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DISCOVERY OF A BLACK FEMALE FORM OF *PTEROURUS APPALACHIENSIS* (PAPILIONIDAE: PAPILIONINAE) AND ADDITIONAL OBSERVATIONS OF THE SPECIES IN WEST VIRGINIA

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ABSTRACT: The univoltine *Pterourus appalachiensis* was described from the southern Appalachian Mountain region of the United States as a sympatric sibling of *P. glaucus* (Pavulaan & Wright 2002). A black form was unrecognized at that time. Subsequent sampling of populations at Spruce Knob, West Virginia, revealed a unique black female phenotype present among typically yellow female *appalachiensis*. We believe that this phenotype represents a black female form of *P. appalachiensis*, thus broadening our understanding of this unusual species and firmly establishing its distinction from *P. canadensis*.

Additional key words: mimicry, female-linked polymorphism, sympatry, introgressive-type hybridization

REVIEW OF THE BLACK FORM OF *PTEROURUS GLAUCUS* (LINNAEUS)

Papilio glaucus was described by Linnaeus (1758) from a black female, which he believed was a distinct species unrelated to the large yellow swallowtails of eastern North America. As was customary in 18th century natural history, no type specimen was designated and the name existed for over two centuries without a name-bearing type. Honey & Scoble (2001) in their exhaustive survey of butterflies in the Linnaean collections found no surviving *P. glaucus* specimens. In the absence of syntypes from which to select a lectotype, we designated a typical black female of the summer brood (Fig. 6) as the neotype of *Papilio glaucus* Linnaeus (see Pavulaan & Wright 2002). This specimen was collected on September 10, 2000, in the Sandbridge section of Virginia Beach, VA, a few hundred feet from the Atlantic Ocean. Scott (1981) introduced the infrasubspecific name *nigra* for the black female to distinguish it from the “normally yellow” form. However, this name has no official taxonomic standing under the rules of the ICZN (1999). The black female of *P. glaucus* is believed to be a mimic of the poisonous model *Battus philenor* (Linnaeus), a dark-colored swallowtail that sequesters aristolochic acids from its larval hosts (Sime et al. 2000). The mimetic black female of *P. glaucus* occurs in differing frequencies within the species range, constituting a greater percentage of females in the southern portion and a lesser percentage in the north. This distribution is believed to be in response to the frequency of *B. philenor*, which is more common in southern United States and less common in the north.

DISCOVERY OF AN UNUSUAL BLACK PHENOTYPE OF *PTEROURUS APPALACHIENSIS*

During our original field study of *Pterourus appalachiensis* in years 1985-2001, no black females corresponding to the size and behavior of typical yellow females were found in the mountains of North Carolina, Virginia, Maryland, and southern Pennsylvania. The few black specimens retrieved for identification proved to be rather typical black females of *P. glaucus*. We inferred that *P. appalachiensis* lacked

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a black female because of its general resemblance to *P. canadensis* (Rothschild & Jordan), a univoltine species known to have no black female (Hagen et al. 1991). On June 10, 2001, two unusual black females were captured among approximately 100 yellow *P. appalachiensis* females on the summit of Spruce Knob (4861 ft.) in West Virginia. These black females (similar to Fig. 2) initially confounded us. Their size matched the distinctive large size of *P. appalachiensis* (Fig. 5), and their overall appearance was noticeably different than the local black female form of *P. glaucus* (Fig. 1). At that point, we were undecided whether they were aberrations or an undescribed black female form of *P. appalachiensis*.

In the following years (2002-2004), several more black females of this phenotype were collected on Spruce Knob, suggesting this form existed in a low but stable frequency in West Virginia. On June 5, 2002, four were collected among approximately 100 yellow *P. appalachiensis* females at Spruce Knob and Spruce Knob Lake. On June 24, 2003, nine were collected or observed at these two locations, again among approximately 100 yellow females. On May 29, 2004, the number increased significantly. Eleven black females were collected or observed among approximately 50 females in two hours on Spruce Knob summit. The reason for this sudden increase is unknown; it may reflect natural fluctuations in population size, local weather conditions, and/or quality of nectar sources. (A sampling bias also cannot be ruled out.)

