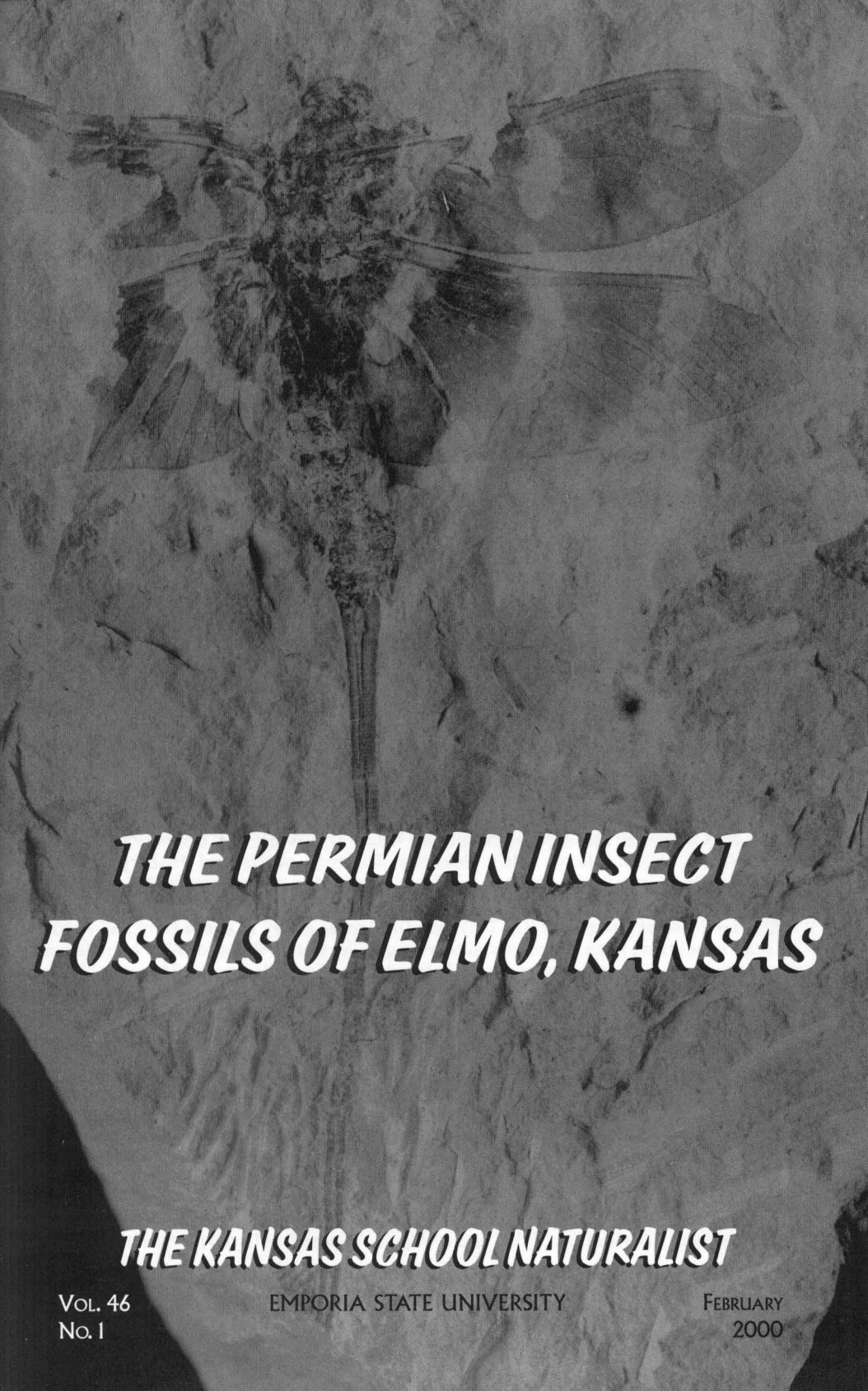

THE PERMIAN INSECT FOSSILS OF ELMO, KANSAS

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I owe a debt of gratitude to a number of people who helped to make this issue possible. Drs. Sonny Ramaswamy and Ralph Charlton (Kansas State Univ. Entomology Department) allowed me to scan fossils in the KSU collection and provided copies of papers on Elmo fossils, including D.A. Wilbur, Sr.'s KSU report. Jason Dinges of Hays, Kansas, who is currently working the Elmo site under lease, allowed me to visit and photograph the site. Rod Asher (Cawthron Institute, Nelson, New Zealand), provided scanned images of the glass plates made to illustrate a number of Dr. R.J. Tillyards' original type descriptions of Kansas Permian Insects, and authorized their use here. Liz Brosius (Kansas Geological Survey) provided copies of her articles and notes on Dr. Frank M. Carpenter and photos of him as well. Tim White (Sr. Collections Manager, Invertebrate Paleontology, Yale's Peabody Museum of Natural History) provided photos of Dunbar and Schuchert as well as images of Elmo fossils in the Yale collection. Dr. Ebbe S. Nielsen (Dir., Australian National Insect Collection, Canberra, Australia) authorized use of a photo of R.J. Tillyard. Dr. George Byers (Kansas Univ.) allowed me to scan specimens from his personal teaching collection of Elmo fossils. Ann Molineux (Collections Manager, Non-vertebrate Paleontology, Texas Memorial Museum, Univ. of Texas) provided a photo and information on E.H. Sellards. The Snow Entomological Museum allowed use of their photo of Frank Carpenter. Special thanks to Liz Brosius, George Byers, and J. Richard Schrock for reviewing and thereby much improving this issue. ~ Roy Beckemeyer, 12/99.

Cover Photo: Palaeodictyoptera: Spilapteridae: *Dunbaria fasciipennis* Tillyard 1924. An extraordinarily well-preserved fossil of an insect, with beautifully patterned wings, from the Permian deposits near Elmo, Kansas, in southeastern Dickinson County. This image was scanned especially for use here by Rod Asher of the Cawthron Institute, Nelson, New Zealand, from the original glass plate negative used to illustrate the type description. Used with permission.

