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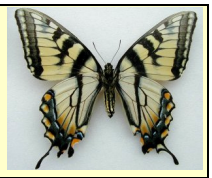

PTEROURUS APPALACHIENSIS (PAPILIONIDAE: PAPILIONINAE), A NEW SWALLOWTAIL BUTTERFLY FROM THE APPALACHIAN REGION OF THE UNITED STATES

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ABSTRACT: A new univoltine species of Tiger Swallowtail, *Pterourus appalachiensis*, is described from the southern Appalachian Mountain region of the eastern United States. This distinct swallowtail has remained unrecognized by lepidopterists since the description of its sympatric congener *Pterourus glaucus* (Linnaeus) in 1758. Historical accounts of Tiger Swallowtails from this region pertain specifically to *glaucus* and cannot be attributed to this new species. Morphology, voltinism, phenology, distribution, and behavioral traits indicate species level status of *appalachiensis*. Although *appalachiensis* shares several phenotypic characters with the recently elevated species *canadensis* (Rothschild & Jordan), preliminary mitochondrial DNA analysis indicates that *appalachiensis* is more closely related to *glaucus*. Additional work is needed to identify the natural hosts and evolutionary origins of this fascinating species.

Additional key words: Cryptic species, sympatry, species complex**.**

REVIEW OF *PTEROURUS GLAUCUS* (LINNAEUS)

The insect commonly known for over 150 years as the Tiger Swallowtail (Miller, 1992) and more recently as the Eastern Tiger Swallowtail (NABA, 1995) has been the subject of intensive investigation in recent years regarding its ecology, genetics, and systematics (Scriber et al., 1995; Scriber, 1996). It was the first butterfly depicted by an artist from the New World. John White, while serving as the expedition leader of Sir Walter Raleigh's third sortie to America ("Virginia" = Roanoke Is., North Carolina), rendered the famous first painting in 1587 which was reproduced in Holland (1931, Pl. 77) (Fig. 1). Despite some exaggerations through artistic license, White otherwise provided accurate detail. The specimen appears to be a male. Among marginalia appended to the original painting is the name "Mamankanois", that is believed to be an equivalent to the Native American Indian name for "butterfly". The painting fell into the hands of Thomas Moffett of London, who directed the making of a woodcut facsimile and its eventual publication in 1634 (p. 98) (Fig. 2). Moffett's figure was copied by Jonstonus in 1657 (Pl. 5) (Fig. 3). The butterfly was described again by Merret (1666) and Petiver (1699), but not figured. Petiver formerly called it "*Papilio Caudatus, luteus, maximus, Virginianus*" and informally referred to it as "Moffet's great yellow

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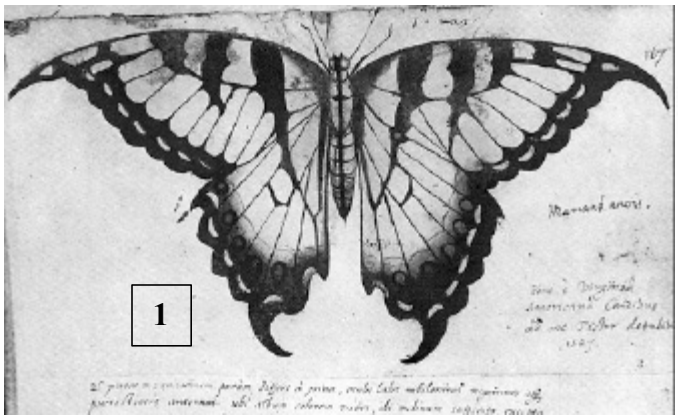

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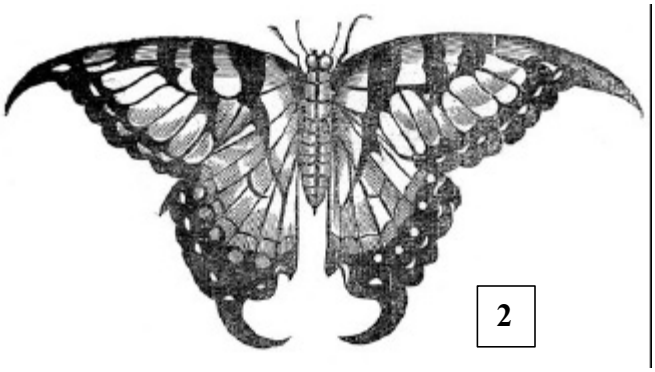

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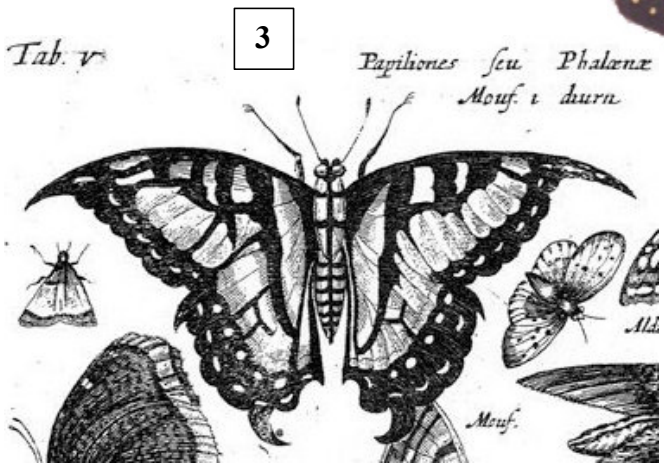

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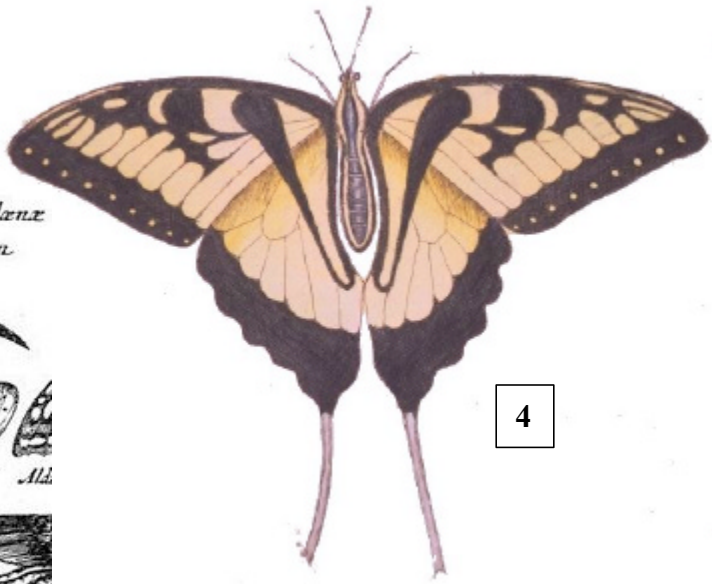

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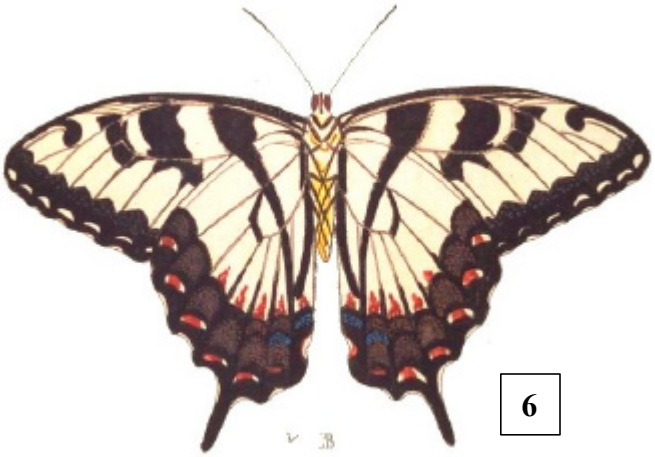

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Figures 1 - 6: Earliest artistic renditions of *Pterourus glaucus glaucus*. **Fig. 1.** Mamankanois from White, 1587. **Fig. 2.** Moffett's 1634 rendition of Mamankanois. **Fig. 3.** Jonstonus' 1657 copy of Moffett's cut. **Fig. 4.** *Papilio caudatus maximus, Carolinianus* in Catesby, 1736. **Fig. 5.** Dorsal, *Papilio alcidamas*, Cramer, 1775. **Fig. 6.** Ventral, *Papilio alcidamas*, Cramer, 1775.

and black Virginia Butterfly". He also cited the works of Moffett, Jonstonus and Merret. The next depiction (Pl. 83) was by Catesby in his The Natural History of Carolina, Florida and the Bahama Islands, Vol. 2 (1736) (Fig. 4). Catesby called it "*Papilio caudatus maximus, Carolinianus*" and cited Petiver's work. These pre-Linnean names have no standing in The Code, however illustrations and descriptions published in this period may be used by authors erecting Latin names in 1758 and afterward (Article 3.2) (ICZN 1999).

The next descriptions came from Linnaeus (1758), whose Systema Naturae (10^{th} ed.) marked the official beginning of zoological nomenclature. Linnaeus first described *Papilio glaucus* (p. 460) from a dark female form. The location was described as "*Habitat in* America." No type specimen was designated and it is believed that none existed. In the same publication, Linnaeus described *Papilio antilochus* (p. 463). He cited the previous works of Petiver and Catesby, and in so doing referred to a male specimen. The location was given as "*Habitat in* America *Septentrionalis*." Similarly, no type specimen was designated, and it is believed that none existed. Linnaeus (1771) later described *Papilio turnus* from the yellow form of the female and the location was described as "*Habitat in* America". No figure or type was provided. Cramer (1775) described *Papilio alcidamas* (Pl. 38) from a male specimen, and gave the location as "Jamaica, but also can be found from New York to Carolina.". The plate depicts a typical summer form *glaucus* male (Figs. 5 & 6). No type specimen is known. Rothschild and Jordan (1906) restricted the type locality to "New York, Carolina".

DISCOVERY OF AN UNUSUAL SWALLOWTAIL

During the interval 1985 to 2001, while conducting research in various sites of the southern Appalachian Mountains, yearly emergences of an unusual Tiger Swallowtail were consistently noted. The annual appearance of this butterfly was interpolated in the staggered emergence of what was considered to be one species *Pterourus glaucus*. Traditionally, offset spring flights of an individual species in the mountain region are attributed to stratified climatic conditions. At higher elevations average colder temperatures directly affect the emergence dates of butterflies, where the first individuals appear later than those at lower elevations. In time, however, it became evident to us that climatic conditions could not account for significant differences between low and high altitude populations. The contrasting phenotypes and differences in voltinism between Piedmont and Appalachian populations were reminiscent of sibling species. We theorized that two taxa were likely involved, i.e. standard *glaucus* and a new species. Privately, we choose a temporary moniker for the latter ("giant *canadensis*") because it was quite large and immediately recognizable by its *canadensis*-like yellow submarginal band on the ventral forewing. Furthermore, it had a single brood and lacked a black female form. Careful subsequent sampling allowed us to establish a primary southern Appalachian distribution for this new taxon.