A repeat search for this black female form in other mountainous portions of Virginia, Maryland, and southern Pennsylvania in 2002-2004 was unproductive. Serendipitously, we received a report from Richard Romeyn, who collected an unusual black female specimen on May 10, 2002, at Buck Creek in western North Carolina (Clay Co.), the type locality of *P. appalachiensis*. Examination of the specimen (Fig. 3) revealed a striking similarity between it and the black females from Spruce Knob. We concluded that they were all black females of *P. appalachiensis*. The presence of the black form in the extreme southern Appalachians and West Virginia implies it occurs throughout the species range. We attribute the apparent scarcity of the black female to its low frequency and the general elusiveness of *P. appalachiensis* females.

Spruce Knob is an excellent natural setting to observe large numbers of females. Why is this peak so attractive to *P. appalachiensis*? The answer most likely involves local topography and behavioral tendencies of the butterfly. *P. appalachiensis* is primarily a forest canopy species and females are rarely seen in the forest understory except when nectaring (Pavulaan & Wright, 2002). At 4861 ft. elevation, Spruce Knob (Fig. 7, Top) is West Virginia's highest peak and resides in the boulder-strewn Canadian Zone. It has a relatively open canopy of *Betula lenta* (Black Birch), *Nemopanthus mucronatus* (Mountain Holly), *Picea rubens* (Red Spruce), *Prunus alleghaniensis* (Allegheny Plum), *Prunus pensylvanica* (Pin Cherry), *Quercus rubra* (Red Oak), *Ribes rotundifolia* (Smooth Gooseberry), *Sambucus canadensis* (Black Elderberry) and *Vaccinium* sp. (Blueberries). *Populus tremuloides* (Quaking Aspen), a host of *Pterourus canadensis* (Canadian Tiger Swallowtail) (Hagen et al. 1991), also occurs in this area. The western side of Spruce Knob slopes gradually away from the summit and is persistently windswept. The landscape here has a distinctly subalpine character. *P. appalachiensis* has been observed flying up this rocky slope toward the summit pushed on by strong westerly winds. On the summit are numerous protected crannies characterized by montane heath vegetation (Fig. 7, Bottom), where adults may rest and nectar. *Rhododendron nudiflorum* (Pinkster Flower or Pink Azalea) is locally abundant and blooms precisely during the peak flight of *P. appalachiensis* (Fig. 8).

To the east of Spruce Knob, the terrain drops steeply from the summit. The forest on the eastern slope is primarily Transition Zone. It consists of a vast variety of trees, including *Acer pensylvanicum* (Striped Maple), *Acer rubrum* (Red Maple), *Acer saccharum* (Sugar Maple), *Acer spicatum* (Mountain Maple), *Betula alleghaniensis* (Yellow Birch), *Betula lenta* (Sweet Birch), *Fagus grandifolia* (American Beech), *Fraxinus americana* (White Ash), *Liriodendron tulipifera* (Tulip Poplar), *Magnolia acuminata* (Cucumber Tree), *Magnolia fraseri* (Fraser Magnolia), *Picea rubens* (Red Spruce), *Prunus serotina* (Black Cherry), *Quercus prinus* (Chestnut Oak), *Quercus rubra* (Red Oak), *Sorbus americana* (American Mountain Ash), *Tilia americana* (Linden or American Basswood), and *Ulmus americana* (American