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THE PERMIAN INSECT FOSSILS OF ELMO, KANSAS

by Roy J. Beckemeyer

INTRODUCTION: BURIED TREASURE BENEATH THE KANSAS PRAIRIE

What does the term "buried treasure" bring to your mind? Perhaps Caribbean beaches and palm trees, pirate ships sporting the Jolly Roger and wooden chests of gold bullion? Or maybe gems mined from beneath the ground? Both of these images have something in common with the fossil treasures that have been found buried beneath the Kansas prairie.

Today Kansas hardly resembles a Caribbean island, but in the Permian period (245 to 280 million years ago) of the late Paleozoic Kansas was tropical. North America and Europe were close to the equator. The oceans were receding, and much of Kansas was a coastal plain at the edge of an inland sea. And while paleontologists may not dig diamonds or gold from beneath the ground, they do unearth gems of knowledge: the fossilized remains of ancient life forms.

Put the two images together to get the treasure that I have in mind: a rich and well-preserved trove of insect fossils that were buried during the tropical Permian period and can now be dug from beneath the Kansas prairie. Paleontologists call such sites "Lagerstatten." Literally translated from the German as "deposits," this word has come to mean a "fossil bonanza," a place where fossils are particularly numerous and valuable.

Few Kansans are aware that their state contains one of the most celebrated sites for Paleozoic insect fossils: the Elmo, Kansas Lagerstatt in southern Dickinson County. I hope this issue of the *Kansas School Naturalist* will help to change that situation. The variety, quantity, and quality of insect fossils found in the Kansas Permian limestone are known to paleontologists around the world. In this issue we will briefly review what the Elmo fossils tell us about the insects that flew over Kansas long ago. We will also learn a bit about the interesting people who discovered, studied, and wrote about the insects of the Kansas Permian. There is still much to be learned about Paleozoic insects; perhaps a reader of this pamphlet will be inspired to carry on the study of the Permian fossil insects of Elmo, Kansas.

Figure 1. The treasure site. The Elmo, Kansas Permian Insect site as it appears today. After the last visit by Frank Carpenter of Harvard in the 1930's, the end of the dig had been marked with a steel rod and the gully refilled. The fill has now been removed and the quarry extended. The pick rests on the insect layer and the shovel blade points to a dark area which is a blackish shale containing fossilized stumps and branches from an ancient swamp that underlies the insect layer of limestone. The site is currently being worked under lease by the team of Jason and Matthew Dinges and Jerry Green of Hays, Kansas. The photo was taken by Roy Beckemeyer on a visit to the site with Jason in September of 1999.

Roy J. Beckemeyer (957 Perry, Wichita, KS 67203-3141, Email address: royb@southwind.net) is a retired aeronautical engineer and an avocational entomologist interested in the mechanics and evolution of flight in nature. He is also the coauthor of the *Kansas School Naturalist* issues on dragonflies and damselflies of Kansas. A checklist of Elmo Permian insects that includes full synonymies is available from the author.

THE ELMO SITE AS PART OF THE KANSAS-OKLAHOMA PERMIAN

Dr. Paul Tasch, Emeritus Professor in the Dept. of Geology at Wichita State University, studied the ecology of Kansas during Permian times (Ref's. 42-48). He described the region of central Kansas and north central Oklahoma during the Permian (Ref. 46) as being " . . . a coastal flat with relict puddles, ponds, and even small-scale lakes that gradually freshened as the epeiric sea regressed. Marine encroachments over this coastal area occurred between times of recurrent fresh-water biofacies."

The Wellington Formation, the shale sequence of sedimentary rocks deposited across Kansas and Oklahoma during the Permian, is about 700 feet thick. Dr. Tasch was able to correlate layers of this formation from location to location in the area and to show that insect beds recurred at approximately 100-foot intervals. The region is generally covered by relatively recent (Quaternary) deposits, and the Permian rocks are only occasionally visible as outcrops. The most prolific and famous of the insect-bearing exposed layers are those in the Midco, Oklahoma area (Noble and Kay Counties) and the Elmo, Kansas beds (Dickinson County). The two areas are each incredibly productive, both in terms of quantity and quality of fossils. About 8,000 specimens were taken from Midco between 1940 and 1957 (Ref. 18). The Elmo site yielded nearly 15,000 specimens (detailed below) in the century since its discovery. One of the world's authorities on fossil insects, Dr. Frank Carpenter of Harvard (we'll learn more about him later), studied and compared the two sites: " . . . the Elmo beds in Kansas and the Midco beds in Oklahoma originated as lakes about 140 miles apart. Both deposits . . . were apparently contemporaneous. However, there appear to have been differences in the environments of the lakes . . . The one in Kansas contained fresh water, derived from an earlier swamp, with plants growing close to the water's edge and with some insect nymphs living in the water. The Midco lake was essentially a playa, containing algae and Conchostraca [clam shrimps]; plants did not grow near it and insect nymphs did not live in it." (Ref 18).

A SHORT HISTORY OF THE DISCOVERY AND STUDY OF THE ELMO FOSSILS

In 1899 Elias H. Sellards was a graduate student working on a PhD in paleontology at Yale University. In going over some fossil plants collected from the Wellington shales southeast of the town of Elmo in Dickinson County, Kansas, he came across two insect fossils. Recognizing the significance of this find, he returned to the site during the summers of 1902 and 1903 and eventually accumulated " . . . some 2,000 specimens, a number which exceeded the combined fruits of nearly a hundred years' collecting from all other American Paleozoic localities . . . " (Ref. 24).

He published a short series of papers (1903-1909, Refs. 36-39) in which he described a number of the insects which seemed to be typical of the fauna. It was his intention to eventually publish a revision, but he was never able to do so (insects were not his primary field). He deposited a small number of fossils in the Peabody Museum at Yale, but kept most of the specimens with him until 1928, when he sent his collection to Harvard.

Fig. 2. E.H. Sellards (1875-1961). Born in Carter City, Kentucky, the son of Wiley W. and Sarah (Menach) Sellards. The family moved to Kansas during his youth. He attended the University of Kansas, where he received his B.A. and M.A. degrees, and Yale University, from which he graduated in 1903 with a doctoral degree in paleontology. Photo and biographical information courtesy Texas Memorial Museum, Austin, Texas.

The next chapter in the story of the Kansas Permian insects opened nearly 20 years later, when Robin J. Tillyard came upon the scene. Tillyard was English. He moved to Australia and became a famous and influential entomologist, known especially for his work with dragonflies and with fossils and the evolution of insects. He wrote two classic books: *The Biology of Dragonflies* in 1917, and *The Insects of Australia and New Zealand* in 1926.