The principal question was did this unusual swallowtail represent an unrecognized population of *Pterourus canadensis* (Rothschild & Jordan) in the southern Appalachians. Allen (1997) included *P. canadensis* in the West Virginia fauna based on phenotypic similarity of mountainous West Virginia populations to *canadensis* populations from areas much further north (Figs. 7 & 8). The primary distinguishing feature of *canadensis* is the strongly developed yellow submarginal band on the ventral forewing. In *glaucus* this band becomes a row of yellow lunules interrupted by black. On June 10, 2001, we sampled and measured several *Pterourus* swallowtails on the summit of Spruce Knob in Randolph Co., WV (4861 ft., Canadian Zone). One segregate of individuals (n=8) was immediately recognizable as *canadensis* by diminutive size (FW costal length 43-48 mm) and a strongly developed submarginal band. This is the only location where we have found *canadensis* in West Virginia, though Allen lists it from five counties. Several attempts to find it at Dolly Sods Natural Area in Tucker Co., WV (Canadian Zone) were unsuccessful. Also flying with standard *canadensis* at Spruce Knob were (n=18) much larger individuals

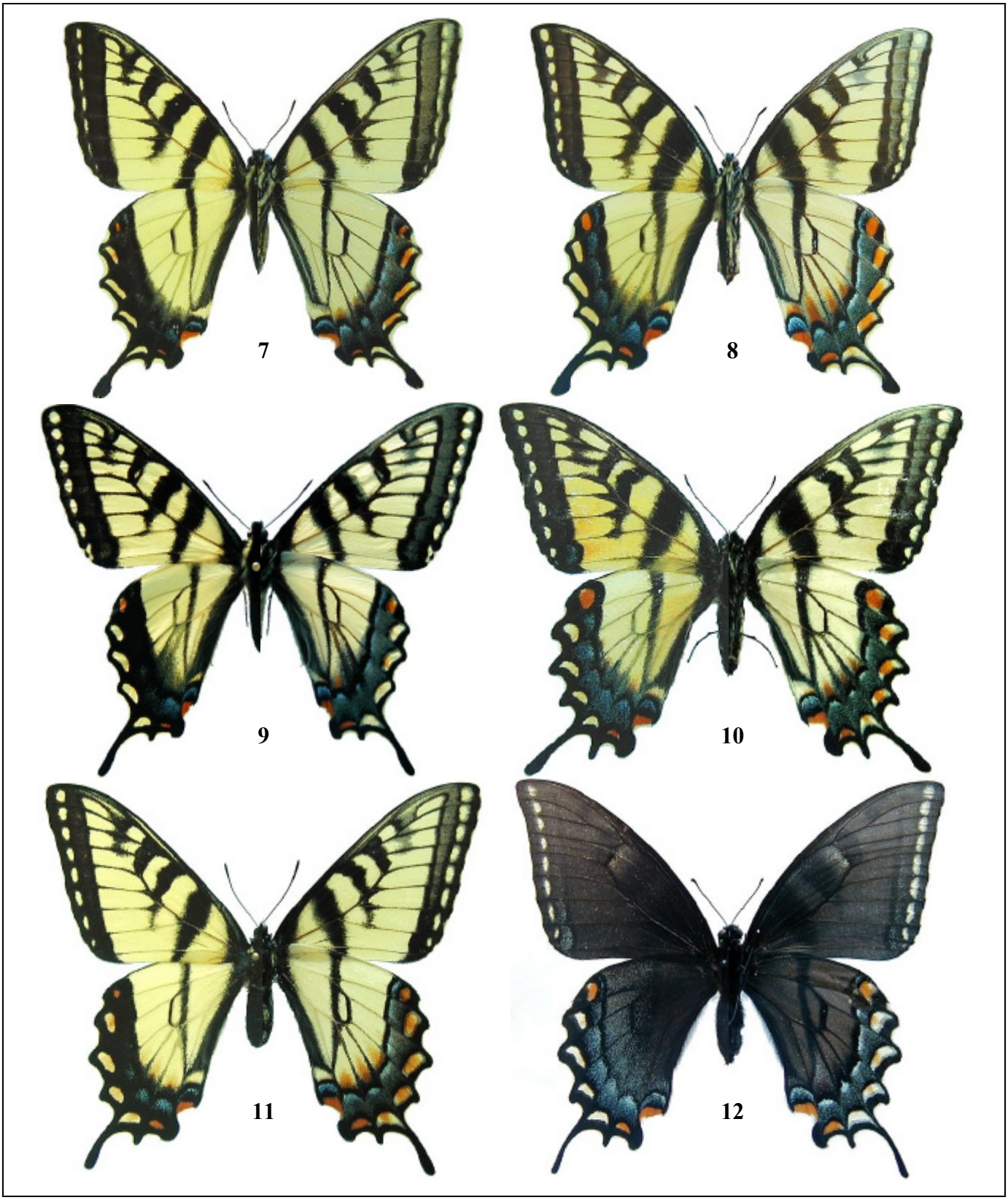
(51-65 mm) of the "giant *canadensis*" phenotype observed elsewhere in the southern Appalachians. With two size segregates clearly present in West Virginia and only the larger phenotype occurring further south in the mountains, we felt it was unlikely that "giant *canadensis*" actually was *canadensis*.

For a time we also entertained the possibility that "giant *canadensis*" represented a hybrid phenotype between low altitude *P. glaucus* and undiscovered populations of *P. canadensis* at higher elevations. Allen (1997) reported that hybridization between *glaucus* and *canadensis* probably occurred in West Virginia and that *canadensis* ranged further south in a hybrid zone through Virginia to western North Carolina. However, an exhaustive search of the mountains of western North Carolina and eastern Tennessee, the Blue Ridge of Virginia, and Dolly Sods Wilderness of West Virginia proved unsuccessful in finding the small *canadensis* phenotype. We also observed that the spring brood of *glaucus* was noticeably absent at higher elevations. Thus in the absence of one parent species or both, hybrids would not be possible. Since the new taxon occurred in such dominant numbers over such broad mountainous regions, we were convinced it was not the product of ongoing hybridization.

It is important to call attention to a confounding situation at low and mid elevations in the Appalachians. Small *canadensis*-like variants of *glaucus* (Fig. 9) occur there regularly in the early spring. These variants often possess strongly developed yellow submarginal bands on the ventral forewing, making them difficult to distinguish from *canadensis* on the basis of that character alone. In some, the black margin of the inner hindwing is also broad, however, this is usually narrower in these variants and aligns with descriptions of this trait in *glaucus*. Virtually all females associated with these early spring, yellow-banded males are readily identified as *glaucus* (Fig. 10), because they have considerable blue on the dorsal hindwing. Also approximately 50% of the early spring females are the black form *glaucus* (Linnaeus) (Fig. 12) in our study area in northern Virginia. Offspring of these early spring *canadensis*-like variants, obtained from ovipositions in captivity on both *Prunus serotina* and *Liriodendron tulipifera*, yield typical summer form *glaucus* adults. Routinely, the early spring populations of *glaucus* (Fig. 11) on the coastal plain and outer Piedmont fail to generate strong *canadensis*-like traits.

The yellow submarginal band on the ventral forewing is a consistent feature of several North American *Pterourus* swallowtails including *P. canadensis* in the north; *P. rutulus* (Lucas), *P. eurymedon* (Lucas) and *P. multicaudatus* (W. F. Kirby) in the west; and *P. alexiares* (Hopffer) in Mexico. *Glaucus* is the exception among the Tiger Swallowtails in having the submarginal band replaced by a row of yellow crescents. We scanned several eastern collections for yellow banded specimens from the Appalachian Mountains in western North Carolina to south-central Pennsylvania and found additional males & females with this character which had been previously labeled "*Papilio glaucus*". All of these specimens were collected within the hypothetical flight period (May-June). The females bore a striking resemblance to *P. canadensis* on the ventral forewings, but departed significantly from *canadensis* on the dorsum. Taken all together, our observations lead us to conclude that we were seeing an unrecognized species. A unique feature of the new taxon is its considerable size, which is in stark contrast to what one would expect in a spring swallowtail in the mountain region.

The most extensive historical coverage of Tiger Swallowtails from this region is found in Clark & Clark (1951). These authors devoted 20 pages to phenotypic variation within *glaucus*, not only in Virginia but also throughout the entire species range, which included at-the-time subspecies *canadensis*. Having carefully read and reread this work, we cannot find clear reference to a unique Appalachian Mountain phenotype. The authors described an early spring phenotype ("late March or early April") from northern Virginia as being comparable to *canadensis* and even to Alaskan *P. canadensis arcticus* (Skinner). Their description is attributable to the early spring *canadensis*-like variant of *glaucus* (Fig. 9) which we found primarily in the Blue Ridge region. Clark & Clark (1951) also described a late-spring phenotype which emerged "ten days or two weeks after the first appearance" of the early spring form. They considered this to be normal *glaucus*, though somewhat intermediate between spring and summer forms. It contained both black and yellow female forms. Their spring form intergraded through an "unbroken series" to "the typical



Figures 7-12: *P. canadensis* and early spring *P. glaucus* (all split dorsal/ventral aspects). **Fig. 7.** ♂ *P. canadensis*: no date, Miners Bay, Ontario, Canada (leg. unknown). **Fig. 8.** ♀ *P. canadensis*: same data as 7. **Fig. 9.** ♂ *P. glaucus*: 4 May 2001, Buck Creek, Clay Co., North Carolina (leg. Gatrelle). **Fig. 10.** ♀ *P. glaucus*: 27 April 1999, Blue Mountain, nr. Linden, Warren Co., Virginia. **Fig. 11.** ♂ *P. glaucus*: 23 April 1993, Germantown, Montgomery Co., Maryland. **Fig. 12.** ♀ *P. glaucus*: 7 April 2002, same data as 10. All leg. Pavulaan except Figs. 7-9. All are actual size. Photos: Joe Mueller.

[summer] form" which appeared shortly after the end of the spring flight; occasionally the two broods overlapped. Our observations of *glaucus* on the Piedmont and in the lower mountain elevations parallel those of the Clarks, which is consistent with a bimodal spring emergence pattern (early spring & mid spring). Clark & Clark (1951) also discussed *glaucus* in other text sections of their Virginia monograph, including a curious reference to "northern 1-brooded forms still persist[ing] in the mountains" (p. 7) and to "[some] pupae…remaining dormant until the following spring" (p. 123). Our interpretation is that they did not recognize these points as referable to a different but fairly cryptic species.

DESIGNATION OF NEOTYPES

We contend that name-bearing types serve to stabilize taxonomic nomenclature and are compelled to designate neotypes for the four names previously published for the species *Pterourus glaucus* (Linnaeus) in the eastern United States. These names are *Papilio glaucus* Linnaeus 1758, *Papilio antilochus* Linnaeus 1758, *Papilio turnus* Linnaeus 1771, and *Papilio alcidamas* Cramer 1775. By erecting name-bearing types, the nomenclature relating to *Pterourus glaucus* is fixed and clarified. This action will help to distinguish *glaucus* from the new species being described below for which there is no available name.

Papilio glaucus Linnaeus 1758. Systema Naturae. 10th ed. Vol.1 Stockholm, 824 pp.

