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A PROPOSED REVISION OF NON-ARCTIC PARNASSIUS PHOEBUS FABRICIUS IN NORTH AMERICA (PAPILIONIDAE)¹

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THE SUBSPECIES OF Parnassius phoebus Fabricius in North America have been in a state of confusion for a number of years. This is, in part, a result of the papers published by Bryk and Eisner in the 1930's and later by Eisner in the 1950's and 1960's. McDunnough, 1936a, b took exception to some of their work, but most of the Bryk and Eisner taxa persist. Additional names have been proposed by Bang-Haas and Wyatt. Other workers who have contributed to the nomenclature in this species include Doubleday, H. and W. H. Edwards, Holland, Neumoegen, Stichel, Wright, and several others whose taxa were sunk into synonomy by dos Passos in 1964. If forms are counted, then there are forty-four names recognized by dos Passos. Four additional subspecies and several form names have been proposed since completion and publication of the dos Passos checklist. Of these more than fifty names, five apply to arctic races and the remainder apply to populations associated with southwestern Canada and the western United States. In addition, Bryk and Eisner have published a number of infraspecific names not recognized by dos Passos.

At this point, one must examine taxonomic philosophy. There are "lumpers" (everything is Parnassius phoebus), "middle-ofthe-roaders" (there are some valid subspecies), and "splitters" (specimen A has a spot that specimen B lacks, thus they are nomenclaturally distinct). Our European colleagues tend to be "splitters" to a greater degree than workers in the U.S. and have carried this process to extremes in some instances. Eisner, 1955b, cites ten "aberrational" names to be applied to both wings in Parnassius, twenty-seven such names to be applied to FW vari-

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ations, and thirty names for HW variants. These apply to ground color, marginal fascia, spot size, color of spots, etc. and are applied singly or in combination, e.g. *Parnassius phoebus sayii* form magna + quadropicta + albopicta + rubroocellata. The latter translates as a specimen of *P. ph. sayii* which is especially large, with four red costal spots on the FW that have white centers, and red spots on the HW. Another specimen from the same colony might not be designated "albopicta" since its FW spots are uniformly red. The foregoing is not intended to belittle any workers, but to indicate the extremes to which nomenclature can be carried; such combinations are found frequently in the Bryk and Eisner literature.

Workers in this country tend to recognize variations within a given species as originating from environmental factors, geographic isolation, genetic variation, etc. Within given colonies of a butterfly species, there can be variations based upon the gene pool, and in multivoltine species, frequent seasonal variations. Blend zones or tension zones are recognized in areas where populations or races overlap. When a strong character, or a group of lesser but consistent characters is recognized which reliably separate groups within a species, then subspecies may be designated. This is the general philosophy espoused by the I.C.Z.N., but the categorization stops at this point. Infraspecific names (forms, aberrations, etc.) are not recognized. In view of the variability of biological entities, this seems a wise policy.

With regard to the above introduction, the intent of this paper is to attempt a rational taxonomic review of *Parnassius phoebus*, with particular regard to the Rocky Mountains. Insufficient study material is available to review the arctic subspecies in detail. Several of these taxa are known only from type series housed in European museums. All are perhaps valid taxa as a consequence of extreme geographic isolation. For completeness, they are listed with their authors, dates, and type localities. The other available taxa are listed according to geographic region, in chronologic order and by page priority. One should refer to dos Passos, 1964, for synonomy.

Arctic Subspecies apricatus Stichel, 1906. Kodiak Island, Alaska. golovinus Holland, 1930. Golovin Bay, Alaska. elias Bryk, 1934. St. Ilya, Alaska. alaskaensis Eisner, 1957. McKinley National Park, Alaska. yukonensis Eisner, 1969. Haines Junction, Yukon Territory, Canada.

West Coast (California and the Pacific Northwest)

behrii Edwards, 1870. Fixed by Brown, 1975, as near the summit of Mt. Lyell, Yosemite Valley, California.

magnus Wright, 1905. Enderby, British Columbia, Canada.

- sternitzkyi McDunnough, 1936 [1936c in Lit. Cited.] Castle Lake, Siskiyou Co., California.
- olympianus Burdick, 1941. Hurricane Ridge, Olympic Range, Clallam Co., Washington.
- guppyi Wyatt, 1969. Mt. Arrowsmith, Vancouver Island, British Columbia, Canada.

Great Basin

hollandi Bryk and Eisner, 1935. La Sal Mountains, Utah.

rubina Wyatt, 1961. Liberty Peak 3120 m., Angel Lake 2900 m., Ruby Mountains, Elko Co., Nevada. [Actually, Angel Lake is in the East Humboldt Range.]

