# THE BIOLOGY OF NEARCTIC LEPIDOPTERA
# I. FOODPLANTS AND LIFE-HISTORIES OF COLORADO PAPILIONOIDEA

By Charles L. Remington
Osborn Zoological Laboratory, Yale University

In recent years the impact of evolutionary studies on taxonomy has greatly enhanced the interest in pairs or groups of species the members of which are almost indistinguishable according to the usual taxonomic criteria but which show no tendency to interbreed in nature and which differ in at least one important environmental specialization. For these Mayr (1940) has coined the convenient term "sibling species". In the Lepidoptera many instances have been discovered in which the siblings differ most strikingly in having special foodplant requirements, the food of each being unacceptable to the other (*e.g.*, Thorpe, 1928; Berger & Fontaine, 1947-48; Rawson & Ziegler, 1950). Some of these situations have been known for many years, and the siblings were formerly characterized as "foodplant races" of a single species.

The exposure of these unrecognized sympatric species in the Lepidoptera is very much hampered by the lack of precise knowledge of the species of foodplants on which each species can develop successfully. By such "success" we ultimately refer to the plant species on which the larvae of the insect will feed readily without fatalities from nutritional failure or from poisoning and on which they can develop to adulthood with normal fertility and inclination to mate. Several instances are now well understood in which: a) females occasionally oviposit on plants on which the larvae cannot thrive; b) larvae appear to prosper on a given plant, but very high losses occur through failure to pupate successfully; c) larvae seemingly develop normally on a given plant, producing adults as usual, but the adults of one or both sexes show no inclination to mate and are apparently sterile. But for most species this precise information is lacking, and even more limiting are the cases in which the food plants are completely unknown.

With the aim of providing some definite information on the foodplants of Lepidoptera I have begun collecting and preserving specimens of the plants, to be submitted to authoritative plant taxonomists for precise determinations. I propose to publish annotated lists of these foodplants from time to time. In the present contribution I have been substantially aided in obtaining plant identifications by my colleague, Dr. John R. Reeder, Curator of the Herbaria at Yale University, and I owe thanks to him and to the determiners: Dr. Reed C. Rollins, Director of the Gray Herbarium at Harvard University; Dr. S. F. Blake, Senior Botanist of the U. S. Division of Plant Exploration and Introductions; and Mr. Carleton R. Ball, of Washington, D. C. Specimens of most of the plants are being preserved for future reference in the Herbarium of Yale University. The initials of the determiner follow each species in brackets. The present paper is devoted to foodplants of Lepidoptera occurring in the state of Colorado. Unfortunately, in the following list little can yet be said about the suitability of the plants as permanent food. Notes on field observations are included. Records of the parasites obtained will be held for future publication.

## Papilionidae

1. *Papilio eurymedon* Lucas. On 15 July 1949, J. D. Eff saw a female oviposit on a leaf of *Crataegus rivularis* Nutt. [R.C.R.] on the western slope of Rabbit Ears Pass, in Routt Co., Colo. The larva eclosed on 29 July and was preserved. In California Comstock recorded the foodplant as *Rhamnus californica*. My correspondent there, W. H. Evans, wrote (*in litt.*): "A *Papilio eurymedon* laid four eggs on cultivated jasmine. Each year this species oviposits occasionally on this plant but I have never seen larvae on this vine. This year I gave them tender leaves on which they nibbled for several days, eating just barely enough to keep alive; then I gave them some of the native food plant, *Rhamnus crocea ilicifolia*. But all died without even tasting these leaves."

2. *Parnassius smintheus* Dbldy. & Hew. A single ovum was found 6 July 1949 attached to a leaf of *Oxytropis*

*lambertii* Pursh. [R.C.R.] near Nederland, Boulder Co., Colo. The ovum was fertile. This appears to be another case of a mistake by an ovipositing female, but there was no opportunity to test the nutritional suitability of *Oxytropis*. The usual foods of *Parnassius* are Crassulaceae, Saxifragaceae, and Papaveraceae. One must question Wright's records of *Viola* and *Vaccinium*. Females of *P. smintheus* from Nederland laid numerous ova on a native *Sedum* in confinement, 11 July 1949. The larvae emerged in the laboratory 12-14 September 1949, although they would normally have overwintered in the egg stage.

