

THE TSETSE FLIES  
OF  
FLORISSANT, COLORADO



F. MARTIN BROWN  
RESEARCH ASSOCIATE  
UNIVERSITY OF COLORADO MUSEUM  
BOULDER, COLORADO

Bulletin No. 1  
Pikes Peak Research Station  
Colorado Outdoor Education Center  
Florissant, Colorado 80816

1986

PIKES PEAK RESEARCH STATION  
COLORADO OUTDOOR  
EDUCATION CENTER  
FLORISSANT, COLORADO 80816

---

Roger A. Sanborn  
Director  
COEC

Boyce A. Drummond  
Director  
PPRS

---

Pikes Peak Research Station is a nonprofit organization dedicated to promoting the understanding of the natural world through research and education. Actively engaged in interdisciplinary research on the ecosystems of the Pikes Peak region, PPRS is a part of Colorado Outdoor Education Center, a pioneer in nature programs for all ages since 1962.

It is with great pleasure that we inaugurate this new series of publications, Bulletin of Pikes Peak Research Station, with a paper by Dr. F. Martin Brown describing fossil tsetse flies from the Florissant Shales. Dr. Brown is known the world over for his knowledge of Florissant fossil insects. A teacher, writer, and scientist of world repute, Dr. Brown is a research associate of many museums and research organizations, including Pikes Peak Research Station.

The Bulletin of Pikes Peak Research Station will be published at irregular intervals as manuscripts on the natural history of the Pikes Peak Region become available. Each bulletin will contain new scientific information resulting from research conducted at the station, but will also be written so as to convey the meaning of this research to the largest possible audience.

Boyce A. Drummond  
Editor

---

COVER ILLUSTRATION

The tsetse fly Glossina morsitans is widely distributed in Africa and is a strong vector of Rhodesian sleeping sickness of man. The word "tsetse" comes from the Sechuana language of Bechuanaland and means "fly destructive to cattle."

THE TSETSE FLIES  
OF  
FLORISSANT, COLORADO

F. MARTIN BROWN  
RESEARCH ASSOCIATE  
UNIVERSITY OF COLORADO MUSEUM  
BOULDER, COLORADO

Bulletin No. 1  
Pikes Peak Research Station  
Colorado Outdoor Education Center  
Florissant, Colorado 80816

1986

## TABLE OF CONTENTS

	Page
PREFACE . . . . .	.iii
INTRODUCTION . . . . .	1
FLORISSANT FOSSIL TSETSE FLIES . . . . .	7
REFERENCES . . . . .	11
FIGURES . . . . .	13

## PREFACE

The Earth has a 4.5-billion-year history, but only in the last few hundred years have scientific theories and explanations of her behavior emerged so quickly. As discoveries continue to appear at an accelerated rate, we are able to grasp a better understanding of how the earth and life began, what has happened since that beginning, how present systems work, and what each of us can do to help it continue.

What is so exciting about the discovery of 35-million-year-old tsetse flies in Florissant, Colorado? For the curious, it brings on a myriad of questions: Why and when did tsetse flies leave North America? What were the ecological relationships of the organisms within the ancient Florissant community? What do the relationships in today's tsetse-fly communities have to tell us about the ecology of the Florissant area 35 million years ago? What changes have occurred since that time? Although scientists called paleontologists are charged with the responsibility of seeking the answers, all of us share an obligation to ask such questions.

We delight in the delicate beauty preserved in the fossils of the Florissant Shales, and marvel at the opportunity they provide to obtain a remarkable view into the past. The thrill of discovery helps complete our understanding of what we experience. We know that discovery is not invention but is a way to view our intimate connection with the complexity of past environments. Discovery enables us to speculate about the consequences of our own presence here and encourages us to take long looks rather than limited glances. We are reminded that humans have evolved to wonder, that understanding offers joy, and that it is important to possess a genuine awareness of our relationship to the total scheme of things.