Rocky Mountains

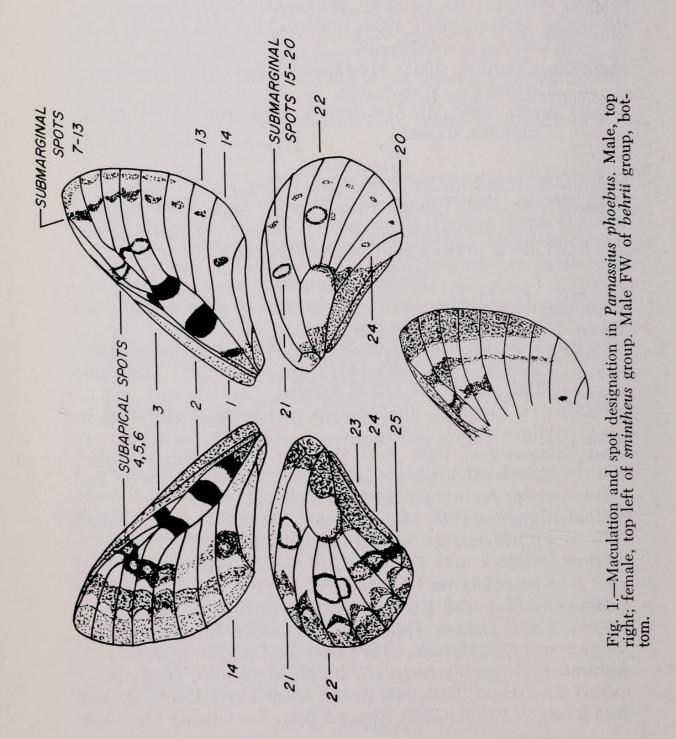
- smintheus Doubleday, 1847. Nr. Laggan (Lake Louise) and Banff, Alberta, Canada.
- sayii Edwards, 1863. Fixed by Brown, 1975, as Running Creek Field Station, 6950' (2118 m.), Elbert Co., Colorado [T9S, R65W, SW 1/2 25 Native.]
- hermodur H. Edwards, 1881. Gilpin or Boulder Co., Colorado, [Brown et al., 1957.]
- nanus Neumoegen, 1890. Fort Calgarry and Spence's Bridge, British Columbia, Canada. [Calgary, Alberta and Spence's Bridge, British Columbia.]
- xanthus Ehrmann, 1918. Moron, Idaho. [Actually Moscow, Latah Co., Idaho; see Avinoff in Holland, 1927.]
- montanulus Bryk and Eisner, 1935. Turah, Missoula Co. and Kiowa, Glacier Co., Montana.
- dakotaensis Bryk and Eisner, 1935. Mt. Roosevelt, Black Hills, South Dakota. [Mt. Theo. Roosevelt, Roosevelt Monument, T5N, R3E, S16, Lawrence Co., South Dakota.]

maximus Bryk and Eisner, 1937. Judith Mountains, Montana.

rotgeri Bang-Haas, 1938. Mt. Evans, Clear Creek Co., Colorado. pseudorotgeri Eisner, 1966. Elwood Pass, Rio Grande Co., Colorado.

Based upon the marginal scaling of the forewings of the males, the North American *Parnassius phoebus* can be divided into two groups: the *smintheus* group and the *behrii* group. This char-

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acter in Parnassius was recognized by Müller, 1954. Table I indicates group assignments for the non-arctic taxa listed above. Those which I consider as valid subspecies, as subsequently discussed, appear to the left with their synonyms offset to the right.

TABLE I

Parnassing phoebus groups

smintheus group smintheus

nanus xanthus magnus sayii hermodur hollandi dakotaensis rotgeri rubina montanulus maximus

behrii group behrii sternitzkyi olympianus guppyi pseudorotgeri

The *smintheus* group:

This group is recognized, as shown in Figure 1, by the reduced unscaled areas from the apex of the FW in the males and along the margin. The aspect is one of marginal chevrons or white spots interspersed with a dark (unscaled) band followed basad by a white band and a dark spot row (spots 7 - 13) which may be obsolete in some examples. Discussion proceeds according to geography from the Great Basin eastward and northward rather than in the chronological order indicated in Table I.

Wyatt's primary basis for describing rubina, 1961, was its geographic isolation from other races. He also cited hollandi from Utah as an isolated race. Careful examination of specimens produces no significant differences between the two subspecies. I can detect only two very slight differences. The FW black spot in cell Cu_1 , spot 14 (see Figure 1 for nomenclature) is slightly smaller and rounder in *hollandi* and the bottom of spot 3 extends distally slightly along the vein in *rubina*, while ending abruptly in *hollandi*. The remaining maculation: spot size, borders, red versus black spots, etc., exhibits the normal range of

variability associated with *phoebus*. I would find it very difficult to separate a specimen of *rubina* from a series of *hollandi* and vice versa without looking at locality labels.

Wyatt's descriptions for both *rubina* and *guppyi* (discussed subsequently) do not satisfy the criteria specified by the I.C.Z.N., as he does not clearly distinguish how his proposed taxa differ from other recognized subspecies. In his description of *rubina*, he briefly mentioned *hollandi* and then stated the physical characters of the two type specimens of *rubina*. No discussion of variation was presented.

Albeit that they are geographically separated by some distance, in facies *hollandi* and *rubina* appear to the the same insect. At best, *hollandi* can be considered only a weak subspecies closely allied to *sayii*. The variation observed in both *hollandi* and *rubina*, including spot 3, is well within the normal range for *sayii*. Although there is geographic isolation from the main populations of *sayii*, since there are no clear phenotypic differences, I am assigning both taxa to *sayii*.

