The taxonomy of *Pieris protodice* Boisduval & LeConte and its relatives in western North America has long been confused, with the relationship of that taxon to *P. occidentalis* Reakirt being a matter of particular contention. Both current "field guides" (Klots, 1951; Ehrlich & Ehrlich, 1961) treat them as conspecific, as does the North American check-list (dos Passos, 1965), while recent faunistic papers by authors in western North America (e.g., Garth & Tilden, 1963) have regarded them as separate species. Chang (1963) provided morphological evidence in support of the latter position and mapped the distribution of *P. occidentalis*. His analysis was followed by Howe (1975). The situation is complicated by the occurrence of named seasonal and/or altitudinal phenotypes in both, as well as one valid subspecies. The present paper summarizes the result of a series of field and laboratory studies in which the biological relationships among these entities have been clarified; these studies are cited individually in the text. It is not intended as a formal taxonomic revision; such a revision should, if undertaken, be on a world-wide basis. All of the taxa are abundantly illustrated in the papers cited.

The only previous American treatment of this group was by Abbott (1957) and Abbott, Dillon, & Shrode (1960). This incompetent study, which "synonymizes" the very different species *Pieris beckerii* Edwards and *P. sisymbrii* Boisduval with *P. protodice* and *P. occidentalis* with total disregard for their biology and extensive sympatry, makes no useful contribution to the taxonomy of the group. Those names in the group which were authored by William H. Edwards have been very thoroughly treated taxonomically by Brown (1973). McHenry (1962) has prepared a bibliography of the original descriptions of all taxa placed in *Pieris* in North America.

The biological entities recognized in this paper are:

I. *Pieris protodice* Boisduval & LeConte
   f. vern./aut. *vernalis* W. H. Edwards
   *nasturtii* "Boisduval MS." (W. H. Edwards)

II. *Pieris occidentalis* Reakirt
   f. vern./aut./alt. *calyce* W. H. Edwards
   II A. ssp. *nelsoni* W. H. Edwards
I. *Pieris protodice* Boisduval & LeConte (Fig. 1).


The type locality makes this name biologically unambiguous, as there is only one member of this species–group in the eastern United States. *Pieris protodice* is distributed over most of the U.S. generally below 2000 m but reaching 3000 m in New Mexico and Arizona. It is absent from the Pacific Northwest, north of the Central Valley of California, and from the northeastern states north of southwestern and southeastern Pennsylvania except along the immediate coast, north rarely to Massachusetts. It occurs in southern Ontario, at least sporadically. Its northern and upslope borders are extremely unstable; in cold-winter areas it is generally dependent on immigration and although it may breed, it overwinters only exceptionally. It is reported southward to southern Baja California, and on the mainland to Guatemala (Hovanitz, 1962), but is rare or absent in subtropical Florida although it has been collected on Cuba. It is striking that Boisduval recorded this species, along with *Colias eurytheme* ("edusa"), so far north so early. We will probably never know whether they occurred naturally or had already been introduced from further south.

*Pieris protodice* is always associated with sunny, warm, and dry environments. It is a "weedy," "colonizing," or "fugitive" species commonly found in highly disturbed, early-successional habitats, especially on sandy soils—often by roadsides, along railroad rights-of-way, or in urban vacant lots. In the west it often occurs in the dry washes and around corrals. In the northeast it is frequent on beaches. In most of its range its preferred hosts are the annual or winter-annual cruciferous weeds *Lepidium virginicum* L. and *L. densiflorum* Schrad. In California at low elevations it breeds extensively on *Brassica geniculata* (Desf.) Ball where no summer *Lepidium* spp. grow, and on the southwestern and Great Basin deserts on native *Lepidium* spp. and *Physaria* spp. and on *Sisymbrium altissimum* L. It rarely breeds on *Brassica nigra* (L.) Koch (a misdetermination by Hovanitz, 1962) but is capable of accepting a great variety of crucifers in captivity.

