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Systematics and Biogeography of the New Zealand Sub-Family Crambinae (Lepidoptera: Pyralidae)

Volume II - plates

A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy (Ph.D) in Zoology at Massey University, Palmerston North, New Zealand.

David Edward Gaskin

1968
NOTE

Where possible each figure in this volume is cross-referenced to the appropriate page or pages in volume I. However in the case of the systematic charts, which are referred to many times throughout the text, this is not practical.
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The method of phylogenetic systematic analysis used in this thesis was propounded by Dr W. Hennig in two important papers ('Systematik und Phylogenese', Ber. Hundertjahr. Deut. Entomol. Ges. Berlin 1957, pp. 50-71, and 'Phylogenetic systematics', Ann. Rev. Ent. 1965, pp. 97-116). He considered that unassailable reconstruction of the history of phyletic groups could only be carried out through detailed comparative study of 'plesiomorphic' (relatively primitive) and 'apomorphic' characters (derived or advanced relative to the primitive condition in any given instance).

By his reasoning, only a pattern of apomorphic characters could be used to demonstrate that species and genera formed truly monophyletic groups with common lines of descent.

The reason for selecting this system is quite straightforward. The author believes that the systematic approach to a group in need of revision should be logical, consistent, and if possible subject to some kind of scaled quantitative plan, to facilitate comparison with other revisions. The only other method which allows this approach is the currently popular discipline generally referred to as 'numerical taxonomy', the mechanics of which have been propounded by Sokal and his co-workers (for example see 'Typology and empiricism in taxonomy', R. R. Sokal, J. Theoret. Biol. 3, pp. 230-67, 1963). One of the tenets of this system is that characters shall not be weighted by the taxonomist; in practice this frequently results in associations of plesiomorphic characters having considerable and unwarranted attention focussed on them (Hennig 1965), since they show a high degree of statistical significance for correlation and hence presumed relationship. The proponents of this system tend to completely or partially ignore the vital factors of parallelism and convergence (Gunther 1963, A critical review of the above paper by Sokal in Ber. Wiss. Biol. A, 191, p. 70, and Hennig, 1965). Hence it is hard to see how their results can be interpreted in terms of real phylogenetic relationships, despite protestation to the contrary. Only in the case of enzymatic studies on micro-organisms could this approach be presently considered to be fruitful, since here a worker can code possible pathways of actual
molecular evolution.

Hennig's approach is essentially relative, and presupposed that detailed consideration of parallelisms and convergence has been carried out so that such can be eliminated from the phylogenetic analysis. Fig. 1 shows a highly simplified study of relationships which might be found to exist between 5 hypothetical species A, B, C, D, and E by analysis using 'Hennig's Principle'. Black squares indicate the derived or apomorphic condition of a character, and a white square the relatively plesiomorphic condition. Arrows indicate the direction of character development. A shaded area between black squares indicates monophyly. In each following figure the small numbers represent the character with the same number in the accompanying key; each number above an arrow, indicating the direction of development has its parallel in the numbers within the matrix of the systematic 'tree' beneath the set of squares. The lower numbers enable one at a glance to make an assessment of the relative positions of the genera or species groups within the figure without looking up among the squares for the same number to see which characters are regarded as representing a major division.

For example, character 1 might, in Fig. 1, be a wing coupling mechanism composed of several elements in the primitive condition, but which shows a relative advance (in species D in this case), to a fused or partially fused condition. Of course the plesiomorphic condition might be found in the rest of this family, and perhaps even in other families too. Common ancestry of species A, B, and C could not be proposed on this point alone. However the three species might share another character (2, derived, judged by the experience of the taxonomist familiar with the group), from a generalized primitive condition present in species D, and perhaps in other species too. In reality of course the monophyletic descent of the ABC complex is unlikely to be based on a single character. Despite the apparent 'apomorphic character development & exchange from D to A, B, C, (indicated by the direction of the arrow, showing development from the primitive to the derived), we still could not postulate common ancestry of D with ABC unless we could find at least one character found in the apomorphic condition in
A, B, C, and D, but not in other species. Similarly, on the strength of the pattern of hypothetical characters shown in fig. i, E is totally unrelated to ABC and D, since they share only the bottom character in the diagram, a plesiomorphic one (white). This could be a negative one such as 'walking legs not modified', shared by many other totally unrelated families of insects, for example. The A–E matrix in this diagram is held together only by the condition of 'symplesiomorphy' (Hennig, 1965), which is not a valid base on which to discuss monophyly.

