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BUTTERFLIES FROM THE MIDDLE EOCENE: THE EARLIEST OCCURRENCE OF FOSSIL PAPILIONOIDEA (LEPIDOPTERA)

By Christopher J. Durden and Hugh Rose

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W. W. Newcomb, Director

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BUTTERFLIES FROM THE MIDDLE EOCENE: THE EARLIEST OCCURRENCE OF FOSSIL PAPILIONOIDEA (LEPIDOPTERA)[1]

By Christopher J. Durden[2] and Hugh Rose[3]

ABSTRACT

Three fossil butterflies recently collected from the Green River Shale of Colorado extend the known range of Rhopalocera eight to ten million years back, to 48 Ma. *Praepapilio colorado* n. g., n. sp., and *P. gracilis* n. sp. are primitive Papilionidae related to the modern *Baronia brevicornis* Salvin, but they require a new subfamily, Praepapilioninae. *Riodinella nympha* n. g., n. sp. is a primitive member of the Lycaenidae, related to modern *Ancyluris, Riodina,* and *Rhetus,* in the tribe Riodinidi.

INTRODUCTION

With approximately 194,000 living species, the Lepidoptera is, after the Coleoptera with some 350,000, species, the second most diverse order of organisms. It is underrepresented in the fossil record (Scudder 1875, 1891, 1892; Handlirsch 1925; Mackay 1970; Kuhne 1973; Shields 1976). Neogene (later Tertiary) reports include 33 ditrysian moths, 18 butterflies, and 16 unplaced Lepidoptera, and more are known from amber of Chiapas and the Dominican Republic. Paleogene (earlier Tertiary) reports include one monotrysian moth, 41 ditrysian moths, 24 butterflies, and one unplaced lepidopteran. Cretaceous finds include only two records of monotrysian moths in amber. The oldest records of butterflies have been the compression fossils of Florissant National Monument, Colorado (Scudder 1889, 1890; Cockerell 1913; Brown 1976; Durden 1962[4]) in age, about 38 Ma[5] of the Sannoisian Stage of the Oligocene Epoch, and the amber inclusions of the Baltic Coast[6] of early Oligocene and probably latest Eocene age.

Through the efforts of Allen Graffham[7] it was possible for us to obtain

[1] Accepted for publication September 12, 1977.
[2] Texas Memorial Museum, 2400 Trinity Street, Austin, Texas 78705.
[3] Governor Wentworth Road, Amherst, New Hampshire 03031.
[4] Unpublished notes on a fossil butterfly in the Florissant Fossil Forest Museum.
[5] Ma = million years in SI units (Systême international d'unités). The Thirtynine Mile Volcanic Series, which dammed south-flowing valleys in which accumulated the Antero and Florissant Formations (Durden 1966), has a K/A age of approximately 38 Ma (Geologic Atlas of the Rocky Mountains Region, 1972, page 235). Age based on mammalian fossils is early Chadronian (MacGinitie 1953).
[6] Berendt 1854-6, Conwentz 1886, Evers 1907. Most amber specimens are reworked float from Baltic strand lines, but even subsurface finds from the "Blue Earth" of Samland are of imprecisely known age.
[7] Geological Enterprises, Ardmore, Oklahoma.

part of the first butterfly found in the Green River Formation[8]. Subsequent inquiry has located two additional specimens, owned by Black Hills Minerals[9]. These have been borrowed for study and are described here with hopes that other material that may be in private collections will be made available for study. The other part of the third specimen found has been loaned for study by David Douglas[10]. These three specimens were collected by Bill Hawes, whose collecting efforts and initial care with the specimens are greatly appreciated.

The fossils were photographed at 0.9 X magnification on the negative. Negatives were made on Kodak Verichrome 120 film (58 X 92 mm), illuminated by 350 watt tungsten. Filters were used to enhance color contrast, with greatest separation using a Wratten No. 50 deep blue filter on the camera, with a 15 second exposure at f.32. Enlargements were made at 3.22 X. Interpretive drawings were prepared on electrostatic copies of these enlargements, with reference to the photographs and with corrections made with reference to the specimens. Specimens were studied under a Leitz stereoscopic microscope at 32 X and 96 X magnification. After interpretive drawings and pattern reconstructions were made, each specimen was run through the family group keys provided by Ehrlich (1958), with reference to the discussion of characters by Munroe (1961) and by Munroe and Ehrlich (1960).

Family PAPILIONIDAE Leach, 1815
(nom. transl. Doubleday, 1846, *ex* Papilionida)

Characters agreeing with the family:

Face anteriorly convex, somewhat protuberant.
Laterofacial sutures separated from eye margins.
Paraocular areas relatively small.
Interantennal distance 0.3 of interocular distance.
Anterior tentorial pits high on face.
Palpi 0.4 of thoracic length.
Cervical sclerites united beneath neck by narrow sclerotic band.
Metatergum not completely overhung by mesotergum.
Vein V3 of forewing present, terminating on posterior margin of wing.
Cell Sc-R present in hindwing.

[8] Scudder 1890, 1891, Shields 1976.
[9] After acceptance of the manuscript a fourth specimen, apparently a satyrine nymphalid, was acquired from the collector, Lloyd Gunther, who found it at the Raydome locality in November, 1976.
[10] The Prehistoric Life Museum, Yachats, Oregon.

Anomalous characters:

Posterior margin of cell trifid.
Hindwing with vein V3 well developed.

Discussion:

Primitive characters deduced by previous students may be evaluated with reference to occurrence in these fossils. Ford (1944, 1944a) supposed the mediocubital tail to be primitive but this was doubted by Ehrlich (1968). Ehrlich supposed the palpi to be of normal length as they are here, contrary to Ford's prediction. Brown (pers. comm.) has suggested that the frequent abnormal length of the palpi in fossil butterflies may be due to compression. One of our fossils (Raydome 2) displays a ventral abdominal structure that may be a sphragis (Eltringham 1912, Bryk 1913). This is a vaginal seal deposited by the male, which prevents subsequent mating. It is found in all living subfamilies of Papilionidae and also in subfamily Acraeinae of the Nymphalidae. Ford considered this character primitive, Ehrlich supposed it to be advanced.