> **Original description**: (p. 460) Glaucus. 9. P. E. alis subcaudatis nebulosis concoloribus: primoribus macula flava; posticus macula ani fulva. M. L. U. *Habitat in* America. Alae Posticus *Linea transversa fusca bifida; ceteratum Troilo similis*. [Wings dark, cloudy & tailed. Yellow spots on forewings. Hindwings with reddish spot in anal region. Found in America. Wing surfaces with dark indistinct forked transverse veins, otherwise similar to *troilus*.]
>
> **Neotype**: A typical black female specimen of the summer brood (Fig. 19) is hereby designated as the neotype of *Papilio glaucus* Linnaeus 1758. It is currently deposited in the Museum of the Hemispheres, Goose Creek, South Carolina, and bears the following labels: A large label which reads: *Pterourus glaucus* female / Summer black form / September 10, 2000 / Sandbridge / Virginia Beach, VA. A small red hand-written label which reads: NEOTYPE / *Papilio glaucus* Linnaeus 1758 / designated by H. Pavulaan & D. Wright. This specimen was collected from an area near to the John White lead settlement on Roanoke Island, NC, and fixes the name-bearing type to a coastal plain population. This population presently contacts neither *P. canadensis* nor *P. appalachiensis*. The type locality is also outside the range of subspecies *P. glaucus maynardi* (Gauthier, 1984).

Papilio antilochus Linnaeus 1758. Systema Naturae. 10th ed. Vol.1 Stockholm, 824 pp.

> **Original description**: (p. 463) Antilochus. 28. P. E. alis caudatis concoloribus flavis: fasciis margineque nigris, caudis albis longitudine alae. *Pet. Mus*. 50. N. 505. Papilio caudatis maximus, striis umbrique nigris. *Catesb. Carol*. 2. T. 83 *Habitat in* America *Septentrionalis*. [Wings yellow & tailed. Black bands and margin. Tail edged longitudinally with white. Petiver's Musei Petiverani, etc. (page) 50. No. 505. Large tailed butterfly with black stripes. Catesby's Natural History of Carolina, Florida and the Bahama Islands. Vol. 2, pl. 83. Found in North America.]
>
> **Neotype**: A typical yellow male specimen of the summer brood (Fig. 17) is hereby designated the neotype of *Papilio antilochus* Linnaeus 1758. It is currently deposited in the Museum of the Hemispheres, Goose Creek, South Carolina, and bears the following labels: A large label which reads: *Pterourus glaucus* male / Summer form / July 17, 1988 / Corapeake / Gates Co., NC. A small

red hand-written label which reads: NEOTYPE / *Papilio antilochus* Linnaeus 1758 / designated by H. Pavulaan & D. Wright. This specimen was collected from a coastal area near to the John White lead settlement on Roanoke Island, NC, and represents a corresponding male to the *Papilio glaucus* neotype.

Papilio turnus Linnaeus 1771. Mantissa Plantarum. 2nd ed. Stockholm, 587 pp.

Original description: (p. 536) Turnus PAPILIO E. A. alis caudatis concoloribus flavis: primoribus fasciis quinque dimidiatis posticeque nigris. *Habitat in* America. *D. Fabricius*. *Corpus* 2: dae magnitudinus, facie P. Machoanis. *Thorax* limeis flavis. *Alae primores* concolores, flavae, fascii, 5 nigris ad margineum. Extetiorem: harum prima in ipsa basi; fecunda excurrens peralam. Posticam; margo posticus late niger lunulis 8 geminatus flavis. ____ *posticae* repundae, caudatae, subconcolores, flavae, versus postica nigrae. *Fascia* 2: da primorum excurrens versus angulum ani. Lunulae marginis postici, 6 lutae (subtus nagis fulvae) praeter totidem. Lineares marginales. Canda lanceolata nigra. [*Papilio turnus*. Wings yellow and tailed. Forewings with five black bands and hindwings with (about) half as many. Found in America. D.(?) Fabricius. Body (abdomen) twice the size, same appearance as *P. machaon*. Thorax with yellow lines. Forewings uniformly yellow with five black bands and exterior margin; First band at the base of wing, others fanning out to outer margin. Wide black border with eight small lunule-like yellow eyespots. Hindwings curved backward, tailed, nearly all yellow, turning black near edge. Bands on forewing twice the size as those on hindwing, tapering toward anal or posterior portion of wing. Six golden yellow lunules near margins of hindwings (underneath more reddish) in addition to just as many tiny marginal lines, separated by small black distinct projections.]

Neotype: A typical yellow female specimen of the summer brood (Fig. 20) is hereby designated as the neotype of *Papilio turnus* Linnaeus 1771. It is currently deposited in the Museum of the Hemispheres, Goose Creek, South Carolina, and bears the following labels: A large label which reads: *Pterourus glaucus* female / Summer yellow form / September 10, 2000 / Sandbridge / Virginia Beach, VA. A small red hand-written label which reads: NEOTYPE / *Papilio turnus* Linnaeus 1771 / designated by H. Pavulaan & D. Wright. This specimen was collected at the same location as the *Papilio glaucus* neotype.

Papilio alcidamas Cramer 1775. De Uitlandsche Kappelen, etc. Vol. 1. Amsterdam, 156 pp.

Original Description: (p. 62) PLAAT XXXVIII. Fig. A. B. *Alcidamas*. Deze Pagie of Grieksche Ridder Kapel (Pap. Eq. Achivi) gelykt eenigermaate naar de zoogenaamde Konings-Pagie (*Podalirius* Sp. 36. Linn.) die Niet allen in Europa, maar ook in de West-Indien zig onthoud. Deze komt von Jamaika, en valt ook in Nieuw-Jork en Carolina. [Plate 38. Fig. A. B. *Alcidamas*. This species of tailed butterfly with Greek name, which resembles a closely related species (*podalirius* Linn.) that is found in Europe, can be found in West Indies. This one comes from Jamaica, but also can be found from New York to Carolina.]

Neotype: A yellow male specimen of the summer brood, which closely resembles Cramer's plate (Fig. 18), is hereby designated the neotype of *Papilio alcidamas* Cramer 1775. It is currently deposited in the Museum of the Hemispheres, Goose Creek, South Carolina, and bears the following labels: A large label which reads: *Pterourus glaucus* male / Summer form / September 10, 2000 / Sandbridge / Virginia Beach, VA. A small red hand-written label which reads: NEOTYPE / *Papilio alcidamas* Cramer 1775 / designated by H. Pavulaan & D. Wright. This specimen was collected at the same location as the *Papilio glaucus* neotype.

Pterourus appalachiensis Pavulaan and Wright, new species

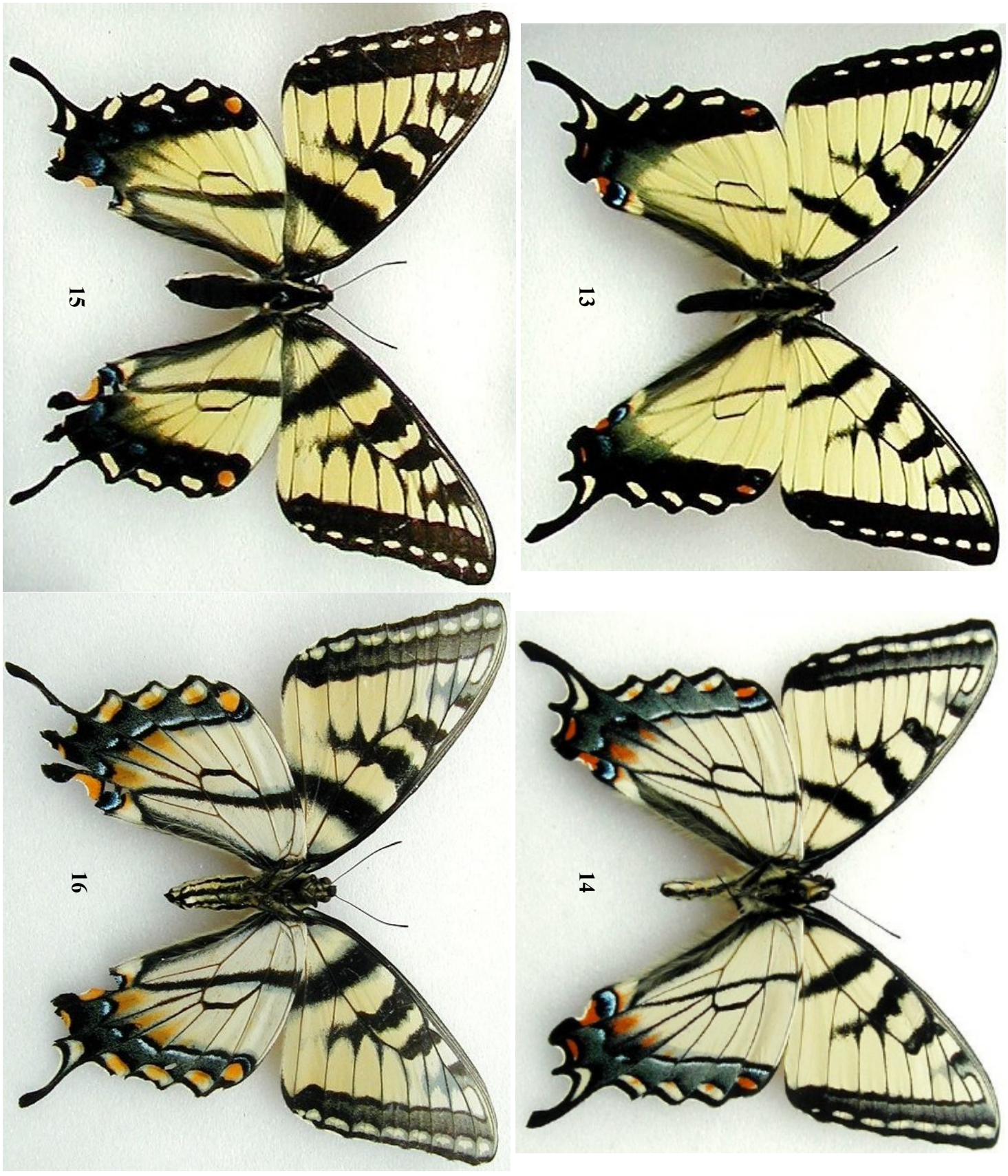
Description. In general, similar to widely sympatric *P. glaucus* and locally sympatric *P. canadensis* (in West Virginia). Size comparable to summer brood of *glaucus*, but larger than variable spring brood of *glaucus* and considerably larger than *canadensis*. Male phenotype most similar to *glaucus* males. Female phenotype most similar to *glaucus* females, but with more contrasting features than males. Both sexes also share morphological features with allopatric *P. rutulus* and *P. alexiares*.

