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A NEW LEPIDOPTERAN FOSSIL FROM THE CANYON FERRY RESERVOIR DEPOSIT IN SOUTHWESTERN MONTANA (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT: A new fossil species in the Satyrinae, *Lethe montana*, **spec. nov.** is described from the Canyon Ferry Reservoir in Southwestern Montana, from a deposit of early Oligocene age (32±.01 Mya). Comparative analyses and discussion with extant taxa are discussed. The proposed ancestral stock originates from Oriental region and the historical biogeography and evolutionary and ecological implications are discussed.

KEY WORDS: Bering Land Bridge, Lethe

INTRODUCTION

Luikart et al. (1995) and CoBabe et al. (2002) reported on a new insect and plant Lagerstätte from a Tertiary lake deposit along the Canyon Ferry Reservoir in Southwestern Montana. The deposit occurs in a thick sequence of nonmarine strata exposed on the west side of Townsend Valley, southeast of Helena, Montana, and the fossils are found in a sequence of interbedded mudstone, sandstone, carbonate and volcaniclastic rocks several hundred meters thick (CoBabe et al. 2002). The wide diversity, exquisite quality and preservation of the fossil plants and insects at this Oligocene site are particularly noteworthy. Subsequent to this original find, O'Brien et al. (2008) found that these paper shales are composed of thin laminae of diatomite that form couplets with alternating smectitic clay laminae. The fossils in these formations are associated with biofilms of extracellular polymeric substances (EPS) secreted by diatoms. They suggested that the decomposition of the organisms was

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arrested during sedimentation by this protective mucus covering, and the properties of this covering limited the further actions of bacteria and grazers and may have further enhanced fossilization. Similar biofilms have been reported in the Eocene Florissant Formation, Colorado, the Miocene Save Canyon Formation, Stewart Valley, Nevada, and the Miocene Shanwang Beds of Shandong Province in northeast China (O'Brien et al. 2008).

The diversity of fossils in the Canyon Ferry Reservoir Deposit includes representatives of 37 families of insects and more than 40 taxa of plants. The density of fossil insects is incredible, sometimes more than several hundred individuals found per square foot. Based on an ash-flow tuff which is stratigraphically located well below the plant/insect horizon, the age of this deposit is interpreted to be 32.0 ± 0.1 Mya (CoBabe, 2002). Among these fossils was a beautifully preserved butterfly wing, first illustrated by CoBabe et al. (2002, fig. 4c), and identified therein simply as a satyr butterfly. Further study and examination of this fossil is the subject of this paper.

MATERIALS AND METHODS

The part (pt) and counterpart (cpt) were examined in detail using a dissecting microscope and comparative measurements (Table 1) (n=2), and analyses were made with a survey of taxa in the Satyrinae. Venation and maculation were examined on representative extant taxa from published illustrations, and specimens in the McGuire Center for Lepidoptera and Biodiversity (FLMNH/MGCL) and the National Museum of Natural History (USNM). The discussion and description follow the venation system of Comstock-Needham as adapted from L. Miller (1970).

DIAGNOSIS TO HIGHER CATEGORIES

The general form of the wings, the development of the unbranched forewing radial veins, and the closed forewing cell indicate that this fossil (Figs. 1, 3) is a member of the superfamily Papilionoidea and not a member of the Hesperioidea. There is no crossvein cu-2a nor development of 3A which eliminates the family Papilionidae (J. S. Miller 1987). Since vein M_1 is not stalked with radial veins, the Pieridae should not be considered. The veins are not simple in that they do not arise from the base or from the radius or cubitus proper, eliminating Riodinidae or Lycaenidae. The forewing is rounded and not angular along the lateral margin, and thus, the Libytheinae is not a possibility, leaving Nymphalidae. Within the nymphalids, the forewing cell is closed and in addition to the enlargement of the forewing subcostal vein and the position of the prominent enlarged ocellus in M_1 - M_2 , suggests the subfamily, Satyrinae (= Satyridae, L. Miller 1968; Harvey, 1991). The forewing cell end is located less than one-half of the forewing length, and vein M_2 arises slightly closer to M_1 than to M_3 .