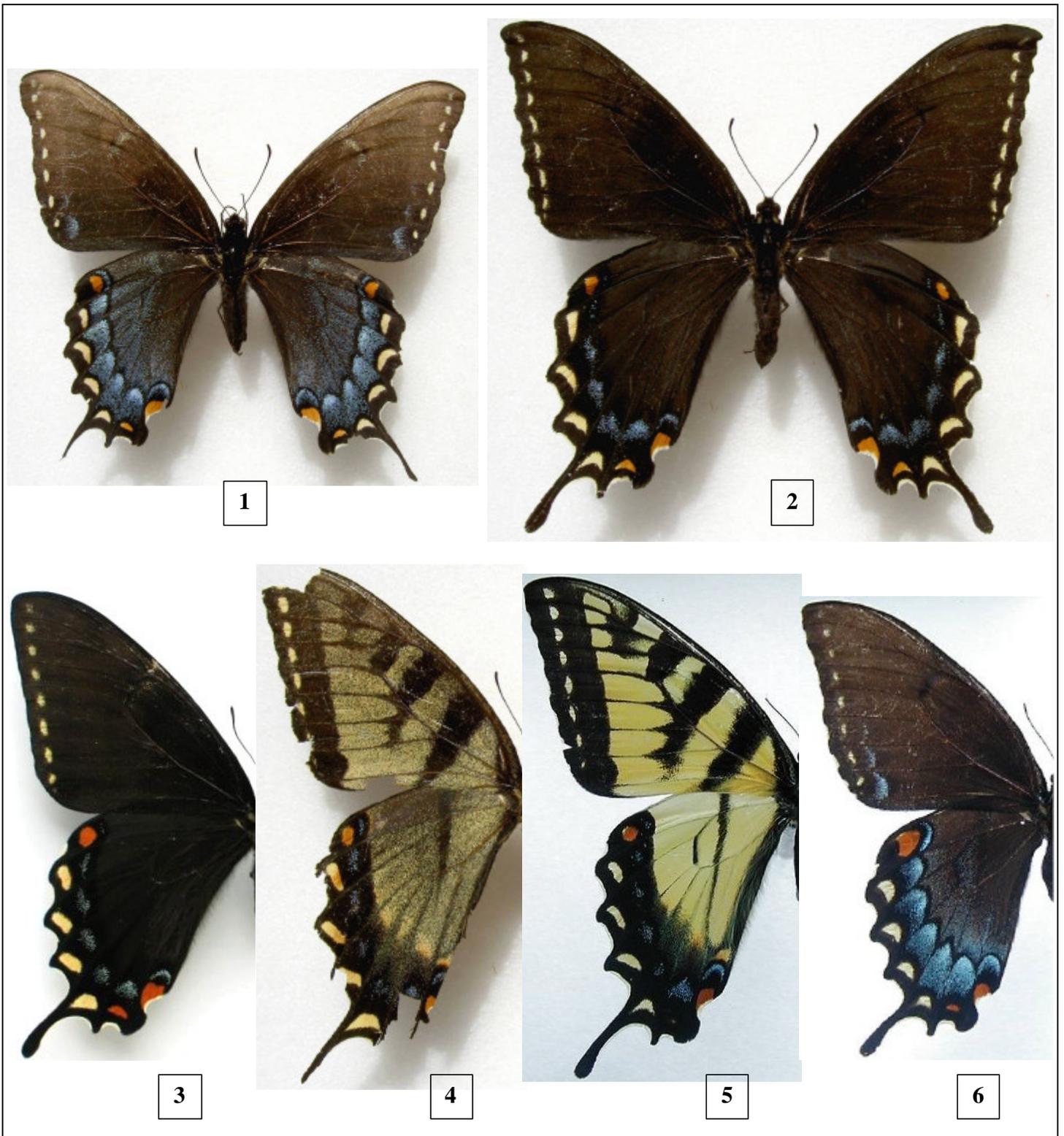


Fig. 1. *Pterourus glaucus*, black ♀ spring form, May 29, 2004, Spruce Knob, near Judy Gap, Pendleton Co., WV. **Fig. 2.** *Pterourus appalachiensis*, black ♀ form, same data as Fig. 1. **Fig. 3.** *P. appalachiensis*, black ♀ form, May 11, 2002, Buck Creek, Clay Co., NC. (*P. appalachiensis* type locality). **Fig. 4.** *P. appalachiensis*, intermediate “dusted” ♀ form, same data as Fig. 1. **Fig. 5.** *P. appalachiensis*, yellow ♀ form, June 10, 2000, Blue Mountain Summit, near Linden, Warren Co., VA. **Fig. 6.** Neotype *Papilio glaucus*, black ♀ summer form, September 10, 2000, Sandbridge, Virginia Beach, VA. All figures natural size.