Subfamily BARONIINAE Bryk, 1913
(nom. transl. Ehrlich, 1958, *ex* Baroniidae)

Characters agreeing with the subfamily:

Patagia with narrow elongate sclerotization.
Vein R is 4-branched.
Hindwing has vein V3 well developed.

Anomalous characters:

Antennae not close together, interantennal distance exceeds width of socket.
Labial palpi not very short, 0.4 of thoracic length and longer than head.
Forewing with distinct basal segment of PCu (crossvein Cu-V of Ehrlich).

Discussion:

Some would argue that, with the posterior margin of the cell trifid, our material falls outside the Papilionidae. There are a number of described varieties of *Baronia brevicornis* including: *brevicornis* Salvin 1893; *eusemna* Dyar 1912; *phronima* Dyar 1912; *puella* Boullet 1913; *aureomaculata* Bryk 1913; *intemerata* Hoffmann 1940; and *luteocincta* Hoffmann 1940. In the varieties with more rounded wings, the trifid condition of the posterior cell margin is approached through proximal recession of the base of M2 into the cell. The well developed vein V3 of the hindwing is shared only with *Baronia* among the Papilionidae.

There is a temptation to separate our material and *Baronia* into a different family. The life history of *Baronia brevicornis* has been reported by Vazquez and Perez (1962). They find a smooth egg, as in other Papilionidae, basally flattened as in Parnassiinae. The larva feeds at night, resting during the day in a shelter formed by drawing the leaflets around a midrib with silk. The foodplant is *Acacia cymbispina* Sprague and Riley. Several species of *Acacia* are reported from Tertiary rocks as old as Paleocene (La Motte 1952). Five larval instars are deduced from measurements of larval head capsules of collected larvae. The larva has an eversible osmaterium which was found by Eisner et al. (1970) to secrete the same acids (isobutyric and 2-methyl butyric) as are secreted by Papilionidi and Leptocircidi, but not by *Battus polydamas* L. in the Troididi, which secretes only a mixture including two unidentified sesquiterpenes. The Parnassiinae have not been investigated for their osmaterial chemistry; the osmaterium of *Parnassius phoebus xanthus* Ehrmann, however, has an odor resembling the osmaterium of *Papilio machaon* L. rather than the osmaterium of *Battus philenor* L. The osmaterium with its butyric acid secretions appears to be a general feature of Papilionidae and probably arose early in the evolution of the family. It may have originated outside the family as a modification of the dorsal gland found elsewhere in the Lycaenidae. Prolegs of the first instar larva are with irregular circles of crochets, already well on the ontogenetic series toward the harmoncopodous condition found in arboreal caterpillars (Hinton 1952). The integument of the larva is ornamented with small short hairs similar to those of the Parnassiinae, the Pieridae, the Satyrinae, the Lycaenidae and the Hesperiidae. The prothoracic plate is large, recalling its usual condition in the Hesperiidae, a condition not found in Papilioninae or in Parnassiinae. The pupa is squat and ovoid as in other ground pupating forms. It is slightly more angular than the pupa of *Parnassius*, which it otherwise resembles. The rugose ornamentation of the pupal integument resembles that of *Parnassius.* Abdominal width in the *Baronia* pupa is appreciably greater than thoracic width, with proportions most closely matched among the Lycaenidae. This condition in *Baronia* is probably to accommodate fat storage in the abdomen to sustain the pupa through aestivation that lasts from midsummer to early summer (May and June) of the following year.

Baronia differs from other butterflies except Lycaenidae, in the dorsal notch or downward curve of the mesodiscrimen at its junction with the furca in the interior of the thorax. Because our material does not have this internal character preserved, and because it differs in a number of characters from *Baronia* it appears best to leave Baroniinae as a subfamily of Papilionidae following Ehrlich (1958) and Munroe and Ehrlich (1960) and to propose a new subfamily for the fossil material, to be placed at present in the Papilioninae.

Subfamily PRAEPAPILIONINAE new
(Type genus: *Praepapilio* new genus)

Characters of the subfamily disagreeing with the Baroniinae:

Interantennal distance exceeds width of socket.
Labial palpi longer than head.
Forewing with distinct basal segment of PCu.
Mediocubital tail present.
Vein R2 base at cell end, not proximal to it.
Bases of recurrent veins M1 and M2 of forewing nearly equidistant from each other, from Rs and from M3 on discocellular crossvein.
Posterior border of cell strongly trifid.
Humeral vein not forked, directed distally and angled in the middle.
Veins M3 and Cu1 forked at, or just distal to discocellular crossvein.
PCu a pigmented, well-sclerotized crease in both forewing and hindwing.

Discussion:

This subfamily is in the ancestry of Papilioninae and Parnassiinae, and, if it bears a lycaenoid mesodiscrimen it may also be in the ancestry of Baroniinae. In some respects it is closer to Lycaenidae *s.1.* than are any other Papilionidae.

PRAEPAPILIO new genus
(Type species: *P. colorado* new species)

Diagnostic characters:

Forewing costa concave at end of Sc.
Vein R1 originates proximal to cell end, terminates on costa.
Vein R2 originates at cell end, terminates at wing apex.
Veins R1 to R4 form a distally expanded anterior pecten which grades evenly into the mediocubital series.
Vein M1, a recurrent vein nearly equidistant from Rs and M2 basally.
M2 a recurrent vein nearly equidistant from M1 and M3 basally.
Vein M3 forked with Cu1 proximal to cell end.
Veins M3, Cu1, Cu2 form a posterior, distally expanded pecten (trifid).
PCu is a conspicuous sclerotized crease in the wing.
Cu-V crossvein, interpreted as base of PCu[11] is as strongly sclerotized as PCu and as weak as it is in some living Papilioninae.

[11] The term PCu is used here for the postcubital vein following Snodgrass (1935) to emphasize its distinctness from the forks of the cubitus. This vein is called Cu2 by Comstock (1918), CuP by Riek (1970), and P by Hamilton (1972).