Within the Satyrinae, a number of potential tribes, subtribes, genera, and species were examined. The genus *Cercyonis* Hübner, [1819], a speciose group in the Maniolina Verity, 1953, was examined as it is widely distributed throughout the U. S. and Canada. This genus was a possibility with the prominent eyespot and rounded apex of the forewing. Upon closer examination of the wing venation, particularly the origin of R_1 , R_2 , and R_3 and the swollen subcostal and medial veins proximad, this genus was eliminated. In addition, the rounded forewing apex, lateral wing margin and enlarged ocelllus also suggested members of the *Coenonympha* Hübner, [1819]. Closer investigation of the wing venation, the location,

origin, and development of the radial veins (especially R_1 , R_2 , and R_3) in conjunction with the origins of M_1 and M_2 indicated Parargini Tutt, 1896 (after Higgins 1975; =Lethini of A. H. Clark, 1948; =Lethini L. Miller, 1968) rather than *Coenonympha*. The swollen subcostal vein proximad in conjunction with the origins of R_1 , R_2 , and R_3 in close proximity to M_1 is characteristic of the extant genus *Lethe* Hübner, [1819]. The only member Lethini represented in the current northwestern North American fauna is *Satyrodes eurydice* (Linnaeus, 1763). *Satyrodes* Scudder, 1975 is now considered by some authors as a subgenus of *Lethe* (Pelham 2008). The forewing apex of *S. eurydice* has multiple ocelli of similar size present along the submargin and a prominent, darker submarginal band present, which is not the same as the fossil satyrid under consideration. Since the climate for this particular deposit was estimated to be considerably warmer and moister than present (CoBabe et al. 2002), other representatives within the Parargini were also examined. Upon further examination of the Oriental region, there are a few representative species in the genus *Lethe* that exhibit the reduced number of ocelli on the ventral forewing in combination with a white postmedian band, which extends from the costal margin to the tornus similar to this fossil.

Based on the review of known lepidopteran fossils by Kristensen and Skalski (1999), the only fossil Satyrinae that provided reliable geological age information was *Lethe corbieri* (Nel et al. 1993). Peña and Wahlberg (2008) in their analyses of prehistoric climate change and diversification of the Satyrinae in association with various larval hostplants, calibrated the relative ages based on the minimum age of *L. corbieri* as 25 Mya. Given the age of this fossil documented as to the early Oligocene at 32.0 ± 0.1 Mya in combination with the morphological features and wing maculation patterns described above indicate that this fossil is best placed in the genus *Lethe*.

Lethe montana, spec. nov. Figures 1-5

Specimen Conservation and Description. The fossil is comprised of the more complete pt and reverse cpt portions of the left forewing of a satyrine butterfly that is well preserved in clayshale and claystone. The proximal portion of the wing is incomplete especially in the cpt. The venation is quite evident but incomplete at base and anal margin. The wing pattern and maculation, especially along the lateral margin are reasonably well preserved showing the pattern elements of both the dorsal and ventral surfaces.

In the pt, the forewing cell is closed, and end cell is located less than one-half the forewing length to the apex. The base of subcostal vein is swollen. The origins of R_1 , R_2 and R_3 are in close proximity to the origin of M_1 ; the origin of R_3 is located at approximately two-thirds of the forewing length with the origins of R_4 and R_5 at two-thirds and three-fourths the length to the apex respectively; the origin of M_2 is closer to M_1 than to M_3 ; vein M_3 is slightly arched and its origin is slightly closer to M_2 than to Cu_1 ; origin of Cu_1 is slightly closer to M_3 than to Cu_2 ; the origin of Cu_2 is closer to Cu_1 than to the hypothesized origin of 2A, the base of which is incomplete.