The subspecies of phoebus associated with the central Rocky Mountains is sayii. Brown, 1975, gives a detailed discussion of the type locality of this subspecies with designation of a neotype to replace the lost type. He also cites the error made by Bryk and Eisner, 1935, in assigning the type locality to the Judith Mountains in Montana. The neotype female is from Elbert Co., Colorado, which is close to the "Pike's Peak" locality cited by Edwards for the original type. The range of sayii is from NE Nevada, central and NE Utah, central Colorado (Pike's Peak region) into central and NE Wyoming, thence into the Black Hills of South Dakota. There appears to be no reason for retaining dakotaensis as a separate subspecies. The maculation exhibited fits well within the normal range for low-altitude sayii. The type series for *dakotaensis* contained specimens from the vicinity of Deadwood, Lawrence Co., South Dakota, undesignated locality specimens from Wyoming, and specimens from the Big Horn and Teton Mountains in Wyoming. As discussed later, material from the two latter localities should be referred to montanulus.

It seems quite evident that *hermodur* is simply the altitudinal form, more pronounced in the females, of *sayii*. There has been quite a bit of confusion in the past as to what exactly is phenotypic *hermodur*. Elrod, 1906 (p. 14-15, figs. 13-14), figured lowaltitude *sayii* as *hermodur* and also reversed the sexes. Howe, 1975, has figured two specimens, neither of which is *hermodur*. The female shown in plate 67, fig. 10 from Mt. Evans, Clear Creek Co., Colorado appears to be low-altitude *sayii* or a poor illustration. The male shown in plate 68, fig. 7 from Telluride, San Miguel Co., Colorado is *pseudorotgeri*, a member of the *behrii* group. The elevation cited, 8000' (2438 m.) is much too low for *hermodur*. The insect is correctly figured in Brown et al., 1957 (p. 234). What Holland, 1898, illustrated as *hermodur* (pl. 39, fig. 6) is closer to high-altitude *montanulus*.

The *hermodur* form appears in most high-altitude populations of North American phoebus. Southeastern Wyoming provides an excellent opportunity to observe sayii from the prairie association high plains through a continuous gradation into the mountains above treeline where hermodur flies. Throughout the Rocky Mountains, low-elevation phoebus tend to be much larger and more brightly marked than specimens taken at high elevations. With increasing altitude, the females become smaller and darker, with the ground color of the wings tending toward charcoal gray. On the other hand, the males become smaller and more lightly marked. This change in color and maculation is easily observed in the continuous cline from the Laramie Plains (ca. 7000', 2134 m.) through the Transition Zone foothills (ca. 8000-9000', 2438-2743 m.) and into timberline habitats on Snowy Range Pass (10,800', 3292 m.) in the Snowy Range Mountains, Albany Co., Wyoming. In this region, there is a continuous band of Sedum lanceolatum Torrey, the hostplant, and there are no barriers that produce isolated colonies. Specimens can be collected nearly everywhere along Hwy. 130 from east of Centennial westward to the summit. Thus hermodur is sunk as the altitudinal form of sayii. The reason for the dark color in the females relates to development at reduced temperature (high altitudes) results in the production of more melanin and hence darker tones. This phenomenon is sometimes called thermal adaptation.

In the north-central to northwestern Rocky Mountains, the picture becomes somewhat more confused. The Red Desert in Wyoming presents a natural zoogeographic barrier of approximately 100 miles (150 km.) between the northern foothills of the Sierra Madre Range (an extension of the Colorado Western Slope) and the southern boundary of the Wind River Range (the northern continuation of the Rocky Mountains). In Utah, *sayii* is found from the SE to NW portion of the state as shown in Figure 2. It occurs in the Wasatch and Uinta Ranges which border Wyoming on the south and west of the Red Desert region.

Parnassius phoebus again appears in numbers in Lincoln Co., Wyoming in the Salt River Range and in the Snake Range in Teton Co., thence into Idaho and Montana. In southern Lincoln Co., a wide variety of forms is taken, indicative of a clinal situation or tension zone. To the north, especially in Park Co., (the Beartooth Plateau) a distinct phenotype emerges. The males are larger than high-altitude sayii (although occurring at comparable altitudes) and the females are more brightly marked. There is a distinct basal cream coloring in the wings of the females, but the outer half of the wings is almost transparent (unscaled) charcoal gray. There is a submarginal FW cream colored spot row as in form hermodur. The two red HW spots (21-22) tend to be pupiled with white. The males appear less inclined toward FW red spotting. As with sayii, one observes a gradual change in facies from the arctic-alpine region inhabitants to those found in the deep canyons at lower elevations.

The population from the two summits of Beartooth Pass on the Beartooth Plateau (Park Co., Wyo. - Carbon Co., Mont.) and extending NE to Red Lodge, Montana shows considerable variability and comprises specimens resembling the holotypes and paratypes of both *montanulus* and *maximus*. About 5 airline miles separate the summit area from the lowest elevation where *phoebus* is found. Elsewhere in Montana, similar specimens can be collected, including the Glacier National Park region. I can see no basis for retaining both names and therefore sink *maximus* as a synonym of *montanulus* which carries publication priority.