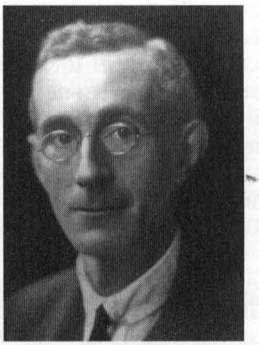


Fig. 3. Robin J. Tillyard (1881-1937) was born 31 January, 1881 in Norwich, England. He earned a BA from Cambridge in 1903 and Dsc degrees from Univ. Sydney (1917) and Cambridge (1920). He was Chief of the Biological Dept., Cawthron Institute, Nelson, New Zealand from 1920 to 1928, when he was named first Chief , Div. of Economic Entomology, Australian Commonwealth Scientific and Industrial Research Organization (CSIRO). Photo courtesy of CSIRO.

Tillyard's studies of Australian fossil insects had led him to the conclusion that the classification of insects would only be understood by serious study of fossils from the Permian, an age when much diversification was taking place. He took a tour in 1920 to look over fossils from other parts of the world. At Yale University he came across Sellards' material, and, in the words of Carl Dunbar (Ref. 24), "his delight was unbounded."

Tillyard's enthusiastic response to these fossils led Professor Charles Schuchert, Curator of the geological collections at the Peabody Museum, to request a grant from the National Academy of Sciences to underwrite an expedition to Kansas in the summer of 1921. The trip, led by Dunbar, was a resounding success, yielding another 2,000 specimens, bringing the total number of Elmo fossil insect specimens to about 4,000.

Fig. 4. Carl Owen Dunbar (1891-1979) was born in Hallowell, Kansas, the son of David and Emma (Thomas) Dunbar. He received a BA from the University of Kansas in 1913 and a PhD in geology from Yale University in 1917. He was the Director of the Peabody Museum of Natural History at Yale from 1942 until his retirement. Dunbaria was his namesake. Photo courtesy Peabody Museum.

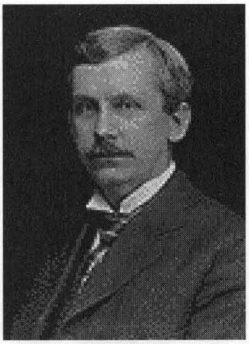


Fig. 5. Charles Schuchert (1856-1942) was born in Cincinnati, Ohio on July 3, 1856 to Philip and Agatha (Mueller) Schuchert. Schuchert went to Yale in 1904. He was Chair of the Geology Department (1909-1921) and administrative head of the Peabody Museum (1904-1923) during the time of the Yale Elmo expedition (1921). Megatypus schucherti and Permohymen schucherti were among the insects named in his honor. Photo courtesy Peabody Museum.

All of the Yale Elmo Expedition insect fossils were shipped to Tillyard in New Zealand, and he worked on them from 1921 until his death in 1937. Tillyard, a prolific author, wrote a series of some 20 papers on the Elmo fossil insects (one with Dunbar) that were published between 1923 and 1937 (Refs. 23, 24, 49-68).

The most thorough study of the Elmo fossils came when Frank M. Carpenter came upon the scene. He had been born in 1902, the year when Sellards began working the Elmo site. Perhaps this was prophetic. Carpenter seems to have been destined to work with fossil insects.

Liz Brosius of the Kansas Geological Survey told how (Ref. 2), as a youngster of 13, Carpenter came across a book containing a picture of a fossil butterfly. Its wings were outstretched and its color pattern was wonderfully preserved. The name of the butterfly was Prodryas *persephone*. He told his father that night that he wanted to work with fossil insects when he grew up. Years later, when Carpenter entered Harvard University to begin his studies, he went into the fossil insect collections. The first box that he took from the drawers of specimens contained that very butterfly fossil. "Like a fairy-tale omen, the sudden manifestation of P. *persephone* must have assured Carpenter that he was on the right path. Some years later he became curator of the Harvard collection. 'I never dreamed [he said], that I would live the rest of my life within 20 feet of that specimen' " (Ref. 2).

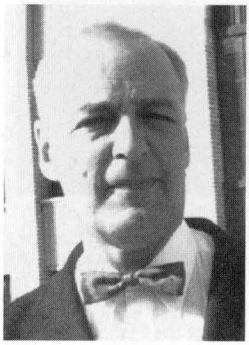


Fig. 6. Frank M. Carpenter (1902-1994) was born and grew up in the Boston area. His first trip away from New England was to the Elmo site in Kansas. Carpenter received his PhD from Harvard. He became the premier American student of fossil insects. Photo courtesy of the Snow Entomological Museum, Kansas University.

Carpenter and one of his professors, Percy Raymond, went to Elmo in 1925 to scout the area and to see if another expedition was warranted given the success experienced by Dunbar for Yale. They found enough specimens at the site to set plans in place for the following year. Carpenter and two graduate students spent 6 months and collected about 2,400 specimens, bringing the total for Elmo to 6,400 fossil insect specimens in the Sellards, Yale, and Harvard collections.

In 1927, Carpenter traveled to Austin, Texas to study Sellards' type specimens. The following year, Sellards sent the remainder of his collection to Carpenter at Harvard. In 1932 Carpenter returned to the Elmo site on a trip to the central and western United States fossil sites, "...where about two thousand specimens were obtained, bringing the total number of insects in the Harvard collection from this locality to some forty-three hundred" (Ref. 9). This brought the total for the Elmo site in all collections together at that time to 8300 specimens.

In 1939 Carpenter wrote about his 1935 collecting trip to Elmo, where he " . . . secured several thousand more insects for the Museum of Comparative Zoology. The Museum collection from this formation now exceeds eight thousand specimens" (Ref 11). D. A. Wilbur of Kansas State University reported (Ref. 69) that from 1928 through 1976 he had collected about 2,800 specimens which, when he retired, he deposited with Carpenter at the Harvard Museum of Comparative Zoology. This brings the total for Elmo, all collections, to an incredible 14,800+.

Carpenter's publications on the Elmo Permian insects spanned sixty years, commencing in 1926 and ending in 1987 (Refs. 3-12, 14-17, 19-22). They were definitive and comprehensive, and went far toward clarifying understanding of the Permian insect fauna.

