 iv 80 (No. 12) (†) VRLF
B287  ♀ Japan: as above but 20 iii 80 (No. 14) (†) VRF
B288  ♂ Japan: as above but 16 iii 80 (No. 9) (†) VRLF
B289  ♂ Japan: as above but 4 iv 80 (No. 7) (†) VRLF
B290  ♂ Japan: as above but 2 iv 80 (No. 8) (†) VRLF
B291  ♂ Japan: as above but 3 iv 80 (No. 2) (†) VRLF
B292  ♀ Japan: as above but 4 iv 80 (No. 13) (†) VRLF
B293  ♀ Japan: as above but 29 iii 80 (No. 15) (†) VRF
B294  ♂ Japan: as above but 3 iv 80 (No. 1) (†) VRLF
B295  ♀ Japan: as above but 4 iv 80 (No. 11) (†) VRLF
B296  ♂ Japan: as above but 3 iv 80 (No. 6) (†) VLF
B297  ♂ Japan: Niigata-ken, Itoigawa-shi, Kotaki bred emerg.
       16 iii 80 (Nishimura in litt. No. 16) (†) VRLF
B298  ♀ Japan: as in B284 but 3 iv 80 (No. 10) (†) VRF
B299  ♂ Japan: as above but 31 iii 80 (No. 5) (†) VRF
B300  ♂ Japan bred emerg. 14 iii 80 E. Yamazaki (Nishimura
       in litt. No. 18) (†) VLF
B301  ♀ Japan: Niigata-ken, Itoigawa-shi, Imai bred emerg. 3
       iv 80 E. Yamazaki (Nishimura in litt. No. 17) (†) VRF
B302  Luehdorfia puziloi Erschhoff ♀ Japan: Nagano-ken, Omachi-
       shi, Inao bred emerg. 20 iii 80 E. Yamazaki (Nishimura in
       litt. ) (†) VRLF

2. Dorsal/Ventral Wing Homoeosis

Hepialidae

D1  Hepialis humilis Linnaeus ♂ UK: Cockayne 1926: 226 VLF
Pieridae

D2  Pieris napi Linnaeus ♀ UK: New Forest vii 23 (Christie)† VRH
D3  ♂ UK: Derry 1898 (Salvage) BMNH† VRLH
D4  ♀ UK; Cockayne 1926: 225* BMNH† VLH
D5  ♂ UK; Inverness, Forres bred 17 vii 10 (Christie)† VLH
D6  ♂ UK; Cornwall, Bude bred 16 vii 08 (Christie)† VRLH
D7  Colias croceus Geoffroy ♀ BMNH† DRF

Lycaenidae

D8  Calliphrys rubi Linnaeus ♀ UK: Surrey, Headley 6 v 35 F. D. Coote (Christie)† VRF
D9  Lycaena phaeas Linnaeus ♀ UK: Near Herne Bay 23 v 20 D. G. Marsh (Christie)† VRF
D10 ♂ UK; Robertson 1969: 89 (No. 37)* (Christie)† VRF
D11 ♂ UK; Robertson 1969: 89 (No. 36)* (Christie)† VRF
D12 Plebejus argus Linnaeus UK; Cockayne 1923: 3 V
D13 ♂ UK; Cockayne 1930: 220* DLF
D14 ♂ UK; Cockayne 1926: 225 DLF
D15 ♂ UK; Cockayne 1926: 225* BMNH† VRF
D16 ♂ UK; Cockayne 1926: 226* DLF
D17 ♂ UK; Cockayne 1930: 221 DRH
D18 ♂ UK: Kent, Snodland 20 vii 28 D. G. Marsh (Christie)† DLF
D19 Polyommatus icarus Rottemburg ♂ UK: Aberdovey 23 vii 49 L. Birch (Christie)† VRLH
D20 ♂ UK: Aberdovey 20 vi 49 L. Birch (Christie)† VRH/VLH
D21 ♂ (as Agriades thetis)♂ UK; Cockayne 1926: 224 VRF
D22 ♂ (as Agriades thetis) UK; Pierre 1922 V
D23 Lysandra coridon Poda ♀ UK; Bright & Leeds 1938: 61* DLF
D24 ♂ (as Agriades ♀ UK; Cockayne 1926: 225* DLF
D25 ♂ (as Agriades) ♀ UK; Cockayne 1926: 227 VLF
D26 ♂ UK; Bright & Leeds 1938: 86 VRH
D27 Lysandra bellargus Rottemburg ♂ UK: Folkestone ix 23 L. W. Newman (Cockayne-Kettlewell) BMNH† VRF

Nymphalidae

D28 Batesia hypochloros hemichrysa Godman & Salvin ♀ Ecuador: Timotou BMNH† VRH
D29 Vanessa cardui Linnaeus (as Pyrameis) UK; Cockayne 1930: 221 VRLH
Satyridae