We now come to the taxon smintheus Doubleday (not W. H. Edwards, see Brown, 1975). Doubleday's material came from Laggan (Lake Louise) and the Banff area in Alberta. From the same general area, Neumoegen described nanus (near "Ft. Calgarry" and Spence's Bridge, British Columbia). The former locality is Calgary, Alberta, while the latter is in British Columbia. I suspect that the Calgary specimens were actually collected in the mountains to the west of the settlement, that is the east slope of the Canadian Rockies. Many old records cite the nearest settlement rather than the actual collection locality. Neumoegen's description (1890) is somewhat confusing. It could apply equally well to the high-alpine sayii from Colorado. Specimens from the upper reaches of Whitehorn Mtn. near Banff fit Neumoegen's description reasonably accurately. Thus nanus appears to be an altitudinal form of smintheus in the same manner as hermodur is to sayii.

Transition Zone *smintheus* resembles *sayii* from the same zone, but there is considerably more red marking in the females. Spots 4 - 6 are generally markedly red as are spots 24 - 25. Spots 21 - 22 are very large and boldly red with 22 extending well into cell M_3 . Both may be white pupiled. Spots 24 and 25 are large and 23 is frequently present. The females are the most boldly marked of the non-arctic *phoebus*.

Specimens of phoebus from central and eastern Washington, eastern Oregon, and Idaho exhibit a cline between smintheus and montanulus. Two names have been applied to Idaho material. In 1918, Ehrmann described xanthus from Moron [sic], Moscow, Latah Co., Idaho (Avinoff in Holland, 1927). Without any reference to Ehrmann's action, Bryk and Eisner described idahoensis from Wallace, Shoshone Co., Idaho in 1931. The type series included specimens from "Pine Creek", Idaho (probably Pine Ck. Pass, Bonneville Co.), and Mt. Spokane, Spokane Co., Washington. Wallace and Mt. Spokane are close to Moscow. In 1964, dos Passos placed idahoensis as a junior synonym of xanthus. Specimens from Yakima Co., Washington are very close to smintheus although a bit lighter colored and less heavily maculated. Some males, however, exhibit the transparent wing borders associated with the behrii group. Yakima Co. appears to represent a tension zone between the behrii complex and the smintheus complex. Material from Idaho is quite variable. Some specimens blend into montanulus, while others are quite close to smintheus, especially in the northern portion of the state where the intrusion of spot 22 into cell M_3 is observed in the females. As would be expected in a clinal situation, there is considerable variation within colonies and throughout the range of phoebus from central Idaho into Oregon and Washington. I do not feel that material from this region merits nomenclatural recognition. Based upon the illustrations which appear in the original description of *idahoensis* and the localities from which both xanthus and idahoensis were described, I am sinking both taxa as synonyms of smintheus, although it should be understood that the two names apply to a very variable cline. Ehrmann described xanthus from a single pair, and the type series of idahoensis contained 17 specimens. Specimens from Cassia Co., Idaho on the Utah border are referable to sayii.

Wright, 1905 (pl. 2, fig. 13, b) described *magnus* from two specimens taken by an unknown collector at Enderby, British Columbia, ca. 1880. His description applies better to *montanulus* than to the type specimens illustrated. Cited are the large size and the more defined markings in both sexes. The type pair which he illustrated fits perfectly into my series of *smintheus* taken south of Banff, Alberta along the Kananaskis Highway. Specimens from Lac La Hache and Pavilion Mtn., near Jesmond, British Columbia are similar. Thus *magnus* appears to be simply the Canadian Rocky Mountain western slope form of *smintheus* parallel to the eastern slope-western slope relationship of *sayii* in Colorado. Recall that *nanus* was described from specimens taken on both slopes. For these reasons, I am sinking *magnus* as a synonym of *smintheus*.

It appears that much of the confusion concerning the true identity of *smintheus* was generated by W. H. Edwards when he applied the name to all red-spotted *phoebus* from North America. This has resulted in the redescription of the insect under other names.

In the Rocky Mountains, *sayii* and *smintheus* respectively, represent the southern and northern phenotypes of the *smintheus* group. The name *montanulus* has been retained to describe the fairly uniform specimens which occur in northern Wyoming and Montana. One could, however, justify retaining only the taxa *sayii* and *smintheus*, with the remainder of the Rocky Mountain population designated as a cline.

The behrii group:

This group is characterized by the diaphanous margins of the FW in the males. From the apex to vein Cu_1 and sometimes to Cu_2 , the margins are virtually unscaled, which gives them a charcoal gray aspect. Unscaled margins are characteristic of the females of both *phoebus* groups. The subspecies *behrii* is rapidly separated from all other U.S. subspecies of *phoebus* by its characteristic yellow-orange rather than red spots. It inhabits the Sierra Nevada of California and detailed discussion of this butterfly appears in Brown, 1975.

In 1936 [1936c in Lit. Cited], McDunnough recognized that the red-spotted northern California *phoebus* was not *smintheus* and he named it *sternitzkyi*. He cited two major characters which separated the new taxon from other *phoebus*. The first is the chalky white ground color, which is apparent in older specimens, but less apparent in freshly caught material. The chalky white color appears in worn specimens from high altitudes in the *smintheus* group. The other character was cited as "the *broad unicolorous dark (unscaled) marginal band on the forewings* extending down to vein Cu₁ and containing none of the

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whitish triangular marks along the outer margin found to a greater or less extent in both the other races [magnus and sayii]."