Roger A. Sanborn  
Director  
Colorado Outdoor  
Education Center

# THE TSETSE FLIES OF FLORISSANT

by F. Martin Brown

---

## INTRODUCTION

You are right! The only place the disease-carrying tsetse fly lives today is in tropical Africa. This has not always been true. About thirty-five million years ago tsetse flies lived in the forests that surrounded ancient Lake Florissant. We do not know if the ancient members of this fly family transmitted disease as do the modern ones. Tsetse flies carry sleeping sickness, a serious disease to which the natives of the land, man and hoofed animals, have acquired some immunity. Europeans and their domestic animals, however, have not developed an immunity to the disease. Thus, the tsetse fly has presented a barrier to those of European background ever since the early Portuguese explorers tried to settle the interior of Africa. For most of this century, medical entomologists and pest-control scientists have waged a slow war against these pesky agents of disease.

During this time, we have learned a great deal about the tsetse fly, one of many kinds of flies that bite and suck blood from mammals and other vertebrates. Tsetse flies are distantly related to our horse flies, deer flies, and other such noxious pests. Mosquitoes are more distantly related, about as close as mice are to us. The females of these distantly related flies, of which the mosquito is a common example, need to have a "blood meal" before they can lay fertile eggs. In almost all cases, only the female of the species does the biting. These insects do not really bite as do you and I; instead, they stab a hole through the skin and into the underlying tissue. A minute drop of saliva is injected through the proboscis, the piercing organ of the insect, and prevents the victim's blood from clotting. Mosquitoes

infected with malaria, yellow fever, or other illnesses inject the disease-causing organisms along with the saliva into the victim, thereby spreading the sickness. Fortunately, public health measures today greatly reduce the chance that one may contract mosquito-borne diseases in the United States. Tsetse flies differ from the great majority of blood-sucking flies in one very important respect: the males are blood-sucking as well as the females---and are just as dangerous. Kipling's old tag, "the female is more deadly than the male," does not hold for tsetse flies!

We find other tsetse fly habits that differentiate them from the majority of flies. One such difference is the birth cycle. Most flies and other insects lay many eggs after mating. These eggs are laid on or near the food of the maggots that develop. In the case of tsetse flies, however, the females give birth to a single, well-developed maggot, which weighs about a quarter the bulk of the mother. When preparing to give birth to a maggot, the mother finds a suitable place. Often the birthplace is the underside of a fallen tree that rests a few inches above the forest floor in the woodland. The female tsetse fly hangs upside down under the tree trunk, drops her young, flies away, and will be ready in fortnight or so to give birth to another maggot, providing she obtains another blood meal in the interim. A maggot is born rather quickly, in only a matter of a few minutes. The husky newborn maggot, usually a quarter of an inch long, immediately digs into the forest duff to live its immature life.

Although the maggots develop under the surface, they are not in a safe hiding place. The larvae of several bee flies (Bombyliidae) in the genus Villa parasitize the maggots. Many newborn maggots do not have time to burrow before being attacked by numerous tiny parasitic wasps, some of which attack even while the maggot is being born. These parasites lay their eggs in or on the maggot, or the pupa, and the developing wasp larva feeds on the developing tsetse fly. Those tsetse-fly maggots that survive their enemies and pupate undergo a change in their entire organization, a process similar to the metamorphosis

of a caterpillar to a butterfly. In the pupal stage, the digestive organs of the fly maggot (like those of the leaf-eating caterpillar) are changed to those that can make use of fluid food. These changes take about a month, after which the pupal shell splits down the back, the fly emerges, and the wings develop. The cycle is then repeated in the next generation.

Today, tsetse flies are found scattered throughout the tropical parts of sub-Saharan Africa and to the east of the Sahara in Somalia. At one time, the smallest of the modern tsetse flies also inhabited the hinterland of Aden at the southeastern corner of the Arabian peninsula. Human development and occupation of the land has largely eliminated the kind of habitat ecologically suitable for tsetse flies. About thirty species of Glossina, the genus to which the tsetse fly belongs, are found in Africa.