Carpenter studied fossil insects from around the world and from many geological eras. His encyclopedic knowledge of the fossil insects as a whole is evident in his sole authorship of the monumental two volumes of the Treatise on Invertebrate Paleontology devoted to insects (Ref. 19). But it was with the Elmo Permian insects that he began his career, and they form a vital and important body of his work, one he always hoped to get back to. As he stated during a 1992 interview, "The fact of the matter is, I haven't even yet had a chance to study all the specimens collected there" (L. Brosius, 1999, personal communication).

THE INSECTS

Nearly all of the fossils taken from the Kansas formations were of winged insects (Subclass Pterygota). However, one primitively unwinged insect fossil (Subclass Apterygota) was described in 1978. Two subdivisions are often used by paleontologists to further differentiate the winged insects: The Palaeoptera (literally ancient-winged) and Neoptera (modern-winged). The Neoptera can fold their wings down flat against the dorsal surface of their abdomen (like the bees, beetles, and flies of today). Most of the paleopterous insects had to hold their wings out at right angles to the body (like the dragonflies or the mayflies), although one order (the Diaphanopterodea) did have a simpler mechanism that allowed them to fold their wings back in a similar manner to the Neoptera.

Checklist of Permian Insects of Elmo, Kansas:

Compiled by Roy J. Beckemeyer. This list contains only the most recent names. Many of the species names used in the literature were later synonymized. Contact the author for a version of this list containing all synonyms. Higher order taxonomy is per Ref. 19.

Key:
No indentation: **Order (Higher taxon) Eras.** Notes:
One tab: Suborder;
Two tabs: Family Author Date described;
Four tabs: Genus Author Date described;
Six tabs: species Author Date described.

Archaeognatha (Apterygota) U.Carb.-Hol. The bristletails are primitive wingless insects with a long "caudal process" or tail, but without cerci. The thoracic segments look very much like the abdominal segments dorsally. One family, 1 genus, 1 species.

Dasyleptidae Sharov 1957
Lepidodasypus Durden 1978
sharovi Durden 1978 (Fig. 7)

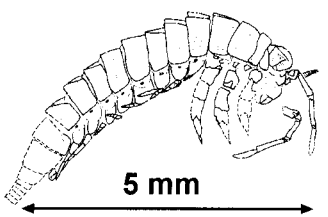


Fig. 7. *L. sharovi* after Durden 1978 (Ref. 25)

Ephemeroptera (Pterygota: Palaeoptera) U.Carb.-Hol. Mayflies are aquatic insects. This is the only palaeopterous order that has existed from the Upper Carboniferous to the present. Current adult mayflies do not have functional mouthparts and do not eat; fossil mayfly adults had chewing mouthparts. The hind wings of modern forms are reduced or absent; in fossil forms the fore and hind wings are almost the same size. Two families, 2 genera, 8 species.

Misthodotidae Tillyard 1932
Misthodotes Sellards 1909
obtusus (Sellards) 1909 (*Dromeus*)
biguttatus Tillyard 1932
ovatus Tillyard 1932
Protereismatidae Lameere 1917
Protereisma Sellards 1907
permianum Sellards 1907 (Fig's. 8, 20)

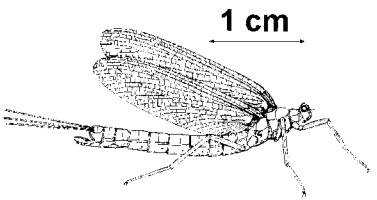


Fig. 8. *P. permianum* after Tillyard, 1932 (Ref. 62)

elongatum (Sellards) 1907 (*Bantiska*)
arcuatum (Sellards) 1907 (*Rekter*)
latum Sellards 1907
insigne Tillyard 1932

Palaeodictyoptera (Pterygota: Palaeoptera) U.Carb.-Perm. These insects had winglets on their prothorax. They held their wings open much like modern dragonflies. They had sucking mouthparts as did the next two orders, Megasecoptera and Diaphonopterodea, which together with the Palaeodictyoptera make up the palaeodictyopterid group. It is thought that these insects fed on plant juices or on the semi-liquid endosperm of Paleozoic plants. Three families, 4 genera, 4 species.

Calvertiellidae Martynov 1931
Calvertiella Tillyard 1925
permiana Tillyard 1925
Elmoboriidae Carpenter 1976
Elmoboria Carpenter 1976
piperi Carpenter 1976
Spilapteridae Handlirsch 1906
Dunbaria Tillyard in Dunbar & Tillyard 1924
fasciipennis Tillyard in Dunbar & Tillyard 1924
(Pictured on front & back covers.)
Uncertain Family
Kansasia Tillyard 1937
pulchra Tillyard 1937

Megasecoptera (Pterygota: Palaeoptera) U.Carb.-Perm. A group very similar to the previous order, but with the fore and hind wings nearly equal in size, and noticeably long and slender. Wing bases often very slender and reminiscent of those of modern damselflies. One family, 2 genera, 5 species.

Protohymenidae Tillyard 1924
Protohymen Tillyard 1924
permianus Tillyard 1924
(Photo on back cover)
elongatus Carpenter 1930
readi Carpenter 1933 (Fig. 9)
tenuis Carpenter 1938

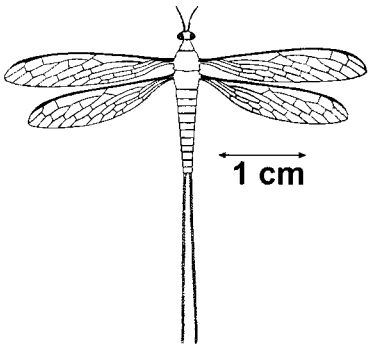


Fig. 9. *P. readi* after Carpenter 1933 (Ref. 9)

Permohymen Tillyard 1924
schucherti Tillyard 1924

Diaphanopterodea (Pterygota: Palaeoptera) U.Carb.-Perm. Similar to the previous order, but have the ability to fold their wings back along the abdomen. Three families, 3 genera, 6 species.