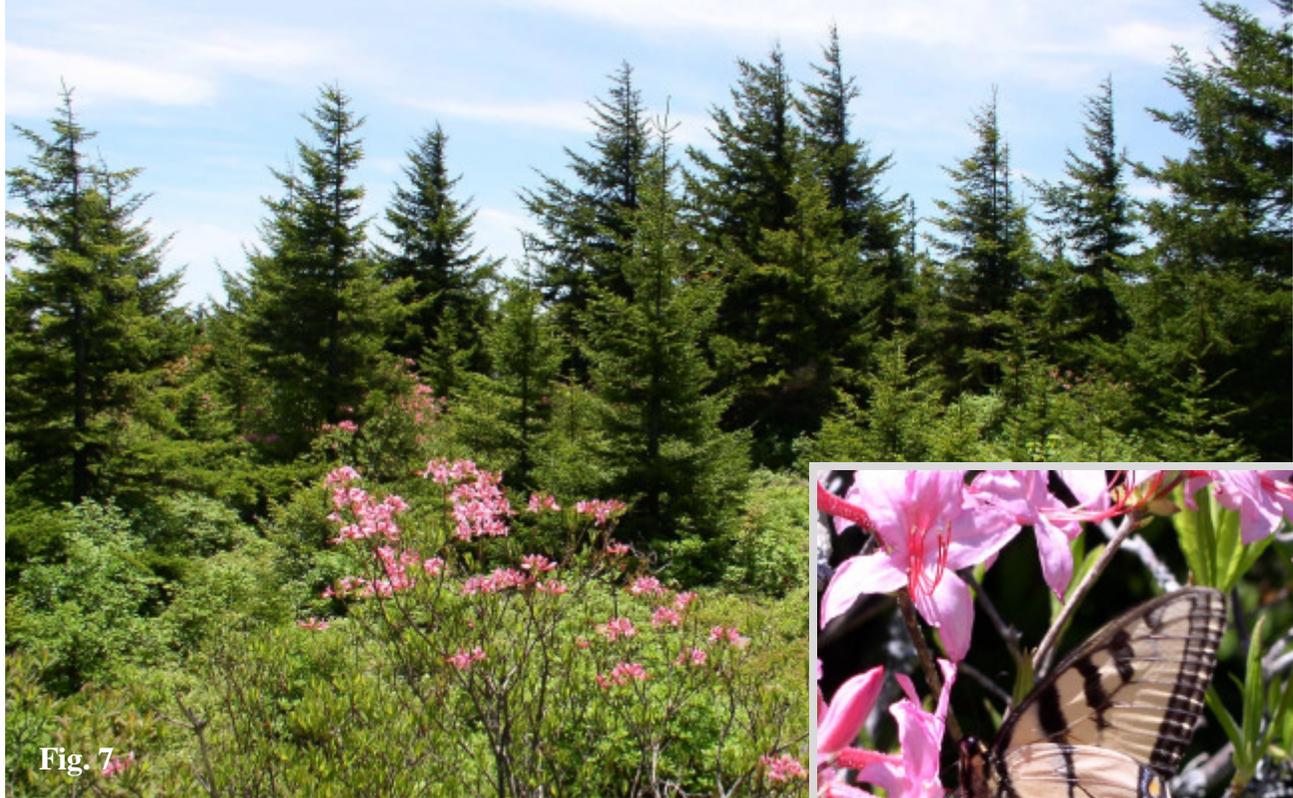


Fig. 7

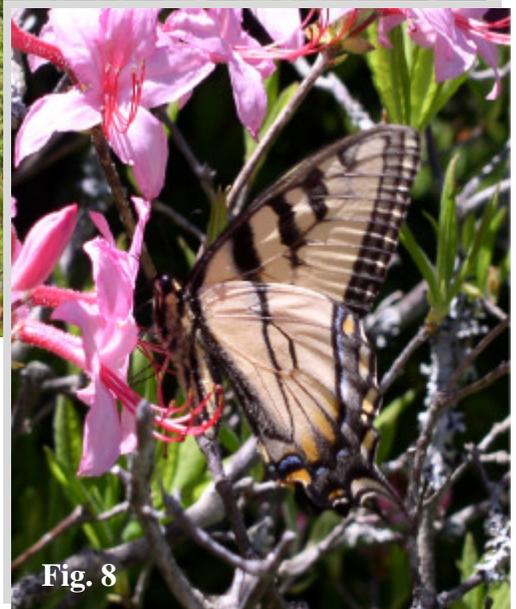


Fig. 8

Fig. 7. Spruce Knob, West Virginia. **Top:** Panorama looking south from summit. **Bottom:** Sheltered area with *Rhododendron nudiflorum*. **Fig. 8.** *Pterourus appalachiensis* female nectaring on *Rhododendron nudiflorum*.

Elm). The dominant trees are well protected from the prevalent winds of the western slope and grow nearly to the summit, forming a solid canopy. From vantage points on the summit trail, one can look over the forest canopy to the east and observe *P. appalachiensis* flying above the treetops. Butterflies flying uphill over the forest canopy suddenly arrive on the summit among abundant blooming azaleas and congregations of swallowtails. The strong westerly winds encountered on the immediate west side of the summit may have the effect of “herding” large swallowtails back to the summit area.

Pterourus appalachiensis black female form

Description. In size and contour, the black female form is similar to the typical yellow *appalachiensis* female. Forewing length = 52-63 mm for known specimens (n = 26). The forewing of the female representing this description (Fig. 2) is 60 mm. There are consistent differences in wing markings between the black females of *P. appalachiensis* and *P. glaucus*.