D30  Morpho terrestris Butler (as M. didius) ♂ Peru; Cockayne 1926: 227* BMNH† VRH

D31  Morpho menelaus Linnaeus ♂ Cockayne 1926: 227 BMNH† VLH

3. Others

Lycaenidae

A1  Plebejus argus Linnaeus ♂ UK: Kent 5 viii 33 H. A. Leeds (Christie) † VRH (partial duplication in mirror symmetry)

Noctuidae

A2(=B257)  Bryoleuca domestica Hufnagel (as Bryophila perla) Cockayne 1930: 219(*) DLH (F in reverse)

Results and Discussion

Geographic distribution of homoeotic specimens examined

The specimens included in the list come from Europe, Africa, Asia and the Americas, whilst no single example of homoeotic Lepidoptera in the Australian region is known to me. An impressive majority derives from the United Kingdom, many of these having been duly reported by indigenous workers there. Next comes the contribution by the Japanese, both in reports and specimens. Although workers from both countries reported cases of exotic species, naturally most of the cases they recorded or assembled originated from their respective home countries. A curious fact is the absence of any record by the American workers. This has resulted in a conspicuous lacuna of known homoeotic specimens among American taxa. This fact of course need not mean that the American Lepidoptera are less prone, and that the British ones are more prone to produce wing homoeosis, but might simply reflect the characteristic attitudes of the lepidopterists of these countries.

Taxonomic distribution of wing homoeoses in the sample

Tables 1 to 3 summarize the number of samples in various taxa at three levels: families, genera and species. Again, they are subject to some human bias: (1) The range of individual higher taxa adopted here: Nymphalidae, including the acraeines, are separated from Danainae and Satyridae, of which the last includes the morphines, a compromise suggested by Eliot (1978); Pieris and Vanessa are sensu lato whereas Argynnis is sensu stricto, hence a frequent occurrence of homoeosis among large fritillaries (B171-177) is not reflected in Table 3. (2) As noted before
(Sibatani, 1980), detection of wing homoeosis depends very largely on the type of wing patterning, that is, good markers which characteristically differ in the crucial areas of the wings subject to homoeotic conversion may or may not occur in various higher taxa. It is true that, as pointed out by previous workers (Cockayne, 1922, 1926, 1930; Robertson, 1969), individual taxa often exhibit characteristic trends in the mode and frequency of homoeosis detected on the wing. This point is clearly indicated in Table 4 in the case of F/H homoeosis (see the last four columns of this table).

Nevertheless, from overall wing patterning it would be expected that distribution of known homoeosis among four different wing surfaces need not be highly asymmetric. The possibility at least of detecting one type of homoeosis should be coupled with that of detecting a reciprocal case, the latter being as frequent. Hence, the taxonomic bias of the homoeosis seems to involve, at least partially, epigenetic biases characteristic of individual species, because most of these homoeoses are presumably produced through phenocopies rather than genetic mutations (see Sibatani, 1980).

**Distribution of homoeoses among different wing surfaces**

The foregoing remarks clearly indicate that the overall figures on homoeosis of the entire Lepidoptera should involve biases due to the taxonomic and morphogenetic heterogeneity of the sample, genetic diversity and non-uniform artefact. Keeping this in mind, I will now analyse some spatially significant disparities in the frequency of homoeosis on the eight wing surfaces of specimens of different taxa.

With respect to the frequency of homoeosis, as controls I chose two near-trivial comparisons: the two sides of the wings and the two sexes. As expected, no significant differences were detected between right and left wings in the entire samples and individual taxa as shown in Tables 1, 2 and 4, except for F/H homoeoses in Pieridae, Satyridae and Coenonympha and for this I have no explanation.

With respect to sex, the frequency of F/H homoeosis was significantly higher for male than for female in Anthocharis, Anthocharis cardamines, Melitcta-Melitae-complex, Melitcta, Melitcta athalia, Coenonympha and Coenonympha pamphilus as well as in the whole Lepidoptera.

Obviously, the picture was strongly influenced by the three species, A. cardamines, M. athalia and C. pamphilus with their significant sex bias and large sample sizes. It is conceivable that the sex difference was a real one in terms of the wing homoeosis either detected or produced; or it may be due simply to the fact that relatively more males than females could exist in collections of these three species. In A. cardamines in particular the conspicuous orange marker on the dorsal surface of forewing tip is male-specific.
Table 1. Fore/hindwing homoeosis in various families of Lepidoptera

<table>
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<tr>
<th>Taxon</th>
<th>Total</th>
<th>Sex</th>
<th>Wing</th>
<th>Surface (wing)</th>
<th>Wing W</th>
<th>Surface</th>
<th>Wing/surface affected</th>
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<tr>
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<td>(1)</td>
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<td>6</td>
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<td>(8)</td>
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<td>37</td>
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<td>63</td>
<td>112</td>
<td>117</td>
<td>5(9) 288 152 150 53...242</td>
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</table>