In my opinion, olympianus and guppyi are synonyms. Wyatt's description of guppyi refers to its larger size, stronger maculation and the more prominent spot in cell Cu_2 (spot 14) of the FW (1969). In comparing topotypical specimens of both taxa, I can find no significant size difference and the other characters are quite variable. The variation is no more extreme, however, than one would find in a somewhat geographically restricted subspecies such as *behrii*.

Burdick, 1941, in his description of *olympianus* compared the new taxon with *behrii* rather than *sternitzkyi*, to which it is both geographically and phenotypically more closely related. The two subspecies are quite closely related, but there are some minor characters in which they consistently differ. These are ground color and degree of maculation, especially in the females where *olympianus* is the more darkly marked. It may be that *olympianus* represents the altitudinal form of *sternitzkyi* in the same manner as the relationship between *sayii* and *hermodur*. This cannot be proved at the present time, as *sternitzkyi* is known only from northern California and southern Oregon, and *olympianus* from northwestern Washington and Vancouver Island.

The Burdick collection is at the University of Colorado Museum in Boulder. I examined the spread (10 pairs) and papered paratypes in the collection. Three of the spread males exhibited quite strongly the FW marginal white chevrons or marks associated with the *smintheus* complex. This maculation also occurs in some imagines of *behrii*.

Material from the San Juan Mountains in southern Colorado and the southern end of the Sangre de Cristo Mountains in northern New Mexico also belongs to the *behrii* group, as the males very strongly exhibit the diaphanous margins of the FW. Chermock proposed the name *pseudorotgeri*, based no doubt upon the insect's small size and superficial resemblance to *rotgeri*, but he did not publish the name. Eisner used the name, credited to Chermock, in a 1964 paper, and then published the taxon with a description of the butterfly under his own name in 1966 [1966a].

The two taxa, rotgeri and pseudorotgeri should be clearly distinguished. The former was described by Bang-Haas from Mt. Evans, Clear Creek Co., Colorado in 1938 and was a redescription of hermodur. Bang-Haas based his action upon Bryk's description of hermodur in Das Tierreich which led him to believe that the Mt. Evans material was significantly different from *hermodur*. Unfortunately Bryk's concept of *hermodur* was incorrect. The type specimens illustrated by Bang-Haas (pl. 1, figs. 6, 9) are clearly high-altitude *sayii* and *rotgeri* falls as a junior synonym of *hermodur*, which is the altitudinal form of *sayii*.

P. ph. pseudorotgeri clearly belongs to the behrii group. Eisner apparently was unable to recognize the diagnostic differences between it and rotgeri, for in his 1966 paper he noted that *pseudorotgeri* matched very closly his [Eisner's] paratypes of rotgeri and suggested that Bang-Haas may have had incorrect locality data. Despite Eisner's sixty-seven descriptors that he has used to separate Parnassius forms, he missed, as did Bryk, the one feature that separates the members of the two phoebus groups in North America, namely the margins of the FW in the males. Table II presents sufficient information to separate pseudorotgeri from high-altitude sayii. It is a small insect and the males are clearly of the behrii form. The females exhibit broad diaphanous wing borders both FW and HW, but the basal and discal areas are white scaled. They do not have the dusky appearance of form hermodur. The tension zone between sayii and pseudorotgeri extends from Trinchera Peak in the Spanish Peaks of Las Animas Co., Colorado through the Wet Mountains in Huerfano Co., into Alamosa and Conejos Cos., Old Baldy Mtn., Costilla Co., and westward into Mineral (Treasure Mtn.), San Juan and San Miguel Cos., as shown in Figure 2. Highaltitude specimens from the tension zone may look like either rotgeri or pseudorotgeri. The females can usually be separated into one or the other; the males look basically like pseudorotgeri, but the white maculation appears in the FW diaphanous margin. Low altitude specimens from the tension zone tend toward more typical sayii.

In New Mexico, *pseudorotgeri* occurs in isolated pockets in the high mountains of the northern part of the state. One specimen in the University of Colorado collection exhibits the yellow spots (both upper- and undersides) associated with *behrii*. It was taken along with normal red-spotted specimens on Chama Peak, 11,500-11,900' (3502-3627 m.), Rio Arriba Co., New Mexico by L. E. Chadwick on August 11, 1935. This specimen, in other respects, looks like *pseudorotgeri*. It has the wide diaphanous FW margins and the relatively light maculation characteristic of male *pseudorotgeri*; *behrii* is a much more heavily marked subspecies. Occasional red-spotted specimens occur in behrii, although yellow is the normal color.

Of the arctic races, *alaskaensis and golovinus* belong to the *behrii* group; *apricatus* appears to belong to this group based upon a rather poor photocopy of the plate accompanying the original description. Specimens or photographs of *elias* males were not available for examination; *yukonensis* belongs to the *smintheus* group.

In several areas, interaction between the two groups occurs, or has occurred in the past. Strong interaction is observed in the southern Colorado tension zone between *sayii* and *pseudorotgeri*. Specimens from Yakima Co., Washington generally represent the *smintheus* group, but occasional specimens exhibit the *behrii* group FW margins, indicative probably of interactions with *olympianus* to the west, while some specimens of *olympianus* show the white chevrons typical of *smintheus*. About ten percent of nearly 100 specimens examined from the Minam area in Wallowa Co., Oregon showed the *behrii* FW border.