Vein V1+2[12] is subparallel to posterior wing margin.
Vein V3 originates on V1+2 distal to crossvein to PCu, terminates on wing margin at 0.15 from base to tornus.
On hindwing, humeral vein is directed distally, strongly bent in midsection, and concave distally.
Basal cell is formed by Sc (with base of humeral vein) and R (bearing base of Rs) which are fused distally at 0.2 to 0.25 discal cell length. Vein Sc+R1 smoothly approaches costa, terminating in series with the medicubital veins.
Rs forms 0.65 to 0.70 of anterior border of discal cell.
Vein M1 is forked with Rs proximal to cell end.
Vein M2 is recurrent, based on discocellular crossvein 0.4 to 0.45 posterior in cell width.
Sc+R1, Rs, M1, M2, M3, Cu1, Cu2, and PCu intervein spaces form a series even in width or, spaces Sc+R1-Rs and M3 to PCu are slightly larger. Vein M3 is forked with Cu1 at or just proximal to cell end, terminates at anterior base of tail.
Vein Cu2 arises 0.6 to 0.7 from cell base, terminates posterior to tail base.
Veins M3, Cu1,Cu2 form an even posterior pecten.
PCu originating on V1+2 distal to origin of V3 as a conspicuously sclerotized crease terminating on wing margin.
Vein V1+2 terminates on abdominal slope of tornus.
Vein V3 terminates on abdominal margin at 0.6 of length to tornus, just distal to end of abdominal lobe.

Praepapilio colorado new species

HOLOTYPE: Figs. 1, 6A, 6B; Raydome butterfly No. 1 (Hugh Rose Collection).
TYPE LOCALITY: Colorado, Rio Blanco Co., Raydome.
TYPE HORIZON: Green River Shale, Parachute Creek Member, upper beds.
AGE: Eocene, Lutetian or Biarritzian Stage; about 48 Ma.

Description:

Based on wing shape, abdominal dimensions preserved as deformation of matrix, and position of abdominal margin of hindwing, this specimen is a female. Forewing proportions are: width, 0.569 of length; cell length, 0.466 of wing length; posterior edge, 0.655 of wing length. Hindwing proportions are: width, 0.742 of length; mediocubital tail, 0.090 of wing length; cell length, 0.371 of wing length; abdominal margin, 0.843 of wing length.

[12] In some butterflies and moths the fused character of this vein is demonstrated by separate bases of V1 and V2, which are fused distally.

Preservation of ground color is light as four shades which are (1) probably brown or black, (2) probably red, (3) probably yellow, and (4) probably white. A row of patches of structural color appears to have been present in the position of scintilla[13] of the first macular band. These patches were blue or green by homology with living Papilionidae. In the forewing there are no "white" spots of shade 4. Patches of shade 3 "yellow" occur in seven locations:

(1) A series of Praemacular lacunae at 0.95 from wing base, from vein M2 increasing in size to vein PCu where they touch and decreasing in size to vein V1+2.

(2) The first intramacular lacunae from 0.8 to 0.9 from wing base in intervein spaces R2-3, R3-4, R4-M1, and M1-2, longest in the first two, shortest in the last.

(3) The 1-2 intermacular lacunae, a band of confluent spots at 0.6 to 0.72 from wing base in intervein spaces from R2 to M1, widest in space Rs-M1, constricted along Rs with veins darkened to isolate a small spot at base of space R3-4.

(4) A posterior reappearance of this band as a row of distally blunt, proximally acute patches at 0.8 to 0.9 from wing base, longest posterior to vein V1+2, shorter but of even width in the anterior spaces to Cu1 where a Y-shaped patch has distal arm continuing the trend into space M3-Cu1 in line with the costal series of this spotband, and the proximal arm angled into intramacular position 2.

(5) A third intramacular small spot just inside cell end.

(6) The 3-4 intermacular, most prominent spot in the cell at 0.35 of wing length, which is narrowly confluent across Cu1 to continue this lacunal band at 0.55 to 0.75 from wing base, widest in space Cu1-2, narrowing posteriorly and cut by dark lines along the veins.

(7) A 4-5 intermacular patch near cell base and in spaces Cu-PCu, PCu-V1+2, and post-V1+2.

Shade 2 "red" is absent from the forewing.

Shade 1 "brown" surrounds the yellow patches and is interpreted to include six bands:

(1) The terminal band.

[13] The system of color pattern description is derived from Nabokov (1944, 1945, 1949). This system was devised for patterns with dark spots on light ground. Application to patterns with light spots on dark ground, formed by fusion of maculae to form bands (probably the reverse of what happened phylogenetically, but the concept is reversible) requires a term for light spots. We call these lacunae. Reference to Papilionidae such as *Parnassius hardwickii* Gray shows that scintilla (structural blue) appears in the intramacular lacunae of macular band 1, and aurora (red, orange, yellow) appears in the intramacular lacunae of band 2. Thus, in *Lycaeides* the semimacular fraction of band 1 is fused with the praeterminal marks of band 2, and macule 1 of Nabokov is, in our terminology, a fused band 1 + 2. Among living Papilionidae, *Parnassius* has a well developed macular pattern, particularly in Asian species, while *Sericinus* and *Zerynthia* have well developed lacunal patterns with similarly located scintilla and aurora. Position of a mark on the wing is given by coordinates, using intervein location as one, and proportion of distance from base to edge of wing as the other.

Fig. 1.—*Praepapilio colorado* n. g., n. sp., HOLOTYPE, Raydome butterfly No. 1 (Hugh Rose Collection). Bar scale is one centimeter.

(2) The first macular band, split anterior to M3 into praeterminal and semimacular fractions.

(3) The second macular band, confluent with praeterminal fraction of third macular band posterior to M3, covering cell end, then forked away from third macular band toward margin, ending at Cu1.

(4) The third semimacular band, setting off cell end spot, but confluent across fork M3 off Cu1 to join praeterminal fraction in space M3-Cu1, then posteriorly parallel to wing margin.

(5) The fourth macular band crossing cell, angled in space Cu1-2, and passing straight to hind margin parallel to third band.

(6) The fifth macular band, sessile as the basal shade.

In the hindwing all pattern elements are present. Shade 3 "yellow" occurs as four bands.

(1) The praemacular lacunae, elongate tornally in space V1+2-V3, largest in space Cu1-2, smallest in space Rs-M1 and obsolete in space Sc+R1-Rs.