Pairs of figures connected by dots have statistically significant differences between them at $P < 0.05$ (italics) and $P < 0.01$ (bold print) on $\chi^2$ tests. For abbreviations see the list in text.
Table 3. Lepidopteran taxa contributing more than one case of wing homoeosis to the present compilation.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>No. of Species</th>
<th>Species</th>
<th>No. of Cases</th>
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<td>Z. filipendulae</td>
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<td>Zygaena</td>
<td>6*</td>
<td>Parnassius apollo</td>
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<td>Luehdorfia</td>
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<td>L. japonica</td>
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<td>Papilio</td>
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<td>P. machaon</td>
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</tr>
<tr>
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<td>Delias</td>
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<td>D. hyparete</td>
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<td>P. napi</td>
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<td>Anthocaris</td>
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<td>A. cardamines</td>
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<td>Colias</td>
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<td>Lysandra</td>
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<td>Morphi</td>
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<td>Danaus chrysipus</td>
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<td>Danainidae</td>
<td>Diorsia</td>
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<td>Catocala nupta</td>
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<td>Orthosia</td>
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<td>Arctia caja</td>
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</table>

*Whole wing homoeosis. Others are all mosaics within a single wing.
Table 4. Wing homoeosis in individual lower taxa

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<tr>
<th>Taxon</th>
<th>Type of Homoeosis</th>
<th>Sex</th>
<th>Wing</th>
<th>Surface</th>
<th>Wing</th>
<th>Surface</th>
<th>Wing/Surface Affected</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>c</td>
<td>?</td>
<td>L/R</td>
<td>L</td>
<td>R</td>
</tr>
<tr>
<td>Luehdorfa (Papilion.)</td>
<td>F/H</td>
<td>19</td>
<td>11</td>
<td>8</td>
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<td>Luehdorfa japonica</td>
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<td>Pieris (Pieridae)</td>
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<td>10</td>
<td>9</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>A. cardamines</td>
<td>F/H</td>
<td>9</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Lycaena phloeas (Lyc.)</td>
<td>F/H</td>
<td>39</td>
<td>20</td>
<td>19</td>
<td>10</td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>Melitta+Melitaea (Nym.)</td>
<td>F/H</td>
<td>56</td>
<td>37</td>
<td>20</td>
<td>17</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>Melitta</td>
<td>F/H</td>
<td>47</td>
<td>31</td>
<td>16</td>
<td>9</td>
<td>20</td>
<td>18</td>
</tr>
<tr>
<td>Melitta athalia</td>
<td>F/H</td>
<td>46</td>
<td>31</td>
<td>15</td>
<td>8</td>
<td>20</td>
<td>18</td>
</tr>
<tr>
<td>Argynini (Nym.)</td>
<td>F/H</td>
<td>15</td>
<td>7</td>
<td>8</td>
<td>3</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Cloissiana (Nym.)</td>
<td>F/H</td>
<td>8</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Coenonympha (Saty.)</td>
<td>F/H</td>
<td>45</td>
<td>28</td>
<td>13</td>
<td>7</td>
<td>12</td>
<td>25</td>
</tr>
<tr>
<td>Coenonympha pamphilus</td>
<td>F/H</td>
<td>42</td>
<td>26</td>
<td>12</td>
<td>7</td>
<td>12</td>
<td>22</td>
</tr>
<tr>
<td>Arctia caja (Arctiidae)</td>
<td>F/H</td>
<td>12</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Peris napi (Pieridae)</td>
<td>D/V</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Lycaena phlaeas (Lyc.)</td>
<td>D/V</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Plebejus argus (Lyc.)</td>
<td>D/V</td>
<td>7</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

For abbreviations and statistical analyses see Table 1. Figures with an asterisk indicate cases where homoeosis appears on both surfaces of a wing.
Concerning the mosaicism in wing homoeosis, the results are clear-cut: the whole wing homoeosis is very predominant in Zygaenidae (although it appears exclusive in the list, several homoeotic mosaics can now be added—Sibatani, to be published); whole-surface homoeosis appears only in genus Clossiana. This point would certainly bear on the mechanism of homoeosis and of epigenetic control of wing morphology in these species.

Homoeosis is evenly distributed between fore and hindwing for the whole Lepidoptera, but this is deceptive because individual taxa in Tables 1 and 4 clearly show a strong tendency of F/H wing non-equivalence in individual species. Hence the tendency towards fore- or hindwing homoeosis is more species-specific, and as stated above, cannot be solely ascribed to the presence of favourable markers for detection.