The ground color of pt (Fig. 1) is dark with a lighter postmedian band that occurs approximately two-thirds the distance to the apex and extends from the costal margin to the anal angle along the lateral margin and is diffused toward the tornus; this band appears irregular proximad and is somewhat broken with veins darkened. There is a faint, broken rectangular marking in the forewing cell about two-thirds the distance from the base to the end cell. There is a prominent ocellus in M_1 - M_2 , which consists of single light pupil inside



Figures 1-2. Lethe montana: 1) Holotype; 2) illustrated wing venation.

a dark circle with faint indication of a lighter, distal posterior circle which extends beyond both M_1 and M_2 ; there are two offset smaller ocelli, one each in R_5 - M_1 and M_2 - M_3 , the latter of which is closely aligned proximad with the lighter postemedian band. There is a distal, lighter submarginal band that outlines the Y-shaped, darker, ocellular patch and a darker submarginal line that extends from the apex to Cu_2 and blends with the postmedian band. This postmedian band is followed distad by a darker submarginal line and another lighter distal submarginal band which extends from R_4 near the apex and to Cu_2 , with another fine, darker line which extends from the apex to the tornus and another lighter band distad. The



Figures 3-4. Lethe montana: 3) counterpart; 4) illustrated wing venation.

wing fringe is evident, especially from the apex to Cu_2 (Figs. 1, 2). The distal portion of 2A is evident but broken toward the base and a portion of it is present on the cpt. The wing base is incomplete on this portion of the fossil.

The ground color of the cpt wing (Fig. 3) is darker and similar in appearance with the wing margins and venation not as complete. The markings are similar with the exception of the following: (1) the faint, broken, rectangular marking in the forewing cell about two-thirds the distance from the base is not evident; (2) the proximal area adjacent to the lighter postmedian band that extends from the costal margin to the anal angle is slightly darker; (3) the lighter postmedian band that extends from the veins darkened; and (4) there is an indication of two smaller ocelli present in R_5 - M_1 and M_2 - M_3 anterior and posterior to larger ocellus in M_1 - M_2 . There is an indication of extra scales on vein Cu₂ a little more than one-half the distance

to the lateral margin. Thus far, no hindwing or body of a satyrine butterfly has been located in the Canyon Ferry Reservoir Deposits.

Holotype designation. The specimen consists of pt and cpt, labeled: MONTANA: Broadwater Co., Canyon Ferry Lagerstätte locality, MOR No. MV-152, ex cliff face. CoBabe/Ivie Excavation, summer 2000. Deposited in the Paleoentomology Collections of the Museum of Rockies, Montana State University, Bozeman.

Etymology. The specific epithet refers to the state in which the fossil was discovered.

DISCUSSION

The extant genus Lethe is distributed in the Palearctic and into southeast Asia. Depending upon the taxonomic authority, there are 60-100 species distributed from Sri Lanka through India to the Himalayas, east to the Amur basin of China, Japan, and south to Sulawesi (Bascomb et al. 1999, Bolzano 1999, Monastryskii 2005a, 2005b, 2010). Members of the genus are generally associated with Capillipedium Stapf and Bambusa Schreb. The type species of Lethe, Lethe europa (Fabricius, 1787) (Figs. 6, 11), possesses a slightly more produced forewing apex as indicated by the measurements in Table 1 (n=2), additional scale tufts at the end of distal veins along the lateral margin, and a recurved, arching spotband on the ventral forewing with the ocelli similar in size. On the ventral surface, there is a white postmedian band which extends from the costal margin to the tornus and a thin, white bar more than half the distance to the forewing end cell. There is, however, another group within the genus in this same biogeographic area with a more rounded forewing, a transverse white band, which extends from the mid-costa toward the tornus on both the dorsal and ventral surface, and a more reduced submarginal band with ocelli. Some characteristic examples include Lethe confusa Aurivillius, 1897, Lethe rohria (Fabricius, 1787), Lethe mataja Fruhstorfer, 1908 (Fig. 12), Lethe verma (Kollar, 1844) (Lethe verma sintica Fruhstorfer 1911, Fig. 13) and Lethe latiaris (Hewitson, 1863) (Fig. 14) among others. However, based on the wing characters, especially the lighter postmedian band, which extends from the costal margin and is diffused toward the tornus, the presence of the lighter bar in the forewing cell approximately two-thirds of the length up the cell, the reduced band of ocelli with the single enlarged ocellus in M₁-M₂ and additional smaller ocelli in R₅-M₁ and M₂-M₂, and the two lighter submarginal bands outlined with the thinner darkened bands which extend from the apex to the tornus, suggests that this species is more closely related to the ancestral stock of three other species, Lethe philemon Fruhstorfer, 1911, Lethe philesana Monastyrskii and Devyatkin, 2000 (Figs. 7-8), and Lethe philesanoides Monastyrskii and Devyatkin, 2003 (Figs. 9-10). There are two slightly offset smaller ocelli in R₅-M₁ and M_2 - M_2 as in L. philesana, but the white band is wider than in L. montana. The ocellus is enlarged in L. montana and fills the cell in M1-M2 which may have been the result of preservation. In L. philesanoides, the width of the white postmedian band is reduced but the number of the ocelli in the ventral submarginal band is increased. The current distribution of both of these uncommon, endemic taxa, L. philesana and L. philesanoides is northern Viet Nam, and more recently Formosa for L. philesana.