(2) The proximal border, convex basally, of each intervein space of intramacular lacunae 2, forming also the anterior halo and posterior border of this lacuna in space Sc+R1-Rs.

(3) The 2-3 intermacular spotband at 0.55 from wing base, narrowed from the costal edge to space Cu1-2.

(4) The 3-4 intermacular patch, at the costa from base to 0.4, narrowed across cell nearly to cell end, then widened in space Cu2-PCu from 0.15 to 0.5 from wing base.

Shade 4 "white" extends as a spotband in the center of the second intramacular lacunae with both edges convex proximally and each spot separated by darkened vein border, largest in space Cu1-2 and absent anterior to Sc+R1 and posterior to V1+2.

Shade 2 "red" occurs in the distal edge of the second intramacular lacunae from Sc+R1 to V3. This shade is the aurora of Lycaenidae and the "applespot" of Parnassiinae. Each patch is a proximal apex chevron, smallest in space PCu-V1+2, largest in space Rs-M1, and a reniform spot, convex distally in space Sc+R1-Rs.

The scintilla "blue" occupies the first intramacular lacunae from Rs to V1+2, largest in space M3-Cu1.

Shade 1 "brown" surrounds the lacunae and is interpreted to include five bands:

(1) The terminal band.

(2) The first macular band fused with the praeterminal fraction of band 2.

(3) The semimacular fraction of band 2 coalesced with band 3 posterior to Cu2.

(4) Macular band 3 coalesced with vannal shade at PCu.

(5) Macular band 4 as basal shade with distal extension on Rs and toothlike projection on Cu and forming vannal shade.

Dimensions:

Forewing: base to apex, 37.0 mm; base to tornus, 23.6 mm; apex to tornus, 27.4 mm. Vein segments[14]: Sc, 21.5 mm; R, 14.3 mm; Ra (R1), 14.0 mm; Rp, 1.6 mm; Rpa (R2), 19.0 mm; Rp^2, 7.5 mm; Rp^2a (R3), 12.1 mm; Rp^3 (R4), 11.5 mm; Ma (M1), 17.1 mm; Mp (M2), 16.2 mm; Cu, 6.8 mm; Cua, 6.8 mm; Cua^2 (M3), 16.5 mm; Cuap (Cu1), 14.9 mm; Cup (Cu2), 20.5 mm; V, 0.6 mm; Va (PCu), 25.2 mm; Vap, 0.6 mm; Vapa (V1+2), 23.3 mm; Vap^2 (V3), 2.2 mm; Cu-V crossvein (base PCu), 0.6 mm; discocellular crossveins, 1.6 mm, 1.9 mm, 1.9 mm. Forewing cell width, 5.0 mm; length, 16.8 mm.

Hindwing: base to tail base, 25.2 mm; base to tail tip, 28.0 mm; tornus to costal edge, 19.9 mm; base to subcostal angle, 18.7 mm; base to tornal angle, 23.9 mm; base to abdominal angle, 10.9 mm. Vein segments: Sc, 1.6 mm; Sca (humeral), 1.9 mm; Scp, 1.6 mm; R, 1.9 mm; Ra, 1.6 mm; Sc+Ra (R1), 17.7 mm; Rp, 5.0 mm; Rpa (Rs), 17.4 mm; Rp^2 (M1), 18.7 mm; M (M2), 14.9 mm; Cu, 6.8 mm; Cua, 4.4 mm; Cua^2 (M3), 15.9 mm; Cuap (Cu1), 16.5 mm; Cup (Cu2), 19.0 mm; V, 1.2 mm; Va, 1.2 mm; Va^2 (PCu), 21.8 mm; Vap (V1+2), 20.2 mm; Vp (V3), 12.7 mm; discocellular crossveins, 1.6 mm, 1.9 mm. Hindwing cell width, 3.1 mm; length, 10.3 mm; subcostal cell width, 0.6 mm; length, 2.5 mm.

Head: width, 3.7 mm; interocular width, 1.2 mm; cephalic length to labrum, 1.6 mm; palpal projection anterior to labrum, 1.9 mm.

Thorax: tegulum length, 2.2 mm; width, 0.8 mm; mesotergum length, 4.4 mm; metatergum (dorsal exposure) length, 1.4 mm; width, 4.4 mm.

Abdomen (outline indicated by matrix distortion): approximate length, 14.6 mm; approximate width, 5.3 mm.

Discussion:

Range of individual variation within sex, between sexes, and within species may be comparable to that found in the modern *Baronia brevicornis* with its sympatric varieties mentioned above, where there is dimorphism of wing shape between sexes, and color pattern and shape polymorphism

[14]The notation for vein segments (Durden 1969) uses *a* for an anterior fork, *p* for a posterior fork. A fragment of an anterior radial pecten, *Rppa*, is abbreviated Rp^2a and is an objective designation of the subjective term R3. V rather than A is used following Ehrlich (1958). Other venational notations are presented by Comstock (1918), Snodgrass (1935), Miller (1969), Riek (1970), Hamilton (1971, 1972, 1972a), and Durden (1969, 1972). This spate of recent proposals of new or modified systems indicates an unsettled terminology. We have elected to follow, with minor modification, Miller's revision of the Comstock system, with the addition of Durden's notation for segments.

among the females. There is a possibility that the next species described is a variety of this one, but size, shape and pattern differences are greater than the extremes known for *B. brevicornis.*

Praepapilio gracilis new species

HOLOTYPE: Figs. 2, 3, 6C, 6D; Raydome butterfly No. 2 (Black Hills Minerals Collection and Hugh Rose Collection).
TYPE LOCALITY: Colorado, Rio Blanco Co., Raydome.
TYPE HORIZON: Green River Shale, Parachute Creek Member, upper beds.
AGE: Eocene, Lutetian or Biarritzian Stage; about 48 Ma.

Description:

Based on abdominal structure this individual is interpreted as female. Forewing proportions are: width, 0.543 of length, cell length 0.533 of wing length, posterior edge 0.629 of length. Hindwing proportions are: width, 0.590 of length (or wider, if compressed), tail, 0.106 of wing length by extrapolation (proportions of preserved wing suggest a possibly longer tail), cell length, 0.400 of wing length, posterior edge, 0.913 of wing length.