## PIERIDIDAE

3. *Euchloe ausonides* Bdv. During the summer of 1949 larvae and ova were found almost everywhere they were sought in Boulder County at all elevations between 5600′ and 9000′. At Nederland on 6 July several ova and a half-grown larva were taken on *Arabis drummondi* Gray and *Arabis fendleri* (Wats.) Greene var. *spatifolia* (Rydb.) Rollins and one small larva on *Erysimum capitatum* (Dougl.) Greene [all R.C.R.]. The next day, in Spring Gulch, several ova and young larvae and one half-grown larva were taken on *Arabis glabra* (L.) Bernh. [R.C.R.]. This *Arabis* has erect pods, and it was noted that *Euchloe* were absent entirely from a co-occurring and similarly common *Arabis* with decumbent pods (*spatifolia?*—not collected) and from *Erysimum*. At Mt. Flagstaff and 6500′ elevation in Boulder Canyon, on 8 July several large larvae were taken on huge plants of *Sisymbrium altissimum* L. [R.C.R.]. The next day a female *E. ausonides* was observed at Nederland ovipositing on small plants of *S. altissimum* [R.C.R.], and on 22 July several large larvae were found there on the same species of plant. Also on the 22nd, a female was seen laying two ova on *A. fendleri spatifolia*. These two ova were laid in a remarkable manner, being fastened by their sides to flower buds, rather than attached by the base and standing out at right angles to the substratum as is uniformly true of the thousands of other ova I have seen laid by females of a score or more species of Pierididae. It is clear that species of *Arabis* and *Sisym-*

*brium* are primary foodplants of *E. ausonides* and that the eggs are laid and the larvae feed largely on the flower buds and seed pods. The suitability of other plants as food remains uncertain. The literature on North American Euchloini too often refers simply to "Cruciferae". In Connecticut we have found that the larvae of *Anthocaris midea* (Hbn.) regularly die on some members of the family, even though wild females occasionally oviposit on them.

4. *Pieris rapae* (L.). On 9 July 1949, at Nederland, females were seen ovipositing on *Thlaspi arvense* L. [R.C.R.], and on the 11th a female oviposited on a large *Sisymbrium altissimum* L. [R.C.R.]. The ova were notably white when laid (see *P. protodice,* below). In general, *P. rapae* is still uncommon in the mountains, perhaps in part because it may not thrive on native Cruciferae, and the weedy forms are not very abundant there. In spite of the presence of *P. rapae, P. napi* is by far the commonest *Pieris* above 7000′; it is believed to have been largely extirpated from New England by *P. rapae* (Scudder, 1889, p. 1198). The much greater success of *P. napi* in the Rocky Mountains, where both species oviposit on *Thlaspi* (see *P. napi,* below), suggests that *Thlaspi* may be nutritionally inadequate or poisonous for *P. rapae.*

5. *Pieris protodice* Bdv. & Lec. There is no unanimity in the name for the Colorado population of low and middle altitudes. However, I am satisfied that it cannot be a species distinct from eastern *protodice.* Near and above timberline there is a very striking form (*calyce* Edw.?), which may be a separate species. *P. protodice* females were seen at Nederland on 9 July 1949, ovipositing on *Sisymbrium altissimum* L. [R.C.R.] and *Thlaspi arvense* L. [R.C.R.]. The new ova were distinctly yellowish, contrasting with some of *P. rapae* taken at the same time (see above).

6. *Pieris napi* (L.). On 5 July 1949, at Eldora in Boulder County, Colo., a female was seen laying several ova on tiny seedlings of *Thlaspi arvense* L. [R.C.R.]. The new eggs were white. At Eldora, on 28 July, many *Thlaspi* plants beside a dirt road were examined. Fifty-six ova and a few young larvae of *P. napi* were found. Fifty-one ova

were on the underside of leaves; five were on the lower surface of large seed-silicles. Thirty of these ova were present singly on leaves or silicles; there were two ova on each of twelve leaves and one silicle (once one ovum was laid on top of the other); one leaf bore three ova. It was not possible to determine how often two or three ova were laid at a single visit of a female, but on 5 July I actually saw the female lay two ova side by side on certain leaves. At Rabbit Ears Pass, Routt Co., Colo., on 15 July, Jeanne E. Remington saw a *napi* female lay several ova on *Arabis drummondi* Gray [R.C.R.]. In Europe *P. napi* has been reared on plants of at least seven genera of Cruciferae (including *Sisymbrium*), but in Coos Co., New Hampshire, the basic, if not exclusive, food is *Dentaria,* according to information received from Donald J. Lennox.

