No. 1.— *The Parasitic Hymenoptera of the Tertiary of Florissant, Colorado.*

By Charles T. Brues.

The present paper is based upon studies on the parasitic Hymenoptera contained in the very extensive collection of fossil insects made many years ago by Dr. Samuel H. Scudder at Florissant, Colorado, and now contained in the Museum of Comparative Zoölogy. In addition, Prof. T. D. A. Cockerell has sent me much material from the same locality obtained by expeditions under his charge during the summers of 1907 and 1908, most of this second series belonging to the American Museum of Natural History. In all I have had the opportunity to examine over 700 well-preserved specimens of insects belonging to this group, among which there are 112 clearly defined species which are described on the following pages. Adding to these the 13 species previously described by Professor Cockerell and the present writer, the total number so far found at Florissant is 125.

The very large number of species of parasitic Hymenoptera represented at Florissant shows it to be by far the richest locality in the world for these insects, as it has already been found to be by Scudder for many other groups. This is shown in the following table which gives a comparison between the several important places where fossil parasitic Hymenoptera have been found.

Number of Tertiary species of parasitic Hymenoptera found in various localities.

Horizon	Locality	Proctotrypoidea	Cynipoidea	Chalcidoidea	Ichneumonidae	Braconidae	Evaniidae	Stephanidae	Totals
Miocene	Florissant	5	3	15	76	23	2	1	125
Upper Miocene	Oeningen	0	0	1	6	0	0	0	7
Lower Miocene	Radoboj	0	0	0	5	0	0	0	5
Lower Oligocene	Baltic Amber	1	3	12	15	6	2	0	39
Lower Oligocene	Aix, France	0	0	1	9	2	0	0	12

With the exception of a single genus and species (Ephialtites) from the Upper Jurassic, no parasitic Hymenoptera are known before the Tertiary. However, the quite typical character of Ephialtites, and the abundance in which the group appears in deposits of Lower Oligocene age show that it must have been clearly differentiated and well developed at least before the beginning of the Tertiary. The discovery of Ephialtites in rocks so much older than those in which other of the higher Hymenoptera have been found has led Handlirsch to derive both the parasitic and aculeate Hymenoptera from this type. In this I cannot agree with him and strongly suspect that the greater antiquity of Ephialtites, if it be a truly ichneumonoid form, must be only apparent, and due to our very imperfect knowledge of the earlier fossil insects. However this may be, we know from the Oligocene and Miocene an extremely large fauna which must of course represent only a small fragment of what actually existed. It will be seen from the taxonomic part of this paper that many species are known only from single specimens, which agrees well with what we find in collections of recent species belonging to this group, and evidences not only their very general occurrence but their high degree of differentiation into numerous closely allied species.

The beautiful preservation of most of the Florissant species makes it possible to refer the great majority of them to living genera with a considerable degree of certainty — that is of course speaking of recent genera in the wide sense as used by the older writers. In some cases it has been possible to place species with still greater certainty, and in these cases the name of the more modern subdivision or genus in the restricted sense has been employed. Even in the case of specimens too poorly preserved to describe, I have rarely been in doubt as to the family to which they should be referred, and well-preserved specimens are usually easily placed in the subfamilies and genera if one is familiar with the details of structure in modern forms, and willing to scrutinize the fossils with great care. This last is extremely important for one is often badly deceived at first sight by obliterated or unduly prominent structures.

On the whole, the wings are the most important characters to be studied. They are usually well preserved, generally lying between the laminae of the shale where it splits in exposing the specimen. Very few specimens show well-preserved legs, although the hind femora and tibiae often show quite prominently. As a rule the specimens can be studied advantageously under a rather strong magnification, and most of those which I have described were examined under a

compound microscope with two-thirds objective and two inch eye-piece.

Since many of the details are indicated by color rather than surface structure, it is necessary to examine both by obliquely reflected light and by as nearly vertical illumination as possible. The latter can be obtained either by using an objective furnished with a prism for vertical illumination, or by placing on the stage of the microscope around the specimen, the rim of a deep pillbox from which the bottom has been removed. This simple device shuts off all very oblique light and renders visible wing venation and other characters which are otherwise often very difficult to make out.