With the closest extant relatives of the genus *Lethe* geographically distributed in the Himalayas, North Viet Nam, Thailand and Formosa, the discovery of this fossil in the Canyon Ferry Reservoir Deposit in Southwestern Montana is of major evolutionary interest. Insect and plant Lagerstätte can provide excellent insight to the environmental and climate conditions at the time of preservation (CoBabe et al. 2002). During this interval, the ocean

Measurements	Lethe montana	Lethe europa
Forewing length	25.5*	31.5
Length of lateral margin (apex to anal angle)	22.9	22
Length of anal margin	21.5*	23.5
Distance across end of cell	4.8	4.2
Length from base to origin of R_2	14.5*	13.0
Length from base to origin of R ₃	*	20.8
Length from origin of R ₃ to apex	13.6*	17.4
Length of origin of M ₁ to lateral margin	16.7	18.2
Length of cubitus to origin of M ₃	16.1	14.5
Length of origin of M_3 to lateral margin	12.5	13.5
Length of cubitus to origin of Cu ₁	12.4	12.5
Length of origin of Cu ₁ to lateral margin	13.3	14.6
Length of cubitus to origin of Cu ₂	12.4*	10
Length of origin of Cu ₂ to lateral margin	16.5	15.8
Length of 2A	21.8*	21.8

Table 1. Comparative measurements. (in mm). Measurements followed by an asterisk (*) indicate that that particular portion of the fossil is incomplete.

temperatures were slowly increasing with a decrease in continental ice during the middle to late Oligocene (Miller et al. 1991), but by the late Oligocene-early Miocene, there is evidence of high-latitude cooling and continental glaciation oscillations (Zachos et al. 1997). Due the close relationship of insects with their associated foodplants, insects are both critical bioindicators of the habitats and provide further information on the ecological relationships and potential coevolutionary relationships (Labandeira 1998, Labandeira et al. 1994, Wheat et al. 2007). Thus, the insect assemblages present in this deposit provide further insight to the climate at the time.

Lee Miller (1968) postulated that the origin of the lepidopteran fauna was initiated in the Cretaceous and subsequent authors (Holloway and Nielsen 1998, Vane-Wright and Boppré 2005, Braby et al. 2006, Wahlberg 2006, Wheat et al. 2007, Peña and Wahlberg 2008, Heikkilä et al 2012) have provided further analysis and documentation. Based on his studies of the butterflies of Viet Nam, Monastyrskii (2010) recently reviewed the origin and biogeography of the lepidopteran fauna in Viet Nam. Both *L. philesana* and *L. philesanoides* have relatives in the Indo-Burmese fauna, which he defined as centers of endemism. The habitat with which these species is associated in Viet Nam is unique with a limestone karst and a distinct vegetation (Averyanov et al. 2003).