MALE: FW = 50-62 mm. (n = 66). Holotype (Figs. 13 & 14) FW is 60 mm. **Dorsum**: Ground color yellow. Forewing with broad black margin, occupying 1/5 of wing area from outer margin through subterminal area. Fringe edged with yellow scaling at the ends of the cells between terminal veins. Fringe black at terminus of veins. Black margin contains a row of 8 submarginal yellow lunules from cell R3 to cell Cu2, forming a straight line broken by the interposed veins. Lowest lunule at tornus in cell Cu2 often faded, appearing only as small spot and sometimes absent. In some individuals (<5%) there is a faint subterminal band of yellow scales superimposed on the black margin, weakly-developed at apical portion of the forewing and rarely extending along the entire length of the forewing (<1%). Four large black stripes, nearly parallel to body and perpendicular to costal margin, cross the forewing: the first (submedian) is most prominent and extends the entire length from the costal margin to the inner (anal) margin, crossing the base of vein Cu2 where it meets the discal cell; the second (inner median) extends inward from the costal margin crossing the discal cell and the base of cell M3, then fading across cell Cu1, accompanied by a thickening of black scaling at the base of veins M3 and Cu1; the third (outer median) extends inward from the costal margin along the upper and middle discocellular veins to an abrupt end at vein M2; the fourth (postmedian) extends inward from the costal margin to vein M1, paralleling the outer wing margin and generally fading (partially-developed) in cells R4 and R5. Part of the outer portion of the fourth stripe, toward the costal half of cell R3, curves outward and connects with the broad black margin. This gives the appearance of a subapical vein segment halfway between veins R3 and R4. The space between this false vein and vein R3 contains yellow ground color, lending to the false vein appearance. The wing veins are clearly defined by black scaling, being more prominent near the apex. The base of the forewing is black, curving outward and merging with the costal margin. The inner half of the costal margin is black and contains a streak of grayish-yellow clouding. The outer half of the costal margin generally consists of black veins R1, R2 and R3, with intermediate stripes of yellow ground color between veins.

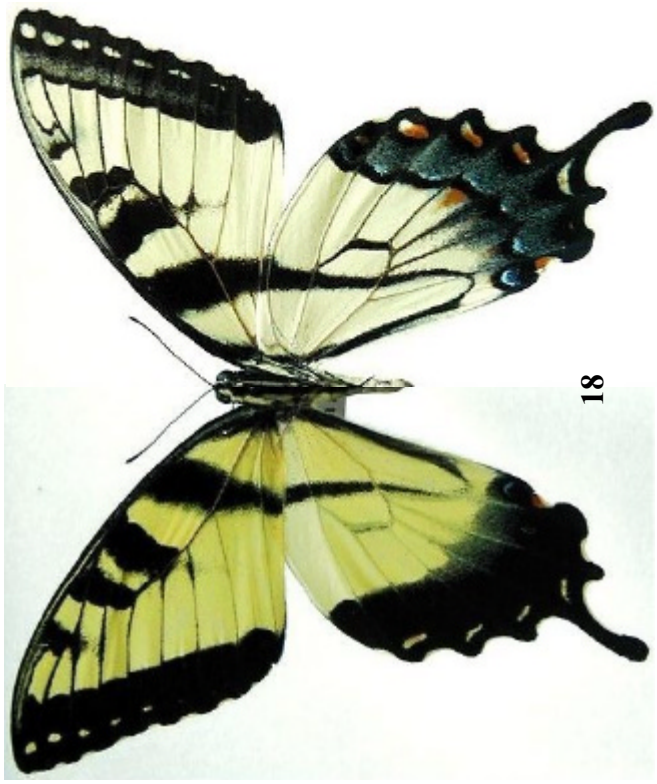
The dorsum of the male forewing resembles *P. glaucus*, but differs mainly in that the black stripes and margin are slightly narrower and the shape of the forewing is slightly more angular in appearance. In most males, the wing appears to have a straighter outer margin. In *glaucus*, especially the summer form, the wing is more rounded in appearance. Within the range of *appalachiensis*, males are considerably larger (50-62 mm) than *glaucus* males of the spring flight (34-53 mm) and are slightly larger than the later summer *glaucus* males (45-58 mm).

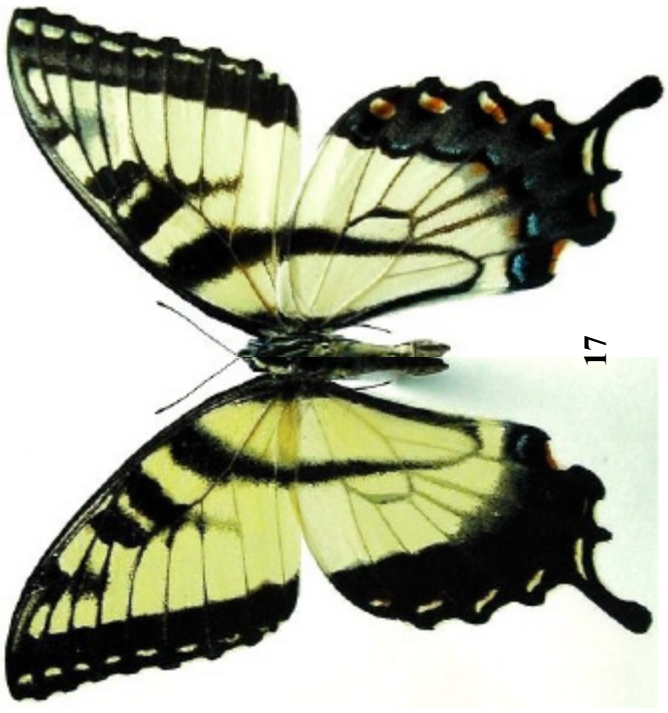
Hindwing with a broad black margin, occupying the outer 1/4 of the wing area; narrower and sharply-defined toward the costal margin. The inner edge of this margin more diffuse and clouded with yellow scaling toward anal angle, most prominent in cells M3 and Cu1. The outer fringe of wing is scalloped. Tail at the terminus of vein M3. Vein Cu1 terminates in a short tail-like stub and vein Cu2 terminates in a large, rounded lobe. Fringe edged with yellow scaling at ends of cells except at vein terminals. Inner edge of the tail lined with a yellow fringe about 2/3 length. Broad black marginal area with row of 6 elongated submarginal lunules. First lunule in cell Sc+R1 smallish, rounded, and deep orange. Lunules in cells RS, M1 and M2 yellow and nearly rectangular in shape. 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 broad black margin is a series of faded blue crescents, most developed in cell Cu1 and usually much faded, almost absent in cell M3. Cell Cu2 with the following characters: Anal angle with large orange crescent, edged with wide yellow fringe. Proximal to orange crescent is black area containing a well-developed, narrow blue crescent. Further proximal is a crescent-shaped area of yellow ground color. The remainder of the cell nearly filled with solid black and covered with long light pile (hairs) giving its surface a gray appearance. This black edge (often referred to as black anal band) occupies most of the width of cell Cu2 and extends cephalad across the wing base to the costal margin. A narrow, straight black stripe extends across the hindwing from near the anal angle to a point on the costal margin, marking the junction of inner third and outer two-thirds of the wing. This stripe often aligns with the first (submedian) stripe of the forewing in the resting position. The wing veins of the outer portion of the discal cell are outlined by black scales that form a black arch, which connects at both ends to the outer portion of the straight black stripe.

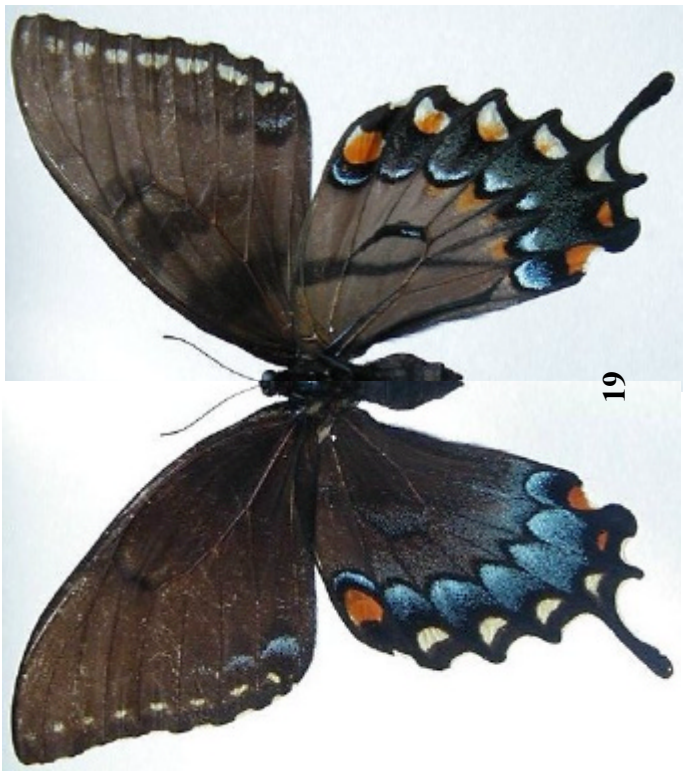
In many aspects, the dorsum of the male hindwing resembles *P. glaucus*. However, the hindwing is noticeably more elongate, narrower and triangular in shape. In *appalachiensis*, the costal margin forms a more squarish angle to the outer margin, whereas in *glaucus* the costal margin arches back and forms a more rounded edge to the outer margin. This difference



Figures 13 - 16: *Pterourus appalachiensis* types. **Figs. 13 & 14.** Holotype ♂ *Pterourus appalachiensis*: 10 May 2001, Buck Creek (3200'), Clay Co., North Carolina (leg. Gatrelle). **Figs. 15 & 16.** Paratype (allotype) ♀ *Pterourus appalachiensis*: 29 May 2001, trail to Scaly Mountain (4300'), Macon County, North Carolina (leg. R. Gatrelle). Specimens are actual size. Photos: Joe Mueller.







Figures 17 – 20: Neotypes (all split dorsal/ventral aspects). **Fig. 17**. Neotype ♂: *Papilio antilochus* Linnaeus 1758 (data in text). **Fig. 18.** Neotype ♂: *Papilio alcidamas* Cramer 1775 (data in text). **Fig. 19.** Neotype ♀: *Papilio glaucus* Linnaeus 1758 (data in text). **Fig. 20.** Neotype ♀: *Papilio turnus* Linnaeus 1771 (data in text). Specimens are actual size. Photos by Joe

is more pronounced between *appalachiensis* and summer brood *glaucus*, as well as the larger individuals of spring brood *glaucus*. The scallops of the hindwing margin are more angular and squarish in *appalachiensis*, while those in *glaucus* are more rounded and arched. The tail is narrower in *appalachiensis*, while in *glaucus* it is thicker and has a more "clubbed" appearance. The yellow submarginal lunules are more rectangular in *appalachiensis*; in *glaucus* these lunules are generally more rounded in appearance, often forming arching crescents.

Venter: Overall pattern repeats that of the dorsal surface with a few modifications. Ventral ground color is light, pale yellow. On forewing, the broad black margin and three inner black stripes generally of the same size and extent as dorsal surface. Fringe as in the dorsum. Distinct yellow submarginal band as in *P. canadensis.* This band is unbroken from cell R3 at the apex to cell M3. In cells Cu1 and Cu2, band broken by interposed veins forming two yellow lunules. The lowest lunule at the tornus (cell Cu2) reduced and generally broken into two small spots within cell. Lowest of these spots smallest, occasionally absent. Proximal to submarginal yellow band is parallel black band with prominent yellow "clouding". Yellow clouding strongly developed from the apical portion of forewing to cell Cu1. Of the four black stripes which cross forewing, only the fourth (outer) stripe departs significantly from the dorsum. On the venter, this stripe primarily occupies only cell R3. The outer portion of cell R3, toward costal half, curves outward and connects with the broad black margin, giving the appearance of a false subapical vein segment halfway between veins R3 and R4. Space between this false vein and vein R3 contains grayish-yellow clouding which connects to the yellow-clouded band. Wing veins clearly defined by black scaling, being more prominent near the apex. Base of forewing black, curving outward and merging with costal margin. Inner half of costal margin black with streak of grayish-yellow clouding. Outer half of costal margin consists of black veins R1, R2 and R3 with intermediate yellow stripes between veins.