Pooled data from the whole Lepidoptera indicate that the dominance of ventral surface over dorsal surface for homoeosis is quite conspicuous. Again, however, this was deceptive because such a trend is limited to butterflies, moths showing exactly the opposite trend. The forewing dorsal surface of moths and both fore and hindwing ventral surfaces of butterflies are the most homoeosis-prone areas. This may be related to the exposed surface of the wing in the resting position of the insect. These parts of the wing tend to be marked more conspicuously and specifically than the other areas which remain unexposed in resting. The detection of homoeotic mosaics seems to be due to the existence of good markers. However, the tendency of individual taxa to show either F/H or D/V homoeosis is unidirectional, indicating that more than just ease of detection causes this bias. Epigenetic factors involved in the generation of homoeosis may well be evolutionarily related to the insect’s behaviour in its resting position.

**Topography of homoeosis within a wing surface**

Figures 1-12 are a schematic mapping of homoeotic mosaics for all the specimens in which I could locate the position of mosaics with a certain degree of accuracy (see Sibatani, 1980 for definition of accuracy). In so doing, I had to resort to one kind of topological anisomorphism regarding the wing base, where anal (A) and subconstal (Sc) veins, and discal and other spaces flanking them meet. Hence the proximal end of the wing spaces including the discal space should be mapped as a point. In my scheme however it is mapped diffusely along a line, and in the case of discal space, on a very long line, thus enormously inflating the relative area of the mosaics proximad, just as in the case of Mercator’s projection of the two poles of the Earth on a two-dimensional map. However, the objective of this mapping is to indicate position and boundary of mosaics relative to individual spaces and veins, and the mentioned anisomorphism does not affect this point.

As already pointed out (Sibatani, 1980), the mosaics of F/H homoeosis
tend to occur most frequently in the posterior half of the wing, the boundary of the anterior and posterior halves occurring somewhere in space Mi-Mi. I regard these halves as equivalents of anterior and posterior compartments in *Drosophila melanogaster* Meigen (Crick and Lawrence, 1975; see Sibatani, 1980 for discussion and further references).

This point can be seen easily from Figures 1-11 illustrating F/H homoeotic mosaics. However, the same is not true with the D/V homoeosis; indeed, even the reverse is sometimes true (Fig. 12). A comparison of the topography for the two types of homoeosis is made in Figure 13, which corresponds to Figure 4 of Sibatani (1980) but which has been revised on the basis of the new data presented in this paper.

Analysis of cases where F/H homoeotic mosaics occurred in the anterior half of the wing is given in Table 5. On the dorsal surface, the homoeotic mosaic appeared in the anterior half of both wings at fairly high frequencies, but the corresponding events were much rarer on the ventral surface. The mosaic was seldom confined to the anterior half of the wing, the majority of these cases exhibiting mosaics in both anterior and posterior halves. Most of these mosaics are discontinuous at the boundary of the putative anterior and posterior compartments, and only a small number of cases exhibited a homoeotic patch lying across the boundary line. The low frequency of such cases is compatible with the assumption that they represent confluent clones arising independently in the two halves of the wing. Although the D/V homoeosis appeared more frequently in the anterior half of the wing (see Fig. 12), there is only one example (D23 Lysandra coridon, on forewing dorsal surface) out of a total of 31 cases, all wings and surfaces inclusive, showing a homoeotic patch continuous between the two halves of the wing. Hence I do not consider that these "confluent" homoeotic patches constitute sufficient evidence to negate the assumption that lepidopteran wings can be divided into anterior and posterior compartments (Sibatani, 1980).

Multiple occurrence of homoeotic mosaics

The above assumption implies that homoeotic mosaics generally represent clones of epigenetically homoeotic cells. Although surely some clones may have been split into some discrete patches, we may assume that the majority of the multiple homoeotic mosaics found in my samples are of independent origin in an individual subject to some homoeotic predisposition (phenocopy). If this is so, the bilateral occurrence of homoeotic patches on either surface of the forewings or hindwings and the multiple occurrence of homoeotic mosaics on the same surface of only one of the paired wings basically represent the same phenomenon. I had a chance to test this hypothesis with a population of *Luehdorffia japonica* having a rather high incidence of homoeotic modification (B284-B301).

These homoeotic specimens were found amongst some 1,550 specimens
reared in several batches from a limited area on the mid-northern slope of Honshu, Japan, in one year (season). Small homoeotic mosaics appeared on the ventral surface of either or both forewings in each of 18 specimens. The right and left wings were pooled and the frequency of the cases exhibiting various numbers of homoeotic patches on a wing was scored (Table 6). The distribution of the mosaics conformed to the Poisson distribution in the homoeotically predisposed specimens but strongly deviated from it in the total population. The results are thus compatible with the assumption that the homoeotic mosaics would appear randomly on the homoeosis-prone surface of either of the bilateral wings in individuals subject to some homoeosis-inducing agent.