Asthenohymenidae Tillyard 1924
Asthenohymen Tillyard 1924
dunbari Tillyard 1924 (Fig. 10)

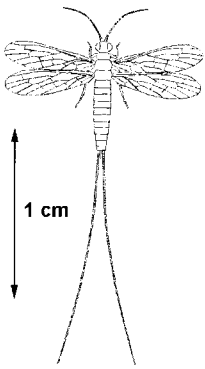


Fig. 10. *A. dunbari* after Carpenter 1939 (Ref. 11)

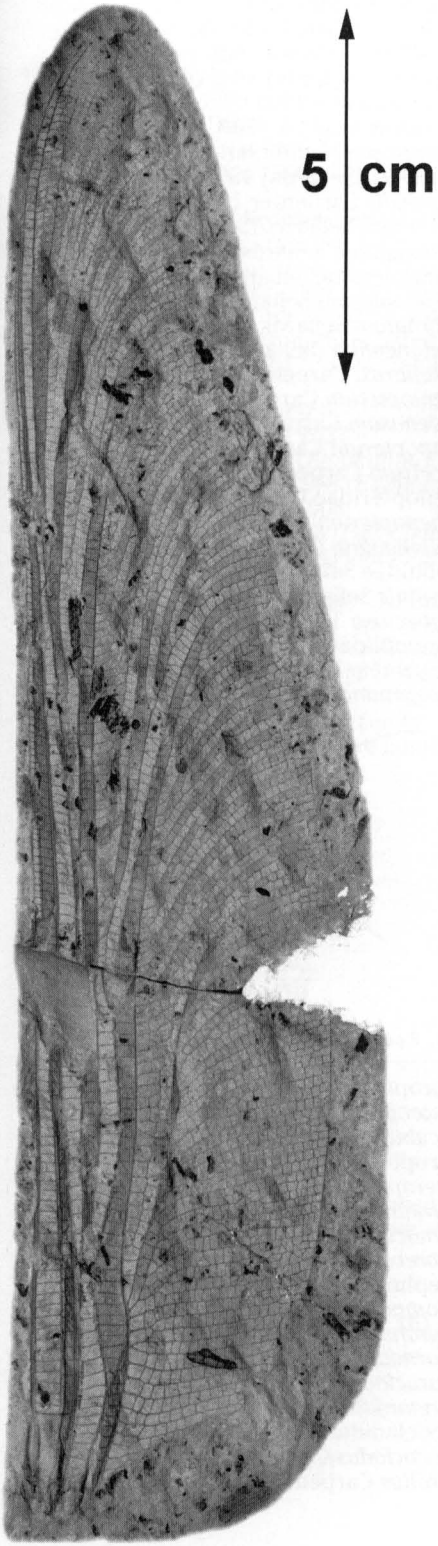
affinis Tillyard 1926
pusillus Tillyard 1926
Elmoidae Tillyard 1937
Elmoa Tillyard 1937
trisecta Tillyard 1937
Martynoviidae Tillyard 1932
Martynovia Tillyard 1932
insignis Tillyard 1932
protohymeniodes(Tillyard) 1932 (*Martynoviella*)

Protodonata (Pterygota: Palaeoptera) U.Carb.-Perm. These dragonfly-like insects were usually large and occasionally gigantic in size. The largest insect known is from Elmo: *Meganeuropsis permiana* is estimated to have had a wingspan of nearly 29 inches. It was likely at the upper limits of size for which tracheal respiration could supply enough oxygen to its flight muscles; it probably also had the ability to actively control its thoracic temperature, making it one of the first endotherms (Ref. 33). Protodonata ruled the Permian skies, preying on flying and perching insects. Probably aquatic as are the Odonata of today. Two families, 4 genera, 7 species.

Meganeuridae Handlirsch 1906
Meganeuropsis Carpenter 1939
permiana Carpenter 1939
Megatypus Tillyard 1925
schucherti Tillyard 1925 (Fig. 11)
ingentissimus Tillyard 1925
Tupus Sellards 1906
permianus Sellards 1906
readi Carpenter 1933
vetustus (Carpenter) 1933 (*Megatypus*)
Paralogidae Handlirsch 1906
Oligotypus Carpenter 1931
tillyardi Carpenter 1931

Fig. 11, (Opposite) A full-sized image of a hind(wing of *Megatypus schucherti* Tillyard 1924. This fossil is in the Kansas State University Entomology Dept. collection. Scanned by Roy Beckemeyer with the permission of Dr. Ralph Charlton of KSU. This 19.5 cm wing, found by two KSU entomology students, Otto Wenger and Floyd Holmes in 1939, is one of the most complete Protodonata wings ever found – nearly all the venation is clear and well-preserved.

Odonata (Pterygota: Palaeoptera) Perm.-Hol. Dragonflies and damselflies quite similar to modern forms were present in the Elmo fauna. Like the protodonates, the odonates were predaceous. It is possible that their generally smaller size was helpful in their survival to modern times. It has been postulated (Ref. 26) that an increase in atmospheric oxygen level to about 35% during the Carboniferous and Permian supported the development of very large flying insects



and that the decrease in oxygen level at the end of the Permian contributed to their extinction. Two families, 4 genera, 7 species.

Archisozygoptera Handlirsch 1906
Kennedyidae Tillyard 1925
Kennedya Tillyard 1925
mirabilis Tillyard 1925 (Fig. 12)
tillyardi Carpenter 1939
reducta Capenter 1939
Progoneura Carpenter 1931

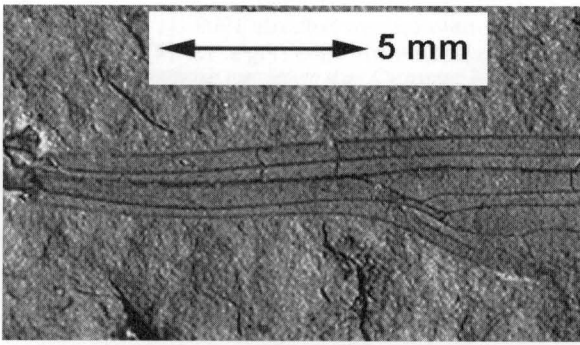


Fig. 12. *K. mirabilis* Tillyard 1925, Peabody Museum specimen No. 5006a, Collector: C.O. Dunbar, 1921. Basal portion of hind wing. Photo courtesy of Yale University.