Dorsum: Forewing uniformly deep black. The ground color in *P. appalachiensis* appears blacker than in *P. glaucus*, which tends more toward a dark brownish gray. In most specimens there is no trace of the black margin or wing stripes. There is a submarginal row of eight yellow lunules from cell R3 to cell Cu2, arranged in a straight line. In most aspects, the dorsum of the female forewing resembles the black female form of *P. glaucus*, but differs mainly in that the shape of the forewing is slightly more angular in appearance and the outer edge of the wing is straighter, while it is often slightly curved in *P. glaucus*. Also the blue crescent frequently present at the tornus in cell Cu2 of black female *P. glaucus* is absent in *P. appalachiensis*. In *P. glaucus*, this blue crescent may be very prominent and there are frequently additional small blue crescents within cells Cu1 and M3 of the submarginal band.

Interestingly, three specimens possess a faded yellow median bar across the outer end of the discal cell. This bar is located between the placement of the second (inner median) and third (outer median) black stripes found on the forewing of typical yellow females. Due to small sample size, it is unknown whether this faded yellow bar is a consistent low-frequency character and an aberration. It is commonly found in black *P. glaucus* females.

Hindwing contour, margin, fringe, and tail as in the typical yellow *appalachiensis* females. There are 6 elongated submarginal lunules, as in the yellow females. The first lunule in cell Sc+R1 smallish, rounded, and deep orange. Lunules in cells RS, M1 and M2 whitish yellow. Lunule in cell M3 is a yellow curved crescent extending somewhat into the base of the tail at vein M3. Lunule in cell Cu1 orange and often reduced to a narrow streak. Within the submarginal area, interior to the submarginal lunules, is a terminal row of six blue crescents as in the yellow females, extending from cell Sc+R1 to cell Cu1. Blue crescents in cells M1, M2 and M3 generally equal in size and extent. Blue crescent in cell Cu1 is generally larger and the most prominent of the blue crescents; crescents in cells RS and Sc+R1 significantly reduced (absent in some individuals). At anal angle, cell Cu2 with large orange crescent edged with wide whitish yellow fringe. Proximal to orange crescent is a narrow blue crescent. The remainder of the hindwing is uniformly black.

In some aspects, the dorsum of the black female hindwing resembles that of the black female form of *P. glaucus*. However, there are noticeable departures between the two taxa. As in the yellow *appalachiensis* females, the black female hindwing is more elongate, narrower and triangular-shaped; the costal margin has a more “suarish” angle at the outer margin; the scallops of the wing margin are more angular; the submarginal lunules are more elongate; the tail is narrower and less “clubbed”. In *P. appalachiensis* the submarginal orange crescent in cell Sc+R1 is smaller than the remainder of the (whitish yellow) submarginal crescents, while in *P. glaucus* it is noticeably larger than the remaining crescents. A major distinguishing character is the extent of blue markings. In *P. glaucus*, the terminal blue crescents form a continuous scalloped band spanning the entire wing. In *P. appalachiensis*, these crescents are significantly reduced and form a row of discrete separate crescents; the blue crescents in cells RS and Sc+R1 are often markedly reduced or even absent. The difference in the extent of blue between both species is noticeable and striking. Furthermore, in *P. glaucus* there is considerable blue overscaling in the postmedian discal portion of the hindwing, which is generally lacking in *P. appalachiensis*. However, in two individuals, a trace of blue overscaling is evident. Within the range of *P. appalachiensis*, yellow and black females are considerably larger (50-65 mm) than *P. glaucus* females of the spring flight (34-53 mm) and slightly larger than the later summer *P. glaucus* females (49-64 mm).

Venter: Typical striped pattern of the yellow females is evident and repeats that of the ventral surface of the yellow females with modification of the ground color. Ground color variably blackish brown, obscuring the black striped tiger pattern.

Forewing darker than the hindwing. Blackish brown ground color obscures the black striped pattern in most individuals, though in some it is evident. When evident, the broad black margin, fringe, and three inner black stripes are generally of the same size and extent as in the yellow females. However, unlike the yellow females, the submarginal yellow band is replaced by a row of eight yellow submarginal crescents as in *P. glaucus*. The lowest lunule at the tornus (cell Cu2) is reduced and generally broken into two small spots within the cell, as in the yellow females. The lowest of these two small spots is smaller and occasionally absent.