The characters 2–6 in the rest of the diagram correspondingly provide a successively finer focus on the relationships firstly between AB and C, and then between A and B. We might postulate that the taxonomist would decide to give generic status to ABC, since it formed a natural grouping, and also generic status to D. Certainly E would merit separate status. Within genus ABC there might be considered to be two species groups, or in older taxonomic terminology, subgenera, with AB in one and C in the other, since B is more closely related to A than to C. AB in Hennig's nomenclature are 'sister species', while AB and C are 'sister groups'.

The weakness of this system of course, as with all systematics, is that in the final analysis, selection of character priorities—their relative importance, must lie with the taxonomist. However experience has shown (Hennig 1965), that this is better than allowing blind mechanical selection of character associations without consideration of environmental pressures which may have led to parallelism and convergence. His system is more rigorously critical of monophyletic postulations than any other yet devised. For deeper discussion the reader is referred to Hennig's original papers (1957, 1965).
Fig. 1. Hypothetical scheme of highly simplified phylogenetic relationships between 5 species using the method of analysis of 'Hennig's Principle'.
Fig. 1. cont.
43. Ostiolar pouch very strongly developed into large bulb. 44. Ostiolar sclerites developed in lateral positions relative to ostium bursae. 45. Ostiolar sclerites developed in dorsal and ventral positions relative to ostium bursae. 46. Sacculus elaborately developed. 47. Hindwing discal cell open. 48. Sterigmal spines developed in intersegmental membrane between seventh and eighth sternite positions, apparently from posterior extremities of ostiolar sclerites. 49. Ostiolar sclerites very strongly developed with large brush of short setae, possibly with sensory function, only basal portions invaginated into ostium. 50. Strong setae developed on valval costa. 51. Aedoeagus apically bifid. 52. Tendency for ostiolar sclerites to be reduced. 53. Reduction of venation, semi-apterous forms. 54. Loss of primary (?) juxtal attachment to posterior extremity of aedoeagus. 55. Pseudosaccus developed. 56. Juxta strongly V-shaped, often apically setulose. 57. Huge cornutus frequently developed. 58. Chaetosemae lost. 59. Strong tendency to total sclerite loss in ostium bursae. 60. Tendency to development of transtill. 61. Vinculum with characteristic lateral transparent "window". 62. Gnathos sharply angled dorsad. 63. Vinculum/saccus with deep anterior cup developed in most species. 64. Hindwings with m_2 stalked. 65. Forewing veins Sc, r_1 concurrent in most species.

Key to numbers within systematic scheme: 1. Ostiolar sclerites invaginated. 2. Ostiolar sclerites evaginated. 3. Strong tendency for eighth abdominal tergite to fuse with ostium bursae. 4. Ostiolar sclerites strongly developed in lateral positions relative to ostium bursae. 5. Ostiolar sclerites strongly developed in dorsal and ventral positions relative to ostium bursae. 6. Strong tendency to loss of anterior apophyses in most genera, and reduction of these structures in remaining genera relative to other tribes. 7. Anal papillae with very
Pyraustines, Scoparines
- Ostiolar sclerites not developed?
Fig. 2. Systematic relationships of *Orocrambus* with *Maoricrambus*, and of the species groups (1-5, shown by uppermost row of numbers) within the genus. Apomorphic characters shown in black, relatively plesiomorphic characters in white.

Fig. 3. cont.

63. Aedoeagus with large thorn developed. 64. Cornuti secondarily lost in O. lewisi. 65. Sacculus flanged.
66. Eighth abdominal sternite weak. 67. Aedoeagus with ornamentation. 68. Saccus truncate apically. 69. Large thorn on aedoeagus. 70. Ostium bursae encircled by eighth abdominal tergite in female. 71. Cornuti reduced.
72. Costa strongly developed dorsally on valve. 73. Valve with subapical point. 74. Gnathos clubbed. 75. Aedoeagus with extra lateral thorn. 76. Costa of valve elongate antero-posteriorly. 77. One signum greatly reduced relative to other. 78. Sacculus flanged. 79. Ostium bursae complex. 80. Gross cornuti present in aedoeagus.
81. Female frenulum element reduced by fusion of one pair of elements. 82. Prong of valval costa clubbed.
83. Gnathos clubbed. 84. Ostium bursae encircled by eighth abdominal tergite. 85. Aedoeagus ornamented.
Fig. 3. cont.
Fig. 3. Systematic relationships within Orocrambus.

Apomorphic characters shown in black, and relatively plesiomorphic characters in white.