The very light preservation of color exhibits three shades interpreted as 1) brown or possibly black; 2) red; 3) yellow. Structural roughness, interpreted as the scintilla ("blue" or "green") is preserved only in space PCu-V1+2 and by extrapolation is expected to have been present in the three next anterior spaces in the first intramacular lacunae.

Shade 3 "yellow" occurs as five bands:

(1) The intramacular lacunae 1 in spaces R2-3 and R3-4 at 0.75 to 0.9 from wing base, and presumed to taper posteriorly.

(2) The 1-2 intermacular lacunae in spaces R1-2, R2-Rs, Rs-M1, M2-3, M3-Cu1 at 0.58 to 0.67 just outside cell.

(3) The intramacular spot 3 at 0.55 near end of cell.

(4) The 3-4 intermacular lacuna at 0.35, tapered posteriorly, curved concentric with wing edge to form outer limb of V-shaped patch.

(5) The 4-5 intermacular lacuna at 0.15, tapered toward tornus as inner limb of V-shaped patch, the apex extending to space Cu2-PCu at 0.4 from wing base.

Shade 1 "brown" surrounds the "yellow" patches and is interpreted to include six bands:

(1) The terminal band.

(2) Macular band 1 split into praemacular and semimacular fractions and presumably confluent with a dark tornal field.

(3) Macular band 2 fused with praeterminal fraction 3 as a bar over cell end.

(4) Semimacular fraction 3 as a bar across cell fused posteriorly with dark ground.

(5) Macule 4 as a tooth-shaped spot from dark costal edge to fork Cu1-Cu2.

(6) Macule 5, the diffuse basal shade.

In the hindwing, shade 3 "yellow" occurs as three bands:

(1) The praemacular lacuna in space Cu2-PCu at 0.95, and by extrapolation is presumed to have been present in the four spaces anterior.

(2) The proximal portion of intramacular lacunae 2 from costal edge to V1+2 at 0.55 to 0.75 with borders convex proximally, separated as spots by dark veins.

(3) The 3-4 intermacular patch from costal edge tapered across cell end to V1+2 at 0.2 to 0.4 from wing base.

Shade 2 "red" aurora forms the distal edge of intramacular lacunae 2 from Sc+R1 to V1+2, convex proximally in each space, widest in space M3-Cu1, of even width posteriorly, narrowed anteriorly.

Shade 1 "brown" surrounds the lacunae and is interpreted to include four bands:

(1) The terminal band.

(2) Macular band 1 containing scintilla and fused with praeterminal fraction of band 2.

(3) Semimacular fraction 2, fused with macular band 3 from costal edge outside cell to fuse with vannal shade, extended tooth-like distally along veins.

(4) Macule 4 as the diffuse basal shade tapered distally as vannal shade posterior to V1+2.

Dimensions:

Forewing: base to apex, 32.6 mm?[15]; base to tornus, 20.8 mm; apex to tornus, 23.9 mm? Vein segments: Sc, 19.7 mm; R, 14.9 mm; Ra(R1), 10.6 mm; Rp, 1.9 mm; Rpa (R2), 14.0 mm? Rp^2, 4.0 mm?; Rp^2a (R3), 10.9 mm; Rp^3 (R4), 9.9 mm?; Ma (M1), 10.9 mm?; Mp (M2), 10.3 mm?; Cu, 7.8 mm; Cua, 5.3 mm; Cua^2 (M3), 12.4 mm?; Cuap (Cul), 11.5 mm; Cup (Cu2), 15.9 mm; V, 0.9 mm; Va (PCu), 21.0 mm; Vap, 0.3 mm; Vapa (V1+2), 19.9 mm; Vap^2 (V3), 1.6 mm; Cu-V crossvein (base PCu), 0.5 mm; discocellular crossveins, 2.1 mm, 1.9 mm, 1.8 mm. Forewing cell width, 4.4 mm; cell length, 17.6 mm.

Hindwing: base to tail base, 24.9 mm?; base to tail tip, 26.4 mm?; tornus to costal edge (underestimated if fan-folded), 16.2 mm; base to sub-

[15] Dimensions inferred from extrapolative reconstruction are indicated "?".

Fig. 2.–*Praepapilio gracilis* n. sp., HOLOTYPE, Raydome butterfly No. 2a (Hugh Rose Collection). Bar scale is one centimeter.

Fig. 3.–*Praepapilio gracilis* n. sp., HOLOTYPE, Raydome butterfly No. 2b (Black Hills Minerals Collection). Bar scale is one centimeter.

costal angle, 18.7 mm?; base to tornal angle, 22.7 mm; base to abdominal angle, 13.1 mm. Vein segments: Sc, 1.2 mm; Sca (humeral), 1.9 mm; Scp, 0.9 mm; R, 1.2 mm; Ra, 0.8 mm; Sc+Ra (R1), 17.1 mm?; Rp, 4.4 mm; Rpa (Rs), 14.6 mm?; Rp^2 (M1), 15.7 mm?; M (M2), 12.4 mm?; Cu, 5.9 mm; Cua, 3.7 mm; Cua^2 (M3), 15.9 mm; Cuap (Cul), 15.5 mm?; Cup (Cu2), 18.0 mm?; V, 1.1 mm; Va, 0.2 mm; Va^2 (PCu), 21.5 mm; Vap (V1+2), 21.0 mm; Vp (V3), 12.0 mm; Discocellular crossveins, 1.1 mm, 1.6 mm. Hindwing discal cell width, 2.3 mm; length, 9.8 mm; subcostal cell width, 0.4 mm; length, 1.9 mm.

Head: width 3.3 mm; interocular width, 1.2 mm; cephalic length to labrum, 1.6 mm; palpal projection beyond labrum, 1.6 mm.

Thorax: tegulum length, 3.1 mm; width, 0.9 mm; mesotergum length, 4.7 mm; metatergum (dorsal exposure) length, 1.2 mm; width, 4.2 mm.

Abdomen length (distorted), 9.8 mm; width (flattened), 4.4 mm. A structure preserved at the end of abdomen is interpreted as a sphragis.