*Pieris protodice* is not known to be a permanent resident anywhere where the breeding season is too short for multiple broods. It has four to six broods in central California and about four at New York and Philadelphia. It is always much commoner and more widespread in late summer and autumn than earlier in the season. Winter is spent as a pupa in diapause under photoperiodic control.

Stocks of *P. protodice* from California, Arizona, Colorado, Texas, New
Fig. 1. *Pieris protodice* from New York (left-hand pair) and California (right-hand pair), summer phenotypes, dorsal and ventral surfaces. The New York male is phenotypically "intermediate," similar to the description of male *nasturtii* (see text).
Mexico, Pennsylvania, New Jersey, and New York have been crossed in various combinations with no significant loss of fertility or viability in continuous culture; wide geographic crosses may, however, disrupt the diapause response (Shapiro, unpublished).

Aspects of the biology of *P. protodice* in California are discussed in Shapiro, 1975a and of its reproductive biology in Shapiro, 1970.

**Pieris vernalis** W. H. Edwards (Fig. 2).


This is the phenotype of *P. protodice* which is produced when the larva develops on a long-night regime, regardless of temperature, and may be induced in the progeny of any female of any brood by appropriate treatment (Shapiro, 1968). Its production is not dependent on the occurrence of diapause, which may be inhibited under inducing photoperiods by high temperatures. Intergrades to the *vernalis* phenotype, and occasionally quite dark examples, are thus produced in autumn. This phenotype has not been reported for many localities where the summer broods of *P. protodice* occur; this is scarcely surprising given the fugitive nature of populations in this species. There are no differences in the expression of the phenotypes in Californian and northeastern stocks.

No type of *Pieris vernalis* exists. Despite information given Brown (1973) by New Jersey collectors, *Pieris protodice* is by no means "nearly extinct" in that state; in 1965 I collected over 500 in an afternoon in Camden. I have not, however, seen specimens of *vernalis* from Red Bank or elsewhere in Monmouth County, although I have several from nearby Staten Island. Because Staten Island is in New York state, I have refrained from designating any of these as a neotype in the hope that a genuine Red Bank specimen may turn up.

**Pieris nasturtii** W. H. Edwards.


This was a Boisduval manuscript name, resurrected by Edwards. Its tangled history is given by Brown (1973). Apparently Boisduval applied it to an animal in the *Pieris napi* group, but the specimens sent by Behr to Edwards as "nasturtii" were "an odd variety of protodice," as Edwards later wrote. No type, nor any specimen which can definitely be linked to this name, is extant.

The only member of this group found in or near San Francisco is *P. protodice* (except for the possible occurrence of *P. occidentalis* in the Santa Cruz mountains, see below). The descriptions strongly sug-
Fig. 2. *Pieris protodice* from New York (left) and California (right), *vernalis* phenotypes, dorsal and ventral surfaces.

suggest the late September–November phenotypes of Bay Area *P. protodice*, which are somewhat transitional to *vernalis*. The “coppery” color of the female is characteristic of old, faded-in-life specimens, as is the hyalinity. It thus appears that the name *nasturtii* W. H. Edwards refers to the
autumn brood of *protodice* and is, thus, infrasubspecific and without taxonomic standing. Its revival would in no way benefit taxonomy or biology, especially since variation from summer to winter phenotypes is essentially continuous in autumn in continuously breeding populations. In my publications the male description of *nasturtii* applies to my “intermediate” phenotypic grade.

**II. Pieris occidentalis** Reakirt (Fig. 3).


*Pieris occidentalis* occurs upslope and northward of *P. protodice* in western North America. The two species have been found sympatric at various locations from 1000–2500 m in the Rocky Mountains and Sierra Nevada, e.g., Donner Pass, California, where *P. occidentalis* is a permanent resident and *P. protodice* a breeding immigrant (Shapiro, 1975a). *Pieris occidentalis* ranges from Arctic Alaska and adjacent Canada south at increasing elevation to the southern Sierra Nevada of California and the Colorado Rockies (both above 2000 m), east to the Black Hills of South Dakota. It may extend into northern New Mexico. Its eastern limits in Canada are poorly understood. Its southern extent in the California Coast Ranges is unknown; it may reach Santa Cruz County, where it was apparently collected (by M. Doudoroff?) in 1930 (U. C. Berkeley collection). However, I have not seen any other Coast Range specimens from Mendocino County southward.