7. *Colias eurytheme* Bdv. This name is used here for all orange members of the *eurytheme-philodice* complex of North America. The pure yellow individuals (*philodice*) are not common in the mountains in Boulder County, but observations suggest that they are permanent residents and survive the winter up to high altitudes. As the season progresses, huge orange individuals (*eurytheme*) begin to appear and increase in numbers for some weeks. There is clearly some hybridizing with *philodice,* as in all other regions where the two species are sympatric; I have a small series from Boulder County taken in 1949 above 8,000′, which includes two males and one female of *philodice,* three males and eight females of "pure" *eurytheme,* two females which look like my laboratory backcrosses to *eurytheme,* one female like my experimental $F_1$ hybrids, and three white females not certainly placeable. The determination of foodplants of these two species of *Colias* in any locality is of great interest, so it is regrettable that the following records are so scanty. On 6 July 1949 a "pure" *eurytheme* female was seen ovipositing on *Thermopsis montana* Nutt. [R.C.R.]. Six days later at Nederland a female *eurytheme* laid several ova on the upperside of leaves of an *Astragalus* which Dr. Rollins tentatively identified as "*racemosus* Pursh.?" (fruit was not collected).

SATYRIDAE

8. *Oeneis brucei* (Edw.). A female taken by J. D. Eff at Berthoud Pass (elev. between 11,000′ and 12,000′), Gilpin Co., Colo., was confined 16 July 1949 over a sedge. It oviposited freely at Eldora, at an altitude about 3,000 feet lower than the normal occurrence at Berthoud. The larvae emerged and fed readily, but all died en route to Connecticut or soon after arrival there.

9. *Oeneis lucilla* B. & McD. A female taken at about 13,000′ on Mt. Evans, Clear Creek Co., Colo., was confined over sedge. At Eldora, over 4,000′ lower than the point of capture, this female laid several ova on 29 July 1949. My records do not show whether the ova were fertile; in the collection are four preserved ova but no larvae.

10. *Erebia epipsodea* Butler. On 11 July 1949 females from Eldora were confined, each over a grass and a sedge. In two days 19 ova were laid, nearly all on the grass, but a few on the sedge; the grass was distinctly preferred for oviposition. The ova were fertile.

NYMPHALIDIDAE

11. *Boloria eunomia alticola* (B. & McD.). On 30 July 1949 females were found in fair numbers in a large alpine bog at Caribou (elev. 10,000′), Boulder Co., Colo. Many were followed closely, but they did not seem strongly-inclined to oviposit and, further, the strong wind made it difficult to keep track of a given individual. However, one female was observed ovipositing and the two ova were recovered. The behavior of this female was unlike that of all others (of both sexes) watched. This one alighted on the lowest plants on small hummocks rising a few inches above the standing water of the bog; the others always came to rest on shrubs and the flowers of tall herbs. The ovipositing female crawled for several seconds into the rather thick low plants (largely Graminales and a tiny *Thalictrum*) and stopped twice to oviposit on leaves of *Thalictrum alpinum* L. var. *hebetum* Boiv. [R.C.R.]. The ova were later lost, and captive females did not oviposit,

so the suitability of *Thalictrum* as a foodplant was not tested.

