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WHY *PIERIS RAPAE* IS A BETTER NAME THAN *ARTOGEIA RAPAE* (PIERIDAE)

ROBERT K. ROBBINS

Department of Entomology, MRC NHB 127, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560

PAMELA M. HENSON

Smithsonian Archives, A & I 2135, Smithsonian Institution,
Washington, D.C. 20560

ABSTRACT. We show that there is no phylogenetic justification for changing the name of *Pieris rapae* to *Artogeia rapae*. We "define" *Pieris* by the presence of androconial basal lobes, and suggest that this grouping, which includes *P. rapae*, *P. brassicae*, and *P. napi*, is monophyletic. Female genital characters indicate that *Perrhybris*, *Itaballia*, and *Ganyra* are the closest relatives of *Pieris*. We discuss criteria for choosing generic nomenclature, and suggest that the following guidelines will best promote nomenclatural stability. If a genus is monophyletic, do not change the name. If a genus is not monophyletic, choose the combination of monophyletic generic groupings that will create the fewest name changes. If another option causes more name changes now but will be more stable in the future because of better evidence for monophyly, then present the reasons and evidence for that choice.

Pieris rapae Linnaeus is one of the best known and commonly encountered temperate area butterflies. Although native to the Palaearctic, it is now nearly ubiquitous in suitable disturbed habitats in North America (Howe 1975), New Zealand (Gibbs 1980), and Australia (Common & Waterhouse 1981). Because *P. rapae* is widely distributed, easily reared, and a pest on cultivated crucifers, it has been extensively studied in the agricultural, ecological, and physiological literature (Harcourt 1966, Dempster 1969, Aplin et al. 1975, Slansky & Feeny 1977, Blau et al. 1978, Kobayashi & Takano 1978, Yamamoto & Ohtani 1979, Wolfson 1980, Chew 1981, Jones et al. 1982, Gilbert 1984, Maguire 1984).

The generic placement of *P. rapae* has recently been changed from *Pieris* to *Artogeia* Verity. Schrank (1801) placed *rapae* in *Pieris* when he originally described the genus, and Klots (1933) retained this generic

placement in his systematic treatment of world Pieridae. Verity (1947) proposed *Artogeia* as a subgenus including *rapae*, and Kudrna (1974) and Higgins (1975) elevated it to generic rank, an action that has been followed in some general works (Pyle 1981, Miller & Brown 1981) but not others (Kawazoé & Wakabayashi 1976, Opler & Krizek 1984). This situation was further complicated when Kudrna later treated *Artogeia* as a subgenus (Blab & Kudrna 1982), and Feltwell and Vane-Wright (1982) suggested that *Artogeia* might not be monophyletic.

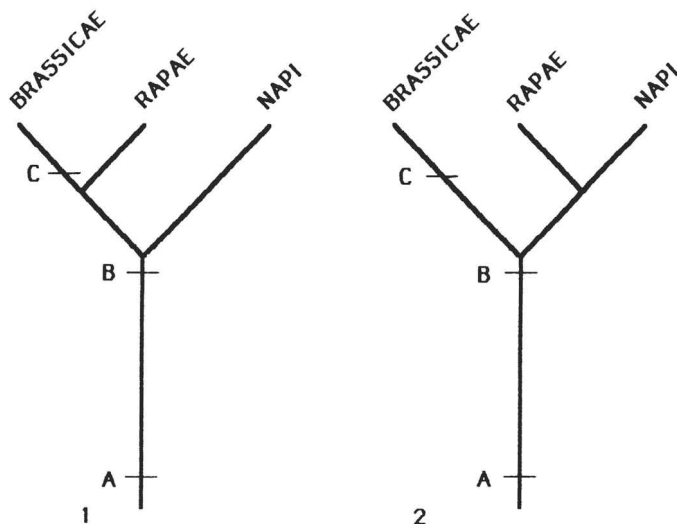
In this paper we assess the evidence for switching *rapae* from *Pieris* to *Artogeia*. We took up this project because of repeated inquiries from scientists in a variety of biological disciplines to the National Museum of Natural History concerning the proper generic name for *rapae*. We address the following questions: "What is the evidence for the change in generic nomenclature and is it compelling?", "What is the 'best definition' for *Pieris*?", "What are the closest relatives of *Pieris*?", and "What criteria will promote stability of generic nomenclature?"