The venter of the female forewing closely resembles that of the black female form of *P. glaucus*. The submarginal yellow band characteristic of the yellow *appalachiensis* females is replaced by a row of eight yellow submarginal crescents as in *P. glaucus*.

Hindwing ground color dark blackish brown with broad black margin and fringe edged with yellow. The classic tiger-stripe pattern is evident. Black marginal area with row of six elongated submarginal lunules as in yellow *appalachiensis* females. The first lunule in cell Sc+R1 rounded and deep orange. Lunules in cells RS, M1 and M2 whitish yellow but variably tinged with orange. Lunule in cell M3 is a yellow curved crescent extending somewhat into the base of the tail at vein M3. Lunule in cell Cu1 orange and often reduced to a narrow streak. Within the submarginal area, interior to the submarginal lunules, is a terminal band of grayish-blue clouding, as in the yellow females, extending from cell Sc+R1 to cell Cu1. Narrow black median stripe crosses wing as in the yellow female. Dark discal veins form an arch. Veins M3 and Cu1 outlined with additional black scaling enhancing thickness. Unlike the yellow females, the cells M3 and Cu1 between these veins do not contain areas of orange coloration.

The venter of the female hindwing departs from the general appearance of the black form of *P. glaucus* primarily by its more elongated submarginal lunules. Unlike yellow *appalachiensis* females, the lunules of known specimens tend not to be rectangular, though they are not as arched as in *P. glaucus*. As in the yellow *appalachiensis* females, the inner edge contour of the broad black marginal area generally forms a straight line in cells RS and M1, angling outward in cell Sc+R1 and angling inward in cell M2. In *P. glaucus* the inner edge of the margin is scalloped inwardly in each cell.

Specimen records. Since infrasubspecific form names have no official standing under the ICZN rules, we refrain from naming this form and prefer to simply designate our specimens as “*Pterourus appalachiensis* black female form”. The specimen in Fig. 2 from Spruce Knob summit, 4861 ft. elev., Pendleton Co., WV, May 29, 2004, is retained in the collection of the senior author. It depicts the key phenotypic features given in the description above. Additional specimens from the same location and forming part of the descriptive study series are as follows: June 10, 2001 (n=2), June 5, 2002 (n=4), June 24, 2003 (n=9), May 29, 2004 (n=10). It is important to note that none were found at this location in mid or late summer after the *P. appalachiensis* flight period. This supports it as a normal *P. appalachiensis* form and not a form of *P. glaucus* or hybrid.

Additional Nectaring Observations in WV. On the summit of Spruce Knob, *P. appalachiensis* adults nectar chiefly on *Rhododendron nudiflorum* (Pinkster Flower or Pink Azalea). This shrub thrives in the rocky landscape (Fig. 7, Bottom), where stands of Red Spruce trees provide shelter from the wind. *Elaeagnus commutata* (Autumn Olive) and *Diervilla lonicera* (Bush Honeysuckle) are used as nectar sources just below the exposed summit area. Along the summit approach road in the Transition Zone forest, adults use flowers of *Crataegus crus-galli* (Cockspur Thorn) at higher elevations and *Erigeron ramosus* (Daisy Fleabane) at lower elevations. At Spruce Knob Lake, 3840 ft. elev., 3 mi. west in nearby Randolph Co., *D. lonicera* is the primary nectar source. South of Spruce Knob, at Seneca State Forest in Pocahontas Co. (Transition Zone), 2600-3600 ft. elev., *P. appalachiensis* adults including black females have been observed and photo-documented on *Kalmia latifolia* (Mountain Laurel).