Our knowledge of foodplants for this genus is in a very confused state. A wide spectrum of plants has been recorded (*e.g.*, see Scudder, 1889, p. 587) as foodplants. However, information is lacking as to the plants **on which larvae were successfully reared.** From our experiences with *B. toddi* (Holland) and *B. selene myrina* (Cramer) in Connecticut, we believe that *Viola* spp. are the only suitable foodplants, but a large series of field observations shows that the females of both species characteristically avoid *Viola* for actual oviposition, although in many instances violets were found a few inches away. Most of the ova were fastened to dead twigs and grass! I suspect that most, if not all, of the recorded "foodplants" of *Boloria,* other than *Viola,* actually represent oviposition observations rather than feeding records. It is doubted that *Thalictrum* is the food of *B. eunomia alticola.*

12. *Boloria selene tollandensis* (B. & Benj.). At the type locality, in the great bogs at Tolland, Gilpin Co., Colo., on 22 July 1949 a female under observation laid an ovum on a dead *Salix* twig several inches above the ground and several feet from the nearest living *Salix.* The ovum was preserved before eclosion. I believe that the actual foodplants at Tolland are *Viola* spp. and that this female exhibited the same habit described above for *B. selene myrina* in Connecticut.

13. *Nymphalis milberti* (Godt.). Several clusters of large larvae were found on 9 and 11 July 1949, on extensively defoliated clumps of *Urtica gracilis* Ait. [R.C.R.] growing in a trash dump near Nederland (elev. 8000′), Boulder Co., Colo. On the same plants were single, concealed larvae of *Vanessa atalanta.* On 25 July many larvae of *N. milberti* of all sizes were found on stream-side clumps of *Urtica* at an elevation of 7200′ in Boulder Canyon. In the same clumps were several full-grown larvae of *V. atalanta* and four solitary larvae of *Polygonia satyrus.* Many larvae and pupae of the Nederland *N. milberti* were preserved; the remainder completed development on *U.*

*gracilis* and emerged during several days beginning on 26 July.

14. *Vanessa atalanta* (L.). Two sites of collection of larvae were mentioned above (see *N. milberti*). In addition a single larva was taken on *Urtica* at Rabbit Ears Pass, Routt Co., Colo., on 15 July 1949. In the Boulder Canyon clumps a pupa of *V. atalanta* was found in one of the webbed-leaf nests characteristic of *V. atalanta*. The larvae of the three *Urtica*-feeding Nymphalididae were easily distinguishable by their habits: *V. atalanta* was always in snug nests and always solitary; *N. milberti* was always gregarious, although the social groups were much subdivided and dispersed toward the end of development; *P. satyrus* constructed at best very simple nests and was not notably gregarious, and in addition the pair of branched head-horns and the broad, creamy dorsal stripe were distinctive. The *V. atalanta* larvae were very heavily parasitized by Larvaevoridae, and four minute Chalcidoidea emerged (as hyperparasites?) from a pupa.

15. *Vanessa cardui* (L.). Many larvae of all sizes were found on *Cirsium undulatum* (Nutt.) Spreng. [R.C.R.] near Spring Gulch, 9 mi. n.w. of Boulder, Colo., on 7 July 1949; two larval webs each contained a dead larva and a cocoon of one of the Ichneumonidae. Females of *V. cardui* were seen on 9 July ovipositing repeatedly on *Artemisia ludovicianus* Nutt. var. *gnaphalodes* (Nutt.) T. & G. [R.C.R.] in clearings in the pine woods near Nederland, Colo. This being an atypical foodplant, special care was taken to be sure that the butterflies were all *V. cardui*, that ova were actually laid, and that the *Artemisia* was always the plant selected. It is not known whether the larvae fed and matured on *A. gnaphalodes*. No thistles were found in these clearings. In 1949 *V. cardui* was unusually numerous in Boulder County as well as elsewhere in North America (see Eff, 1950), and these ovipositing females were probably second generation descendants of immigrants. *V. cardui* appears to oviposit commonly on plants of doubtful adequacy during these great emigrations and then to use only *Cirsium* and other thistles during the

intervening years of much less abundance. In the vicinity of St. Louis, Missouri, I never found larvae of *V. cardui* on anything but thistles except in the years of great influx, but then garden hollyhocks (*Althea rosea* Cav.) were always heavily infested. There is a very long list of recorded foodplants for *V. cardui* in North America and Eurasia, but *Artemisia* seems to be previously unlisted. Careful tests of the whole range of recorded plants for their suitability to *V. cardui* for development would be valuable.