In the limited area occupied by the forest around ancient Lake Florissant, at least four species of tsetse flies were living. The first of these species was discovered by S. H. Scudder of Harvard, who first made extensive excavations at Florissant in the 1870's. He did not recognize the fact that he had found a fossil tsetse fly. He thought his discovery was a bot fly such as we find today on cattle and wild animals. In 1892, Scudder named this fly Paloestrus oligocenus. Translated into English, the name means "the ancient botfly . . . from the Oligocene period." In 1907, T. D. A. Cockerell, from the University of Colorado, studied a specimen of Scudder's oligocenus and found it to be a tsetse fly. Cockerell's correction of Scudder's work is ironic, for, in 1892, Scudder had pointed out the precise feature that had shown Cockerell that the specimen belonged to the genus Glossina. This feature was the peculiar path of the fourth vein in the wing that is found only in the tsetse fly (Figure 1). It is interesting to note that before Cockerell made his discovery, Henry Fairfield Osborne, the great student of fossil mammals, had written an article about the extinction of many species of hoofed mammals in America at the approximate time that Lake Florissant existed. He suggested that this disappearance might have been caused

by blood-sucking flies carrying diseases.

We think we have a better reason for the change in the hoofed animal fauna at the time: the land was drying out and grasslands were beginning to develop. At the time of Lake Florissant, the hoofed mammals were primarily browsers, feeding on the twigs and leaves of trees and shrubs. Today most hoofed mammals are grazers, which need differently designed teeth to cope with grasses rather than with leaves and twigs. So, although browsers disappeared, they were replaced by grazers. We still have both.

There is another point that speaks against Osborne's idea: tsetse flies and grazing mammals have lived together in tropical Africa for thousands of years. Only introduced cattle and horses are fatally stricken with sleeping sickness disease; the native animals of the region have gained a measure of immunity. Even so, however, Dr. Frank Lambrecht recently (1985) published a most interesting paper discussing the possibility that the tsetse flies of Africa had a marked influence upon the development of modern man by eliminating the Australopithican branch, allowing the genus Homo to survive as the sole representative of the hominid lineage.

Thus, even if the tsetse flies of Florissant did carry a disease, the hoofed mammals probably had an acquired immunity to the sickness. At the present we have no way of learning about the role of ancient American tsetse flies as disease carriers, but who knows what new discoveries and understanding the future will bring?

It is interesting that tsetse flies of Africa do not invade the grasslands to any great distance. The fly is essentially an insect of the shade, brush, or open forest. This type of environment was precisely the habitat of the ancient species around Lake Florissant thirty-six million years ago. The fossil tsetse flies of Florissant belong in the same genus as do the modern ones of Africa. Since we find no real difference between the ancient and modern tsetse flies, and their habitats are the same, we can reasonably suppose that their life histories are similar.

The Florissant tsetse flies may have been a

little larger than modern ones, but not by much. Curiously, this does not seem uncommon when modern and fossil insects are compared, for the ancient ones are often a little larger than their modern descendants, as shown by the following measurements: the largest and smallest of the modern tsetse flies have wing lengths of approximately 13.5 mm and 6mm, respectively. The largest and smallest of the Florissant fossilized tsetse flies have wing lengths of 16 mm and 7 mm, respectively.

The very detailed studies that have been made upon African tsetse flies suggest something about the climate in the vicinity of ancient Lake Florissant. The span of temperatures that prevail in areas where tsetse flies maintain breeding populations today is from 64°F (18°C) to 86°F (30°C), for above and below those limits, the females are unable to produce larvae. Other evidence at the Florissant fossil beds suggests that at some times during the year the mean temperature fell below 64°F. During such times of low temperatures, it is probable that tsetse fly reproduction ceased, leading to pulses in the appearance of new tsetse flies during favorable times of the year in the Lake Florissant area. However, our educated guesses about paleoclimates have, as yet, no sound empirical basis. The temperature may never have dropped too low for reproduction of the flies. Research is continuing on this problem.

We have no idea why or how the tsetse flies disappeared from North America. During the time they lived around ancient Lake Florissant, the Atlantic Ocean was opening between the New and Old Worlds. Millions of years earlier, North and South America, Europe, and Africa were one huge land mass. When the continents were in this combined state, the tsetse flies were probably living in all of the scrub and forest country that supported herds of hoofed animals. We also find it probable that these flies lived along broad rivers and lakes where the forerunners of tapirs provided a good food source. The tapir, a semi-aquatic relative of the horse, is now restricted to two regions -- namely, Malaya in Asia and the tropical Americas. Today, one such animal, the hairy tapir,

lives close to treeline in South America. It is found in the eastern Andes of east central Ecuador at about 11,000 feet above sea level. As the Andes rose gradually from sea level, this tapir stayed with the land and somehow acquired a good coat of thin fur!