Upper row of numbers indicate species as follows:

1. Orocrambus apicellus. 2. O. haplotomus. 3. O. dicrenellus.
4. O. flexuosellus. 5. O. horistes. 6. O. mylites. 7. O. aethonellus.
8. O. catacaustus. 9. O. fugitivellus. 10. O. tritonellus.
26. O. jansoni. 27. O. lectus. 28. O. lewisi.
32. O. ordishi. 33. O. heteraulus. 34. O. harpophorus.
35. O. ramosellus. 36. O. siriellus. 37. O. tuhualis.
41. O. paraxenus. 42. O. vittellus. 43. O. callirrhous.
44. O. enchophorus. 45. O. xanthogrammus.

Key to numbers in systematic scheme: 1-16 as in fig. 2.

17. Aedeagus with apical thorn greatly reduced. 18. Eighth abdominal sternite reduced or absent in female.
21. Aedeagus with spur developed. Aedeagus also far longer and narrower than in any other species in this group.
22. Compound eye diurnal type, with nude periorbital strip. 23. Strong aedeagal thorn at dorso-posterior apex.
Fig. 4. Systematic relationships within Pareromene. Species groups (1-10) shown by upper row of numbers. Apomorphic characters shown in black, relatively plesiomorphic characters in white.

Fig. 5. cont.
partly divided. 34. Uncus and gnathos swollen apically, strongly hooked. 35. Valval costa with two prongs.
42. Juxta stellate. 43. Juxta anteriorly truncate.
44. Ostiolar pouch present, distinctly stalked.
45. Tendency for elongation or splitting of thorn.
53. Tapered juxta. 54. Very elongate costal prong.
55. Juxta drawn posteriorly into two sharp prongs.
56. Juxta elongate. 57. Strong external thorn developed.
63. Juxta deeply cleft posteriorly. 64. Internal cornuti totally lost or permanently everted. 65. Very heavily sclerotised juxta.
Fig. 5. Systematic relationships of the species of Pareromene. Species shown by upper row of numbers as follows:


Key to numbers in systematic scheme, apomorphic characters shown in black, relatively plesiomorphic characters in white: 1 - 22 as in Fig. 4. 23. Costal prong of valve strongly developed. 24. One large cornutus greatly elongated. 25. Accessory cornuti lost. 26. Length of costa reduced relative to valve. 27. Costa with two prongs. 28. Costal length reduced relative to valve. 29. Juxta reduced posteriorly to narrowing lobe. 30. Cornutus with swollen base. 31. Length of costa relative to valve much reduced. 32. Ductus with sub-apical swollen region in female. 33. Cornutus fish-hooked,
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Key to symbols: A. Tawhitia pentadactyla, B. Tawhitia glaucophanes. Numbers within systematic plan:
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Above: vapidus, nexalis form (Lake Tekapo).
Centre: typical vittellus (Palmerston North).
Below: eonopias form.

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Centre: typical form (Macetown).
Below: leonina form (Takitimus)

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Legends: 7t, seventh tergite; teg., tegumen; un., uncus; gn., gnathos; c.f., costal flange; v.c., valval cucullus; v., valve; c.l., costal lobe; saccl. fl., sacculus flange; saccl., sacculus; tr., transtilla; psd., pseudosaccus; sacc., saccus; 7st., 7th sternite; k., keel of saccus; aed., aedoeagus; anl., anellus; cr., cornuti; th., aedoeagal thorn; a/j.h., anellar/juxtal horn; j., juxta; acc.gl.f., fused portion of accessory gland; acc.gl.pr., paired portion of accessory gland; tst.cp., testis capsule; v.d.&v.s., vas deferens with seminal vesicles; d.e.gl., glandular part of ductus ejaculatorius; d.e.cl., clear portion of ductus ejaculatorius; h.s., hydrostatic (?) sac; ans., anus; r., rectum; ev.vs., everted vesica; o.b., ostium bursae; d.b., ductus bursae; d.s., ductus seminal o., ostium; vinc., vinculum; A. Form of saccus in Tawhiti B. Form of saccus in Gadira; C. Form of saccus in Pareromene.
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Fig. 41 Generalized diagram of ectodermal structures in crambine female genitalia (Tribe Crambini). (see pp.32)

Fig. 42 Generalized diagram of ectodermal structures in crambine female genitalia (Tribes Chiloini and Diptychophorini). (see pp.35,37).

Legends: an.p., anal papillae; 8t, eight tergite; 7t, seventh tergite; d.s., ductus seminalis; c.b., corpus bursae; sg., signum; d.b., ductus bursae; 7st, seventh sternite; o.b. ostium bursae; l.av. lamella antevaginalis; o.ostium; l.pv., lamellae postvaginalis; 8st, eighth sternite; r, rectum; ovl., ovariole; glr.p., glandular region of oviduct; acc. accessory glands; ovd., oviduct; spm., spermatophore with proximal chitinised hood and distal bulla.

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Note: In this and all following
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