One of the most remarkable facts connected with the preservation of the Florissant insects is the apparent fidelity with which colors are usually preserved or indicated. It is not so difficult to understand the preservation of metallic colors which are dependent upon physical structure, but the distinction between red, black, and yellow is usually also retained as well as the difference between hyaline and infuscated wings. This is proven beyond all doubt by the similar color of different specimens belonging to the same species, and the general color tendencies of fossil species as compared with those of recent related forms. In a small proportion of the specimens carbonization has proceeded to the point of blackening the entire specimen but this is unusual. There is probably no doubt that a part of the color differentiation both in recent and fossil insects of these groups is dependent upon the thickness of the chitin covering the different parts of the body, and it is much easier to see how this may have been preserved than to understand the retention of actual pigment colors or their proper representation. The peculiar method of entombment of these fossils must be, I think, in great part responsible for this. The volcanic ash of which the matrix was formed, was evidently very fine, and its similarity to cement rock has led me to believe that the rapidity with which it originally hardened must have been very great. This would account in great measure for the failure of the chitin to macerate as it will do in the presence of much water, and perhaps also for the presence of pigment. In his Tertiary Insects ('90, p. 24) Scudder quotes Dr. M. E. Wadsworth who examined specimens of these insect-bearing shales, to the effect that they probably originated from a moya, or mudflow which was rapidly deposited in the shallow waters of the Florissant lake without any preliminary erosion. That the deposition and hardening of the shales was unusually rapid seems to me undoubted, for in no other way can I account for the presence of

pigmental colors and the preservation of microscopic structures like wing hairs with such wonderful perfection.

The distribution of the Miocene parasitic Hymenoptera among the various groups is very interesting and I have attempted to represent graphically in the accompanying diagram (Plate 1) the comparative abundance of the several families and smaller groups during Recent, Miocene, and Oligocene times. In order to make the diagram more easily understood, the comparative numbers and not the actual ones are shown by the width of the black lines for each period since the numbers of species known vary much in proportion for the three periods.[1]

Only one family, the Ichneumonidae, was proportionately more abundant in Miocene times than at present and its abundance was caused entirely by the occurrence of a much larger number of species in two of its subfamilies, the Ophioninae and Pimplinae; the other three subfamilies, Ichneumoninae, Cryptinae, and Tryphoninae were about as well represented then as now. The Braconidae appear to have become less numerous, and I believe the change has been even greater than is shown by the diagram, since fossil Braconidae are usually more poorly preserved than the Ichneumonidae, due probably to their softer bodies and wings. The Evaniidae appear to have become less abundant in recent times, but this may possibly be due to the small number of species on which the calculation is based. The Chalcidoidea (exclusive of the Mymaridae which are omitted on account of their disproportionate abundance in amber) seem to be on the ascendent, but the number of species of Proctotrypoidea and Cynipoidea is so small that they do not furnish a satisfactory basis for any deductions of this nature.

I have not been able to find much evidence bearing on the probable relationships of the Florissant fauna from a study of the Parasitic Hymenoptera. This is disappointing, but really to be expected, for the group, with minor exceptions, is very widely distributed at the present time and extremely similar the World over. A few points of interest may however be worthy of review. The occurrence of a fig insect shows a tropical element in the fauna, but only serves to strengthen the evidence offered by the presence of fossil fig leaves in the flora. Australian and South African affinities are suggested by

[1] I have used as a basis for the number of recent species, Cresson's Catalogue of North American Hymenoptera. It is now rather old, but I think the proportion of species to be placed in the several families has not changed materially since the time of its publication.

the occurrence of Leptobatopsis and Ormyrodes respectively, but these may have no general significance, and I do not believe that they have. The abundance of Ophioninae and Pimplinae, particularly of the former, would appear to be expressions of Neotropical tendencies, and I think they may quite probably be so.

The exact relationships of the present fauna of the United States and of that of Florissant during Miocene times can be traced in the accompanying table. The number of fossil species are contrasted with the number of recent species occurring in the United States (according to Cresson, 1888) and the third column of figures gives the proportionate number of species in the two faunae.

GROUP	Number of recent species in the U. S.	Number of fossil Florissant species	Proportionate number.
Proctotrypoidea	75	5	100:6.6
Cynipoidea	191	3	100:1.5
Chalcidoidea	413	15	100:3.6
Evaniidae	31	2	100:6.4
Ichneumonidae	1326	77	100:5.6
Ichneumoninae	343	13	100:3.8
Cryptinae	280	6	100:2.1
Pimplinae	211	17	100:8.0
Tryphoninae	249	13	100:5.2
Ophioninae	243	28	100:11.5
Alysiidae	40	2	100:5.0
Braconidae	292	19	100:6.5
Stephanidae	4	1	100:25.0

The designation of the special localities for certain of the species collected by Professor Cockerell's expeditions is in accordance with his numbers of stations as given in one of his recent papers (:07). The specimens in the Scudder collection have no indication of which specific localities or beds they were taken from, except that all were taken from the Florissant lake basin.