The venter of male forewing resembles *P. glaucus*, but differs mainly in having yellow submarginal band and slightly narrower black stripes and margin. Yellow submarginal band in summer form *glaucus* replaced by row of yellow oval-shaped spots. The spring form of *glaucus* is polytypic and many spring individuals, especially males (Fig. 9), may possess yellow submarginal band to varying degrees. Smallest individuals in first *glaucus* emergence in April often possess a strongly-developed band and take on the appearance of *P. canadensis*.

Hindwing with broad black margin. Fringe edged with yellow as on dorsum. Broad black marginal area with row of 6 elongated submarginal lunules. First lunule in cell Sc+R1 smallish, rounded, yellow with orange central area. Lunules in cells RS, M1 and M2 are yellow, centered with orange, and nearly rectangular in shape. These rectangular lunules are minimally arched along concave portion of scalloped wing edge. (In *glaucus*, these lunules are generally more rounded in appearance, often forming regular arched crescents.) As on dorsum, lunule in cell M3 is a yellow curved crescent extending into base of tail at vein M3. Lunule in cell Cu1 orange and often reduced to a narrow streak. Inner portion of broad black margin dusted with grayish-blue scales extending from cell Sc+R1 to cell Cu1. Cell Cu2 at anal angle with large orange crescent, edged with wide yellow fringe. Proximal to orange crescent is black area containing a well-developed, narrow blue crescent. Further proximal is a crescent-shaped area of pale yellow ground color that may contain varying amounts of orange. The remainder of cell Cu2, as on dorsum, includes wide black anal edge covered with long light pile (hairs). A narrow, straight black stripe extends across the hindwing as on the dorsum and the dark veins of the outer portion of the discal cell connect to this straight black stripe, forming an arch. Wing veins M3 and Cu1, from this straight black stripe to the broad black margin, often outlined with additional black scaling enhancing thickness. Toward the margin, these veins sometimes outlined by grayish clouding. Between these dark enhanced veins, cells M3 and Cu1 contain inward pointing V-shaped areas of orange with bases at edge of black margin. In some individuals, cell M2 contains a reduced amount of this orange scaling.

The male ventral hindwing departs from *P. glaucus* primarily in the more rectangular shape of submarginal lunules.

FEMALE: FW = 50-65 mm. (n = 42). Paratype female (allotype) (Figs. 15 & 16) is 63 mm. **Dorsum**: Ground color yellow. Some females with very slight ochreous tint. No black form. Forewing with broad black margin, fringe and submarginal lunules as in the male. Black margin slightly wider than male. Frequently a trace of blue dusting toward the tornus in cell Cu2 which corresponds with band of blue crescents on hindwing. Four large black stripes cross the forewing. These are generally wider than in the male, forming broad black bands. The second (inner marginal) band extends into cell Cu2, while in male it generally only extends into cell Cu1. Wing veins defined by black scaling, being more prominent near the apex. Base of forewing and costal margin as in male.

In most aspects, dorsum of the female forewing resembles *P. glaucus*, but differs mainly in that the shape of the forewing is slightly more angular in appearance. Other minor differences include less ochreous orange than *glaucus* (especially the summer brood), the second (inner median) stripe extends into cell Cu2 (in *glaucus* this stripe usually ends at vein Cu2), and blue crescent at tornus in cell Cu2 of black margin is reduced to a trace of blue dusting. In *glaucus*, this blue

crescent is very prominent, and there are frequently additional small blue crescents within cells Cu1 and M3 of submarginal band.

Hindwing contour, margin, fringe, and tail as in male. Broad black margin with 6 elongated submarginal lunules. The first lunule in cell Sc+R1 smallish, rounded, and deep orange. Lunules in cells RS, M1 and M2 yellow and nearly rectangular in shape. 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 broad black margin is a terminal row of 6 blue crescents, 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 generally larger; crescents in cells RS and Sc+R1 significantly reduced (absent in some individuals). Near anal angle, inner edge of black marginal area diffused and clouded with yellow scaling which is most prominent in cells M2, M3 and Cu1. At anal angle, cell Cu2 with large orange crescent edged with wide yellow fringe. Proximal to orange crescent is black area containing a well-developed, narrow blue crescent. Further proximal is a crescent-shaped area of yellow ground color. Remainder of cell partially occupied with a solid black margin covered with long light pile (hairs). Black anal band of HW inner margin occupies half of width of cell Cu2 (or more) and extends cephalad across the wing base to costal margin. A narrow, straight black stripe extends across the hindwing from near the anal angle to a point on the costal margin, marking the junction of inner third and outer two-thirds of the wing. This stripe broader than in the males and aligned with the first (submedian) stripe of the forewing. Veins of outer discal cell outlined by black scales, forming a black arch.

In some aspects, the dorsum of the female hindwing resembles *P. glaucus*. However, there are noticeable departures between the two taxa. The *appalachiensis* hindwing is more elongate, narrower and triangular-shaped; the costal margin has a more "squarish" angle at the outer margin; the scallops of the wing margin are more angular; the submarginal lunules are more rectangular; the tail is narrower and less "clubbed"; and the anal black band occupies one half (or more) of the width of cell Cu2. In *appalachiensis* the submarginal orange crescent in cell Sc+R1 is smaller than the remainder of the (yellow) submarginal crescents, while in *glaucus* it is noticeably larger than the remaining crescents. A major distinguishing character is the extent of blue markings. In *glaucus*, the terminal blue crescents form a continuous scalloped band spanning the entire wing. These crescents in *appalachiensis* 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. Furthermore, in *glaucus* there is generally some blue overscaling in the yellow postmedian area (most evident in black females) which is lacking in *appalachiensis*. Within the range of *appalachiensis*, females are considerably larger (50-65 mm) than *glaucus* females of the spring flight (34-53 mm) and are slightly larger than the later summer *glaucus* females (49-64 mm).

Venter: Overall pattern repeats that of the dorsal surface with a few modifications. Ground color light yellow. Forewing broad black margin, fringe, and three inner black stripes generally of the same size and extent as dorsal surface. Black margin contains a yellow submarginal band as in *P. canadensis*. This band is unbroken from cell R3 at the apex to cell M3. In cells Cu1 and Cu2, band broken by interposed veins forming two yellow lunules. Lowest lunule at the tornus (cell Cu2) reduced and generally broken into two small spots within the cell. Lowest smaller and occasionally absent. Yellow subterminal "clouding" parallelling the submarginal yellow band. Fourth (outer) stripe, false subapical vein segment, prominent apical vein scaling, wing base, and costal margin as in male.

In most aspects, the venter of the female forewing resembles *P. glaucus*, but differs mainly in having yellow submarginal band. The submarginal area in summer *glaucus* consists of a row of yellow oval-shaped spots. In polytypic spring *glaucus* brood, a small portion of females possess a yellow band which is not as straight as it is in *appalachiensis* and appears more like a connected row of crescents or scallops.

Hindwing with broad black margin and fringe edged with yellow. Black marginal area with row of 6 elongated submarginal lunules with coloration and shape as in male. Terminal band of grayish-blue clouding in black margin. Cell Cu2 characters as in male, including black anal edge. Narrow black stripe crosses wing as in the male. Dark discal veins form an arch. Veins M3 and Cu1 outlined with additional black scaling enhancing thickness. These veins outlined by grayish clouding toward margin. Cells M3 and Cu1 between these veins contain inward pointing V-shaped areas of orange coloration. In some individuals, cell M2 also with a small amount of this orange scaling.

The female ventral hindwing departs from the general appearance of *P. glaucus* primarily by its more rectangular shaped submarginal lunules and the inner edge contour of the broad black marginal area. In *appalachiensis* this edge generally forms a straight line in cells RS and M1, angling outward in cell Sc+R1 and angling inward in cell M2. In *glaucus* the inner edge of the margin is scalloped inward in each cell.

Note: Small *glaucus* individuals appear in early spring with a yellow submarginal band on the ventral forewing and/or wide black stripe on the HW inner margin (Fig. 9). These variants are usually males and less frequently yellow females (rarely black females). They occur more commonly in the mountain region. This *canadensis*-like form of *glaucus*

should not be confused with *appalachiensis*. A positive identification of *appalachiensis* in any given region is best achieved by finding both sexes as described above. The female phenotype is an especially strong confirmation. Size is also a helpful feature.

Types and Type Locality. Holotype male (Figs. 13 & 14): Buck Creek Serpentine Barrens, 3200' elev., Clay County, North Carolina, 10 May 2001, deposited in the Museum of the Hemispheres, Goose Creek, South Carolina. Paratype female (allotype) (Figs. 15 & 16): Scaly Mountain, 4300' elev., Macon County, NC, 29 May 2001, deposited in the Museum of the Hemispheres, Goose Creek, South Carolina. Type location elevation: 3200-3400 ft. 72 additional paratypes, are numbered as follows: (1 – 19: all Buck Creek Serpentine Barrens, 3200-3400' elev., Clay Co., NC): (#1) female, May 14, 2001; (#2-3) females, June 18, 2001; (#4-5) males, May 29, 2001; (#6) male, May 4, 2001; (#7) male, May 29, 2001; (#8) male, June 18, 2001; (#9-15) males, May 29, 2001; (#16), May 18, 2001; (#17) male, May 18, 2001; (#18) male, May 31, 2001; (#19) male, May 18, 2001. All above paratypes currently deposited in the Museum of the Hemispheres, Goose Creek, SC. Numbers 20 – 72 currently retained in the TILS collection of Harry Pavulaan as follows: (#20-23) 4 males, May 10, 2001, Buck Creek Serpentine Barrens, 3200-3400' elev., Clay Co., NC; (#24-26) 3 males, June 1, 1988, Nantahala National Forest, near Bryson City, Swain Co., NC; (#27-37) 10 males, 1 female, June 10, 2000, Blue Mountain, near Linden, Warren Co., VA; (#38-40) 2 males, 1 female, May 28, 2001, Blue Mountain, near Linden, Warren Co., VA; (#41) 1 female, June 8, 2001, Blue Mountain, near Linden, Fauquier Co., VA; (#42-44) 3 males, May 29, 2002, Blue Mountain, near Markham, Fauquier Co., VA; (#45) 1 male, June 10, 2000, Blue Mountain, near Berrys, Clarke Co., VA; (#46) 1 male, May 17, 2002, Blue Mountain, near Berrys, Clarke Co., VA; (#47) 1 female, June 20, 1982, Front Royal, Warren Co., VA; (#48) 1 male, May 19, 1985, near Stanley, Page Co., VA; (#49-50) 1 male, 1 female, May 17, 1986, near Stanley, Page Co., VA; (#51) 1 female, May 31, 1986, near Stanley, Page Co., VA; (#52), 1 male, May 5, 1985, Sugar Grove, Pendleton Co., WV; (#53), 1 male, July 4, 1999, Dolly Sods Wilderness, near Hopeville, Tucker Co., WV; (#54-55) 2 females, June 10, 2001, Spruce Knob, near Riverton, Pendleton Co, WV; (#56-72) 7 males, 10 females, June 5, 2002, Spruce Knob, near Riverton, Pendleton Co, WV.

Etymology. *Appalachiensis* is named for the species' fundamental Appalachian Mountain distribution. We propose the common name Appalachian Tiger Swallowtail.