It is not our intent to produce a definitive work on *Pieris* systematics. Besides reporting the results of a few representative female genitalic dissections, we discuss published information only, all of which was available to Kudrna and Higgins, with the exception of two recent papers on isozymes. We discuss characters sequentially, note their states and distributions, and generally limit our discussion to those species for which we have information. Many species level decisions, particularly in the *P. napi* group, are controversial (Warren 1961, Bowden 1972, Eitschberger 1983, Geiger & Scholl 1985); we avoid entering the fray because it is largely irrelevant to our purpose. Finally, we show that treatment of all *Pieris* species would not alter our conclusions.

PIERIS RAPAE OR ARTOGEIA RAPAE

In this section, we ask whether *rapae* is more closely related to *napi* Linnaeus—the type of *Artogeia*—or to *brassicae* Linnaeus—the type of *Pieris*. The classification of Kudrna (1974) and Higgins (1975) implies that the former is correct, while others (Mariani 1937, Geiger 1981, Geiger & Scholl 1985) suggest the opposite. These two possibilities are represented by alternative phylogenies (Figs. 1 & 2).

To determine primitive character states among these species (the state at point A in the phylogenies), we used two sets of outgroup species. The first set is *Pontia daphidice* Linnaeus and *Synchlœ callidice* Hübner. Pierid specialists (Klots 1933, Bernardi 1947) considered them to be closely related to the *brassicae-napi* complex, and sometimes included them in *Pieris*. Kudrna (1974) placed them next to *Pieris* and *Artogeia*. They are the immediate outgroups of the *brassicae-napi* lineage in dendrograms constructed from isozyme data (Gei-

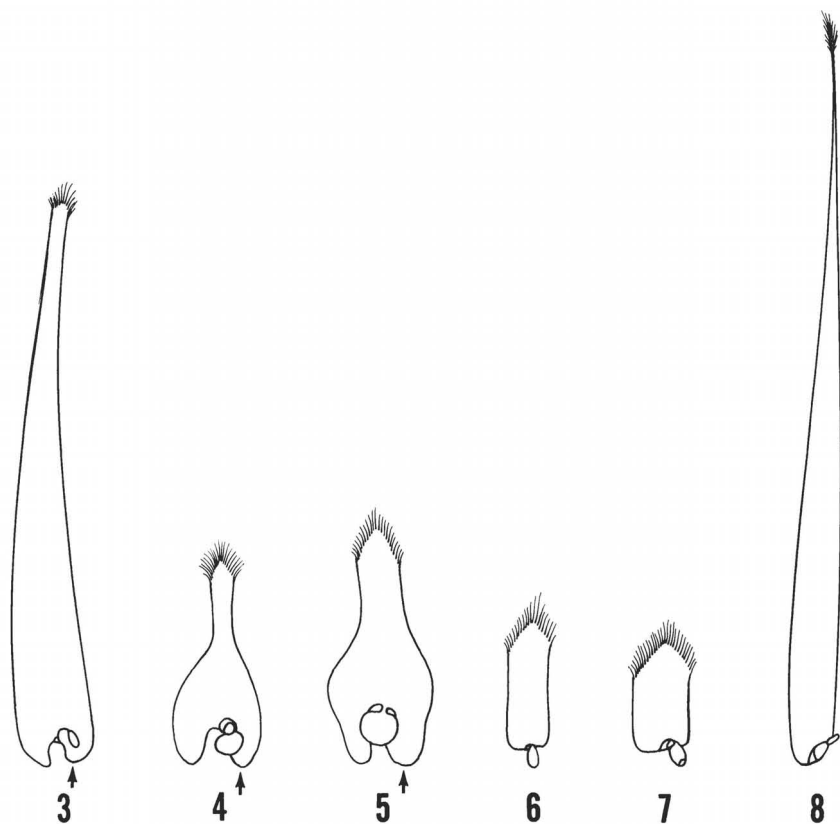


FIGS. 1 & 2. Phylogenies showing cladogenesis among *Pieris brassicae*, *P. rapae*, and *P. napi*. The letters designate ancestral species in the branching sequence.