I wish to gratefully acknowledge the courtesy of the authorities of the Museum of Comparative Zoölogy for the loan of the Scudder collection and the assistance given by Professor Cockerell who first suggested to me the great interest attaching to the Florissant fauna, and who aided by the sending of much material. I am indebted to Dr. H. C. Bumpus and Mr. R. W. Miner of the American Museum

of Natural History for the fine figures of the types belonging to that institution, which they had made as illustrations.[1]

The task of working up the material has consumed much more time than I anticipated when I undertook it fully two years ago, due not only to many interruptions, but to the necessarily slow methods of studying and comparing the specimens which belong to a group unusually difficulty to classify. For these reasons the work has been very tedious but I hope that future students may not be misled into thinking it uninteresting. On the contrary, it is extremely fascinating.

BETHYLIDAE.

Handlirsch in his recent work (:07) on fossil insects records the presence of a species of this family in Baltic Amber and I have already figured (:06) a strange species from Florissant which most likely is a bethylid.

In the present series there is one very finely preserved species belonging to the genus Epyris.

Epyris deletus, sp. nov. (Fig. 1.)

Female. Length 5.5 mm. Black; the antennae brownish, except at the

Fig. 1.— Epyris deletus, sp. nov. Type.

base, and the abdomen brownish toward the tip. Head (as preserved) but slightly wider than long. Antennae of the typical attenuated form, stout basally and involute, the number of joints not ascertainable; those near the middle quadrate. Surface of head faintly shagreened. Prothorax about one-third longer than the mesonotum, which seen from the side is about as long as the metanotum. The latter carinate laterally, i. e. with a raised margin, its lateral angles rather prominent, quadrate. Abdomen slightly longer than the head and thorax together, seen from the side of the typical form or perhaps slightly more slender or elongate. Legs, except one of the anterior ones not preserved; this is very strongly incrassated, and

brownish yellow on the tibia and tarsus. Wings hyaline, with elongate,

[1] The manuscript of the present paper was completed before the writer severed his connection with the Milwaukee Public Museum, and he wishes to take this opportunity to thank Mr. H. L. Ward, the Director of the Museum, for the interest taken by him in the progress of the work.

narrow, fuscous stigma; two basal cells; marginal cell open, but the radial vein is very long, four or five times as long as the short basal vein; veins, except the costal, pale.

One specimen, No. A3, very nicely preserved in lateral aspect from Professor Cockerell's Station No. 17. Type in the Amer. Mus. Nat. Hist.

This is a very typical bethylid and is perhaps better referred to Mesitius than to Epyris. As however, Kieffer believes that the American recent species of Mesitius which this approaches in the short basal and long radial veins are not generically distinct from Epyris, I have placed it here. The scutellar fovea, which is the only character to distinguish the two genera as restricted by Ashmead does not show, and Kieffer restricts Mesitius to a group of species with the lateral angles of the metathorax produced, to which the present form certainly does not belong.

CERAPHRONIDAE.

A single species belonging to Ceraphron is recorded by Burmeister ('31) as occurring in Baltic Amber.

PROCTOTRYPIDAE.

This group as here restricted is for the first time recorded in the fossil state.

Proctotrypes exhumatus, sp. nov. (Fig. 2.)

Female. Length 5.5 mm. Black, the abdomen reddish except at the base and the tip of the terebra, the black extending farther back on the venter

Fig. 2.—Proctotrypes exhumatus, sp. nov. Portion of wing and profile of abdomen of type.

than on the dorsal surface, although the tips of the second and third segments appear to be blackened above. Antennae 13-jointed, the first flagellar joint

one and one-half times as long as the second; second and the ones immediately following between two and three times as long as thick. Head not thick anteroposteriorly. Metanotum and metapleurae irregularly rugose; the mesonotum without distinct parapsidal furrows. Base of second abdominal segment fluted along the sides; terebra a little shorter than the posterior tibia, the last abdominal segment being much extruded also. Spur of posterior tibia indistinctly preserved. Wings more or less infuscated toward the middle. Costal cell present; veins and stigma dark, marginal cell rather small, shorter than the stigma. This is a typical representative of the genus closely allied to the recent *P. caudatus* Say.

Six specimens.

Type.— No. 2055, M. C. Z., Florissant, Col. (No. 4391, S. H. Scudder Coll.). Other specimens, M. C. Z., Nos. 2056–2059, Nos. 845, 8389, 10894, 8111, S. H. Scudder Coll.); and A 97 from Professor Cockerell, the latter in the Amer. Mus. Nat. Hist.