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minuta Carpenter 1931
Protanisoptera Carpenter 1931
Ditaxineuridae Tillyard 1926
Ditaxineura Tillyard 1926
anomalostigma Tillyard 1926
celulosa Carpenter 1933
Uncertain Suborder
Uncertain Family
Campotaxineura Tillyard 1937
ephialtes Tillyard 1937

Uncertain Order (Pterygota: Palaeoptera)
One genus, 1 species.
Uncertain Family
Permoneura Carpenter 1931
lameerei Carpenter 1931

Protorthoptera (Pterygota: Neoptera: Exopterygota) U.Carb.-Trias. This is a large group of orthopteroid insects that dominated the entomofauna of the Paleozoic and is the most common order found at Elmo. Many of the taxa (especially the family Lemmatophoridae) are obviously related to today's stoneflies (Order Plecoptera) and were probably aquatic in their immature stages. There are many species for which even body parts were well preserved. Thirteen families, 24 genera, 34 species.

Blattinopsidae Bolton 1925
Blattinopsis Giebel 1867
kukalovae Carpenter 1966
Glaphyrophlebia Handlirsch 1906
speciosa (Sellards) 1909 (*Sindon*)
ovata (Sellards) 1909 (*Pursa*)

Chelopteridae Carpenter 1950
Chelopterum Carpenter 1950
peregrinum Carpenter 1950
Demopteridae Carpenter 1950
Demopterum Carpenter 1950
gracile Carpenter 1950
Heteroptilidae Carpenter 1976
Heteroptilon Carpenter 1976
costale Carpenter 1976
Lemmatophoridae Sellards 1909
Lemmatophora Sellards 1909
typa Sellards 1909 (Fig's. 13, 14)

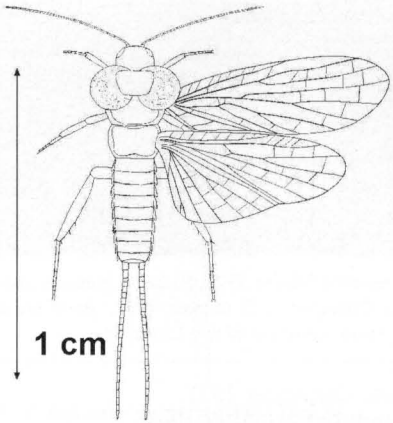


Figure 13. *L. typa* after Carpenter 1935 (Ref. 10)

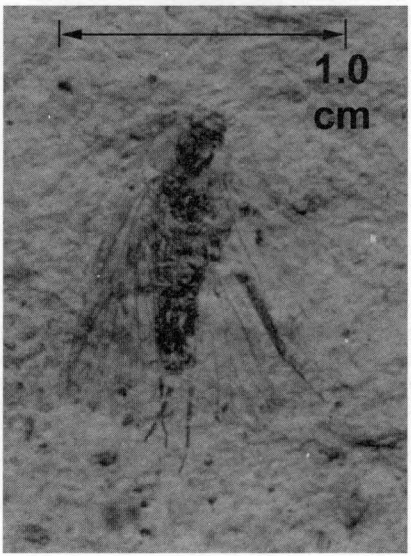


Fig. 14. *L. typa* fossil from teaching collection of Prof. George Byers of the University of Kansas. Fossil identified and image scanned by Roy Beckemeyer, Oct. 1999.

Artinska Sellards 1909
clara Sellards 1909
sellardsi Tillyard 1928
ovata (Sellards) 1909 (*Orta*)
Lisca Sellards 1909
minuta Sellards 1909
Paraprisca Handlirsch 1919
fragilis (Sellards) 1909 (*Prisca*)
grandis Carpenter 1935
Lecorium Sellards 1909
elongatum Sellards 1909
Liomopteridae Sellards 1909
Liomopterum Sellards 1909
ornatum Sellards 1909
elongatum (Sellards) 1909 (*Horates*)
sellardsi Carpenter 1950
Semopterum Carpenter 1950
venosum Carpenter 1950
Tapopterum Carpenter 1950
celsum Carpenter 1950
Phenopteridae Carpenter 1950
Phenopterum Carpenter 1950
elongatum (Sellards) 1909 (Lepium)
Probnidae Sellards 1909
Probnis Sellards 1909
speciosa Tillyard 1939
Protembiidae Tillyard 1937
Protembia Tillyard 1937
permiana Tillyard 1937 (Fig. 15)

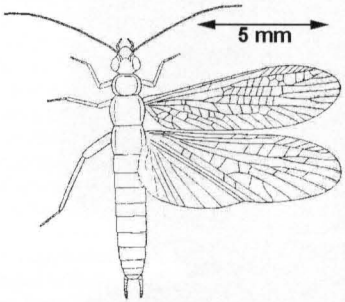


Fig. 15. *P. permiana* after Carpenter 1950 (Ref. 14)

Psoropteridae Carpenter 1976
Psoroptera Carpenter 1976
cubitalia Carpenter 1976
Steropteridae Carpenter 1950
Steropterum Carpenter 1950
rotundum Carpenter 1950
maculosum Carpenter 1966
breve Carpenter 1966
Strephocladidae Martynov 1938
Homocladus Carpenter 1966
grandis Carpenter 1966
ornatus Carpenter 1966
Paracladus Carpenter 1966
retardatus Carpenter 1966
Tococladidae Carpenter 1966
Tococladus Carpenter 1966
rallus Carpenter 1966

Opisthocladius Carpenter 1976
arcuatus Carpenter 1976
strictus Carpenter 1976
Uncertain Family
Atava Sellards 1909
ovata Sellards 1909
Lecopterum Sellards 1909
delicosum Sellards 1909

Blattaria (Pterygota: Neoptera: Exopterygota) U.Carb.-Hol. The cockroaches were one of the largest orders of insects in the late Paleozoic. Carpenter (Ref. 19) did not revise the nomenclature for this order in his Treatise, so the taxonomy is listed here as defined by Tillyard. One family, 2 genera, 4 species.

Spiloblattinidae Handlirsch
Permoblattina Tillyard 1937
curta (Sellards) 1908 (*Etoblattina*)
permiana (Sellards) 1908 (*Etoblattina*)
Pycnoblattina Sellards 1908
compacta (Sellards) 1908 (*Puknoblattina*)
curvata (Sellards) 1908 (*Puknoblattina*)

Protelytroptera (Pterygota: Neoptera: Exoptery-gota) Perm.-Cret. An order of small insects that are related to cockroaches and are ancestral to modern earwigs (Order Dermaptera). The front wings, called elytra, are actually hard covers like those of beetles. Five families, 9 genera, 15 species.