Fifty years ago some scientists believed that the forerunners of Glossina, the tsetse fly genus, lived in what is now Colorado. These proposed forerunners inhabited the region now covered by Eocene shales, the Green River Formation in northwestern Colorado, northeastern Utah, and southwestern Wyoming. Cockerell (1924) described this proposed forerunner as Eophlebomyia claripennis, which he placed in Trypetidae, a family of fruit flies.

When Cockerell (1925b) discovered a second specimen of this fossil, he sent it to the British Museum (Natural History) hoping that Major E. E. Austen, who was the world authority on tsetse flies at the time, would examine his find. Austen wrote to Cockerell stating that ". . . I am, for the moment at any rate, inclined to consider Eophlebomyia as possibly representing an annectant form between the Anthomyiidae and the blood-sucking Muscidae, as represented by Glossina."

Dr. Curtis Sabrosky of the Systematic Entomology Laboratory, U.S. Department of Agriculture, kindly examined for me Cockerell's type of Eophlebomyia claripennis in the National Museum's Department of Paleobiology. He came to the conclusion that the fly is acalyperate (lacking curious leaf-like structures at the base of each wing), as Cockerell had said, and thus cannot be an ancestor of the Glossinidae.

In 1930, Joseph Bequaert prepared a synopsis of our knowledge of tsetse flies to that time. [In large part this is based upon Hegg (1929).] In this synopsis Bequaert noted (p. 159) that Cockerell had described from Florissant four "apparently quite distinct species of flies, which unmistakably belong to the genus Glossina." Cockerell did describe four fossil Glossina in his several papers, one of which he fully acknowledged as being of Scudder's authorship.

# FLORISSANT FOSSIL TSETSE FLIES

## Muscoidea: Diptera Glossinidae

Among the Glossinidae, the median (4th) vein is "hooked" upward toward a very short cross-vein. According to Austen's Handbook of the Tsetse Flies (1911) this is a unique feature for Glossina, the type genus for Glossinidae. In 1938, C. T. H. Townsend published a note about the Florissant fossil glossinids. In this brief article, less than two pages long, he proposed two new fossil genera. These are noted below in the synonymy of Glossina. Hegh (1946) and Henning (1973) relegate these genera of Townsend to synonymy. James (1945) noted a number of other cases where Townsend was in serious error.

A key to the described Colorado fossil Glossinidae

1. Wing over 9 mm long.....3  
Wing under 9 mm long.....2
2. Distal end of discal cell, ignoring  
the bulge, at about right angle  
to its costal side, body rela-  
tively stout.....osborni Ckll.  
Distal end of discal cell, ignoring  
the bulge, at an angle of about  
45° to the costal side, abdomen  
slender and banded.....armatipes Ckll.
3. Wing about 16 mm long.....oligocena (Scudd.)  
Wing about 10-12 mm long.....veterna Ckll.

Glossina Wiedemann

Wiedemann, C. E. W., 1830, p. 253.

Type species: longipalpis Wiedemann 1830.

Geological horizon: Recent to Oligocene.

These are robust flies with the median vein (4th vein) uniquely, abruptly bent or looped upward where the anterior cross-vein meets it. The proboscis is staunch, encased in the palpi and directed forward. There may be as many as 30 modern species or as few as a dozen, depending upon whose taxonomy you follow. Today there are no American species. Several genera have been suggested for various species groups, but on the whole these generally are considered to be worth only subgeneric status or to be synonyms.

Synonyms of fossil Glossina:

Paloestrus Scudder, 1892, pp. 18-19. Type species: oligocenus Scudder, 1892. Cockerell, 1907, recognized that Scudder's genus is synonymous with Glossina Wiedemann.

Cockerellitha Townsend, C. T. H., 1938, p. 166. Type species: Glossina osborni Cockerell, 1909.

Lithoglossina Townsend, C. T. H., 1938, p. 166. Type species: Glossina armatipes Cockerell, 1917.

oligocena (Scudder) (Paloestrus), 1892, p. 19, pl. 2, figs. 1, 4. Type locality: Florissant, Colorado, probably from one of Scudder's pits in the vicinity of Fossil Stump Hill.

