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A NEW OLIGOCENE FOSSIL BUTTERFLY, *VANESSA* †*AMERINDICA* (LEPIDOPTERA: NYMPHALIDAE), FROM THE FLORISSANT FORMATION, COLORADO

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Introduction

Numerous fossil insects, including 10 butterflies, have been excavated from the Florissant Lake Bed Shales, which date from the early Oligocene, approximately 35 million years ago. Recently two butterfly specimens were located and upon further examination were determined to represent a new fossil species. The first fossil is the best preserved and was one of the fossil specimens presented as gifts to tour guides leading groups through the area. The specimen was given to F. Martin Brown by the late Fred Bischoff and was collected in the early 1930's from the southwestern portion of the present Florissant Fossil Beds National Monument. The area was later excavated by E. R. Nelson, Jr. for the Milwaukee Public Museum, and although Nelson did not find any further butterflies, he did locate some interesting moths.

The second specimen is incomplete and was found some 3.12 km due north of the Florissant Fossil site on the old Stoll Ranch. This area is adjacent to the much older but now back-filled site originally excavated by George Wilson and H. F. Wickham. The specimen was recovered in 1981 by Frederick Sanborn.

Phylogenetic Relationships

Determining the phylogenetic relationship between these two butterfly specimens and modern taxa has proved to be interesting. The outline of the forewing apex is similar to that of †*Barbarothea florissanti* Scudder (1892), a libytheid, the type of which has been lost or misplaced. While both specimens under study are comparable in size to this taxon (24-27 mm), the presence of a labial palpus with the distal segment approximately one-third the length of the second segment argues that this family should not be considered

as a possible relative.

The wing veination provided clues to the taxonomic placement of these new fossil butterflies. The apical forewing venation in the two present specimens is markedly different from the recently described species, †*Oligodonta florissantensis* Brown (1976). The branching of forewing radial veins and the presence of R_5 effectively eliminated the family Pieridae. The possibility that these two fossils are related to the family Hesperiidae was discarded due to the branching of the forewing apical veins. The faint indication of the hindwing humeral vein effectively eliminated the Lycaenidae, and with the staggered origin of hindwing medial veins, the Riodinidae were also rejected. Since there was no evidence of the basal swollen forewing veins nor any indication of 3A, the butterfly families Satyridae and Papilionidae were also disregarded from further consideration.

The only remaining butterfly family is the Nymphalidae, and one of the diagnostic features of this family, the presence of reduced forelegs, is evident on the first fossil. The produced apex of the forewing with the characteristic lobe at M_1-M_2 is indicative of the genus *Vanessa*. In 1965, Nekrutenko described two fossil species from Miocene deposits in the northern Caucasus, one in the genus *Vanessa*, *Vanessa* †*karaganica*, a fossil that is actually associated with the modern genus *Aglais*. The second species described was *Pyrameis (=Vanessa)* †*fossilis*. The proportional size and venation of the present fossils are comparable to that described in the genus *Pyrameis (=Vanessa)* by Nekrutenko; however, the produced lobe at the forewing apex and the smooth transition along the lateral margin posteriad to the anal angle, in addition to the distinctive wing pattern elements, differentiates these two fossils from those taxa previously described. However, the wing venation, produced apical area of the forewing in conjunction with certain forewing pattern elements in these fossils is reminiscent of the Old World taxon *Vanessa* indica and is herein described.

Vanessa †*amerindica*, new species

Figs. 1-4

This description is based on examination of two fossil specimens, both preserved in shale with the ventral surface exposed: (1) a specimen which is relatively complete with four wings and body, and (2) a partial specimen comprised of the distal three-fourths of two left wings. In both specimens the hindwings are superimposed over the forewings. The principal portion of this description is based on fossil 1 (Figs. 1, 3) with comparative wing venation verification in fossil 2 (Fig. 2, 4).

The squashed condition of the body makes the examination and study of body parts difficult. The outline of the eyes, and in particular the inner eye ring which encircles the ommatidia proper, are recognizable. Neither of the antennal shafts nor the antennal clubs have been preserved. The anterior margin of the head is outlined in prominent setal tufts. There is a single labial palpus preserved in the lateral view along the ventral prothorax. The distal segment is approximately one-third the length of the second segment, but the present position of the palpus gives no indication as to whether it is erect or porrect in relation to the labrum and frons. The ventral surface of all three segments is clothed heavily in setae and scales. There is no indication of the proboscis.