As noted in the introduction, Chang (1963) has described morphological differences between these two species. There are useful color and pattern differences; both sexes characteristically are more heavily and completely marked in *P. occidentalis* than in *P. protodice*; the wings of *P. occidentalis* appear thicker and more heavily scaled; the body is proportionally larger and usually hairier. The larva is more contrastingly colored and the pupa tends to be shorter and broader than in *P. protodice*. The chaetotaxy is uninvestigated. In areas of sympatry occasional interspecific matings may occur, but only 2 of 339 specimens collected at Donner Pass in 1973 were phenotypically ambiguous (Shapiro, 1975a). Although conspecific pairs are readily formed in cages, interspecific ones are not.

*Pieris occidentalis* is characteristically found at low densities in mountainous regions, where most captures are of “hilltopping” males. It normally breeds on montane crucifers such as *Arabis* and *Streptanthus* species and *Thlaspi alpestre* L., but becomes “weedy” and breeds at high density when presented with the opportunity, as in the railroad yard at
Fig. 3. *Pieris occidentalis* from the California Sierras, summer phenotypes, dorsal and ventral surfaces.

Donner Pass where its host is *Lepidium virginicum*. It is double-brooded at moderate elevations southward and possibly partially triple-brooded at its lower elevational limit in both Colorado and California (see below). Winter is spent as a diapausing pupa.

*Pieris calyce* W. H. Edwards (Fig. 4).


Edwards (1876) speculated that *calyce* might be a spring form of *Pieris occidentalis*, and in this he was correct. Brown (1973) demonstrates that the type was probably collected by Henry Edwards at Virginia City (elev. 1921 m) in March 1868 or 1869. At Virginia City a March specimen would be a very early example of the phenotype emerging from overwintering pupae in a bi- or trivoltine population of *occidentalis*. In such populations Shapiro (1973) has shown that *calyce* is the equivalent of *vernalis*, a seasonal, photoperiod-induced phenotype (although in *occidentalis* the control is less absolute). It can thus be obtained in the laboratory from the progeny of any female *occidentalis*. In its original
Fig. 4. *Pieris occidentalis* from the California Sierras, *calyce* phenotypes, dorsal and ventral surfaces.

sense, then, although proposed as a species-group name, *calyce* clearly refers to a seasonal phenotype and is infrasubspecific.

The name *calyce* has been used by some authors (e.g., Garth & Tilden, 1963) in a subspecific sense to apply to the univoltine animal of this group which occurs at or above tree-line in the Rockies, Sierras and Great Basin ranges. This animal is phenotypically indistinguishable from specimens collected one or two months earlier 1000 m lower. When stock of univoltine "*calyce*" from Loveland Pass, Colorado (3600 m) was reared under continuous light at 25°C it did not diapause, but developed directly in less than a month and produced light, *occidentalis* "summer" phenotypes (Shapiro, 1975b). These animals were successfully crossed with *P. occidentalis* from Donner Pass, California, with no decrease in fertility or viability. An apparently spring-univoltine "*calyce*" stock from Haystack Mountain in the eastern foothills of the Colorado Rockies has also been studied (Shapiro, 1976b).

The various populations of univoltine "*calyce*" are completely disjunct from one another on mountaintops. Present evidence implies that
each is independently derived locally from the multivoltine populations found downslope from it. Whether or not one is willing to accept "polytopic" subspecies, the use of *calyce* as a subspecific name is rendered inappropriate by the holotype data presented by Brown and should be discontinued. The name *calyce* is appropriately applicable to a phenotype, *not* a population.