Holotype: a somewhat broken specimen but with critical areas of the wings intact; Scudder number 13703 and 14086 (obverse and reverse) now in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts,

No. 3490a,b. The large size of this species, with a wing about 16 mm long and very stout body and long forward projecting proboscis, makes it easily recognized among the Florissant Glossina.

AMNH: a specimen, field number 295, collected in 1908 by the Cockerell party, including William Morton Wheeler who probably presented it to the museum. A second specimen, AMNH 18839, was labeled "Type" in error. This may be from the same expedition.

BM(NH): a specimen, No. I. 8421, was recovered by George N. Rohwer from UCM (Cockerell) pit 14 in the Florissant area. It was sent to the British Museum by Cockerell in 1907 or 1908. Dr. Paul Whalley informed me that the specimen is marked "Florissant station 10." Cockerell (1907a, b, and 1909b) only mentions a specimen collected by G. N. Rohwer at station 14.

UCM: a fine specimen both obverse and reverse collected by Frederick Sanborn in 1982 in the Stoll pit, Wilson and Wickham's site on the old Wilson Ranch, located west of Florissant. The specimen was given to the museum by its finder. It is the best specimen of the species yet discovered.

veterna Cockerell, 1916, p. 17. Type locality: Wilson Ranch, west of the present town of Florissant.

Holotype: collected by George Wilson and sent to Cockerell by F. H. Ward, now USNM 66281. The species is markedly smaller than oligocena, having a wing length of only 10.9 mm.

AMNH: a specimen number 39554. Its source is not known to me.

osborni Cockerell, 1909a, p. 128. Type locality Florissant, Colorado.

Holotype: British Museum (Natural History) IN. 19223. Collected in 1908. This is the only specimen known. The wing is 7 mm long.

Glossina (Lithoglossina)

Townsend, C. T. H., 1938, p. 166.

Type species: Glossina armatipes Cockerell, 1917.  
Geological horizon: Recent to Oligocene.

Buxton (1955, p. 23) questioned placement of armatipes in the genus Glossina. He wrote "in one species (G. armatipes) the hind basitarsus carries a pair of stout longitudinally striated spines, which may indicate that it does not ap-pertain to Glossina." This supports the evidence noted in the holotype description (below) setting the species apart from the other three. It might be well to consider retaining the genus Lithoglossina Townsend, 1938, for this species.

armatipes Cockerell, 1917, pp. 19-20. Type locality: Florissant, Colorado, the pit on the Wilson Ranch (NW1/4, SE1/4, NE1/4, Sec 3, T 13S, R 71W.) to the west of the present town.

Holotype: A male collected by George Wilson and sent to Cockerell by F.H. Ward. This is now USNM 66282. It is the only known specimen. The strongly banded, long and slender abdomen sets this species apart from all of the other Florissant Glossinidae. The wing measures 7.5 mm long and the abdomen 6.5, and its depth about one-quarter of that.

## REFERENCES

- Austen, Maj. E. E. 1911. Handbook of the Tsetse Flies. The Imperial Bureau of Entomology, London. 110 pp., 10 colored plates.
- Austen, Maj. E. E. & Emile Hegg. 1922. Tsetse-flies, Their Characteristics, Distribution and Bionomica. The Imperial Bureau of Entomology, London. ix & 186 pp., 19 ff., 5 pls. This is a classic.
- Bequaert, Joseph. 1930. Tsetse Flies - Past and Present (Diptera: Muscoidea). Entomological News 41: 158-164, 202-203, 227-233.
- Buxton, Patrick A. 1955. The Natural History of Tsetse Flies - An account of the biology of the genus Glossina (Diptera). London School of Hygiene and Tropical Medicine, Memoir 10. H. K. Lewis & Co., Ltd, London. xviii & 816 pp., 47 pls., 165 figs.
- Cockerell, Theodore Dru Alison. 1907a. A fossil Tsetse Fly in Colorado. Nature 76: 414.
- \_\_\_\_\_. 1907b. Some Old World Type of Insects in the Miocene of Colorado. Science (n. s.) 26: 446.
- \_\_\_\_\_. 1909a. Another fossil Tsetse Fly. Nature 80: 128.
- \_\_\_\_\_. 1909b. Fossil insects from Florissant. Bulletin of the American Museum of Natural History 26: 67-76.
- \_\_\_\_\_. 1916. The third fossil Tsetse-fly. Nature 98: 70.
- \_\_\_\_\_. 1917. A fossil Tsetse Fly and other Diptera from Florissant, Colorado. Proceedings of the Biological Society of Washington 30: 19-22.
- \_\_\_\_\_. 1918. 3. Fossil Tsetse Flies. Proceedings of the United States National Museum 54: 308-311, pl. 55.
- \_\_\_\_\_. 1919. Glossina and the extinction of Tertiary mammals. Nature 103: 265. [A reply to G. D. H. Carpenter, Nature 103: 46, 1919.]
- \_\_\_\_\_. 1924. Fossil insects in the United States National Museum. Proceedings of the United States National Museum 64, Article 13 (No. 2503): 15 pp., 2 pls.