ger 1981, Geiger & Scholl 1985). The second outgroup set is *Ganyra* Billberg, *Itaballia* Kaye, and *Perrhybris* Hübner (*sensu* Klots 1933). We discovered that they share female genitalic characters with the *brassicae-napi* complex (detailed below), and may be more closely related to them than has been previously realized.

The first character that Kudrna (1974) and Higgins (1975) used in their taxonomic analysis was androconial structure (illustrations in Dixey 1910, 1932, Bernardi 1947, Warren 1961). There are four major shapes in the "*Pieris* group" with slight quantitative interspecific variation within each type: *P. brassicae* has one type of androconium (Fig. 3), *rapae* and *A. napi* a second (Figs. 4 & 5), outgroups *P. daphidice*, *Perrhybris*, and *Itaballia* a third (Figs. 6 & 7), outgroup *Ganyra* a fourth (Fig. 8), and outgroup *S. callidice* lacks androconia. On either phylogeny this distribution of character states can be explained, no matter which outgroup state occurred at point A, by the *rapae-napi* androconium evolving at point B and the *brassicae* androconium evolving at point C. Although there are other equally parsimonious possibilities, either phylogeny could produce the distribution of character states simply—each androconium type evolved once. Thus, although *rapae* and *A. napi* share a similar androconial structure, this distribution provides no evidence for choosing between the phylogenies in Figs. 1 and 2.

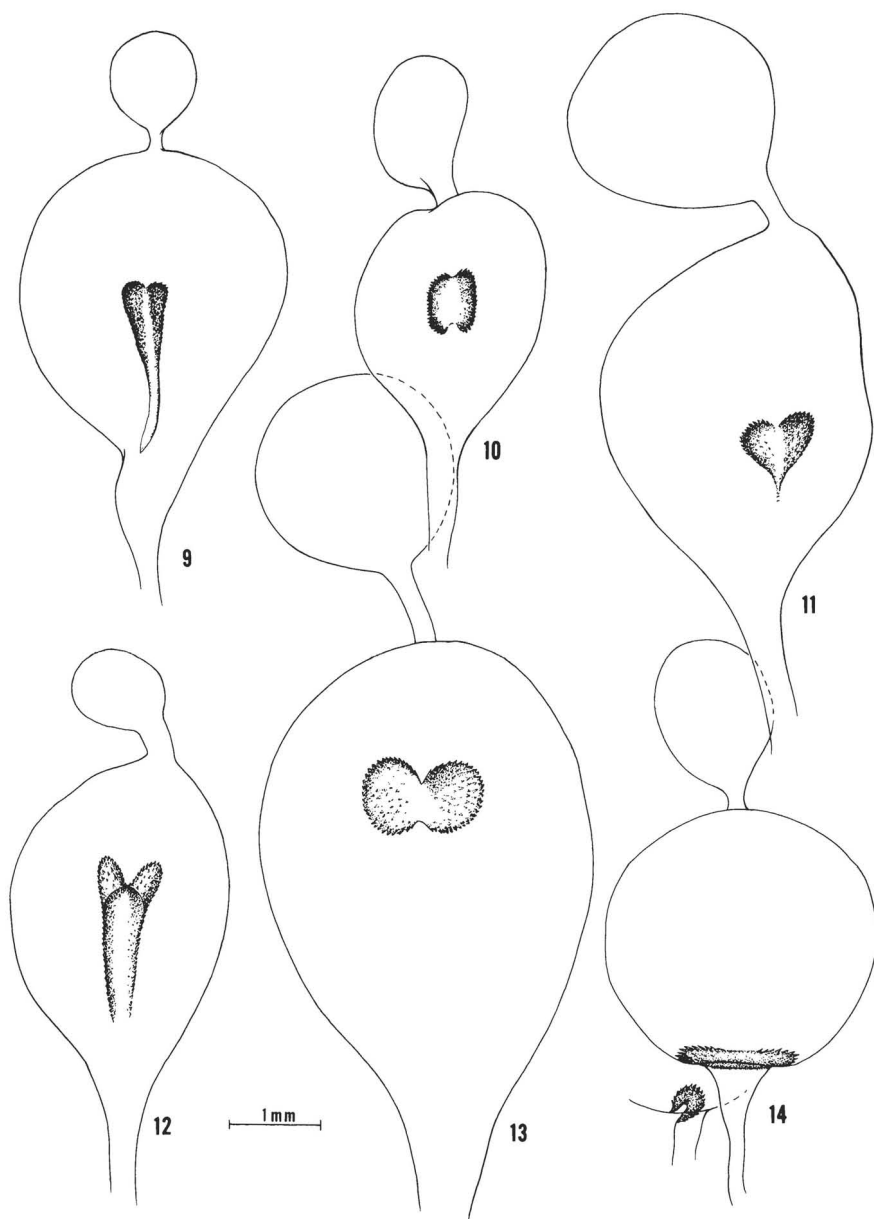
Kudrna (1974) and Higgins (1975) also used male genitalic charac-