Univoltine high-elevation populations have been found associated with *Thlaspi alpestre* and *Smelowskia calycina* (Desv.) Meyer in Colorado and *Erysimum perenne* (Wats. ex Cov.) Abrams at Sonora Peak, California. No definite host records are known to me. *Erysimum* is not a normal *Pieris* host (Chew, 1975), though *P. rapae* has been found on it at least once (Shapiro, 1975a).

**IIA. *Pieris occidentalis nelsoni* (Fig. 5).**

*Pieris nelsoni* W. H. Edwards.


This entity has been "lost" since its original description, although many reports of *P. occidentalis* in Alaska have been made. In July 1974, I studied a population at Fairbanks, Alaska in which "nelsoni" is the most frequent male phenotype, and subsequently bred it in the laboratory, crossed it with Sierran *occidentalis*, and obtained genetic data which are being reported elsewhere (Shapiro, 1976a). The *nelsoni* phenotype is
expressed with or without diapause. Ventrally, *nelsoni* is about as dark as *calyce*, but some specimens reared without diapause are as light as summer *occidentalis* (Shapiro, 1975c).

St. Michael's, now St. Michael, is on the south coast of Norton Sound in western Alaska. Now that *nelsoni* has also been found in interior Alaska, it appears that it is not an aberration but a valid and recognizable geographic subspecies, and I so treat it. It remains to be seen how far it extends into western Canada and the nature of its contact with nominate *occidentalis*. Some *nelsoni* characters are recognizable in populations of *occidentalis* as far south as Modoc Co., California (Shapiro, unpublished).

*P. o. nelsoni* has some resemblance to the *vernalis* phenotype of *P. protodice*, especially in the male. This is presumably the basis for its classification as a subspecies of *protodice* by Howe (1975). Although *nelsoni* has not been tested genetically with *protodice*, its conspecificity with that taxon can be ruled out on Chang's characters, on the shape of the pupa, and on geographical grounds—*nelsoni* is distributed some 2000 mi. from the nearest known *protodice* populations, and in a totally different climatic and vegetational region.

The only confirmed host of *nelsoni* is *Lepidium densiflorum*, a weed in the railroad yard at Fairbanks. As noted in Shapiro, 1975c and 1975d there is reason to suspect that this population may be facultatively bi-voltine.

**Relationships with Palaearctic Taxa**

Higgins & Riley (1970) treat *P. occidentalis* (and by implication *P. o. "calyce"*) as subspecies of the Palaearctic *Pieris callidice* Hübner. Brown (1973) follows this usage, under which there would be two Nearctic subspecies, *occidentalis* and *nelsoni*, as interpreted in the present paper. There are no genetic data bearing on the relationship. It is evident that there is great phenotypic similarity among these taxa, particularly between *callidice* and *nelsoni*. All populations of *callidice* known to me have a yellow ventral hindwing, a character unknown in any North American population; in this respect they parallel many Palaearctic members of the *Pieris napi* complex. W. H. Edwards wrote Henry Edwards concerning Nelson's specimen, March 15, 1882: "There is 1 male Pieris which I think is certainly Callidice. The upper side agrees perfectly with a male Callidice I have from Europe. The underside is not so heavily green dusted on the nervures and branches. If this is Callidice, it is the first American example I ever saw." The plausibility of the conspecificity hypothesis is increased by a report from K. M. Philip,
of the University of Alaska, that he has a male callidice from the River Omolon, Magadansk Oblast, NE Siberia—bridging the gap between the Alaskan populations and the nearest callidice recorded by Higgins and Riley, in Mongolia. It is very likely that further study will confirm the Higgins-Riley-Brown usage.

ACKNOWLEDGMENTS

I thank: K. M. Philip for data on Alaskan and Siberian material; R. & K. Stanford and M. Fisher for help in Colorado; and F. M. Brown for many kinds of aid, including the letter from W. H. Edwards, quoted above. This study has been supported by Grant D-804 from the Committee on Research, U.C. Davis.

LITERATURE CITED