The legs have been relatively well preserved in the first fossil specimen. The forelegs are located in the normal position and reduced in size, a characteristic of the family Nymphalidae. The femur and tibia (in part) of the meso- and metathoracic legs can be easily distinguished on the left half of the thorax. The outline of the femur of the meso- and metathoracic legs on the right thoracic half is barely discernable. Posteriad along the abdominal midline approximately at segments A3-6, the preserved tibial and tarsal segments of the right metathoracic leg are evident. In addition, the tibial and tarsal segments of the mesothoracic leg are located just to the left and anterior to the metathoracic leg. The distal margins of these legs are outlined heavily in setae. However, there are no prominent setae nor scales outlining the distal leg margins associated with the thorax proper.

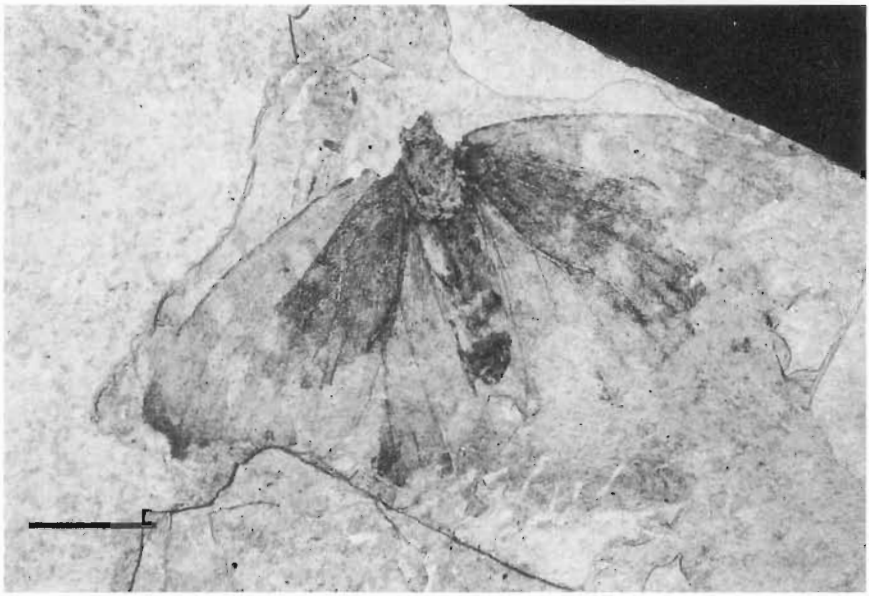


Figure 1. Ventral view of Holotype, *Vanessa †amerindica*, n. sp. (Bar scale = 1 cm) (Allyn Museum Photo no. 880308/36A).

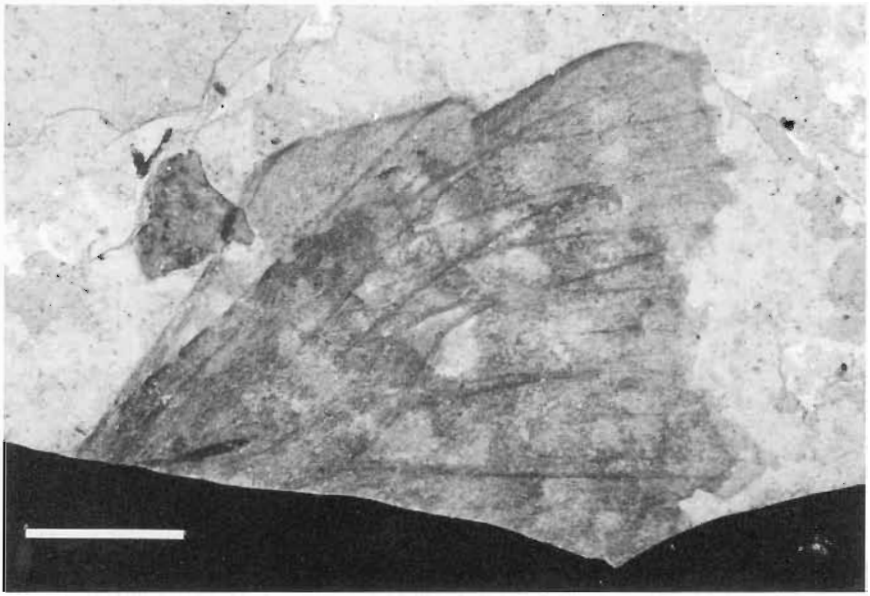


Figure 2. Ventral view of Paratype, *Vanessa †amerindica*, n. sp. (Bar scale = 0.5 cm) (Allyn Museum Photo no. 880309/10).

There are 10 distinct abdominal segments with individual scales evident on the posterior margin of each segment, particularly on segments A7 and A8. There are no discernible sclerotized structures preserved on segment A10, but the irregular intersegmental development of the posterior margin of segment A7 indicates the presence of sclerotized structures, possibly the female sterigma.