**Trends in individual taxa**

Quite apart from the tendency of individual taxa to generate detectable

Table 5. Homoeotic mosaics occurring in the putative anterior compartment of the wings in Lepidoptera

<table>
<thead>
<tr>
<th></th>
<th>Forewing</th>
<th>Hindwing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dorsal</td>
<td>Ventral</td>
</tr>
<tr>
<td>Total number of homoeotic wings examined</td>
<td>18</td>
<td>147</td>
</tr>
<tr>
<td>Number of wings with homoeotic mosaics occurring in the anterior half of the wing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1*</td>
<td>11</td>
<td>6-7</td>
</tr>
<tr>
<td>Group 2**</td>
<td>10</td>
<td>6-7</td>
</tr>
<tr>
<td>Group 3***</td>
<td>(1)</td>
<td>1</td>
</tr>
<tr>
<td>Percent of total</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1</td>
<td>0.61</td>
<td>0.04-0.05</td>
</tr>
<tr>
<td>Group 2</td>
<td>0.56</td>
<td>0.04-0.05</td>
</tr>
<tr>
<td>Group 3</td>
<td>(0.06)</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*Cases in which any homoeotic mosaics occurred on or rostral of M1. The higher figures include cases where homoeosis did not extend rostral beyond veing M1.

**Cases where homoeotic mosaic occurred on both sides of the putative compartment boundary somewhere in space M1-M3. Higher figures as in Group 1.

***Cases where a homoeotic mosaic occurred, which lay astride the putative boundary, thus solidly connecting homoeotic patches which extended rostral of M1 and caudad of M3. Figures in parentheses represent some ambiguous cases without clearly defined mosaic outlines in my records. These cases comprised the following specimens, the taxa in parentheses corresponding to the figures in parentheses: FD, (B252 Danaus chrysippus); FV, B104 Lynandra coridon; HD, B264 Graphiphora augur, B283 Pericallis matronula, B103 Lycaena phlaeas, B180 Aglais urticae; HV, B196 Maniola jurtina, (B202 Pyronia tilanus).
Table 6. Frequency of isolated homoeotic patches on the forewing in a population of *Luehdorfia japonica*.

<table>
<thead>
<tr>
<th>Number of Homoeotic Patches on a Wing</th>
<th>Number of Homoeotic Wings Found</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>In a whole population examined</td>
</tr>
<tr>
<td></td>
<td>Among specimens carrying homoeosis</td>
</tr>
<tr>
<td>0</td>
<td>3072*</td>
</tr>
<tr>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>3100*</td>
</tr>
<tr>
<td><em>p</em></td>
<td>&lt;0.005</td>
</tr>
</tbody>
</table>

*Based on a rough estimation.

**χ² test for a significant deviation from Poisson distribution.

homoeosis on a particular wing surface, which may be partially related to the characteristic patterning of the taxon, there are other trends in the appearance of homoeosis in individual taxa. Variables involved are frequency and degree of mosaicism and propensity for general bilateral mosaicism.

Table 4 lists some of the taxa showing a higher frequency of wing homoeosis. In the descending order of number of cases examined at the species level, they include *Mellicta athalia*, *Coenonympha pamphilus*, *Lyncaena phlaeas*, *Luehdorfia japonica*, *Arctia caja*, *Anthocaris cardamines* and *Pieris napi* for F/H homoeosis, and *Plebeius argus*, *Pieris napi* and *Lyncaena phlaeas* for D/V homoeosis. In the genera of *Mellicta*, *Melitaea* and the arginine group including *Aegynnis*, *Mesoaclidia* and *Fabriciana* as well as in *Luehdorfia*, the mosaics tend to appear in small patches, often in large numbers and also on both wings (Figs. 4, 7-9, 14). In *Arctia caja* (plus one case of *Pericallia matronula* belonging to the same family Arctiidae) the mosaics were larger but occurred frequently widespread in multiple patches on the dorsal (but sometimes even on the ventral) surface of both wings. In *Lyncaena*, the F/W homoeosis tends to appear on the ventral hindwing, whereas the D/V homoeosis, albeit so far known only in small number, appears on the ventral forewing, though other modes of appearance should have been recognized as easily. Also noteworthy is the fact that no D/V homoeosis has been known in males of *Favonius*, *Neozephyrus* and *Chrysozephyrus* of the same family (Lycaenidae) with their green dorsal surfaces very distinct from the grey or brown ventral surfaces. In view of the fact that these taxa are very much sought
after by collectors in Japan, the D/V homoeoses appear more readily in some species of *Lycaena* and *Plebejus* than in the thecline genera including the above and the English or European *Quercusia quercus*, in which detection of a D/V homoeosis would also be easy.

Further, no homoeosis in *Melitaea*, *Mellicta*, argynnine genera, *Plebejus* and *Lycaena* have been reported from Japan, although they are rather common in that country whence a number of wing homoeoses in Lepidoptera has been reported. This suggests that the same or related species in different countries may not display comparable propensity for wing homoeosis.