The specimen from Professor Cockerell was collected by Mr. S. A. Rohwer at Station 13. M. C. Z., No. 2059 (No. 8111 S. H. Scudder Coll.) may not be the same species as the terebra and last abdominal segment are more strongly exserted and apparently longer.

BELYTIDAE.

This family is known fossil only at Florissant so far as I am aware, although some of the earlier references to Proctotrypidae may possibly be based on members of the present group. In addition to *Pantoclis deperdita* Brues (:06), I have the following:

Belyta mortuella, sp. nov. (Fig. 3.)

Male. Length 2.25 mm. Probably entirely dark colored, black or piceous, perhaps the legs and antennae a little lighter. Antennae as long or somewhat exceeding the body in length, filiform but rather stout, the extreme apex not preserved. Several joints before the middle of the flagellum subequal, each about four times as long as thick, those following to near the tip similar but somewhat shorter. Body shining, the mesonotum with deep and complete parapsidal furrows; metathorax carinated and quite distinctly areolated on the sides. The specimen is seen in

Fig. 3.— Belyta mortuella, sp. nov. Type.

lateral view and the absence or presence of a median carina cannot be made out. Abdomen nearly as long as the head and thorax together, the petiole nearly twice as long as thick, coarsely striated. Second segment very large, covering nearly the entire surface; entirely smooth, following all short, transverse-linear, together only about one-sixth the length of the second. Wings and legs not preserved.

One specimen, A32, collected by Mr. S. A. Rohwer at Station No. 14. Type in the Amer. Mus. Nat. Hist.

This is a typical belytid, not very readily assignable with assurance to any particular genus, and therefore left in Belyta, *sensu lato*.

DIAPRIIDAE.

Two genera, one of them new, are represented each by a single species in the present series from Florissant.

PARAMESIUS DEFECTUS, sp. nov. (Fig. 4.)

Female. Length 4–5 mm. Black; antennae at base and legs reddish brown. Antennae probably 13-jointed, gradually clavate, all of the flagellar joints however longer than wide. Thorax oval, rather long, the mesonotum with complete but rather delicate parapsidal furrows. Scutellum with a large, broad transverse median fovea at the base. Metathorax very short, with three longitudinal carinae. Abdomen rather short, twisted at the base in the type so that the petiole is not preserved; broadest just beyond the middle. Wings slightly, but distinctly infuscated; submarginal vein long, two-thirds the length of the wing, stigmated. Basal vein obsolete. Legs long and slender.

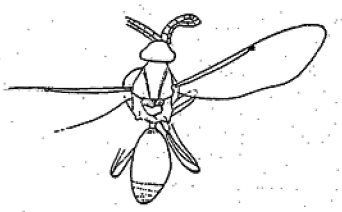

FIG. 4.— Paramesius defectus, sp. nov. Type.

One specimen.

Type.— No. 2061, M. C. Z., Florissant, Col. (No. 13,394, S. H. Scudder Coll.). The specimen is not well preserved, but undoubtedly is a member of this genus or of a very closely related one. The head of the type is peculiarly constricted, but I think this is undoubtedly due to the pressure of the matrix.

GALESIMORPHA, gen. nov.

Head produced as in Galesus, elongate. Wings with a submarginal vein distinct from the margin, ending in a stigma at one-half the length of the wing. Basal vein very distinct.

Type.— *G. wheeleri*, sp. nov.

This is very much like Galesus to which it appears to be more closely related than to any other genus so far described, but differs by its distinctly veined wings.

GALESIMORPHA WHEELERI, sp. nov. (Fig. 5.)

Female. Length 3.3 mm. Black, with the legs and antennae brownish. Head longer than wide when seen from above, the ledge above the antennae emarginate on each side of the middle which is produced as a tooth; just at

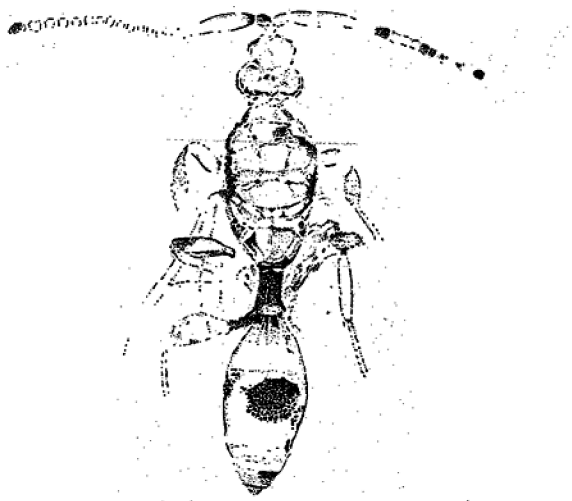

FIG. 5.— Galesimorpha wheeleri, sp. nov. Type.