In the introduction to his dissertation and research on the evolutionary history of the butterfly subfamily Satyrinae, Peña (2009), summarized his work to that date. Based on the review of described fossils by Kristensen and Skalski (1999), Peña and the Wahlberg Working Group used the fossil *Lethe corbieri* (Nel et al. 1993) as a calibration point to ascertain age estimates. Since it was the only taxon that could be used with any degree of confidence, they assumed that this fossil was of Oligocene age (25 Mya) (Peña and Wahlberg 2008). As mentioned above, the Satyrinae are closely associated with various grasses and



Figures 5-10. Venation in extinct and extant *Lethe* and diagrammatic representations of wing pattern elements in *Lethe*: 5) combined wing venation drawings of pt and cpt of Holotype *Lethe montana*; 6) wing venation of *Lethe europa* (after Miller, 1968); 7) *Lethe philesana*, dorsal view; 8) *Lethe philesana*, ventral view; 9) *Lethe philesanoides*, dorsal view; 10) *Lethe philesanoides*, ventral view.

are widely distributed worldwide. Based on molecular phylogenetic analyses Peña et al. (2006) and refined by Peña et al. (2011), it was proposed that the Satyrini originated either in the Neotropical or Eastern Palaearctic, Oriental, and/or Indo-Australian Regions and underwent a major radiation between 32-24 Mya. The expansion and radiation of grasses during the Oligocene (Willis and McElwain, 2002) enabled the diversification and radiation of the Satyrini throughout the world (Peña and Wahlberg 2008). The Satyrinae had the ability to adapt and ecologically shift from forested environments to open non-forested areas



Figures 11-14. Examples of extant *Lethe*, dorsal views left, ventral views right: 11) *Lethe europa*; 12) *Lethe mataja*; 13) *Lethe verma sintica*; 14) *Lethe latiaris*.

where larval resources were abundant. Peña et al (2011) proposed further that if the Satyrini did indeed originate in either Europe or Asia and migrated into the Americas, this migration would have occurred around 37 Mya (late Eocene). Although deposits of fossil insects in Alaska date from the late Miocene (Grimaldi and Engel 2005), there was a continuous belt of forest that extended from Asia to North America across the Bering Land Bridge from the Paleocene (60 Mya) through the Oligocene (30 Mya), which provided ample opportunity for migration and dispersal of the Satyrinae and other fauna and flora in both directions (Elias et al. 1996). The discovery and now description of *Lethe montana* in the Canyon Ferry Reservoir Deposit (32 \pm 01 Mya) in Southwestern Montana fits into the scenario that the ancestral stock for this fossil did indeed arise in the Old World and migrated to North America during the Oligocene via the Bering Land Bridge.

There are other insects in the Tertiary Canyon Ferry Lagerstätte which share a similar, interesting geological history (CoBabe et al. 2002). These include a giant female hornet (Hymenoptera: Vespidae: *Vespa* sp.) which today are restricted to the Palearctic and Oriental regions. One European member of this group has been introduced into eastern North America (Krombein et al. 1979), but extant native members are absent. Another example is the family Osmylidae (Neuroptera, Lacewings), which are now extinct in North America (New 1991). There is an exceedingly well-preserved larva of the osmylid subfamily Kempyniinae from the Canyon Ferry deposit. An adult of this subfamily is reported from the Florissant deposit (Carpenter 1943, 1992). These are the only known examples of this family in the

North American Tertiary record. The Kempyniinae today are restricted to temperate South America, Australia, and New Zealand. Thus, it is evident that there were a number of groups migrating across the Bering Land Bridge in both directions during the Tertiary.

Grimaldi and Engel (2005) documented the Pre-Pliocene fossil Rhopalocera (butterflies and close relatives) and ten Nymphalidae were described from the Oligocene of which four are placed in the Satyrinae. As discussed above, the preservation of Lepidoptera in the fossil record is a complex process and the discovery of a specimen in such superb condition such as *Lethe montana* is a very rare event. This is the only butterfly thus far reported from the Canyon Ferry Reservoir Deposit. The fact that a stratum somewhat below this Lagerstätte site has been accurately dated to the Oligocene $(32\pm.01 \text{ Mya})$ is exceedingly significant as it provides a baseline for future research. In this case, this specimen also provides supportive documentation for the Indo-Australian Region as the potential origin of some ancestors of the neotropical Satyrinae, which is exceedingly significant in our quest for knowledge on the historical geology, biogeography and the evolutionary history of this subfamily.

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