- \_\_\_\_\_. 1925a. The Tsetse Flies. Entomological News 36: 62-63. [A review of E.W. Austen's Handbook of the Tsetse Flies, 1911.]
- \_\_\_\_\_. 1925b. The Eocene fossil fly *Eophleomyia*. Psyche 32: 229-230.
- Curran, Charles Howard. 1934. The Families and Genera of North American Diptera. 512 pp.; many plates and text figures not sequentially numbered. Privately printed, New York.
- Hegh, Emil. 1929. Les Tsé-Tsés. Tome premier. Généralités. Anatomie. Systematique. Reproduction. Gites & Pupes. Ennemis Prédateurs et Parasites. A. J. Engelterzi, Brussels. xiv + 742 pp, 327 text figs., 15 color plates.
- \_\_\_\_\_. 1946. Les Tsé-tsés: Description, Biologie -- Moyens de Destruction. Royaume de Belgique, Bruxelles. 102 pp, 29 text-figures.
- Henning, W. 1973. Diptera. In Klükenthal's Handbuch der Zoologie, Volume 4, Part 2, Number 31, pp. 1-337, text figures 1-143.
- James, M. T. 1945. C. H. Townsend. Annals of the Entomological Society of America 38: 143-144.
- Lambrecht, Frank L. 1985. Trypanosomes and hominid evolution. Bioscience 35(10): 640-646.
- Scudder, Samuel Hubbard. 1892. Some insects of special interest from Florissant, Colorado, and other points in the territories of Colorado and Utah. United States Geological Survey, Washington, D.C. Bulletin 93: 25 pp., 3 pls.
- Townsend, Charles H. T. 1938. Five new genera of fossil *Oestromuscaria* (Diptera). Entomological News, 49:166-167.
- Wiedemann, Christian Rudolph Wilhelm. 1830. Aussereuropäischer zweiflügeliche Insecten, als Fortsetzung des Meigenschen Werkes, Vol. 2. Schultz, Hamburg. xii + 684 pp., 4 pls.

Plate 1. *Glossina oligocena*. Dorsal view of body and right wing. Specimen collected by Frederick Sanborn. Note the looped course of median (4th) vein.