Archelytridae Carpenter 1933
Archelytron Carpenter 1933
superbum Carpenter 1933
Elytroneuridae Carpenter 1933
Elytroneura Carpenter 1933
permiana Carpenter 1933
Megelytridae Carpenter 1933
Megelytron Tillyard 1931
robustum Tillyard 1931
Permelytridae Tillayrd 1931
Permelytron Tillyard 1931
schucherti Tillyard 1931
Blattelytron Tillyard 1931
permianum Tillyard 1931
Parablattelytron Tillyard 1931
subincisum Tillyard 1931
rectum Tillyard 1937
elongatum (Tillyard) 1931 (*Acosmelytron*)
delicatum (Tillyard) 1931 (*Acosmelytron*)
latum Carpenter 1937
Protelytridae Tillyard 1931
Protelytron Tillyard 1931
permianum Tillyard 1931 (Fig. 16)
angustum Carpenter 1933
furcatum Carpenter 1939
Permelytropsis Carpenter 1933
cubitalis Carpenter 1933
Uncertain Family
Protelytropsis Tillayrd 1931
grandis Tillyard 1931

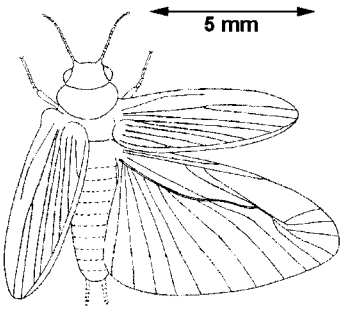


Fig. 16. *Protelytron permianum* after Carpenter & Kukalova, 1964 (Ref. 21)

Orthoptera (Pterygota: Neoptera: Exopterygota) U.Carb.-Hol. Carpenter placed in this order only the fossils of saltatorial, or leaping, insects similar to our grasshoppers. Four families, 5 genera, 7 species.

Oedischiidae Handlirsch 1906
Paroedischia Carpenter 1966
rectu Carpenter 1966
maculata Carpenter 1966
Permelcanidae Sharov 1962
Promartynovia Tillyard 1937
venicosta Tillyard 1937
Anelcanidae Carpenter 1987
Anelcana Carpenter 1987
dilatata (Carpenter) 1966 (*Parelcana*)
Petrelcana Carpenter 1966
elongata Carpenter 1966
Permoraphididae Tillyard 1932
Permoraphidia Tillyard 1932
americana Tillyard 1932
grandis Carpenter 1943

Psocoptera (Pterygota: Neoptera: Exopterygota) Perm.-Hol. Psocids are still found today and are called bark lice or book lice. They are diminutive insects with large heads, prominent eyes, and chewing mouthparts. Three families, 7 genera, 12 species.

Psocidiidae Tillyard 1926
Dichentotum Tillyard 1926
tinctum Tillyard 1926 (Fig. 17)
minimum (Tillyard) 1926 (*Psocidium*)
latum Carpenter 1932
parvulum Carpenter 1932
grande Carpenter 1933
Permopsocidae Tillyard 1926
Prognopsocus Tillyard 1926
permianus Tillyard 1926
Permopsocus Tillyard 1926
latipennis Tillyard 1926
ovatus Carpenter 1939
Lithopsocidium Carpenter 1932

permianum Carpenter 1932
Orthopsocus Carpenter 1932
simgularis Carpenter 1932
Lophioneuridae Tillyard 1921
Cyphoneura Carpenter 1932
permiana Carpenter 1932
Cyphoneurodes Becker-Migsisova 1953
reducta (Carpenter) 1932 (*Cyphoneura*)

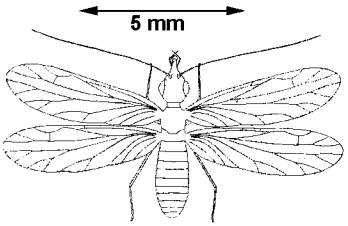


Figure 17. *D. tinctum* after Carpenter 1933 (Ref. 9)

Caloneurodea (Pterygota: Neoptera: Exoptery-gota) U.Carb.-Perm. Considered to be related to the Protorthoptera, but the latter have different fore and hind wings, while the wings of Caloneurodea are similar. Chewing mouthparts and long, slender antennae. Five families, 5 genera, 6 species.
Anomalogrammatidae Carpenter 1943
Anomalogramma Carpenter 1943
parvum Carpenter 1943
Apisdoneuridae Carpenter 1961
Apisdoneura Carpenter 1943
flexa Carpenter 1943
Paleuthygrammatidae Carpenter 1943
Paleuthygramma Martynov 1930
acutum Carpenter 1943
Permobiellidae Tillyard 1937
Permobiella Tillyard 1937
perspicua Tillyard 1937
Pleisiogrammatidae Carpenter 1943
Pleisiogramma Carpenter 1943
mediale Carpenter 1943
reducta Carpenter 1943

Miomoptera (Pterygota: Neoptera: Exopterygota) U.Carb.-Perm. Small to very small insects with biting mouthparts, short cerci, and nearly identical fore and hind wings. Little is known of the bodies of species of this order. One family, 1 genus, 4 species.
Palaeomanteidae Handlirsch 1906
Palaeomantis Handlirsch 1904
minutum (Sellards) 1904 (*Delopterum*)
elongates (Sellards) 1909 (*Delopsocus*)
latus (Sellards) 1909 (*Delopsocus*)
kansasum (Carpenter) 1939 (*Delopterum*)

Hemiptera (Pterygota: Neoptera: Exopterygota) Perm.-Hol. The Elmo Permian Hemiptera: Homoptera were mostly small. Like today's Homoptera (cicadas, plant hoppers, etc.), the Permian forms had sucking mouthparts. One family, 4 genera, 10 species.
Homoptera Leach 1815
Archescytinidae Tillyard 1926
Archysctina Tillyard 1926
permiana Tillyard 1926
muiri (Tillyard) 1926 (Permoscytina)
Permoscytina Tillyard 1926
kansasensis Tillyard 1926
Permopsylla Tillyard 1926
americana Tillyard 1926
cubitalis (Carpenter) 1933 (*Lithoscytina*)
grandis Carpenter 1933
anomala Carpenter 1933
minuta Carpenter 1931
permiana Carpenter 1931
Paleoscytina Carpenter 1931
brevistigma Carpenter 1931