*D/V homoeosis*

I wish to discuss this subject in a separate paper addressed to developmental biologists (but see Figs. 15-17 in this paper). However, I should point out that two of the three D/V homoeoses I record here of *Lycaena philaeas* (D10 and D11) are those described by Robertson (1969) as heteromorphosis rather than homoeosis, a treatment which I followed previously (Sibatani, 1980). However, reexamination of these specimens has now revealed that not only the golden orange ground colour but also black spots on the discal areas of the forewing dorsal surface appear on the ventral surface of the same wing, the latter being superimposed on the black spots on the ventral surface, which are slightly smaller than the corresponding ones on the dorsal surface (compare left (normal) and right (homoeotic) forewings in Figs. 15 and 16). Hence I am now inclined to regard them as examples of true D/V homoeosis.

*Structural modifications*

The homoeotic mosaics featuring the F/H wing pattern conversion does not usually entail a conversion of venation or wing shape. In the case of a complete conversion of the hindwing posterior half (compartment) ventral surface to the corresponding part of the forewing in B193 *Acroa eponina* (Sibatani, 1980), I have now ascertained that vein 3A which exists only in the hindwing is atrophied in the homoeotic wing carrying a forewing pattern on the ventral surface posterior half.

In the case of such extensive conversion of the posterior half of the wing occurring in a tailed papilionid taxon, there is some sign of change in the wing form: in B21 *Papilio machaon* (see Fig. 3, K) in which the dorsal surface of the most part of the posterior half of the left hindwing is converted into the corresponding forewing part, the tail, or the extension of vein M3, on the hindwing is truncated but fringed, showing that it was not broken off. A corresponding reverse case (B18 *P. machaon*, see Fig. 3, D), the allotypic (= homoeotic) M3 on the forewing exhibits only a slight protrusion (see Cockayne, 1926: pl. 62, fig. 3).
Unusual cases

There are a few unusual cases which deserve attention and probably careful study. There are two cases (B45 Pieris melete and B280 Arctia caja) in which both dorsal and ventral surfaces of one wing appear to have homoeotic mosaics. *P. melete* (Fig. 5, L) exhibits entirely different distributions of mosaic areas on the two surfaces of a hindwing, whereas *A. caja* (Fig. 2b) has mosaics on the corresponding areas of the dorsal and ventral surfaces of the wing. The authenticity of the homoeotic nature on the ventral surface of these examples would need further verification.

Further there is a unique example of D20 *Polyommatmus icarus* where two entirely independent D/V homoeotic mosaics appeared on ventral surfaces of the right forewing and the left hindwing (Fig. 12, E, K). Apart from this, I examined two female specimens of this species (in the L. Christie collection) which exhibited blue areas on the ventral surface of a wing. But since the dorsal surface of these female specimens was dark rather than blue as in the male, those blue areas could not be held as a D/V homoeosis. This gives a warning to accepting blue scales resembling those of the dorsal surface of a male wing in most polyommatine taxa, when they appear on the ventral surface, as D/V homoeosis.

Finally, as mentioned before, genus Clossiana shows a high frequency of F/H homoeosis occurring on the whole wing surface which is rarely found in nature. I will discuss the whole wing conversion often observed in Zygaenidae in a separate article as a supplement to this paper, and in which I will also supply selected additional data having some remarkable implications.

Two unusual cases of duplication in reverse polarity were included in the list under the heading of “3. Others.” One is illustrated here (Fig. 18). This specimen, A1 Plebejus argus has a normal dorsal surface pattern, but the ventral surface of its right hindwing exhibits a mirror-symmetry duplication in part, presumably covering the spaces between Rs and Mz. If the symmetry axis lies, as it appears, on vein Mz, it deviates slightly from the putative compartment boundary in mid space Mi-Mz. Moreover, there exists a complete complement of the posterior half of the wing, so that analogy to engrailed phenotype in *Drosophila* (Morata and Lawrence, 1976) in which the posterior compartments in meso- or metathorax are converted into a mirror image of the anterior compartment, does not hold. Hence it is doubtful that this represents a phenocopy of “engrailed”-type homoeosis.

Another example of mirror-symmetry duplication of a forewing, A2 Bryoleuca domestica has already been commented on (Sibatani, 1980).

Acknowledgments. I express my sincere gratitude to all those who provided me with facilities and help in investigating and registering the existing records of, and actual specimens carrying, wing homoeoses and related aberrations; especially to
the British Museum (Natural History) and its staff, particularly to Richard I. Vaneghton, and David J. Carter, for generously allowing me to examine and publish on many homoeotic specimens in its vast and well-curated collection of the world and British Lepidoptera; to L. Christie of London for a similar favour with his extensive personal collection of homoeotic Lepidoptera; and further to the following colleagues and friends of different continents and islands: Greg Daniels, C. D. Ferris, Toshiro Haruta, Geoff Holloway, T. Graham Howarth, Hiroshi Inoue, Tatsuo Ishizaki, Akira Kawazoe, Yoshihiko Kurosawa, David K. McAlpine, Max S. Moulds, Ichiro Nakamura, Masatoshi Nishimura, Masami Ogata, Tom S. Robertson, Takashi Shirou, Courteney N. Smithers, Hiroshi Tsukiyama and Kazuo Watanabe. I also acknowledge Eve Ahearn and Anne Neville for good library services, Ian Franklin and Bruce Sheldon for statistical analyses, Graham A. Rockwell and Judith Howard for improvements of the manuscript, and Peter Watt and Graham Johnson for the art work.