A REEVALUATION OF TIGER SWALLOWTAILS IN WEST VIRGINIA

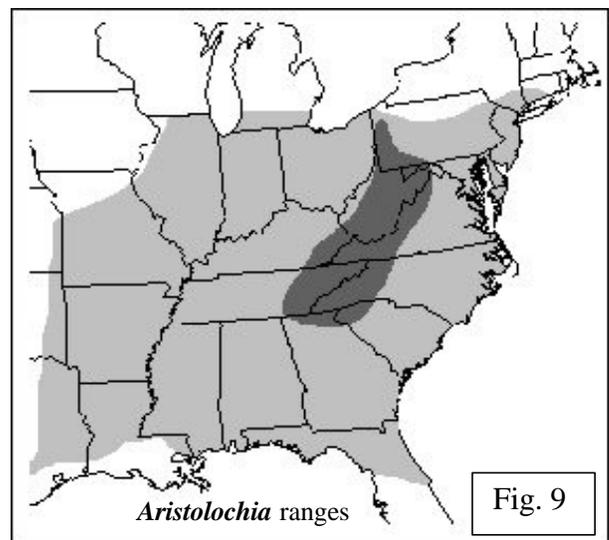
In reexamining *The Butterflies of West Virginia and Their Caterpillars* (Allen 1997), an important observation surfaced regarding the tiger swallowtails in Plate 3 (p. 253). Three specimens in this color plate display key features described for *Pterourus appalachiensis* in Pavulaan & Wright (2002) and for the black female form described above. In Row 1, the left specimen [Rt. 41, Prince, Fayette Co., WV, May 22, 1987] fits the criteria for an *appalachiensis* male, while the right specimen is a rather typical spring form *glaucus* male. In Row 2, the left specimen is a rather typical summer form *glaucus* female, whereas the right specimen [East Fork of Glady Creek, Randolph Co., WV, June 18, 1984] fits the key characters of the black female form of *appalachiensis*. In Row 3, the left specimen [East Fork of Glady Creek, Randolph Co., WV, June 18, 1984] is a female specimen of intermediate “dusted” phenotype fitting the general features of *appalachiensis* and is also similar to a “dusted” specimen we collected at Spruce Knob (Fig. 4); the right specimen is a rather typical black summer form *glaucus* female. It is interesting to note that all six specimens in this plate were photographed together in a single frame. From this perspective, a general comparison of their relative sizes can be made. The *appalachiensis* specimens are noticeably larger than the *glaucus* specimens. We also regard the male in Plate 20 (p. 286), Row 1, right specimen [Lanesville, *sic*, Tucker Co., WV, June 18, 1973], as a typical *P. appalachiensis* male.

In Pavulaan & Wright (2002), we reported that many of the small individuals from the mountainous regions of West Virginia were phenotypically *canadensis*-like and we suspected that the small phenotype might represent relictual *P. canadensis*. It appeared that *P. canadensis* and *P. appalachiensis* overlapped in a small area of sympatry in the highlands of West Virginia, as evidenced by the two size segregates that flew contemporaneously. However, we now believe that true *P. canadensis* is absent from West Virginia. A preliminary electrophoresis study of the small *canadensis*-like phenotypes from Spruce Knob found only *glaucus* allozymes (Scriber & Ordning, unpublished results). This new evidence confirms the presence of *glaucus* at higher altitudes of the Appalachians, albeit as diminutive forms which are far outnumbered by *P. appalachiensis*. These small variants of *glaucus* are more common at low and mid elevations in early spring and can be easily confused with the northern species (Scriber 1990b).

To our knowledge only *P. appalachiensis* and *P. glaucus* occur in West Virginia. The southern limit of true *P. canadensis* populations in eastern United States is poorly defined, but it is at least several hundred miles north of West Virginia in northern New York (Adirondacks) and northern New England. Immediately south, the two species *P. canadensis* and *P. glaucus* hybridize in a narrow zone across central New York, northern Pennsylvania, and Massachusetts. Individuals from these hybrid populations exhibit a composite of *canadensis* and *glaucus* traits (Scriber et al. 2003) and fly in polymodal fashion (Hagen & Lederhouse 1984). It had been predicted that the southern Appalachians might provide a corridor for the extension of the present hybrid zone or altitudinal refugia for *canadensis* types (Scriber 1996). Currently, *P. appalachiensis* satisfies neither hypothesis fully. Although Allen (1997) concluded they were hybrids, *appalachiensis* individuals differ in many details from those in the present hybrid zone (e.g. size, yellow female phenotype, black female, female behavior, neonate larva, flight mode, mtDNA). Instead of viewing *P. appalachiensis* as a relictual “*canadensis* type” in a southern Appalachian refuge, a preferable treatment is to view this species as a relictual montane “*glaucus* type”.