Immature Stages: Egg green and globular. Small sample indistinguishable from *glaucus*. A single first stage larva was indistinguishable from *glaucus*. Body black with one distinct white saddle, as opposed to three in *canadensis;* a faint tan mark was observed at the rear saddle position. Gatrelle (pers. com.) obtained a single first stage larva with identical saddle marks. Second stage larva like first stage. Third stage larva with two well-developed saddles in middle and rear sections. Mature green larva indistinguishable from *glaucus*.

Larval hosts. One of the greatest challenges to date has been ascertainment of the larval host. The habits of this species have frustrated all our efforts to determine its host(s). The females have proven to be exceedingly elusive, even in locations where males were abundant. It is our opinion that the females remain high in the tree canopy throughout much of the day, and seem to be more frequent along ridge tips or on mountain summits. We routinely observed males patrolling the canopy and we suspected mating probably occurs there. A single observed courtship near the summit of Blue Mountain in northern Virginia (Warren-Fauquier Co. line) took place in the tree canopy. The forest at this site featured a broad variety of tree species dominated by *Quercus* (Oak), *Fraxinus* (Ash), *Acer* (Maple), *Juglans* (Walnut), *Carya* (Hickory), *Magnolia* (Magnolia), *Ostrya* (Hornbeam), *Ulmus* (Elm), and also *Fagus grandifolia* (American Beech), *Liriodendron tulipifera* (Tuliptree), and *Platanus occidentalis* (American Sycamore). Despite hours of field work, we have witnessed no ovipositions along forest edges, roadsides, or utility cuts where *Prunus serotina* (Black Cherry), *Lindera benzoin* (Spicebush), *Hamamelis virginiana* (Witch Hazel), and *Sassafras albidum* (Sassafras) are common. The females on occasion were noted to descend briefly to sunlit lower branches and immediately return to the canopy. Rarely were they observed sunning or nectaring. On the summit of Spruce Knob in Pendleton Co., WV (the only location where we have observed females in abundance), various species of *Betula* (Birch), *Fagus grandifolia* (American Beech) and *Prunus alleghaniensis* (Allegheny Plum) are common. Yet no ovipositional interest was observed. The only potential incident of ovipositional behavior that we have observed occurred on the Blue Ridge in Page Co., VA, where a female was observed flying around a medium-height (15') *Prunus serotina* for several minutes, landing frequently, and curling her abdomen. However, upon close inspection, no eggs were found. Her *appalachiensis* phenotype was confirmed when she briefly rested with wings open. In northern Virginia, *glaucus* females oviposit avidly on many of these trees during both the spring and summer flights. Also *glaucus* females commonly oviposit on trees in the understory, easily allowing for identification of immatures and rearing. Gatrelle (pers. com.) observed ovipositional behavior by a female *appalachiensis* on a species of *Crataegus* (Hawthorn) at the type locality, though no ova were found in a brief and awkward search of this thorny shrub.

Several attempts to obtain ova from captive livestock during the period of 1999 to 2001 failed. Repeated attempts using sleeved females on *Prunus serotina* were wholly unsuccessful. Various types of confinement cages ranging from small portable size (1'x 1'x 2') to large sturdy size (3'x 3' x 5') were also employed. Many small tree species were placed in these cages as planted, potted, or fresh cut specimens. These included wild or in some cases nursery stock of *Prunus serotina*, *Prunus cerasus* (Domestic Cherry), *Fraxinus americana* (White Ash), *Liriodendron tulipifera*, *Betula populifolia* (Gray Birch), *Populus tremuloides* (Quaking Aspen), *Ptelea trifoliata* (Wafer Ash or Hop Tree) and *Syringa vulgaris* (Common Lilac). Again, no ovipositions took place.

More interesting results occurred in 2001. The large cage size was used to confine several females in a multiple host choice experiment with a blooming *Buddleia davidii* (Butterfly Bush) provided as a nectar source. After 15 days, a meager thirteen eggs were discovered. Seven were deposited on the screening near the top of the cage on the sun-exposed side, five were deposited on *Prunus serotina* leaves touching or very near the screening, and one was deposited on a *Buddleia* leaf. We could only conclude from these results that females laid few eggs in captivity and/or the natural host was not present among the offered selections. Most of the first instar larvae emerged and crawled away. None were found on the offered leaves in the cages. Only a single first instar larva was discovered on a cage support. This larva was provided *Prunus serotina* solely. After initially refusing to eat, it reluctantly nibbled on leaves and grew slowly. The resulting pupa went into diapause. It was placed in refrigeration (4^0 C) in late summer, then removed to indoor conditions (22^0 C) in early March, 2002. After approximately 30 days, a typical female *appalachiensis* emerged. Gatrelle (pers. com.) obtained a single ovum from an *appalachiensis* female (laid on spreading board) which produced a single larva. The first stage larva was offered a choice of *Prunus serotina* and *Liriodendron tulipifera*, but it did not feed and subsequently died.

A control group of *glaucus* females was tested under the same conditions of cages and sleeves over a two-year period. Females of both the yellow form *turnus* (Linnaeus) and the black form *glaucus* (Linnaeus) oviposited abundantly in the cages and sleeves, often within a few hours. In spring of 2000, a black female *glaucus* deposited over 30 eggs on *Liriodendron tulipifera* and *Prunus serotina* in the first day of captivity. In summer of 2000, another confined black form female deposited over 25 eggs on the first day. Females of *appalachiensis* laid no eggs in the same system during this period.

Flight Period. *Appalachiensis* is single-brooded and an obligate pupal diapauser. The flight period may be described as being interpolated between the main spring and summer flights of multivoltine *Papilio glaucus* where these taxa co-occur (Phenograms: pg. 17). This situation is most pronounced in the southern Appalachians (Gatrelle, pers. com.). At Blue Mountain, Fauquier Co., VA, the first emergence of *glaucus* precedes *appalachiensis* by approximately three weeks. This flight consists of small to medium-sized *glaucus* early spring phenotypes. A second *glaucus* emergence is observed there at lower elevations at approximately the same time that *appalachiensis* emerges. This emergence occurs primarily in the inner Piedmont and in low valley elevations of the Appalachians; it consists of a highly polymorphic mixture of *glaucus* phenotypes ranging from early spring types to late spring types to intermediate-sized individuals resembling *appalachiensis* (possibly hybrids). At higher elevations (>1800') the flight of *appalachiensis* essentially replaces *glaucus*. To date *appalachiensis* has not been collected or observed in late summer, a finding consistent with the premise that *appalachiensis* is univoltine. The flights of *appalachiensis* and *canadensis* are essentially synchronic where they are sympatric in higher elevations of West Virginia. RECORDED FLIGHT: North Carolina: May 4 (2001) - June 1 (1988); Virginia: April 22 (2001) - June 23 (2000) with mid-late May peak; West Virginia: May 25 (2002) - June 5 (2002); Maryland: June 3 (1990); Pennsylvania: May 19 (2001).

Habitat. *Appalachiensis* is a denizen of the densely forested southern Appalachian Mountain chain, being found at all elevations from valley bottoms (Upper Austral Zone) to lofty mountain summits (Canadian Zone). Dense, rich mixed forest is the primary habitat type and we believe it will be found to chiefly utilize hosts in the Transition Zone. *Appalachiensis* replaces *glaucus* as the spring representative of the genus at higher elevations of the southern Appalachians. Very few spring brood specimens of *glaucus* have been documented or observed on the summits. There is reason to believe that *glaucus* may not be able to survive winter temperature minimums characteristic of higher elevations. Limited cold tolerance of overwintering *glaucus* pupae may restrict the species distribution and its ability to acclimatize to high altitude (Kukal et al. 1991). In the Blue Ridge of northern Virginia most *glaucus* individuals in the spring are found in the valleys and the foothills. By late summer, however, *glaucus* is common in flowering meadows along Skyline Drive. Summer individuals on the summit are believed to be descendants of spring migrants and/or summer migrants from lower elevations. (Note in support: In April, 2002, at Blue Mountain in Fauquier Co., VA, during the early spring *glaucus* emergence, virtually no *glaucus* individuals were observed at elevations over 1200 ft. despite large numbers present at lower elevations. During the second *glaucus* emergence (mid-May), very few *glaucus* adults were observed near the 1800 ft. summit despite similarly large numbers present at lower elevations. Finally, on May 29th, one black form *glaucus* female was observed ovipositing on *Prunus serotina* on the summit, indicating that the spring females do produce some of the summer adults of higher

elevations.) *Appalachiensis* may be prone to periodic irruption. On May 23, 2001, during a major emergence of *appalachiensis* on the Blue Ridge, strays were recorded on the Piedmont as far as 20 miles to the east (Warrenton, VA). Curiously, none were recorded further east on that date or the following days despite an intensive search. In the spring of 2002, strays were not observed.

Adult Behavior. Both sexes fly primarily in forested habits. They will cross open breaks in the forest, but seldom stray far from wooded areas. In the first few days of an emergence following a warm spring rain, males congregate at mud puddles and damp earth along watercourses, woodland trails, and road shoulders. Away from human disturbance, they may congregate in very large numbers. The puddle parties are often shared with other species such as *Pterourus troilus, Eurytides marcellus, Everes comyntas, Celastrina neglectamajor, Phyciodes tharos, Erynnis juvenalis* and *Erynnis icelus*. Interestingly, we have rarely observed *Pterourus glaucus* at these puddle parties when *appalachiensis* was present. Roadside congregations can be disturbed by passing automobiles and the presence of road-kill specimens is not uncommon. These road-killed individuals curiously may attract additional individuals. On occasion we have seen flying *appalachiensis* males suddenly dive to inspect road-killed individuals. *Appalachiensis* males also seem to be particularly fond of cow droppings. As the emergence progresses greater numbers appear at higher altitudes. Males are often seen in hurried flight on ridge tops and summits. They can be distinguished from *glaucus* by their more majestic, sailing, looping flight. (Virginia's Skyline Drive on the Blue Ridge is an excellent place to observe *appalachiensis* during flight.)

Females are extremely elusive. They have never been observed at puddle parties. They are usually seen in short glimpses in hurried flight, often 30 ft. high (and higher) in the forest canopy. They prefer to remain in the forest canopy where patrolling males give chase. During courtship encounters, the pair may temporarily descend to the forest floor and then just as quickly return to the forest canopy with the male pursuing the female. Courtship observations have been very difficult to secure while traversing dense rocky habitats at higher elevation. It is usually these same habitats though where female nectaring takes place.

Adult Nectar Sources. The adults nectar chiefly on *Rubus allegheniensis* (Blackberry) and *Rosa multiflora* (White Multiflora Rose), both common bramble-like plants which cover sunny patches in the woodland habitat. They have also been observed nectaring on *Kalmia latifolia* (Mountain Laurel), *Prunus serotina* (Black Cherry), *Crataegus crus-galli* (Cockspur Thorn), *Diervilla lonicera* (Bush Honeysuckle), *Rhododendron roseum* (Early Azalea), and *R. nudiflorum* (Pink Azalea). Near the end of the flight period, *Asclepias syriaca* (Common Milkweed) becomes a favorite nectar source.