Literature Cited


KUZUYA, T., 1969. Two cases of homoeosis of Pieris napi japonica Shirouzu and Pieris


Appendix: Glossary of some technical terms

Compartment. In the development of Drosophila from early embryo to early pupal stage, the prospective adult structures in the head, thorax and genitalia arise and grow in the form of imaginal discs. Descendants of a single cell in a developing imaginal disc can be identified in the adult if that cell has undergone a somatic chromosome recombination which converts the cell’s genotype from the heterozygous to the homozygous state of a recessive gene affecting the adult’s phenotype. Hence, the descendants of a cell, or the clone, may form a genetically labelled mosaic in the adult structure. Analysis of clones started at various stages of development has revealed that development of the imaginal disc proceeds through successive binary partitionings of the cell population of the disc into regions which will follow alternative developmental pathways. Such regions are compartments, their boundaries not usually being transgressed by the clones derived from those multiple cells which are founders of a compartment. For instance, parts of the wing and halteres discs are first allotted to the anterior and posterior compartments, and then each of them is further partitioned into the dorsal and ventral compartments, and so on.

Epigenetic. Adjective of ‘epigenesis’ which is an expression coined in the 18th century (hence preceding introduction of the word ‘genetics’) as a concept opposite to ‘preformation’. With the introduction of the concept of ‘epigenetics’ (developmental biology as analysed in terms of unfolding gene functions during embryogenesis), the meaning of the word ‘epigenetic’ has recently been relaxed and expanded to cover the changes in genetic expression during development.

Phenocopy. Experimental analyses of Drosophila indicate that external agents, such as ether or heat shock, applied at some early crucial stage of development cause some mutant phenotypes to appear in individuals with wild-type genotype. Such a phenomenon is called the phenocopy.
Figs. 1-12. Maps of homoeotic mosaics in Lepidoptera wings. All the examined specimens are included herein as far as sufficient data were obtained by direct examination or through photographic records, description and/or illustration in the literature. Each surface of the wing is mapped by a horizontal array of quadrangles and a broad triangle, representing the intervenous and discal spaces, respectively, the vertical lines representing veins as indicated at the bottom of each column. Unusual abbreviations: c, costa; d, dorsum; A or 1A, 1A+ 2A; Cu, CuA; Sc, Sc+Ri. Homoeotic mosaics appearing on the dorsal and ventral wing surfaces and the left and right wings are all pooled, but they are distinguished by thick (U, dorsal surface; V, ventral surface) and thin (on the corresponding sides of the column) vertical lines, respectively. The broken vertical lines between M3 and M4 indicate the approximate position of the putative boundary of the anterior and posterior compartments. Numbers on the right (occasionally left) end of each horizontal array indicate identification numbers of the recorded specimens as compiled in the list on pp. 3-16; plain numbers refer to B series (F/H homoeosis). Those grouped together in a column with a number preceded by D at the bottom of the column all belong to the D series (D/V homoeosis). Capital alphabet letters and single-brackets on the left indicate individual species as indexed in the legend. Black areas are homoeotic mosaics with definite boundaries; obliquely hatched areas are homoeotic areas whose boundaries are obscure in the available data; vertically hatched areas contain numerous small mosaics difficult to map. Stippled areas represent parts of the wing whose homoeotic nature is questionable or uncertain.


Fig. 1. Moths (except for Arctiidae) and some butterflies. (a), (c) and (d), forewings; (b) hindwings.
(a), Noctuidae—A, Noctua pronuba Linnaeus; B, Catocala nupta Linnaeus.
(b), Lasiocampidae, Geometridae, Saturniidae and Noctuidae—C, Dendrolimus pini Linnaeus; D, Semiothisa (Macaria) notata Linnaeus; E, Philosamia cynthia Drury; F, Diarsia rubi Vieweg; G, Diarsia mendica Fabricius; H, Graphiphora augur Fabricius; I, Orthosia angulipennis Matsumura; J, Orthosia gothica Linnaeus; K, Tholera cespitosa Schiffermüller; L, Mythinna conigera Schiffermüller; M, Xestia alpicola Zetterstedt.
(c), Hesperidae—N, Hasora taminatus Hueber.
(d), Lycaenidae—O, Eumaeus atala Poe; P, Thecla betulae Linnaeus; Q, Favonius cognatus Staudinger; R, Favonius orientalis Murray; S, Lycaena phlaeas Linnaeus; T, Lysandra coridon Poda.