SIGNIFICANCE OF BLACK FEMALE AND THE TAXONOMIC STATUS OF *P. APPALACHIENSIS*

The discovery of a black female in *P. appalachiensis* is consistent with our previous conclusion that this univoltine species evolved primarily from a *glaucus* genome. In many yellow *Pterourus* swallowtails the black female is genetically suppressed (West & Clarke 1988). It is absent in the northern species *canadensis* and the western species *rutulus* (Lucas), *eurymedon* (Lucas), and *multicaudatus* (W.F. Kirby). Its presence in both *P. appalachiensis* and *P. glaucus* underscores the critical importance of mimicry to achieve maximal fitness in habitats where a poisonous model exists. *Battus philenor* is very common in the southern Appalachians. The abundance of *Battus philenor* in the mountains can be attributed in part to the density of its local larval host, *Aristolochia macrophylla* (Dutchman’s Pipe). *A. macrophylla* flourishes in the mountains of West Virginia (Strausbaugh & Core 1978), where it is reported to be the host for *philenor* (Allen 1997). (See Fig. 9. *A. macrophylla*, dark gray. *A. serpentaria*, light gray. FNA 2000.) A single plant of this broad-leaved species can support the growth of several larvae, whereas a single plant of *A. serpentaria* (Virginia Snakeroot) is not enough for one *philenor* larva to mature to pupation (Rausher 1980). The role of ecological factors in natural selection and in speciation cannot be overstated. The absence of a black mimetic female may have selected against *P. canadensis* and other hybrid “*canadensis* types” in this region.



The distinctive large size and reduced blue scaling of the *P. appalachiensis* black female suggest a possible aberration or developmental abnormality. We doubt this is the case, since this phenotype appears regularly at Spruce Knob year after year and seems to be unchanged. An extensive search of the literature relating to aberrations of tiger swallowtails found no natural examples matching the *P. appalachiensis* black female (Clark 1932, 1936; Clark & Clark 1951; Clarke & Clarke 1983; Edwards 1884; Gunder 1927; Heithaus 2003; Howard 1899; Scriber 1990a; Scriber & Evans 1988; Scriber et al. 1987; Strecker, 1878; Tyler et al. 1994). To understand the development of the mimetic wing pattern we must turn to *glaucus* where it has been studied extensively (Clarke & Sheppard 1959). The pattern is constructed from several independently inherited characters that evolved in several steps. A single sex-linked gene controls the black background. Any gene that produces a great deal of black will produce tolerable mimicry. This female-limited gene appears to be an efficient switch because intermediates are rare. The other elements in the mimetic pattern (blue scaling and red spots) are under polygenic control. The suite of genes responsible for these elements are distributed on one or more autosomal chromosomes and inherited independently of black. The regulation of autosomal blue scale genes is poorly understood. Interspecific hybridization is a significant causal mechanism of unusual color morphs, and, occasionally, dark females with reduced blue scaling result from hand-paired laboratory crosses (Scriber & Evans 1988; Scriber et al. 1987; Scriber et al. 1995). However, these hybrid individuals are predisposed to chromosomal alterations that severely jeopardize their integrity and they (or their progeny) rarely survive. In contrast, the black female phenotype in *P. appalachiensis* appears to be unique in nature and fixed as part of a stable female-linked polymorphism.

We presently consider *P. appalachiensis* to be an established species and the dominant species at higher elevations of the southern Appalachians. Its range is fully sympatric with *P. glaucus* and the two species are easily distinguishable in the field. In our earlier paper (Pavulaan & Wright 2002) we speculated that *P. appalachiensis* evolved initially as a montane race of *P. glaucus*, either independently or through the introgression of unique genes. A recent electrophoresis study of specimens from Spruce Knob discovered that *appalachiensis* individuals carry a mix of allozyme alleles (*canadensis*-type LDH, *glaucus*-type PGD), suggesting introgressive-type hybridization and a relatively modern origin (Scriber & Ording, unpublished results). The acquisition of favorable genes, such as an obligate diapause gene and genes expanding tolerances of larvae and pupae, may have acclimated proto-*appalachiensis* to the southern Appalachians. The full extent of introgressive-type hybridization in evolution and animal diversification is unclear. Unlike plants, hybrid animal taxa appear to be relatively rare. However, this may be due to negative attitudes toward hybridization and the difficulty in detecting such examples (Dowling & Secor 1997). Recently, *Papilio joanae* Heitzman (in the Ozarks) and *P. brevicauda* Saunders (in eastern Canada) of the *machaon* group of black swallowtails have been put forth as examples of taxa of hybrid origin (Sperling 2003; Sperling & Harrison 1994). Finally, we caution that further detailed studies are needed to establish the age and origin of *P. appalachiensis*. Presently, it cannot be ruled out that *P. appalachiensis* is ancestral to *P. canadensis*. *P. appalachiensis* may have independently evolved unique adaptive genes and launched proto-*canadensis* into the vast northern territories.

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[Editor's note. A photo of the venter of the black *P. appalachiensis* female can be found at the TILS web site photos section.]

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