16. *Vanessa virginiensis* (Drury). Several solitary larvae were found on 9 July 1949 in their familiar nests on *Antennaria aprica* Greene [S.F.B.] near Nederland, Colo. This is an uncommon butterfly in the mountains, and its larvae were found more easily than the adults.

17. *Polygonia satyrus* (Edw.). On 25 July 1949 one full-grown and three half-grown larvae were found on streamside *Urtica* (*U. gracilis?*) clumps at an elevation of 7200′ in Boulder Canyon, Colo. These were interspersed with larvae of *Vanessa atalanta* and *Nymphalis milberti* (see above). One larva was allowed to complete development, and the imago emerged on 8 August 1949. From the fact that they are allopatric and from the appearance and foodplant of the larvae I suspect that *P. comma* and *P. satyrus* are actually conspecific; the pattern and color differences of the adults are slight enough.

18. *Limenitis weidemeyerii* Edw. A female was seen laying several ova on the tips of leaves of *Salix* along a stream, at Eldora, Boulder Co., Colo., on 18 July 1949. One ovum laid on *Salix drummondiana* Barratt var. *subcaerulea* (Piper) Ball [C.R.B.] was recovered; the larva emerged on 30 July and was preserved.

## References

Berger, L. A. and M. Fontaine.

1947-48. Une espèce méconnue du genre *Colias* F. Lambillionea, 47:91-98; 48:12-15, 21-24, 90-110, 1 pl.

Eff, J. Donald.

1950. Rocky Mountains — New Mexico, Utah, to Alberta, *in* The Field Season Summary of North American Lepidoptera for 1949. Lepidopterists' News, 3:90-93.

MAYR, ERNST.
1940. Speciation Phenomena in Birds. Amer. Naturalist, 74:249-278.
RAWSON, GEORGE W. and J. BENJAMIN ZIEGLER.
1950. A new species of *Mitoura* Scudder from the Pine Barrens of New Jersey. Journ. N. Y. Ent. Soc., 58:69-82.
SCUDDER, SAMUEL HUBBARD.
1889. The Butterflies of the Eastern United States and Canada. 1: 766 pp. Cambridge, Mass.
THORPE, W. H.
1928. Biological Races in *Hyponomeuta padella* L. Journ. Linn. Soc. (Zool.), 36: 621-634.

---

HETEROPONERA MAYR REINSTATED (HYMENOPTERA: FORMICIDAE). — *Heteroponera* Mayr (1887, Verh. zool.-bot. Ges. Wien, *37*: 533) has remained suppressed as a synonym of *Acanthoponera* Mayr for many years. Wheeler (1923, *loc. cit.*) has shown, however that *Acanthoponera* can be split into two groups; one group (*Acanthoponera* s. str.) having the tarsal claws with an extra, strong tooth and a basal lobe (or tooth), while the second group (*Anacanthoponera* Wheeler) has the tarsal claws at most with a single, weak median tooth. In this second group, Wheeler included *Heteroponera carinifrons* Mayr, and since *Heteroponera,* with the genotype *H. carinifrons,* has precedence, it must be **reinstated as a good genus.** *Anacanthoponera* Wheeler (1923, Psyche, *30*: 176, as a subgenus of *Acanthoponera*) is a **new synonym** of *Heteroponera,* since the genotype, *Ponera dolo* Roger, is congeneric with *H. carinifrons.*

*Acanthoponera* is neotropical, and has well developed propodeal teeth and the petiolar apex produced as a long tooth or spine; Kusnezov (*in litt.*) finds *A. mucronata* to have 6, 4 palpal segmentation. *Heteroponera* is neotropical and Australasian, and the propodeal teeth and dentiform petiolar apex are absent or feebly developed; *H. imbellis* Emery has 3, 3 palpal segmentation (my dissection). Until more species can be critically examined, *Acanthoponera* and *Heteroponera* should be considered as distinct genera. *Acanthoponera* appears to be the most generalized living member of the Ectatommini, and is probably close to the stem from which the proceratiines, the myrmicines and *Paraponera* arose. — W. L. BROWN, JR., Museum of Comparative Zoology, Harvard University.