FIGS. 3-8. Outlines of androconia, redrawn from Dixey (1932). Arrows in first three figures point to the right basal lobe. 3, *Pieris brassicae*; 4, *P. rapae*; 5, *P. napi*; 6, *Pontia daplidice*; 7, *Itaballia demophile*; 8, *Ganyra josepha*.

ters for defining *Artogeia*. The male genitalia of *A. napi* and *rapae* are similar to each other, and differ from *P. brassicae* (illustrated in Klots 1933, Bernardi 1947, Kudrna 1974, Higgins 1975). The penis of *P. brassicae* has a dorsal hump and each valva has a distal pointed process while *rapae* and *A. napi* lack the dorsal hump and the process. The outgroups, like *rapae* and *A. napi*, lack a penial dorsal hump and process on the valva (except for *Ganyra*, which has a differently shaped valva process). Thus, the *P. brassicae* penis and valva morphology is derived, defines only *P. brassicae* (evolved at point C on either phylogeny), and provides no information about the phylogenetic position of *rapae*.

Higgins (1975) also used haploid chromosome numbers to differentiate *Pieris* from *Artogeia*. Reported haploid chromosome numbers (De



FIGS. 9-14. Right dorsolateral view of the corpus bursae and anterior portion of the ductus bursae (except for *Pontia callidice*, which is a dorsal view with an additional lateral aspect of the cervix). 9, *Pieris napi*; 10, *P. rapae*; 11, *P. brassicae*; 12, *Perrhybris pyrrha*; 13, *Ganyra josepha*; 14, *Pontia callidice*.

Lesse 1967, 1970, De Lesse & Brown 1971, Robinson 1971) are *P. brassicae*—15, *rapae*—25–26, *A. napi*—25–28, and for the outgroups *P. daplidice*—26, *S. callidice*—26, *Itaballia*—25–26, and *Perrhybris*—27–29. We infer that the lower haploid chromosome number of *P. brassicae* is a derived character state that defines only *P. brassicae*—it evolved at point C in the phylogenies—and that provides no information on the systematic position of *rapae*.

Since the characters used by Kudrna (1974) and Higgins (1975) provide no evidence for choosing between the phylogenies in Figs. 1 and 2, the placement of *rapae* in *Artogeia* was phylogenetically unjustified. We now ask whether other published characters provide information on the generic placement of *rapae*.