A most unusual record is the collection of three phoebus by the late A. H. Moeck near Victoria, Tamaulipas, Mexico. Through the courtesy of Dr. Allen M. Young of the Milwaukee Museum, where the Moeck collection is housed, I was able to examine a pair of these specimens. They represent the smintheus group and are closest to low-altitude sayii. Except for the spots (4, 6, 21, 22) which were orange on the specimen studied, the male was quite similar to typical sayii. The same spots on the female were red and the submarginal spot row (spots 15-20) was formed of very distinct chevrons, much more distinct than in any other female phoebus examined. Otherwise, the specimen appeared as typical sayii. The pair was collected at 1500' (457 m.) on 3 July, 1952. No more specific locality data were given than cited above. After examining the specimens, I have no reason to question the validity of this record. These specimens may represent a describable subspecies, but to do so based upon two specimens would be foolish.

BIOLOGY

The life history of several of the *phoebus* subspecies, *sayii* in particular, is well known. David Bruce and W. H. Edwards collaborated in the collection of ova and the rearing of *sayii* at Hall Valley, Park Co., Colorado. The ova are broadcast by the

females as they flutter close to the ground. The newly hatched larvae are thus forced to seek out the foodplant. Throughout its range, *phoebus* is associated with *Sedum*, primarily *lanceolatum* Torrey. Tietz, 1972 listed a variety of hostplants, including *S. debile* S. Wats., *S. obtusatum* Gray, and *S. wrightii* A. Gray. His records for *Carex*, *Gayophytum* and *Phlox* should be considered doubtful. *Saxifraga* has also been cited as a foodplant. In Wyoming, *S. lanceolatum* seems universally to be the larval hostplant. In southern Colorado, *pseudorotgeri* uses *S. rhodanthum* A. Gray and *S. integrifolium* Hook. (B. Rotger *in litt.*).

The larvae feed until late summer, in some areas, hibernate over the winter, and complete the life cycle the following summer. On Vancouver Island, the larvae emerge during the winter and apparently remain dormant until spring (R. Guppy *in litt.*). It has not yet been determined if the life cycle there is completed in one or two years. The mature larvae are velvety black with conspicuous yellow spots. The smooth brownish pupae are formed in the debris on the ground and are covered by loosely woven cocoons. Typically the pupal stage lasts from 2 to 3 weeks.

Detailed descriptions of the immature stages are to be found in W. H. Edwards, Butterflies of North America, 3rd Series, 1897; J. A. Comstock, Bull. S. Cal. Acad. Sci. 25:62, 1926; 29: 135-136, 1930.

SUMMARY

Several factors have become apparent during the course of this study which have contributed to the taxonomic problems surrounding *P. phoebus* in North America. Many of the taxa have been erected by European workers who have studied isolated specimens in museum collections. In addition, it is quite evident that they had no appreciation of North American geography and topography. In many cases, only a very limited number of specimens was examined. With as highly variable a species as *phoebus*, this practice can lead to misconceptions. Examination of many original descriptions has indicated that the authors were totally unfamiliar with prior publications in the field. In several instances, taxonomic findings were based upon interpretations of other workers without checking source material. This has resulted in the establishment of unnecessary taxa and the redescription of subspecies. The source specimens used by several European authors were primarily purchased from dealers. In many cases, locality data was sketchy or incorrect. Museum specimens tend to fade which leads to erroneous concepts concerning facies. Anyone studying *Parnassius* should have long series of fresh specimens before him before making taxonomic pronouncements. He should also be aware of geography and existing literature; three factors it seems that our European colleagues have neglected.

In the present paper, an attempt has been made to arrange the taxa according to consistent characters as noted in the text and delineated in Table II. This may not be the optimum arrangement, but it presents a rational approach to resolving the long-standing confusion concerning *phoebus*. Based upon the analysis cited in this paper, a checklist is given below in which the major synonomies are listed. As previously noted, additional synonomies are shown in dos Passos, 1964.

PARNASSIUS phoebus Fabricius apricatus Stichel, 1906 * golovinus Holland, 1930 * elias Bryk, 1934 alaskaensis Eisner, 1957 * yukonensis Eisner, 1969 ** smintheus Doubleday, 1847 nanus Neumoegen, 1890 magnus Wright, 1905 xanthus Ehrmann, 1918 idahoensis Bryk and Eisner, 1931 montanulus Bryk and Eisner, 1935 maximus Bryk and Eisner, 1937 sauii Edwards, 1863 hermodur H. Edwards, 1881 Altitudinal form hollandi Bryk and Eisner, 1935 dakotaensis Bryk and Eisner, 1935 rotgeri Bang-Haas, 1938 rubina Wyatt, 1961 behrii Edwards, 1870 sternitzkyi McDunnough, 1936 olympianus Burdick, 1941 guppyi Wyatt, 1969 pseudorotgeri Eisner, 1966 arctic race, behrii group arctic race, smintheus group

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TABLE	
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Spot Characteristics in Parnassius phoebus