The third specimen is very different and indicates that at least two families of Papilionoidea differentiated before middle Eocene time.

Family LYCAENIDAE Leach, 1815
(nom. transl. Stephens, 1829, *ex* Lycaenida).

Characters agreeing with the family:

Eyes emarginate at antennae.
Paraocular areas absent.
Interantennal distance 0.3 of head width.
Labial palpi 0.8 of head length.
Metatergum not completely overhung by mesotergum.
Posterior margin of discal cell trifid in forewing.
Vein V3 present in hindwing.
Prothoracic femur 0.6 of mesothoracic femur in female.

Anomalous characters:

Face protuberant.
Patagia sclerotized.

Subfamily RIODININAE Grote, 1895
(nom. repl. Grote, *pro* Erycinidae Swainson, 1872
Riodina Westwood, 1851 = *Erycina* Fabricius, 1807;
nec Erycina Lamarck, 1805)

Characters agreeing with the subfamily:

Single recurrent vein at end of forewing cell.
Forewing with five radial branches.
Humeral vein in hindwing.
Vein Sc+R1 parallel to costal margin of hindwing.

Tribe RIODINIDI Grote, 1859
(*nom. transl.* herein, = Ancyluridi Stichel, 1911)

Diagnostic characters of the tibial spurs and tarsal claws are not preserved in the fossil.

Subtribe RIODININI Grote, 1895
(*nom. transl.* Clench, 1955, = Ancylurini Stichel, 1911)

Characters agreeing with the subtribe:

Hindwing costal edge thickened basally, vein-like.
Veins Rs and M1 not stalked beyond cell in hindwing.
Vein M2 a recurrent vein in hindwing.
Male genitalia with a prominent Y-shaped furca.

Anomalous characters:

Face protuberant.
Patagia sclerotized.

Discussion:

The anomalous body characters are shared with other families of Papilionoidea outside the Lycaenidae. Retention of these characters is to be expected in early members of the family. The male genitalia are definitely comparable to modern members of this subtribe.

RIODINELLA new genus
(Type species: *R. nympha* n. sp.)

Diagnostic characters:

Forewing costa concave at end of Sc.
Vein R1 originates proximal to cell end, terminates on costa.
Vein R2 originates distal to cell end, terminates at wing apex.
Veins R1 to R4 form an anterior pecten equidistant from each other and from Sc.

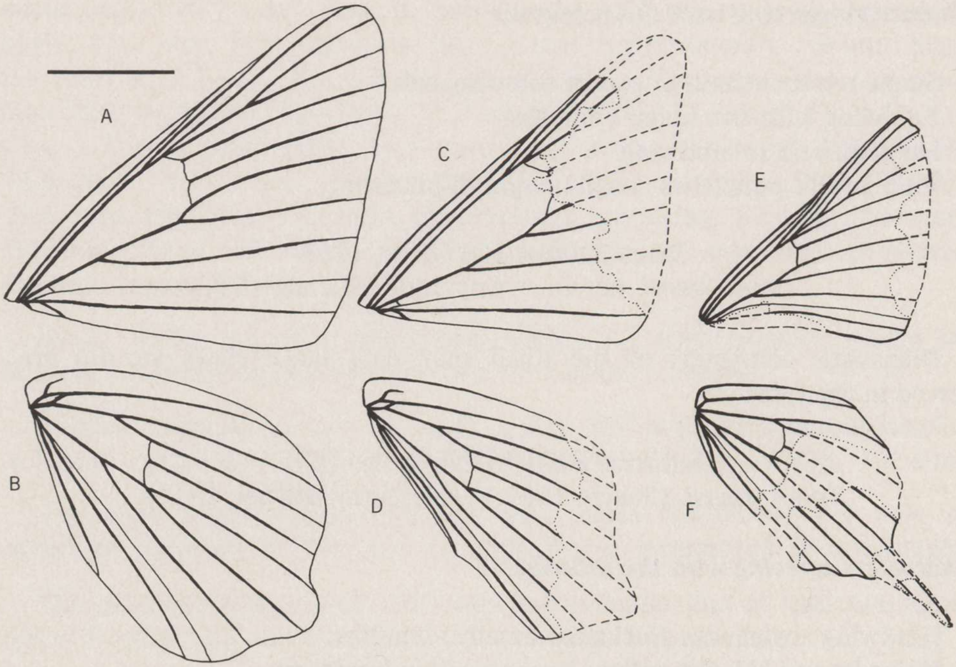

Fig. 6.–Reconstruction of wing venation. (A) *Praepapilio colorado* n. g., n. sp., forewing. (B) Same, hindwing. (C) *P. gracilis* n. sp., forewing. (D) Same, hindwing. (E) *Riodinella nympha* n. g., n. sp., forewing. (F) Same, hindwing. Bar scale is one centimeter.

Intervein space R4-R5 is of width equal to those of the mediocubital series of spaces.

Vein M1 arises at the anterior corner of the cell.

Vein M2 is recurrent.

Vein M3 is forked with Cu1 proximal to cell end.

Veins M3, Cu1, Cu2 form a posterior pecten (trifid).

PCu is a conspicuous crease in the wing.

Vein V1+2 is subparallel to posterior margin.

Hindwing costal edge is thickened at the angle.

Humeral vein is directed toward costal angle, and smoothly concave distally.

Vein Sc+R1 lacks a basal cell and borders costal edge with anterior space narrowed distally, abruptly angled at base of humeral vein.

Rs forms 0.8 of anterior border of cell.

Vein M1 is forked with Rs at 0.15 of wing length, distal to discocellular crossvein.

Vein M2 is recurrent, based on discocellular crossvein at 0.6 posterior in cell width.

Sc+R1, Rs, M1, M2 to M3 intervein spaces form a series of even widths.

M3, Cu1, Cu2, PCu, to V1+2 intervein spaces form a narrower series of even widths.

Vein M3 forms the leading edge of the tail, and is forked with Cu1 at or just proximal to cell end.

Vein Cu1 forms posterior basal strut of tail.

Vein Cu2 arises on basal 0.3 of cell.