Mariani (1937) and Bernardi (1947) examined "*Pieris*" female genitalia, and reported interspecific variation in morphology of the single signum (often called "lamina dentata" in the pierid literature) on the corpus bursae. The signum of *A. napi* has a long posterior process ("flagello" of Mariani, "tail" of Chang [1963]) that is lacking in *rapae* and *P. brassicae* and in all outgroup species (Figs. 9–14, figures in Mariani and Bernardi). Thus, the posterior process is a derived character state that apparently evolved once on the lineage leading to *A. napi*, and does not give us information with which to distinguish the phylogenies in Figs. 1 and 2.

Geiger (1981) and Geiger and Scholl (1985) electrophoresed enzymes from species of *Pieris*, *Artogeia*, *Pontia*, and *Synchlœe*, but not for the other outgroups. They obtained a dendrogram of relationships by using an unweighted pair-group average clustering method on genetic similarities. They found that *rapae* is more similar to *P. brassicae* than to *A. napi* and that all three are more similar to each other than to *Pontia* and *Synchlœe*. This result supports the phylogeny depicted in Fig. 1. There are numerous methods for coding and analyzing electrophoretic data, and Mickevich and Mitter (1981) propose criteria for judging different methods. Before uncritically accepting their dendrograms, we would want to know if other methods of coding and analysis corroborate their results.

In summary, analysis of published characters indicates that the use of *Artogeia* as a genus or subgenus including *rapae* is phylogenetically unjustified. Although the male genitalia, androconia, and haploid chromosome numbers of *rapae* are more similar to *A. napi* than to *P. brassicae*, the opposite relationship is true with regard to the female genitalia and isozymes. Further, these similarities are based on primitive character states, as Feltwell and Vane-Wright (1982) had predicted, and do not provide the information necessary to choose between the phylogenies in Figs. 1 and 2. Characters of "*Pieris*" immature

stages may provide the information necessary to decide this point, but have not been used in *Pieris* revisions.

THE GENUS *PIERIS*

Since *rapae* is such a widely known species and since Kudrna and Higgins' concept of *Pieris* and *Artogeia* leave *rapae* without certain generic placement, we ask in this section whether there are other, more reasonable definitions for *Pieris*. Klots (1933) revised the world pierid fauna. Although he narrowed the definition of *Pieris*—it previously had been a catchall genus for many questionably related pierines—subsequent authors have split the genus further. We ask whether any of these groupings are monophyletic. For outgroup comparisons, we use those genera that Klots considered to be most closely related to *Pieris*: *Leptophobia* Butler, *Itaballia*, *Perrhybris*, *Ascia* Scopoli (including subgenus *Ganyra*), *Tatochila* Butler, *Phulia* Herrich-Schäffer, and *Baltia* Moore.

Three different concepts of *Pieris* besides that of Kudrna and Higgins have been used since 1933. For ease of communication, we list representative species for each grouping, and refer the reader to the original work for a complete list. Klots (1933) placed *brassicae*, *rapae*, *napi*, *callidice*, *daplidice*, and *pylotis* in *Pieris*. Mariani (1937) and Bernardi (1947) put the first four of these species in *Pieris*, while Higgins and Riley (1970) restricted *Pieris* to the first three. (Note that Higgins [1975] later narrowed the genus further, like Kudrna, to include only *brassicae* and close relatives.)

Klots (1933) defined *Pieris* with a paragraph of character states. For the most part, however, they are too ambiguous to code accurately. For example, how does one code "antenna long, with abrupt club" (*Pieris*), "antenna long, with usually somewhat abrupt club" (*Ascia*), and "antenna long, with flattened abrupt club" (*Tatochila*)? Further, each of Klots' generic character states is shared with at least one outgroup genus. Because of character state ambiguity and the lack of unique, potentially defining character states, we found no evidence in Klots' work to indicate that his concept of *Pieris* is monophyletic.