Range. (maps A & B pg. 20). The range at this writing is believed to be primarily the southern Appalachian Mountain region of the eastern United States. The type locality is situated near the southernmost, presently-known location in the Appalachians. Strays have been taken on the Piedmont at locations not far from the mountains. The northern extent is currently undetermined and must be distinguished from the hybrid zone in the northeast between *canadensis* and *glaucus* (Scriber 1990). Additional research is needed to determine the northern limit in Pennsylvania and possibly in New York and New England. Known localities include: **GEORGIA:** RABUN CO.: Sky Valley. **MARYLAND:** ALLEGANY CO.: Flintstone, Green Ridge State Forest; FREDERICK CO.: Catoctin Ridge (Frederick City Municipal Watershed), Gambrill State Park. **NORTH CAROLINA:** CLAY CO.: Buck Creek Serpentine Barrens (Gatrelle, 2001); HAYWOOD CO.: Pisgah National Forest; JACKSON CO.: Pisgah National Forest; MACON CO.: Scaly Mountain, State Hwy 106 west of Highlands; SWAIN CO.: Great Smoky Mountains National Park. **PENNSYLVANIA:** CUMBERLAND CO.: South Mountain (Michaux State Forest); FRANKLIN CO.: Caledonia, South Mountain (Michaux State Forest). **VIRGINIA:** ALBEMARLE CO.: Blue Ridge (Shenandoah National Park); AUGUSTA CO.: Blue Ridge Parkway (George Washington National Forest); CLARKE CO.: Mount Weather (Blue Ridge); FAUQUIER CO.: Blue Mountain (Blue Ridge), Warrenton; FREDERICK CO.: Gore, Great North Mountain (George Washington National Forest); GREENE CO.: Blue Ridge (Shenandoah National Park); LOUDOUN CO.: Mount Weather (Blue Ridge); MADISON CO.: Rapidan State Wildlife Management Area, Blue Ridge (Shenandoah National Park); NELSON CO.: Blue Ridge Parkway (George Washington National Forest); PAGE CO.: Blue Ridge (Shenandoah National Park); RAPPAHANNOCK CO.: Amissville, Blue Ridge (Shenandoah National Park), Sperryville, Washington; ROCKINGHAM CO.: Blue Ridge (Shenandoah National Park), Briery Branch, Massanutten Mountain; WARREN CO.: Blue Mountain (Blue Ridge), Front Royal, Blue Ridge (Shenandoah National Park). **TENNESSEE:** SEVIER CO.: Great Smoky Mountains National Park. **WEST VIRGINIA:** GRANT CO.: Dolly Sods Wilderness Area, Hopeville; GREENBRIER CO.: Kates Mountain; HAMPSHIRE CO.: Capon Bridge. HARDY CO.: Great North Mountain (George Washington National Forest); PENDLETON CO.: Reddish Knob (George Washington National Forest), Spruce Knob; RANDOLPH CO.: Dolly Sods Wilderness Area; TUCKER CO.: Dolly Sods Wilderness Area.

GENETIC AND EVOLUTIONARY RELATIONSHIPS.

The eastern *Pterourus* species (*glaucus*, *canadensis*, and *appalachiensis*) share an extensive suite of morphological and biological features which is a strong indication of common ancestry. Hagen et al. (1991) recently summarized the evidence demonstrating significant differentiation between *glaucus* and *canadensis*. These two species are distinguished by genetically-controlled differences in adult, larval, and pupal stages. *Canadensis* has a gene for obligate pupal diapause which offers a selective advantage in colder climates where the growing season is shortened and the butterflies are limited to one generation (Hagen & Scriber 1989). On the other hand, diapause in *glaucus* appears to be environmentally determined. A zone of thermal unit accumulations necessary to complete two successful generations (Hagen et al. 1991) delineates the northernmost limit of *glaucus*. Under these control systems, the *glaucus* range cannot expand northward but the *canadensis* range may expand southward. The isotherm that corresponds to the thermal watershed between bi- and univoltine populations coincides with a complex plant ecotone and a narrow zone of butterfly hybridization. This isotherm is sharply defined across the Great Lakes region, but is much less regular and uncertain further east. The isotherm follows a southward course through Pennsylvania and rides the high elevations of the Appalachian Mountains to North Carolina (Scriber & Cage 1995). It has been predicted that the Appalachians provide altitudinal refugia for *canadensis* types and that an inability to complete two generations would select against *glaucus* (Scriber et al. 1996). Many individuals from the mountainous regions of West Virginia are phenotypically *canadensis*; also the highest elevations of the state support very small phenotypes that may be true relict *canadensis*. The southernmost limit of these small *canadensis* types is in West Virginia. They are not found further south in the Appalachians, a situation that is analogous to distributions of other northern butterflies (*Colias interior*, *Lycaena epixanthe*, *Celastrina lucia*, *Speyeria atlantis*).

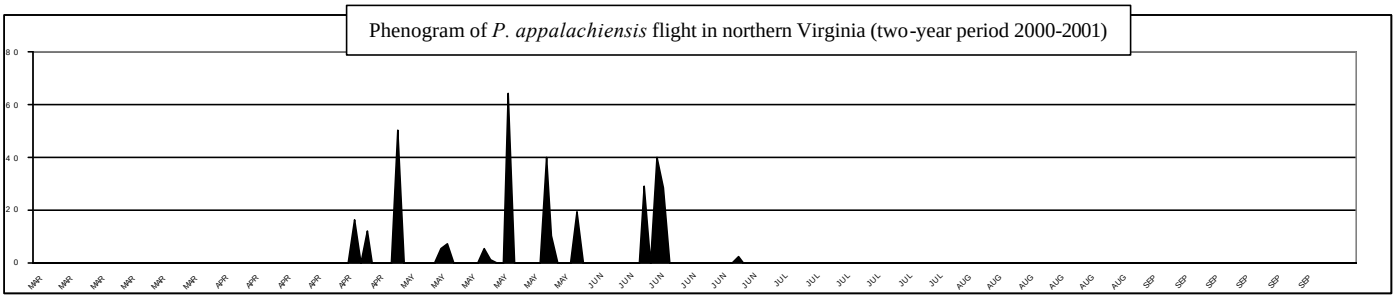
Pterourus appalachiensis appears to replace *canadensis* in the Appalachians south of West Virginia. This large univoltine swallowtail combines the phenotypic markings of *canadensis* and the large size of summer *glaucus*. Its origin is unknown. However, because a considerable portion of its mitochondrial DNA is similar to *glaucus*, we conclude that it is neither *P. canadensis* nor a predominately *canadensis* hybrid. The latter have the external appearance of typical *canadensis,* but their larvae can also detoxify tuliptree (Scriber, 1998). Instead we suspect *appalachiensis* evolved principally from a *glaucus* genome initially as a physiologic race or through introgression of unique genes. It is possible that *appalachiensis* independently evolved genes advantageous for life at high elevation or acquired them during past periods of interbreeding. Climatic variation during the Pleistocene could have expanded the range of *canadensis* to contact ancestral *appalachiensis* in the southern Appalachians. The acquisition of an obligate diapause gene (among others) may have accelerated the acclimatization of *appalachiensis* to the southern Appalachian highlands in the post Pleistocene period.

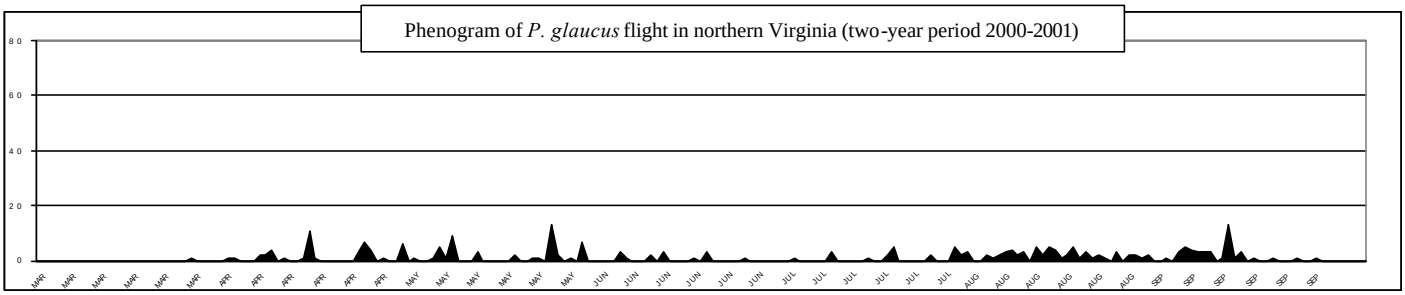
Very little is known about isolating mechanisms between *appalachiensis* and *glaucus* in nature. Their nearly allochronic flights, differing altitude preference, and contrasting behaviors (especially of females) would seem to keep their zone of contact confined to a narrow ecological gradient. To the extent that hybridization occurs, it has not diluted the essence of either taxa. Lastly, we raise the intriguing possibility that *appalachiensis* is older than *glaucus* and is more closely related to a shared common ancestor with *canadensis*. Perhaps *appalachiensis* provided the advantageous genes that spurred *canadensis* radiation in the north.

Hybridization study. In a limited breeding study, a reared black form female *P. glaucus* (*ex* larva, 9/10/00, on *Prunus serotina* from Virginia Beach, VA) was crossed with a male *P. appalachiensis* (captured at Blue Mountain, Warren Co., VA, on April 22, 2001) and placed inside a breeding cage with *P. serotina*. This female oviposited readily and produced 24 ova in two days before dying. All ova yielded first instars with a single white saddle mark and a very faint tan rear saddle mark, thus appearing like the two documented *appalachiensis* larvae. Eight died in the first instar stage. An additional six larvae died during development and the remaining ten reached pupal stage. These pupae diapaused and were placed outdoors in a protected location before being taken indoors in late February, 2002. Seven pupae produced large males of intermediate phenotype between *appalachiensis* and *glaucus*. The three largest pupae (females) failed to eclose. The apparent failure to produce eclosed hybridized females parallels our inability to find naturally-occurring intermediate females (esp. black forms) in our study sites and may be indicative of an isolating mechanism at work.

A NOTE ABOUT THE NORTHERN LIMIT OF *APPALACHIENSIS*.

More work is needed to ascertain the northern limit of *appalachiensis.* Field observations in Rhode Island from 1983 to 2001 recorded a regular sequence of emergences of Tiger Swallowtails throughout the state. The season began with flights of both standard *glaucus* and *canadensis*-like phenotypes in April, which often lasted until early June. No black females were recorded in RI during the spring. A second emergence, consisting of very large *appalachiensis*-like phenotypes emerged during the month of June and flew into early July. Likewise, no black females were recorded in this emergence. During the latter half of July, a second brood of *glaucus* appeared and flew into early September. The latter consisted of a variety of forms, including large ochreous yellow females and occasional black females in years of abundance (M. Schenck, pers. obs.) In 1983, captive females of both spring *glaucus* and *canadensis*-like phenotypes oviposited freely on *Prunus serotina*. The *glaucus* progeny produced typical summer specimens in the same year (second brood). The progeny of *canadensis*-like females went into diapause (pupae desiccated during the following winter). Females of the *appalachiensis*-like phenotype captured in June also oviposited on *P. serotina* and produced diapausing pupae (pupae desiccated during the following winter). The experiment with RI *appalachiensis*-like females was repeated in 1994. Diapausing pupae successfully survived the winter and produced *appalachiensis*-like adults in early July of the following year. We intentionally did not include Rhode Island in the formal range of *appalachiensis* in our paper, and leave open the question of its occurrence in southern New England to future investigation. The issue of a potential hybrid zone of *glaucus* x *canadensis* (and/or *glaucus* x *appalachiensis*) in this region needs clarification.