Fig. 2. Arctiidae. (a), forewings—Arctia caja Linnaeus. (b), hindwings—A, Pericallia matronula Linnaeus; B, Arctia caja Linnaeus.

Fig. 3. Papilionidae. (a), forewings—A, Pachliopta aristolochiae Fabricius; B, Atrophaneura febanus Fruhstorfer; C, Atrophaneura horishanus


Fig. 4. *Luehdorfia* species (Papilionidae), forewings. (a) and (b) A, *L. japonica* Leech; (b) B, *L. puizoi* Erschoff.


Fig. 6. *Lycaena phlaeas* Linnaeus (Lycaenidae), hindwings. Also see Fig. 1(d) S.

Fig. 7. Nymphalidae. (a), forewings—A, *Clossiana euphrosyne* Linnaeus (R is included and mapped as conjoined with Rs and R as it is in situ); B, *Clossiana selene* Schiffermüller; C, *Argynnis paphia* Linnaeus; D, *Fabriciana adippe* Schiffermüller; E, *Mesoacidalia aglaja* Linnaeus; F, *Inachis io* Linnaeus; G, *Aglais urticae* Linnaeus; H, *Polygona c-album* Linnaeus.


Fig. 8. *Melitaca-Melitica* (Nymphalidae), forewings. (a) A, *Melitaea cynthia* Linnaeus; B, *Melitica varia* Meyer-Dur. (b), *Melitaca athalia* Rottemburg (continuing to Fig. 9).

Fig. 9. *Melitaca athalia* Rottemburg (Nymphalidae), forewings, continued from Fig. 8(b).

Fig. 10. *Coenonympha* (Satyridae), hindwings. (a), (b) and (c) A, *C. pamphilus* Linnaeus; (c) B, *C. tullia* Mueller.

Fig. 11. Satyridae and Danaidae. (a) and (b), forewings—A, *Coenonympha pamphilus* Linnaeus; B, *Maniola jurtina* Linnaeus; C, * Danaus chrysippus* Linnaeus.


Fig. 12. D/V homoeotic mosaics. (a), forewings—A, *Colias croceus* Geoffroy; B, *Callipryrs rubi* Linnaeus; C, *Lycaena phlaeas* Linnaeus; D,
Plebejus argus Linnaeus; E, Polyommatus icarus Rottemburg; F, Lysandra coridon Poda; G, Lysandra bellargus Rottemburg.
(b), hindwings—H, Heptalus humuli Linnaeus; I, Pieris napi Linnaeus; J, Plebejus argus Linnaeus; K, Polyommatus icarus Rottemburg; L, Lysandra coridon Poda; M, Vanessa cardui Linnaeus; N, Batesia hypochloros hemichrysa Godman & Salvin; O, Morpho terrestris Butler; P, Morpho menelaus Linnaeus.

Fig. 13. Distribution of mosaic areas and boundaries on the homoeotic wings of Lepidoptera. A revised version of Figs. 4c-f of Sibatani (1980) now based on the expanded data. The horizontal axes are divided as in Figs. 1-12, but superimposed with D which represents the discal cell, of which the rostral and caudal halves were scored and shown separately on both sides of the vertical line of M1 which serves as the dividing midline of the discal cell given in broken lines. The empty and solid portions of each column represent mosaic boundaries encompassing only a part of the length of a space, and those running over 90% or more of it, respectively. The cross-hatched portion of each column signifies the ‘solid’ space covered over its (not necessarily proximal) 90% or more by the homoeotic element and thus virtually devoid of mosaic boundaries. (a), (b), F/H homoeosis; (c), (d), D/V homoeosis; (a), (c), forewings; (b), (d), hindwings. Total number of wing surfaces examined: (a) 173, (b) 158, (c) 13, and (d) 20.

Figs. 14-17. Color Plate, see page 46 for figure explanations.

Fig. 18. A partial duplication of the pattern on the ventral surface of right hindwing of Plebejus argus Linnaeus A1 σ from England in the L. Christie collection.
Figure 2
Figure 5
Figure 8
Figure 9
Figure 13
Figs. 14-17. Some examples of wing homoeosis from England; all from the L. Christie collection. They will be further analysed elsewhere using black and white prints. For data, see the accompanying compilation list using the identification numbers. All the photographs including Fig. 18 were made available to me through the courtesy of R. L. Vane-Wright of the British Museum (Natural History).

Fig. 14. B130 Mellicta athalia Rottentenburg ♀ ventral surface. F/H homoeosis on right forewing (X 1.19). See also Fig. 9.

Fig. 15, 16. Lycena phlaeas Linnaeus D11 (15) and D9 (16) ♀ ventral surface. D/V homoeosis on right forewings (15 = X 1.36; 16 = X 1.27). See also Fig. 12(b).

Fig. 17. Plebejus argus Linnaeus D18 ♀ dorsal surface. D/V homoeosis on right hindwing (X 1.50). See also Fig. 12(b).