Mariani (1937) and Bernardi (1947) apparently ignored *pylotis* (a neotropical species that does not "look" like other *Pieris* species) and moved *daplidice* to *Pontia*. *Pontia daplidice* has forewing veins R_3 and R_{4+5} fused while they are separate in the other *Pieris* species. Outgroups *Phulia* and *Perrhybris* have the fused veins while the other outgroups have separate veins (Klots 1933). Because both character states are found in the outgroups, the primitive character state is ambiguous. Phylogenetic interpretation of this character is thus equivocal.

Higgins and Riley (1970) joined *callidice* with *daplidice* in *Pontia*,

so that their *Pieris* grouping consisted of *brassicae*, *rapae*, *napi*, and close relatives. The androconial lateral edges of these species and their close relatives protrude basally to form lobes (Dixey 1932, Bernardi 1947, Warren 1961) (Figs. 3–5) while the androconial basal edge is flat in *daplidice* and relatives (Bernardi 1947) (Fig. 6), *pylotis* (Dixey 1932), and all outgroup genera (Dixey 1932) (Figs. 7 & 8). Since *daplidice* and *pylotis* share the primitive state—that which occurs in the outgroup genera—the androconial basal lobes would appear to be a derived, defining character for the *brassicae-napi* complex. This situation contrasts with the one in the previous section, in which *rapae* and *napi* share an androconium type that does not reflect phylogenetic relatedness because *brassicae* does not possess the primitive character state.

We “define” *Pieris* by the androconial basal lobes. Although we are reluctant to define a genus on the basis of one character state, there are no alternatives in this case. From published illustrations of androconia (Dixey 1932, Bernardi, 1947), we place the following specific taxa—listed in Bernardi—in *Pieris*: *brassicae*, *deota* de Niceville, *brassicoides* Guerin, *krueperi* Staudinger, *tadjika* Groum-Grshimailo, *canidia* Sparrman, *manni* Mayer, *rapae*, *dubernardi* Oberthur, *extensa* Poujade, *stoetzneri* Draeseke, *napi*, *virginiensis* Edwards, *ochsenheimeri* Staudinger, *ergane* Geyer, *melete*, and *dauidis* Oberthur. Although there are other taxa, particularly in the *napi* group, that are given specific rank by some authors, we leave species level decisions to others.

We believe that this grouping is the most reasonable and stable one for *Pieris*. There is an enormous biological literature on *Pieris brassicae*, *Pieris rapae*, and *Pieris napi*, and the name *Pieris* is widely recognized by nontaxonomists in connection with these species. Our grouping will preserve this association, and because it is based on the best available evidence for monophyly, it is most likely to be stable in the future.

There are three morphologically distinct groups within *Pieris*. The *P. brassicae* group (*brassicae*, *deota*, *brassicoides*) has the androconial and male genital structures of *brassicae*, and is probably a monophyletic lineage defined by these structures. The *P. napi* group (*napi*, *virginiensis*, *ochsenheimeri*, *ergane*, *melete*, *dauidis*, and presumably *stoetzneri*, *extensa*, and *dubernardi*—Bernardi [1947]) has a posterior process on the signum, which probably defines this group as a monophyletic lineage. The *P. rapae* group (*krueperi*, *tadjika*, *canidia*, *manni*, *rapae*) lacks derived character states. There is no evidence to indicate whether it is monophyletic or whether it is phylogenetically more closely related to the *P. brassicae* or *P. napi* groups. Thus, even if we had examined all *Pieris* species in the previous section, it would

not have provided us with evidence on the phylogenetic position of *P. rapae*. Interestingly, the same three groups result when isozyme data are analyzed phenetically (Geiger & Scholl 1985).

THE RELATIVES OF *PIERIS*

In this section we ask which genus or genera are most closely related to *Pieris*. From the work of Mariani (1937) and Bernardi (1947), it appeared that the bursa copulatrix, particularly signum location and shape, had states that might provide information on the phylogenetic position of *Pieris*. Because this character was promising, but unrecorded for many of the outgroups, we dissected the female genitalia of species in *Pieris* and related genera.