		[These are average characters over a series; extreme individuals occur in any series.]	racters over a series; e	xtreme individuals	occur in any series.]	
Subspecies		Spot 1	Spots 4-6	Spots 7 - 13	Spot 14	Spots 15 - 20
sayii	E	variable, weakly present in LA, usually absent HA	distinct	distinct ex 13	faint-to-absent	faint & freq absent ex LA
	f	present	na	na	usually black	na
montanulus	E	variable, weakly present HA, LA	faint ex LA	faint	absent ex LA	absent
	H	well-developed	na	na	often red-ctr	na
smintheus	E 4	usually absent less onaque	usually sm 4 6 prominent	faint na	absent lg usually	absent na
	-	than montanulus			red-ctr	
behrii	Ξ	absent	variable, some- times, orange-ctr dark smear.	present	absent	present, 15, 16 freq missing
	f	absent	sometimes lg with orange centers	na	distinct & black	na
sternitzkyi	Е	absent	lg, red-ctr	present	small	variable
	f	faint when present	lg, red-ctr	na	lg, usually black	na
olympianus	Ш	absent	small	present	absent	variable
	f	present	lg red-ctr	na	lg, red-ctr	na
pseudorotgeri	В	absent	faint, 6 may be red-ctr	present 11, 12 absent	small-to- absent	variable, faint
	f	faint	present, freq red-ctr	na	black	na
Abbreviations us tude; $LA = low$	ed: c altitu	Abbreviations used: $ctr = center/centered$; esp tude; $LA = low$ altitude; $lg = large$; $na = not$	esp = especially; ex = except/excepting; freq : not applicable as a distinguishing character; sm	x = except/excepting; freq distinguishing character; sm		frequently; HA = high alti- small.

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		TABI	TABLE II (Continued)	(pai	
Subspecies		Spots 21, 22	Spot 23	Spot 24	Spot 25
sayii	E f	small ex LA freq white-pupiled, but not extending into cell M_3 ex LA	absent very sm or absent	very faint if present sm, some red in LA	absent sm to indistinct
montanulus	f f	prominent freq white-pupiled & extending into $cell M_3$	absent faint-to- absent	absent, present LA, black sm, often red-ctr	absent sm, usually black
smintheus	f B	sm & often white-pupiled lg, freq white- pupiled & extends deeply into cell M ₃	absent usually present	absent lg & red-ctr	absent distinct & freq red-ctr
behrii	f H	sm, orange-ctr sm, orange-ctr	absent absent	absent sm, black	absent sm, black
sternitzkyi	f H	lg, often white-pupiled lg, extends into cell M_3	absent small	small red-ctr	variable red-ctr
olympianus	E f	sm, often white-pupiled lg, freq white- pupiled, extends into cell M ₃	absent indistinct	absent red-ctr	absent red-ctr
pseudorotgeŗi	f II	sm, esp 21 medium, often white-pupiled	absent absent	absent sm, black	absent sm, black
In the line of the line line line line line line line lin	he fer lighte	In the females of the high-altitude specime the lightest colored and <i>sayii</i> is the darkest.	e specimens of th e darkest.	the high-altitude specimens of the <i>smintheus</i> group, <i>smintheus</i> is d and <i>sayii</i> is the darkest.	ntheus is

PARNASSIUS PHOEBUS

Figure 2 shows the distribution of P. phoebus in the region treated by this paper. To conserve space, individual locality records are not cited. Many hundreds of specimens were examined during the course of this study. Records by province, state and county are: smintheus: BRITISH COLUMBIA: southern portion; ALBERTA: southern portion in and along Rocky Mountains. montanulus: ALBERTA: Waterton Park; IDAHO: Bonneville, Fremont, Teton; MONTANA: Beaverhead, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis and Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Sweet Grass; WYOMING: Big Horn, Fremont, Johnson, Lincoln, Park, Sheridan, Sublette, Teton, Washakie, Yellowstone N. P.; sayii: COLORADO: Boulder, Chaffee, Clear Creek, Custer, Delta, Dolores, Douglas, Eagle, Elbert, El Paso, Fremont, Garfield, Gilpin, Grand, Gunnison, Jackson, Jefferson, Lake, Larimer, Mesa, Moffat, Montrose, Ouray, Park, Pitkin, Pueblo, Routt, Saguache, Summit, Teller; NEBRASKA: Sioux; NEVADA: Elko; SOUTH DAKOTA: Lawrence, Pennington; UTAH: Cache, Davis, Duchesne, Emery, Grand, Rich, Salt Lake, San Juan, Summit, Tooele, Uintah, Utah, Wasatch, Weber; WYOMING: Albany, Carbon, Converse, Crook, Sweetwater, Weston. behrii: CALIFORNIA: Alpine, Amador, Calaveras, El Dorado, Fresno, Madera, Mariposa, Mono, Nevada, Placer, Plumas, Sierra, Tulare, Tuolumne. sternitzkyi: CALIFORNIA: Shasta, Siskiyou, Trinity; OREGON: Jackson, Josephine. olympianus BRITISH COLUMBIA: Vancouver Island; WASH-INGTON: Clallam, Okanogan. pseudorotgeri: COLORADO: Archuleta, Hinsdale, La Plata, Rio Grande, San Miguel; NEW MEXICO: Mora, Rio Arriba, Santa Fe, Taos. sayii - pseudorotgeri intergrades: COLORADO: Alamosa, Conejos, Costilla, Huerfano, Las Animas, Mineral, San Juan. montanulus - smintheus "xanthus" intergrades: IDAHO: Ada, Adams, Blaine, Boise, Clearwater, Custer, Latah, Lemhi, Shoshone; OREGON: Baker, Grant, Morrow, Umatilla, Union, Wallowa; WASHING-TON: Asotin, Chelan, Garfield, Klickitat, Okanogan, Pend Oreille, Pierce, Skagit, Spokane, Whatcom, Yakima.