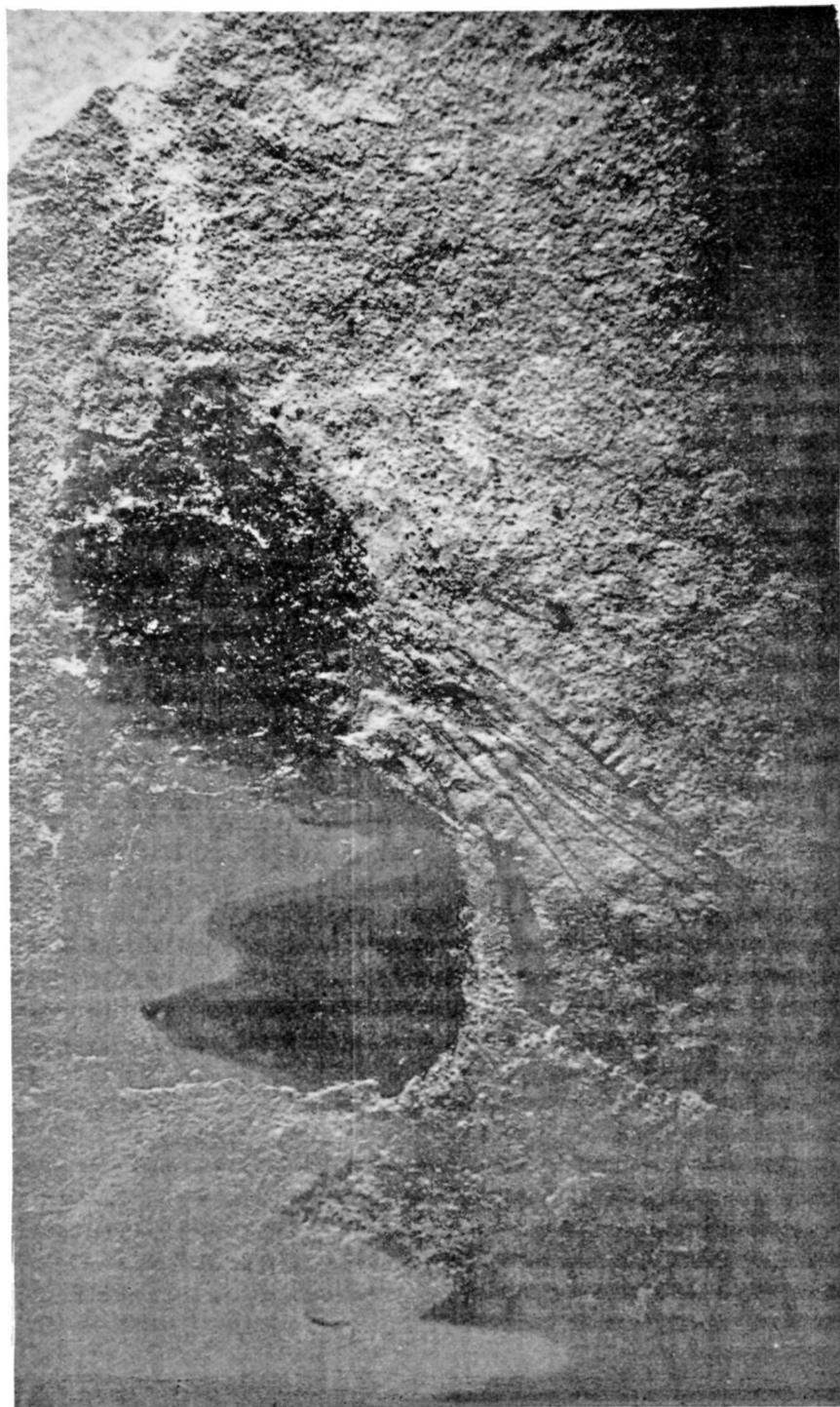
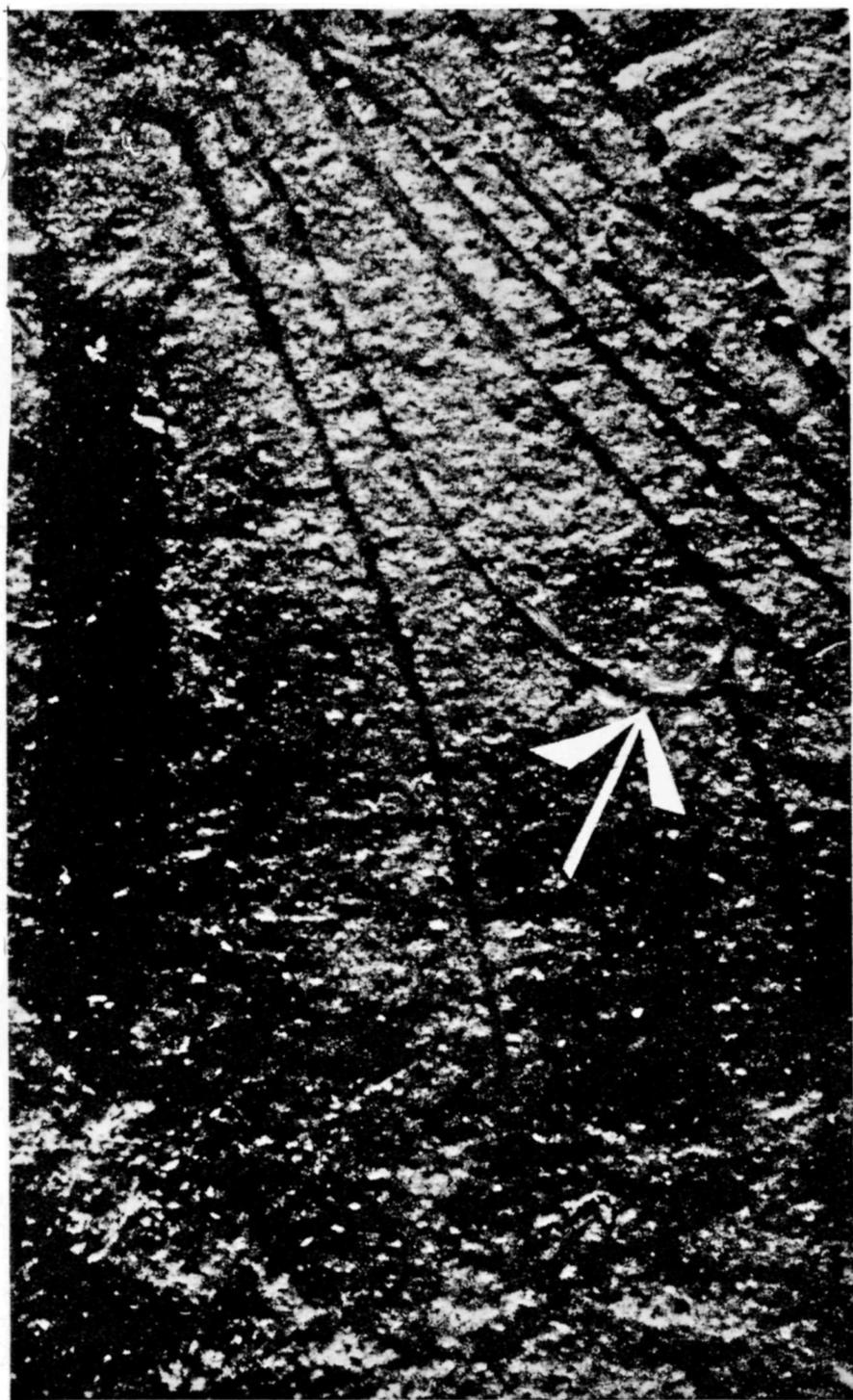