Veins M3, Cu1, Cu2 form an even posterior pecten.

PCu is a sclerotized crease, terminating at margin in a vein-like undulation.

Vein V1+2 terminates just distal to tornus.

Vein V3 terminates on abdominal margin at 0.3 to 0.4 of its length to tornus.

Discussion:

In venation but not in pattern, it resembles species of *Ancyluris* Hubner, 1819, *Rhetus* Swainson, 1829, and *Riodina* Westwood, 1851. In *Ancyluris* vein R5 terminates at wing apex, PCu is weak in both fore- and hindwings, fork Rs-M1 is nearer mid-cell in hindwing, anterior pecten of forewing radius is tighter, and the base of M1 lies closer to the forewing costa. In *Rhetus*, vein R4 terminates at the apex of the forewing, R1 arises at end of cell, and there is a remarkable trace of sclerotization and lineation of scales in the position of the base of PCu, a character found elsewhere only in some Papilionidae. In *Riodina*, vein R4 also terminates at apex. *Corrachia* Schaus, 1913, of uncertain tribal affinity, has a transverse pattern similar to *Riodinella* but wing shape is different and details of venation are unknown. *Dodona* Hewitson, 1861, of subtribe Zemerini Stichel, 1928 in tribe Hameairidi Stichel, 1928, has a similarly transverse pattern but differs in venational characters of tribal significance, and has a tail on Cu2 as in Lycaenidi.

Riodinella nympha new species

HOLOTYPE: Figs. 4, 5, 6E, 6F; Raydome butterfly No. 3 (Black Hills Minerals Collection, and David Douglass, Prehistoric Life Museum Coll.)
TYPE LOCALITY: Colorado, Rio Blanco Co., Raydome.
TYPE HORIZON: Green River Shale, Parachute Creek Member, upper beds.
AGE: Eocene, Lutetian or Biarritzian Stage; about 48 Ma.

Description.

The well preserved portion of the abdomen, seen best in the David Douglass portion, shows a male genitalic capsule of the Riodinine configuration. A Y-shaped sclerotized structure straddling the aedeagus in the anterior

Fig. 4.–*Riodinella nympha* n. g., n. sp., HOLOTYPE, Raydome butterfly No. 3a (David Douglass, Prehistoric Life Museum Collection). Bar scale is one centimeter.

Fig. 5.–*Riodinella nympha* n. g., n. sp., HOLOTYPE, Raydome butterfly No. 3b (Black Hills Minerals Collection). Bar scale is one centimeter.

third of the capsule is interpreted as the furca. Apices of the valvae are papillose-hirsute, while the shanks are smooth.[16].

Forewing proportions are: width, 0.554 of length; cell length, 0.405 of wing length; posterior edge, 0.676 of wing length. Hindwing proportions are: width, 0.500 of length; mediocubital tail, distally 0.284 and tornally, 0.239 of wing length; cell length, 0.261 of wing length; posterior (abdominal) edge, 0.545 of length.

Preservation of color is dark, with three shades interpreted as originally 1) dark brown or black, 2) light brown or red, and 3) white. There is no preserved evidence of scintilla or cyanic overlay such as occurs in modern *Ancyluris*.

Spots of shade 3 "white" occur in the forewing as three bands:

(1) The 3-4 intermacular lacuna 0.85 distally in cell.

(2) The 1-2 intermacular lacunal spotband in spaces R2-3, R3-4, R5-M1 at 0.65 from wing base, and offset distally in spaces M1-2, M2-3, and M3-Cu1 with this last touching the praemacular lacuna.

(3) Intramacular spot 2 in space M3-Cu1 at 0.5 from wing base.

Shade 2 "light brown" occurs as three bands.

(1) The praemacular lacunae from R4 to V1+2 at 0.9, with spots confluent but constricted across PCu and largest at Cu1-Cu2.

(2) Intramacular lacuna 2 and intermacular lacuna 2-3 joined posterior to Cu1 to form a Y-shaped band, and anterior to Rs-M2 space at 0.35 and 0.5 from wing base.

(3) Intermacular spot 4-5 at 0.2 in the cell.

Shade 1 "dark brown" surrounds the lacunae and is interpreted to include six bands.

(1) The terminal band.

(2) Macule 1, possibly split into praeterminal and semimacular fractions.

(3) Macule 2, divided posterior to Rs, the semimacular fraction extending only to Cu1.

(4) Macule 3, on the discocellular crossvein.

(5) Macule 4, a spot in the cell confluent with dark ground posteriorly.

(6) Macule 5, as the basal shade.

In the hindwing, shade 3 "white" is an intramacular lacuna 3 spot at 0.45 outside cell in space M2-3.

Shade 2 "light brown" occurs as four bands.

(1) Intramacular lacunal band 3, across wing at 0.45.

(2) Intermacular lacunae 2-3, from M1 to Cu2 in midwing.

[16] Additional characters preserved in these specimens including cephalic and body anatomy, venational details, scales, and hairs, will be illustrated in larger format by photomicrographs in *Bull. Tex. Mem. Mus.* as part of a series on fossil butterflies. Specialists in lepidopteran phylogeny and anatomy are invited to contribute their analyses of these fossils, of which they may obtain study enlargements from the first author. Descriptions and redescriptions of other fossil material is also solicited.

(3) Intramacular band 2, of uncertain extent.

(4) Intermacular band 1-2 is scarcely preserved in peripheral fragments.

Shade 1 "dark brown occurs as three bands.

(1) Portions of the praeterminal fraction of band 2 in spaces Rs-M1, M2-3, and PCu-V1+2 at 0.85.

(2) Semimacular band 2, confluent anteriorly and posteriorly with band 3 at M1 and Cu2.

(3) Semimacular band 3 proximal to discocellular crossvein, beginning the basal shade.