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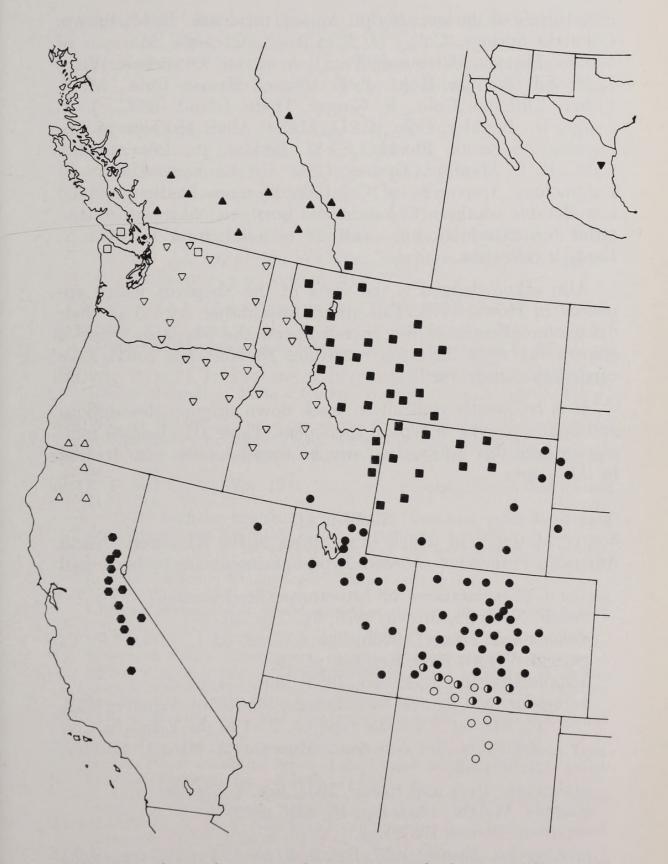


Fig. 2.—Distribution by county of non-arctic *P. phoebus* in North America. Solid triangles = *smintheus*; open triangles = *sternitzkyi*; inverted solid triangle = Mexican race; inverted open triangles = clinal forms; hexagons = *behrii*; solid circles = *sayii*; open circles = *pseudorotgeri*; half-open circles = *sayii* - *pseudorotgeri* cline; solid squares = *montanulus*; open squares = *olympianus*.

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Also acknowledged is the work of the Shepards which appeared in Howe, 1975. This author was rather critical of their discussion (Ferris, 1976). In retrospect, the Shepards made a step in the right direction regarding *phoebus* but could have carried the study further.

It is frequently difficult to track down original descriptions and figures of type or typical specimens. Table III (below) indicates where this information can be found for the taxa treated in this paper.

TABLE III

Source Materials in which Illustrations of the Non-arctic North American *Parnassius phoebus* Type Specimens are to be Found

(See citations in Literature Cited section)

behrii: Neotype, Brown, 1975, fig. 3, p. 10.

dakotaensis: Eisner, 1966b, figs. 4, 5, pl. 22.

guppyi: Wyatt, 1969, figs. 1-4, pl. 15.

hollandi: Paratypes, Eisner, 1955a, figs. 1-4, pl. 23.

hermodur: Not figured by Edwards; figured by Skinner, 1916, pl. XII, fig. 8, female type no. 2791 in the Edwards Collection of the American Museum of Natural History, New York.

idahoensis: Bryk and Eisner, 1931, figs. 4, 5, p. 5.

magnus: Wright, 1905, figs. 13, 13b, pl. 2.

maximus: Eisner, 1957, figs. 1, 2, pl. 4.

montanulus: Eisner, 1957, figs. 5, 6, pl. 4. Typical specimens in Eisner, 1964, figs. 1, 2, pl. 2.

nanus: Not figured by Neumoegen; figured by Skinner, 1916, pl. XII, figs. 4-6.

- olympianus: Burdick, 1941, p. 118. Typical specimens in Eisner, 1964, figs. 3, 4, pl. 2.
- pseudorotgeri: Not figured by Eisner. A typical male is figured incorrectly as hermodur by Howe, 1975, fig. 7, pl. **68**.
- rotgeri: Bang-Haas, 1938, figs. 6, 9, pl. 1.
- rubina: Wyatt, 1961, figs. 1, 2, pl. 11.
- sayii: Neotype, Brown, 1975, fig. 2, p. 7.
- smintheus: Doubleday, 1847, fig. 4, pl. 4.
- sternitzkyi: McDunnough 1936c, p. 273.
- xanthus: Not figured by Ehrmann; figured by Howe, 1975, figs. 13, 14, pl. 69, Wallace, Shoshone Co., Idaho specimens (close to smintheus).

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Note: Lee D. Miller of the Allyn Museum of Entomology has pointed out that the noted collection locality for Moeck's phoebus is thorn desert. Most probably the specimens were taken in the high mountains southwest of Victoria (Sierra Madre Orientale).



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