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APPENDIX

Provided below is the DNA nucleotide base sequence of the mitochondrial gene COI (cytochrome oxidase subunit I) from the *Pterourus appalachiensis* male holotype and female paratype, plus the comparable sequence from a typical male & female *P. glaucus* collected at the *appalachiensis* type locality. A total of 1460 residues of this 1.5 kb gene were aligned for comparison. In the display we have highlighted the two nucleotide positions that were found to vary between these closely-related taxa.

Pterourus appalachiensis

TGAGCAAGAATATTAGGAACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAACTCCGGTTCTTTAATTGGAGATGCCAAATT
TATAATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGACT
AGTACCTTTAATATTAGGGGCACCTGATATAGCCTTTCCTCGAATAAATAATATAAGATTTTGACTTTTACCCCCTTCTTTAACT
CTTTTAATTTCAAGAATAATTGTTGAAAGTGGAGCTGGAACTGGATGAACTGTTTATCCCCCTCTTCTTCCAATATCGCTCATGG
AAGAAGATCAGTAGATTTAGTTATTTTTTCCCTTCATTTAGCAGGGATTTCTTCAATTTTAGGAGCAATTAATTTTATTACTACAA
TTATTAATATACGAATTAATAATATATCATTTGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTACAGCTTTATTATTACTT
CTTTCATTACCTGTTTTAGCTGGAGCTATTACAATACTATTAACAGATCGAAACTTAAATACATCATTTTTTGATCCTGCAGGAG
GGGGAGATCCAATTTTATATCAACATTTATTTTGATNNNNNNNNNNNNNNNNNTTTATATTTTAATTTTACCTGGATTTGGAA
TAATTTCTCATATTATTTCTCAAGAAAGAGGAAAAAAGGAAACATTTGGATGTTTAGGTATAATTTATGCTATAATAGCAATTG
GATTATTAGGATTTATTGTTTGAGCTCATCATATATTTACAGTAGGAATAGATACAGATACTCGAGCTTATTTTACCTCAGCAAC
AATAATTATTGCAGTTCCTACTGGAATTAAAATTTTTAGATGATTAGCAACTCTTCATGGAACTCAAATTAATTATAGTCCATCA
ATTTTATGAAGTTTAGGATTTGTATTTCTATTTACAGTAGGAGGATTAACTGGAGTAATTTTAGCTAACTCTTCTATTGATGTTAC
CTTACATGATACATATTATGTAGTAGCTCATTTTCATTATGTTTTATCTATAGGAGCTGTATTTGCTATTATAGGAAGATTTATTC
ATTGATACCCATTATTTACCGGTCTTTCTTTAAATCCTTATCTTTTAAAAATTCAATTTTTTACAATATTTTTTGGGGTAAATTTA
ACCTTTTTTCCCCAACATTTCTTAGGATTAGCTGGAATACCTCGCCGATATTCAGATTATCCTGATAATTTTACCTCATGAAATAT
TATTTCTTCTTTTGGATCTTATATTTCTTTATTGTCATTAATAATAATAATAATAATTATTTGAGAATCAATAATTAATCAACGAA
TTATTTTATTTTCTCTTAATATACCATCATCTATTGAATGACTTCAAAACTTACCTCCTGCAGAACATTCATATAATGAACTTCCT
ATTTT

Pterourus glaucus

TGAGCAAGAATATTAGGAACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAACTCCAGGTTCTTTAATTGGAGATACCAAAT
TTATAATACTATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGAC
TAGTACCTTTAATATTAGGGGCACCTGATATAGCCTTTCCTCGAATAAATAATATAAGATTTTGACTTTTACCCCCTTCTTTAACT
CTTTTAATTTCAAGAATAATTGTTGAAAGTGGAGCTGGAACTGGATGAACTGTTTATCCCCCCTTTCTTCCAATATCGCTCATGG
AAGAAGATCAGTAGATTTAGTTATTTTTTCCCTTCATTTAGCAGGGATTTCTTCAATTTTAGGAGCAATTAATTTTATTACTACAA
TTATTAATATACGAATTAATAATATATCATTTGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTACAGCTTTATTATTACTT
CTTTCATTACCTGTTTTAGCTGGAGCTATTACAATACTATTAACAGATCGAAACTTAAATACATCATTTTTTGATCCTGCAGGAG
GGGGAGATCCAATTTTATATCAACATTTATTTTGATNNNNNNNNNNNNNNNNNTTTATATTTTAATTTTACCTGGATTTGGAA
TAATTTCTCATATTATTTCTCAAGAAAGAGGAAAAAAGGAAACATTTGGATGTTTAGGTATAATTTATGCTATAATAGCAATTG
GATTATTAGGATTTATTGTTTGAGCTCATCATATATTTACAGTAGGAATAGATACAGATACTCGAGCTTATTTTACCTCAGCAAC
AATAATTATTGCAGTTCCTACTGGGATTAAAATTTTTAGATGATTAGCAACTCTTCATGGAACTCAAATTAATTATAGTCCATCA
ATTTTATGAAGTTTAGGATTTGTATTTCTATTTACAGTAGGAGGATTAACTGGAGTAATTTTAGCTAACTCTTCTATTGATGTTAC
CTTACATGATACATATTATGTAGTAGCTCATTTTCATTATGTTTTATCTATAGGAGCTGTATTTGCTATTATAGGAAGATTTATTC
ATTGATACCCATTATTTACCGGTCTTTCTTTAAATCCTTATCTTTTAAAAATTCAATTTTTTACAATATTTTTTGGAGTAAATTTA
ACCTTTTTTCCCCAACATTTCTTAGGATTAGCTGGAATACCTCGCCGATATTCAGATTATCCTGATAATTTTACCTCATGAAATAT
TATTTCTTCTTTTGGATCTTATATTTCTTTATTGTCATTAATAATAATAATAATAATTATTTGAGAATCAATAATTAATCAACGAA
TTATTTTATTTTCTCTTAATATACCATCATCTATTGAATGACTTCAAAACTTACCTCCTGCAGAACATTCATATAATGAACTTCCT
ATTTT

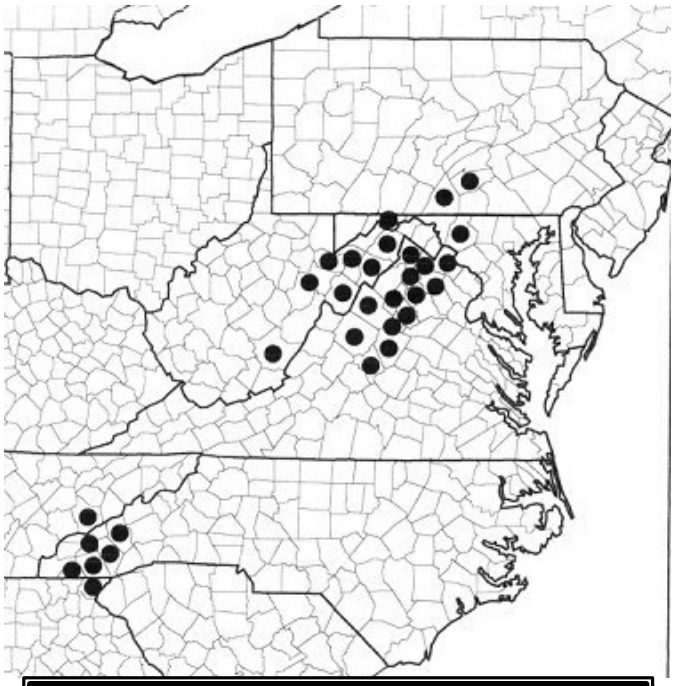
In order to compare *P. appalachiensis* mtDNA with other *Pterourus* swallowtails of the *glaucus* group, COI gene sequences were downloaded from the internet site of the National Center for Biotechnology Information (NCBI) available at http:www.ncbi.nlm.nih.gov/. Gene data were available for *Papilio (Pterourus) glaucus* from Potomac, MD [Accession no. AF044013]; *P. canadensis* from Richford, NY [AF044014]; *P. rutulus* from Orcas Island, WA [AF044015], and *P. multicaudatus* from Black Hills, SD [AF044016]. Collection localities were given in Caterino & Sperling (1999). The *P. glaucus* samples from the Appalachian Mountains and the Piedmont share the same gene sequence, while other taxa diverge from *glaucus* to varying degrees. From this preliminary comparison (Table 1), it can be concluded that *appalachiensis* is much more closely related to *glaucus* than to *canadensis* or any other North American *Pterourus* swallowtail.

Table 1

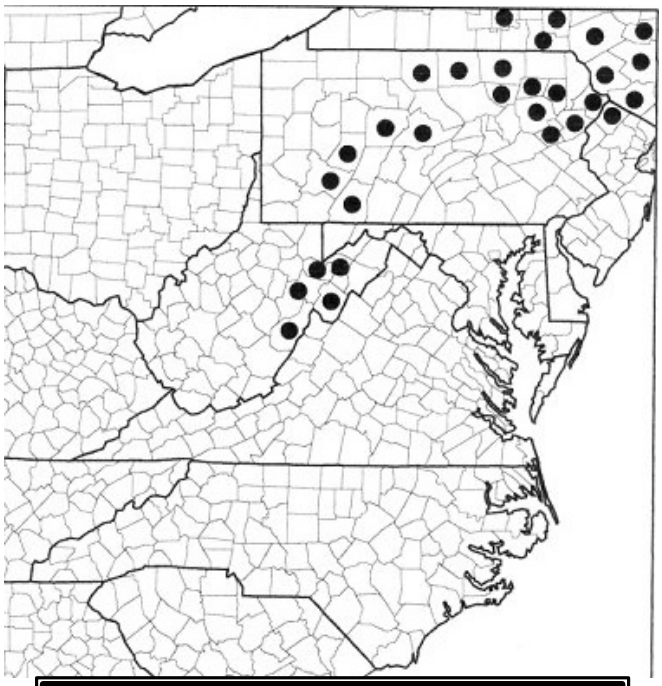
COI Gene		No. of nucleotide base differences					
		A	B	C	D	E	F
P. glaucus 1	A		0	2	24	35	45
P. glaucus 2	B	0		2	24	35	45
P. appalachiensis	C	2	2		25	36	45
P. canadensis	D	24	24	25		27	41
P. rutulus	E	35	35	36	27		47
P. multicaudatus	F	45	45	45	41	47	

1 = North Carolina (Mts.)
2 = Maryland (Piedmont)

Mitochondrial DNA data can only be evaluated in view of maternal lineages. Our limited sampling may have failed to detect considerable intraspecific variation in *appalachiensis.* Small polymorphisms, such as those between *P. appalachiensis* and *glaucus* above, could be interpreted either as a retained ancestral polymorphism or as evidence of recent gene flow through hybridization. Molecular studies of multiple genes, particularly nuclear genes inherited from both parents, may provide a balanced picture of the genetic history of *appalachiensis.* The combination of genetic, morphological, and biological data will help define the limits of this species.



Map A. Study area distribution of *P.*



Map B. Study area distribution of *P. canadensis*.