The wing venation of this new fossil taxon is illustrated in Figures 3 and 4. The left forewing of the first specimen is the most complete and best preserved with a forewing costal length of 27 mm. Just to the left of the head and anterior to the base of the left forewing, there is a separate, preserved portion of either the tegula, or more likely, the base of the forewing costa. R_4-R_5 branch approximately 13.5 mm from the apex or about three-fourths of the forewing length. R_2 and R_3 are well separated with the origins respectively at 16.5 mm and 14.5 mm from the apex. The end of the forewing cell occurs at less than one-half of the forewing length with the cell open. The origins of M_1 and M_2 are incomplete in both fossils but the origin of M_3 is apparent. The relative positions of M_1, M_2, and M_3 are equidistant from each other along the lateral margin. Because of the preservation of the specimen on the ventral surface, the base of the forewing cubitus and anal veins cannot be distinguished.

The arrangement of the veins on the hindwings is rather well preserved in both fossils. The veins illustrated are those which are easily discerned, with those interconnecting faint veins indicated by the broken line. The relative position of the veins has been somewhat distorted during preservation. There is a faint indication of a humeral vein at the wing base in fossil 1 (Fig. 3). M_1 arises approximately 5.8 mm from the base. The origin of M_2 is near that of M_1 but the interconnecting portion of the medius is absent. The hindwing cell is also open. Cu_2 arises approximately 9 mm from the base with M_3 markedly arched.

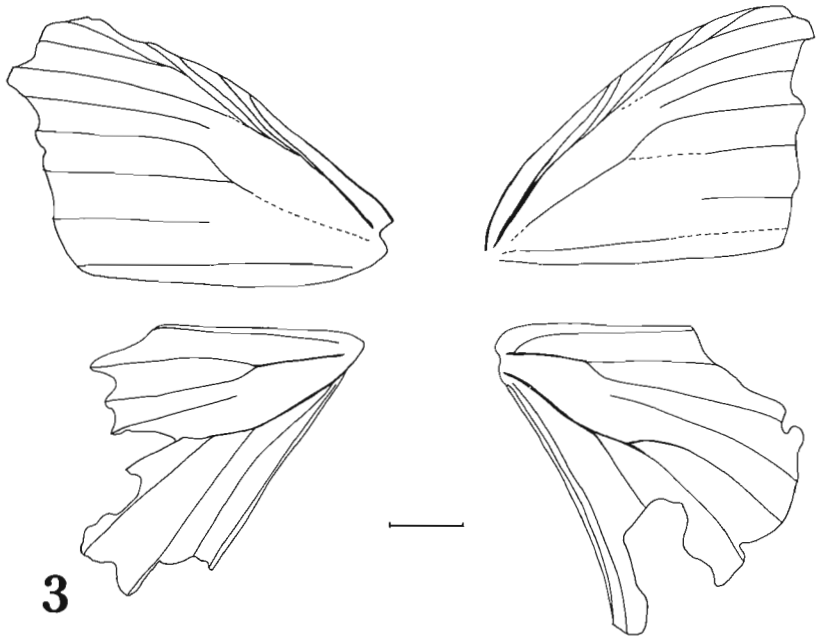


Figure 3. Wing venation of *Vanessa* †*amerindica*, Holotype, ventral view, drawn from the original fossil. (Scale = 0.5 cm)

The relative positions of veins M_1, M_2, and M_3 are equidistant from one another along the lateral margin on the left hindwings of both fossils. Veins 2A and 3A are present in fossil 1 with both veins compressed along the lateral margins of the abdomen. The lateral margins of the hindwings are incomplete in fossil 1 but relatively complete in fossil 2, with numerous scales and setae of the hindwing fringes distinct in both fossils.

One diagnostic feature is present on the lateral margin of the forewing. The whole area of the wing from the apex is markedly angled and produced to M_1-M_2 with the remainder of the lateral margin slightly tapered toward the anal angle. These features are particularly evident on the right forewing margin of fossil 1, and these, taken in conjunction with the wing venation, are similar to the modern Palearctic taxon *Vanessa indica* (Figs. 5, 6). The apical portion of the forewing is absent in part on the left forewing (fossil 1) in M_1-M_2 and not quite as produced in fossil 2.