We recorded three character states of the bursa copulatrix. In the first, the signum is a narrow transverse band located at the posterior end of the corpus bursae just around the entrance to the ductus bursae (Fig. 14). We recorded this state in *Pontia* (*daplidice*, *protodice*), *Synchlœ* (*callidice*), *Leptophobia* (*eleone* Hewitson, *aripa* Boisduval), and *Ascia* (*monuste* Linnaeus). It also occurs in *Tatochila*, *Phulia*, *Baltia*, and close relatives (Field 1958, Herrera & Field 1959, Field & Herrera 1977), in the pierine *Aporia* Hübner (Mariani 1937) and the coliadines *Colias* Fabricius (Mariani 1937) and *Eurema* Hübner (Field 1950).

In the second character state, the signum is located on the right dorsolateral side of the corpus bursae well anterior to the entrance of the ductus bursae (Figs. 9–13). Signum shape varies, particularly in how far it extends posteriorly and in the amount of sclerotization of the median line. We recorded this character state in *Pieris* (*brassicae*, *rapae*, *napi*, *melete*), *Ganyra* (*josepha* Godman & Salvin, *limona* Schaus), *Itaballia* (*demophile* Linnaeus, *viardi* Boisduval, *pisonis* Hewitson), and *Perrhybris* (*pyrrha* Fabricius, *pamela* Cramer [= *lypera* Kollar], *lorena* Hewitson). Mariani (1937) noted its occurrence in all 12 *Pieris* species that he examined.

A third character state is limited to *Glennia pylotis*. There is no signum. The corpus bursae and ductus bursae are greatly modified into a long tube that occupies the length of the abdomen. This tube gradually increases in diameter anteriorly, and the usual abrupt change in size that distinguishes the corpus from the ductus is absent.

The closest relatives of *Pieris* appear to be *Perrhybris*, *Itaballia*, and *Ganyra*. The position of the signum on the right dorsolateral side of the corpus bursae is an unusual character state that is apparently restricted to these four genera. The other genera that Klots (1933) placed near *Pieris* have the signum at the posterior end of the corpus bursae, which is probably the primitive state for the pierines because it is also

found in the coliadines *Eurema* and *Colias*. A definitive survey of the distributions of female genital structures is obviously desirable.

Those holarctic species that Klots (1933) put in *Pieris*, but which have recently been placed in *Pontia* (Higgins 1975, Miller & Brown 1981) are often considered to be close relatives of *Pieris*. However, we know of no evidence that this group is more closely related to *Pieris* than to other genera, such as *Tatochila*, *Phulia*, and relatives (Shapiro 1979). Further, we have found no published characters to determine whether this group is monophyletic. In short, there is a glaring need for a worldwide treatment of the pierines.

The placement of *Glennia pylotis* remains a problem. Although Klots (1933) treated *Glennia* as a subgenus of *Pieris*, it lacks the androconial basal lobes and signum of *Pieris*. There is currently no evidence to decide whether the divergent female genitalia of *Glennia* evolved from the *Pieris* type or from the *Pontia* type.

STABILITY AND GENERIC NOMENCLATURE

In this section we use the confusion over the generic nomenclature of *P. rapae* as an example to discuss the relationship between taxonomic method and nomenclatural stability.

We suggest that butterfly generic nomenclature can be more objectively chosen than in the past by using the criteria of "stability" and "monophyly". The Preamble to the International Code of Zoological Nomenclature (Int. Comm. on Zool. Nomenclature 1985) states that "... the object of the Code is to promote stability and universality in the scientific names of animals" Ehrlich and Murphy (1982) discuss the widespread support for a stable generic nomenclature.