the middle the head is strongly constricted. Mesonotum shining, convex, with two strong, complete parapsidal furrows distinctly convergent behind. Scutellum large, with a large fovea on each side at the middle, the two con-

nected by an impressed arcuate line which bows forward nearly to the base of the scutellum. Postscutellum with a pair of median foveae basally, a posterior impressed line and an oblique impressed line. Metathorax short, smooth, with three longitudinal carinae, the median one not furcate. Abdomen as long as the head and thorax together, rather slender; petiole one-third as long as the abdomen, longitudinally fluted. Second segment three times as long as the following together, less than one-half as broad as long and coarsely striated at its extreme base. Wings faintly infuscated; submarginal vein about one-half as long as the wing. Legs long and slender, clavate.

One specimen, beautifully preserved, No. A52, collected at Station 13 by Prof. W. M. Wheeler. Type in the Amer. Mus. Nat. Hist. In general appearance it is very much like a true Galesus.

FIGITIDAE.

The single species of this family in the present collection seems to be the first one discovered in the fossil state.

FIGITES SOLUS, sp. nov. (Fig. 6.)

Male. Length 2.7 mm. Probably entirely black, except metathorax, base of abdomen, and the legs which are rufous or dark reddish brown. Antennae dark brown, 13-jointed, slender, the club very slightly thickened, two-jointed, its second joint shorter and narrower than the first. First flagellar joint long, fully twice as long as the second which is equal to the pedicel; following to the club about equal, ovate in form. Thorax seen in latero-dorsal view, enough of the dorsum being visible to show the presence of parapsidal furrows, and the probable absence of a cupuliform shape to the scutellum. Abdomen subsessile, about as long as the head and thorax together, apparently not pubescent at the base, although this character may have been lost in the process of preservation. Legs rather stout for this group. Wings hyaline, the veins pale brown; radial cell apparently about two times as long as wide.

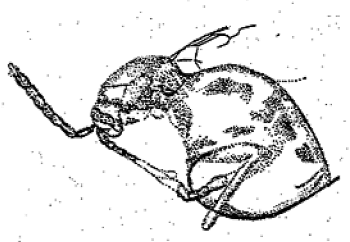

FIG. 6.— Figites solus, sp. nov. Type.

One specimen, A60 collected by Mr. S. A. Rohwer at Station 17. Type in the Amer. Mus. Nat. Hist.

Hormiopterus petrinus Scudder, Tertiary insects N. Amer., 1890, p. 608. (Ichneumon).

Oligocene; White River, Col.

STEPHANIDAE.

Protostephanus ashmeadi Cockerell, Bull. M. C. Z., 1906, 50, p. 57.

Miocene; Florissant, Col.

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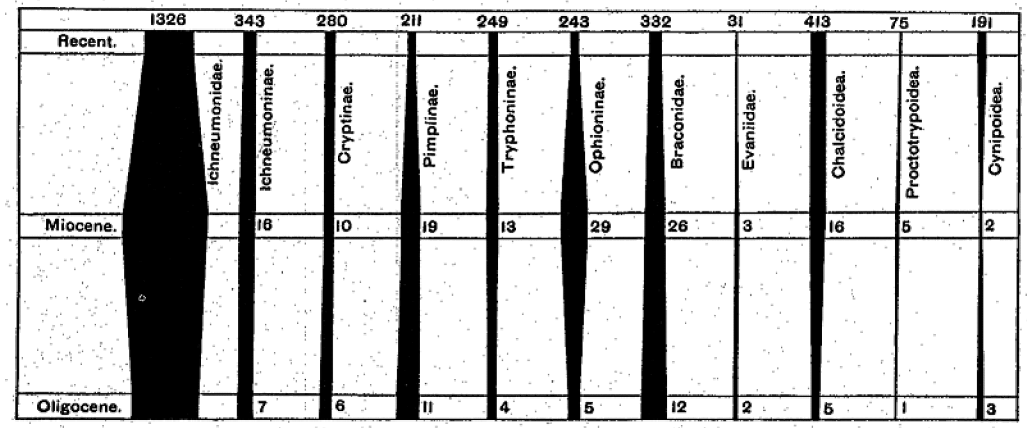

RELATIVE ABUNDANCE OF PARASITIC HYMENOPTERA IN RECENT, MIOCENE, AND OLIGOCENE TIMES.