Plate 2. Close-up of wing of Glossina oligocena shown in Plate 1. Note "hooked" median (4th) vein (see arrow), diagnostic of the Glossinidae.



Brown, F. Martin. 1986. The Tsetse Flies of Florissant, Colorado.<sup>1</sup> Bulletin of Pikes Peak Research Station, Number 1. iii & 12 pp., 2 pls.

---

<sup>1</sup>Manuscript received 01 September 1985; revision accepted 10 December 1985.

Date of Publication: 31 May 1986

---

BULLETIN OF PIKES PEAK RESEARCH STATION is published at irregular intervals by Colorado Outdoor Education Center, Florissant, Colorado 80816.

BUSINESS OFFICE: Requests for information about subscriptions, back issues, and other noneditorial matters should be addressed to Search Publications, Colorado Outdoor Education Center, Florissant, Colorado 80816, USA.

EDITORIAL OFFICE: Manuscripts and correspondence concerning editorial matters should be addressed to Dr. Boyce A. Drummond, Editor, Bulletin of Pikes Peak Research Station, Colorado Outdoor Education Center, Florissant, Colorado 80816, USA.

EDITORIAL ADVISORY BOARD:

Anthropology:

Botany: William A. Weber, Curator of the Herbarium, University of Colorado Museum, Boulder, Colorado 80309, USA.

Geology: R. A. Wobus, Department of Geology, Williams College, Williamstown, Massachusetts 01267, USA.

Paleontology: F. Martin Brown, 6715 South Marksheffel Road, Colorado Springs, Colorado 80911, USA.

Zoology: Thomas C. Emmel, Department of Zoology, University of Florida, Gainesville, Florida 32611, USA.