By monophyly, we refer to taxa defined by derived characters. As Jordan (1898) noted, "... we have here an instructive illustration of the fact—so very often entirely disregarded in classificatory work—that the presence of the same character in two different [taxa] . . . is, evidence of closer relationship only, if the character is a specialisation and not of the ancestral type." Jordan's logic is simple, but has been largely ignored by butterfly systematists.

The application of stability and monophyly to groups with an established generic nomenclature, such as the bulk of the butterflies, is straightforward. If a genus is monophyletic, do not change the name. If a genus is not monophyletic, choose the combination of monophyletic generic groupings that will create the fewest name changes. If another option causes more name changes now but will be more stable in the future because of better evidence for monophyly, then present the reasons and evidence for that choice.

Ehrlich and Murphy (1982) suggested that the concept of balance

(the equivalence of categorical rank in related taxa, *sensu* Mayr 1969) also be used to decide generic nomenclature. Despite Mayr's discussion of how balance might be applied, this method is subjective, particularly since it is unclear exactly what the method is supposed to estimate. Although objectivity is not itself justification for using a criterion, we believe that an obviously subjective one, such as balance, will promote instability of butterfly generic nomenclature.

Kudrna (1974) and Higgins (1975) used the criterion of "similarities and differences" to justify their recognition of *Artogeia*, and did not mention stability and monophyly. For example, Higgins (1975) stated, "Their [*Artogeia*] genitalia, androconial scales and chromosome numbers differ from those of *P. brassicae* and it is not satisfactory to include them in the same genus." Neither worker suggested that *Pieris*, as used by Klots (1933) or Bernardi (1947), was polyphyletic. Neither discussed the possible confusion that would result from changing the generic nomenclature of *P. rapae* and *P. napi*.

There are many problems with the criterion of similarities and differences. (1) The similarities and differences used by Kudrna and Higgins do not provide information on the phylogenetic position of *P. rapae*. This example is a clear illustration that similarities and differences alone are insufficient to establish monophyly. (2) If Kudrna and Higgins had examined female genitalia and isozymes (as opposed to male genitalia, androconia, and chromosome numbers), they would have put *rapae* in *Pieris*. When taxonomic conclusions depend upon the character set used, the result is instability. (3) We are certain that Kudrna and Higgins believed that *Artogeia* should be split from *Pieris* because it is "sufficiently different." However, if one "authority" states that a difference is sufficient to split a genus, but another disagrees, then how can these conflicting views be resolved? It is evident that the criterion of similarities and differences promotes instability, and should not be used.

Kudrna (1974) and Higgins (1975) assumed that the divergent morphology of *P. brassicae* is the result of phylogenetic distance, but did not consider that it might be the result of rapid evolution. We hypothesize that rearrangement of genes caused by extensive chromosomal fusion—haploid chromosome number decreased from about 26 to 15 at point C in Figs. 1 and 2 (discussion in White 1973)—affected gene expression during development (the "position effect"; Dobzhansky 1957, White 1973), and is causally related to the divergent male genital, androconial, and larval (D. Weisman, pers. comm.) morphology of *P. brassicae*. Chromosomal rearrangements would not be expected to affect the protein products of structural genes, however—an expectation consistent with isozyme data (Geiger 1981, Geiger & Scholl 1985). Our

hypothesis generates the testable prediction that morphology and chromosome numbers are perfectly correlated; all species in the *P. brassicae* group should have reduced haploid chromosome numbers (about 15) while none in the *P. rapae* and *P. napi* groups should have the reduced numbers.

J. H. Comstock (1893) wrote: "Here I believe lies the work of the systematist of the future. The description of a new species, genus, family or order, will be considered incomplete until its phylogeny has been determined so far as is possible with the data at hand." Comstock's vision of the holarctic butterfly "systematist of the future" is, by and large, still just a vision. Until we have reasonable phylogenies, generic nomenclature is bound to be unstable. In the meantime, suggested changes in generic nomenclature will hopefully be based on evidence of monophyly, and proposed with due regard for stability.

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