Glosselytrodea (Pterygota: Neoptera: Endoptery-gota) Perm.-Jur. Although the body structure of this order is very poorly known, Carpenter considers these small insects to be Endopterygota, i.e. insects with complete metamorphosis. This is because the wings have traits that are found in the endopterygote Order Neuroptera: rows of setae on the wing veins, cross veins, and wing margins, and the position of the wings at rest. One family, 1 genus, 1 species.
Permoberothidae Tillyard 1932
Permoberotha Tillyard 1932
villosa Tillyard 1932

Mecoptera (Pterygota: Neoptera: Endopterygota) Perm.-Hol. Small to medium-sized insects with a long, beaklike face. They have chewing mouthparts. Modern forms are predaceous or eat dead insects. Modern Mecoptera are often found in wooded areas. Called scorpionflies because of upturned genitalia of males of the modern family Panorpidae, which resemble the tails of scorpions. Four families, 6 genera, 8 species.
Permopanorpidae Tillyard 1926
Permopanorpa Tillyard 1926
formosa Tillyard 1926
inaequalis Tillyard 1926 (See Fig. 18)
schucherti Tillyard 1926
Permochoristidae Tillyard 1918
Protochorista Tillyard 1926
tetraclada Tillyard 1926
Protopanorpa Tillyard 1926
permiana Tillyard 1926
Agetopanorpidae Carpenter 1930
Agetopanorpa Carpenter 1930
maculata Carpenter 1930
Lithopanorpidae Carpenter 1930
Lithopanorpa Carpenter 1930
pusilla (Tillyard) 1926 (*Protopanorpa*)

Uncertain Family
Anormochorista Tillyard 1926
oligoclada Tillyard 1926

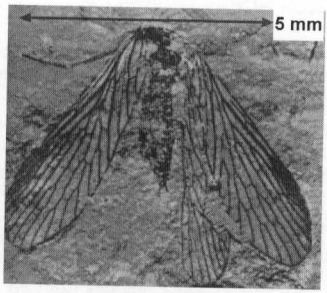


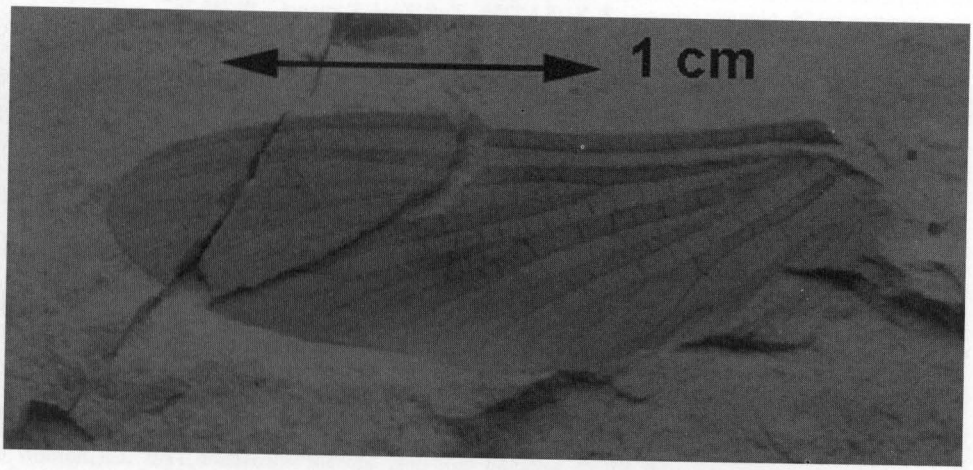
Fig. 18. *P. inaequalis* from Carpenter 1930 (Ref. 4)

Uncertain Order (Pterygota: Neoptera)
Eight genera, 9 species.
Uncertain Family
Apheloneura Carpenter 1976
minutissima Carpenter 1976
amplia Carpenter 1976
Choristosialis Tillyard 1932
enigmatica Tillyard 1932
Elmothone Carpenter 1976
martynovae Carpenter 1976
Gelasopteron Carpenter 1976
gracile Carpenter 1976
Nugioneura Tillyard 1937
problematica Tillyard 1937
Permembia Tillyard 1928
delicatula Tillyard 1928
Platychorista Tillyard 1926
venosa Tillyard 1926
Trachopteryx Carpenter 1976
martynovi Carpenter 1976

Numbers of taxa known from Elmo:
Apterygota: 1 Order, 1 Family, 1 Genus, 1 Species
Palaeoptera: 6 Orders, 13 Families, 20 Genera, 38 Species
Neoptera: 10 Orders, 38 Families, 72 Genera, 110 Species
Total: 17 Orders, 52 families, 93 Genera, 149 Species

(left) Fig. 19. Frank M. Carpenter working at the Elmo site in 1927. On a good day he and his team would find fifty fossil specimens. Photo courtesy of Liz Brosius, Kansas Geological Survey

(below) Fig. 20. Ephemeroptera: Protereismatidae: *Protereisma permiana* Sellards 1907. A mayfly hind wing. scanned by Roy Beckemeyer, October 1999. Fossil is in the teaching collection of George Byers, Emeritus Professor, University of Kansas.



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(Above) *Protohymen permianus* Tillyard 1924. Wing is 11 mm long. From an extinct insect order, Megasecoptera. The wing venation is remarkably well-preserved, as is that of many of the Elmo insect fossils. Often wings, since they are relatively durable, are the only part of insects found as fossils.

(Right) *Dunbaria fasciipennis* Tillyard 1924. The counterpart to the fossil on the front cover. When the rock layer was split, these two fossils were on the respective halves of the rock. From an extinct insect order, Palaeodictyptera. Wingspan 36 to 37 mm. These insects lived in the Permian Period about 260 million years ago. The pictures on the front and back covers are from the original glass plate negatives used to illustrate the type descriptions by R.J. Tillyard in 1924, and are provided courtesy of The Cawthron Institute, Nelson, New Zealand.