Dimensions:

Forewing: base to apex, 23.0 mm; base to tornus, 15.5 mm; apex to tornus, 18.0 mm. Vein segments: Sc, 14.3 mm; R, 7.8 mm; Ra (R1), 5.9 mm; Rp, 1.6 mm; Rpa (R2), 12.7 mm; Rp^2, 1.6 mm; Rp^2a (R3), 11.5 mm; Rp^3, 4.3 mm; Rp^3a (R4), 7.6 mm; Rp^4 (R5), 6.8 mm?; Ma (M1), 9.3 mm; Mp (M2), 10.8 mm?; Cu, 4.0 mm; Cua, 2.0 mm; Cua^2 (M3), 12.7 mm?; Cuap (Cu1), 12.1 mm?; Cup^2 (Cu2), 13.0mm?; V, 0.9 mm; Va (PCu), 15.2 mm; Vp (V1+2), 14.6 mm. Cell width, 2.0 mm; length, 9.3 mm.

Hindwing: base to tail base, 19.0 mm; base to tail tip, 26.4 mm?; tornus to costal edge, 13.7 mm; base to subcostal angle, 12.7 mm; base to tornal angle, 15.2 mm. Vein segments: Sc, 0.9 mm; Sca (humeral), 0.6 mm; Scp (Sc+R1), 12.1 mm; R, 5.9 mm; Ra (Rs), 9.3 mm; Rp (M1), 11.2 mm?; M (M2), 10.9 mm; Cu, 1.9 mm; Cua, 5.0 mm; Cua^2 (M3), 19.6 mm?; Cuap (Cu1), 15.5 mm?; Cup (Cu2), 17.4 mm; V, 0.6 mm; Va, 0.3 mm; Va^2 (PCu), 16.2 mm; Vap (V1+2), 14.3 mm; Vp (V3), 4.4 mm.

Head: Width, 2.5 mm; interocular width, 0.8 mm; cephalic length to labrum, 1.6 mm; palpal projection anterior to labrum 0.6 mm; bilobed frons width, 0.9 mm.

Thorax: tegulum, 0.8 mm long by 0.5 mm wide; mesotergum length, 3.1 mm; metatergum length, 0.8 mm; width, 3.0 mm.

Abdomen: preserved (distorted) length, 10.7 mm; width (flattened), 3.4 mm.

Legs: forefemur length, 2.5 mm; midfemur length, 3.1 mm.

Discussion:

The range of individual variation within the species may have been as great as in some modern *Ancyluris* spp. where there is strong sexual dimorphism of wing shape and tail length.

Preliminary conclusions concerning the relationships of these fossils to the higher taxa of butterflies, are presented graphically in Fig. 7.

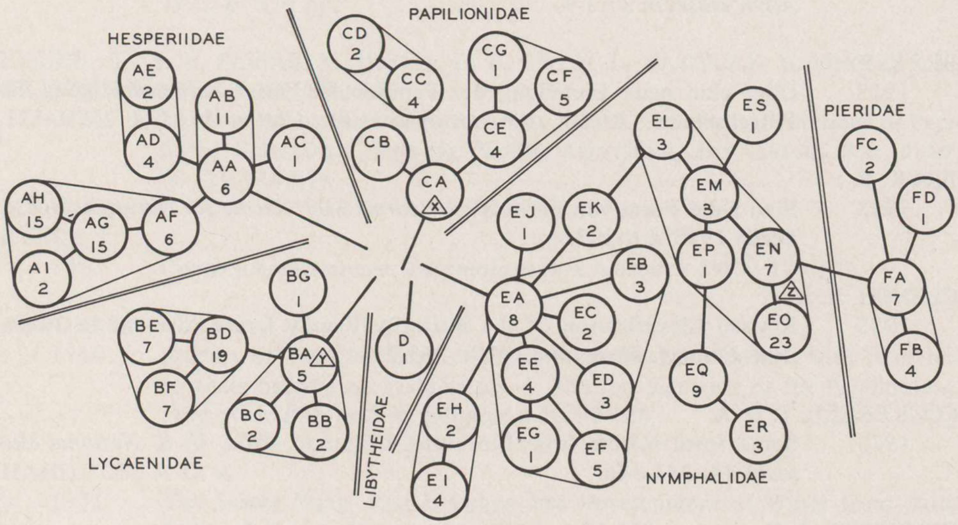

Fig. 7.–Cross section of phylogenetic tree of the Rhopalocera at the present time. Triangles represent the location of Eocene genera projected onto the same plane, with X, *Praepapilio* in Praepapilioninae (extinct), Y, *Riodinella* in Riodinidi, and Z, Raydome butterfly No. 4 (position based on preliminary study of undescribed specimen). Lines between taxa represent similarity but are not necessarily true projections of phylogenetic branches of actual descent. Numbers indicate diversity of subtribal and suprageneric groups within each tribe. Circles represent tribes and are lettered as follows: AA Urbanidi, AB Pyrgidi, in Pyrginae; AC Euschemoninae; AD Pyrrhopygidi, AE Coeliadeidi, in Pyrrhopyginae; AF Trapezitidi (includes "Megathymidae"), AG Hesperiidi, AH Apaustidi, AI Heteropteridi, in Hesperiinae; BA Riodinidi, BB Hamearidi, BC Euselasiidi, in Riodininae; BD Lycaenidi (includes "Lycaeninae," "Plebeinae," "Theclinae," "Strymoninae"), BE Liphyridi, BF Liptenidi, in Lycaeninae; BG Styginae; CA Praepapilioninae (extinct); CB Baroninae; CC Luehdorfiidi (includes "Zerynthiinae"), CD Parnassiidi, in Parnassiinae; CE Leptocircidi (includes Graphiidi, "Teinopalpidae"), CF Troididi (includes "Cressidinae"), CG Papilionidi, in Papilioninae; D Libytheidae; EA Nymphalidi (includes "Argynninae," "Vanessiinae"), EB Heliconiidi, EC Biblidi, ED Eunicidi, EE Melitaeidi, EF Limenitidi (includes "Marpesiinae"), EG Ageroniidi, in Nymphalinae; EH Apaturidi, EI Charaxidi, in Charaxinae; EJ Acraeinae; EK Morphinae; EL Brassolidi, EM Biidi, EN Satyridi, EO Elymniidi (includes "Lethinae"), EP Haeteridi, in Satyrinae; EQ Ithomiinae; ER Danainae; ES Calinaginae; FA Pieridi, FB Coliadidi, in Pierinae; FC Dismorphiinae; FD Pseudopontiinae.

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