With the hindwings superimposed over the forewings in both fossils, the wing pattern elements, especially those of the hindwings, are not easily distinguished. However, there is a reduced forewing apical band and an enlarged irregularly shaped spot at the end of the forewing cell near the orgin of R_3 evident in both fossils. These pattern elements coupled with the produced forewing apex and lateral margin are reminiscent of the modern taxon, *Vanessa indica* (Fig. 6) as compared with the more complex pattern elements of *V. virginiensis* (Fig. 7) or the subtle patterns of *V. cardui* (Fig. 8). These latter taxa are widely distributed in North America today. Therefore, the name *amerindica*, for this nearctic fossil reflects its systematic position near *Vanessa indica*, which presently has a range throughout the Palearctic and Indomalayan zoogeographic regions.

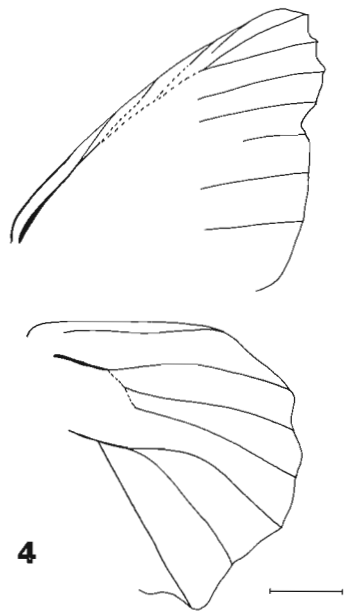


Figure 4. Wing venation of *Vanessa* †*amerindica*, Paratype, ventral view, drawn from the original fossil. (Scale = 0.5 cm)

Holotype (Fossil 1) (Figs. 1, 3): A fossil with four wings and body compressed, preserved in shale with the ventral surface exposed. Forewing length, 27 mm and that of the hindwing is approximately 24.5 mm. Colorado, Florissant Fossil Beds National Monument, T13S R71W, Section 26 and bears the following typed gummed label, "Holotype of *Vanessa amerindica*, n. sp., J. Y. Miller and F. M. Brown, 1988 (UF 21999)." Paratype (Fossil 2) (Figs. 2, 4): a specimen with the greater portion of the left wings preserved in shale and with the ventral surface exposed. Colorado, Stoll Ranch, N. Florissant Fossil Beds National Monument (T13S R71W NE.25, Section 3) and bears the following typed gummed label, "Paratype, *Vanessa amerindica*, n. sp., J. Y. Miller and F. M. Brown, 1988. (UF 22000)." Both the Holotype and Paratype are deposited in the invertebrate palaeontological collections of the Florida Museum of Natural History and are on indefinite loan to the Allyn Museum of Entomology.

In his description of two new taxa in the genera Vanessa *(=Aglais)* and *Pyrameis (=Vanessa)*, Nekrutenko (1965) based his findings not only on wing pattern and venational elements but also on a set of comparative morphometric measurements between the origin of hindwing veins and the hindwing cell. While these measurements provided a convenient method with which to compare modern taxa with the potential ancestors, such measurements are relative and vary with preservation of the fossil specimen. Such size variation may be affected by a number of other ecological factors at the time of preservation. Despite the imperfect preservation of these fossils, including the absence of the interconnecting vein between M_1 and M_2, measurements of the easily discerned

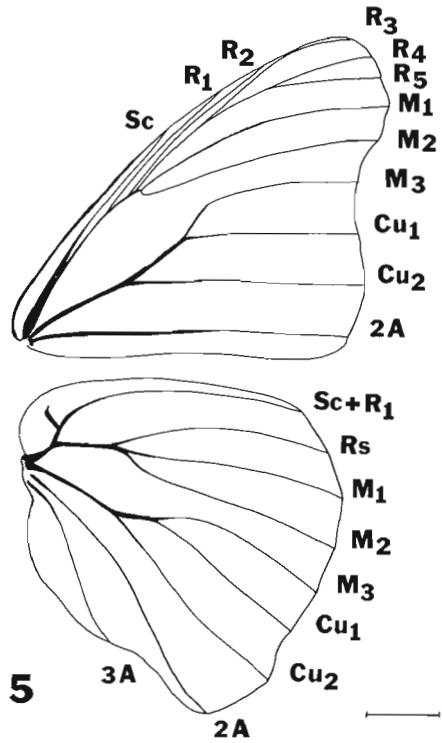


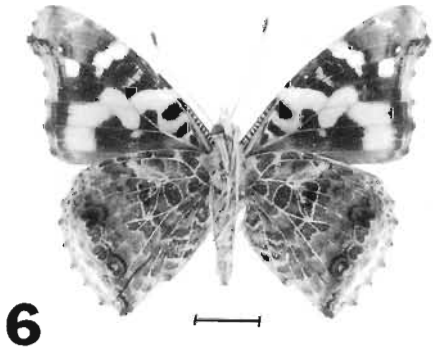
Figure 5. Wing venation of *Vanessa indica*. (Scale = 0.5 cm)

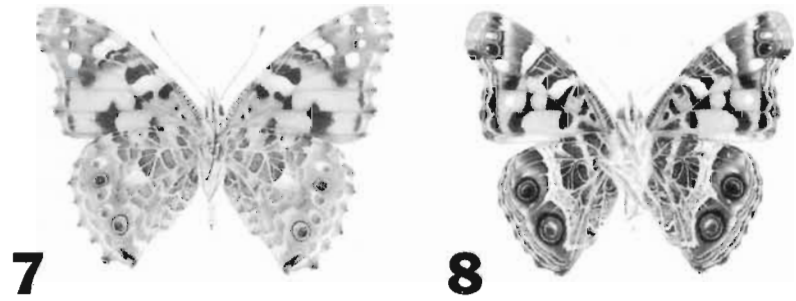
veins of *V. amerindica* are similar in position and relative proporation to those of *V. indica* (+0.2-0.5 mm).

Discussion

It is difficult to determine relationships of extant butterfly taxa with any degree of certainty through the examination of incomplete 35 million year old fossils. The usual diagnostic features, such as the dorsal and ventral wing pattern elements and genitalia, used in standard taxonomic treatments are either incomplete or unavailable for further examination in fossils. In addition, our knowledge of the fossil record in Lepidoptera and particularly that of butterflies, is very limited with only 26-28 specimens described.

Previous descriptions of fossil butterflies from the Oligocene Florissant Shales included a number of taxa with relationships found in modern neotropical butterfly taxa, such as †*Barbarothea florissanti* Scudder, *Hypanartia (*†*Prodryas) persephone* Scudder (1892), *Chlorippe* †*willmetae* Cockerell (1913), and †*Oligodonta florissantensis* Brown (1976). Even a castniid moth, †*Dominickus castnioides* Tindale (1985) has been described from this site. This new species, *Vanessa* †*amerindica* is the first described taxon from the Florissant shale deposits closely aligned with extant species from the Holarctic and Indomalayan geographical regions. *Vanessa* is today a nearly cosmopolitan butterfly genus with a broad geographical range throughout the Holarctic to New Zealand, through central and southern Africa, to Central and South America, and east even to the small island of San Juan de Fuca east of the Falkland Islands. Such a broad geographical range and conspecificity is not completely unknown within the Nymphalidae (Miller and Miller, in press) and is





Figures 6-8. Ventral view of three extant taxa within the genus *Vanessa*: (6) *V. indica*, (7) *V. virginiensis*, and (8) *V. cardui*. (Scale = 1 cm)

found in other butterfly families (Higgins and Riley, 1970; Higgins, 1975). In addition, species within the genus *Vanessa* are notably migratory, a fact which may explain in part the presence of this fossil in the Florissant shales.

Durden and Rose (1978) described two new fossil taxa in the Papilionoidea from the Middle Eocene deposits of the Green River Shales in Colorado, and these discoveries markedly altered our conception of the age of butterflies. While none of these Middle Eocene fossils were precisely comparable to extant taxa, certain morphological attributes placed one species, †*Praepapilio colorado*, in an intermediate sister subfamily between the Papilioninae and the Parnassinae and their more synapomorphic counterparts, the Baroniinae (Durden & Rose 1978). While the taxonomic relationships of †*Praepapilio colorado* have been the subject of further refinement and interpretation (Hancock, 1983; J. S. Miller, 1987), clearly this fossil evidence supports the hypothesis that the Papilionidae are more than 48 million years old! Most of the early records for the Lepidoptera date from the lower Cretaceous (Whalley, 1977, 1978), the period during which the angiosperms arose. Thus, most of the lepidopteran evolutionary history apparently took place sometime between the early Cretaceous and middle Oligocene.

The advanced morphological attributes for the genus *Vanessa* (Nymphalidae) are represented in fossils from both Miocene and these significant Florissant Oligocene deposits. This fossil evidence renders the previously held position that the most of extant butterfly species and genera date from the Pleistocene untenable and indicates an earlier origin. Indirect evidence from phylogenetic studies in other groups suggests a similar evolutionary history. This is illustrated dramatically in the recent description of a stingless bee, *Trigona prisca* (Michener and Grimaldi, 1988), discovered in Cretaceous New Jersey amber, but significantly still another species referable to a contemporaneous genus. The evolutionary history of the Lepidoptera is far from completely known and further investigation of the higher classification of the butterflies in relation to other Lepidoptera is warranted.

Acknowledgments

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