BURROWING MAYFLIES OF OUR LARGER LAKES AND STREAMS : : : : By James G. Needham

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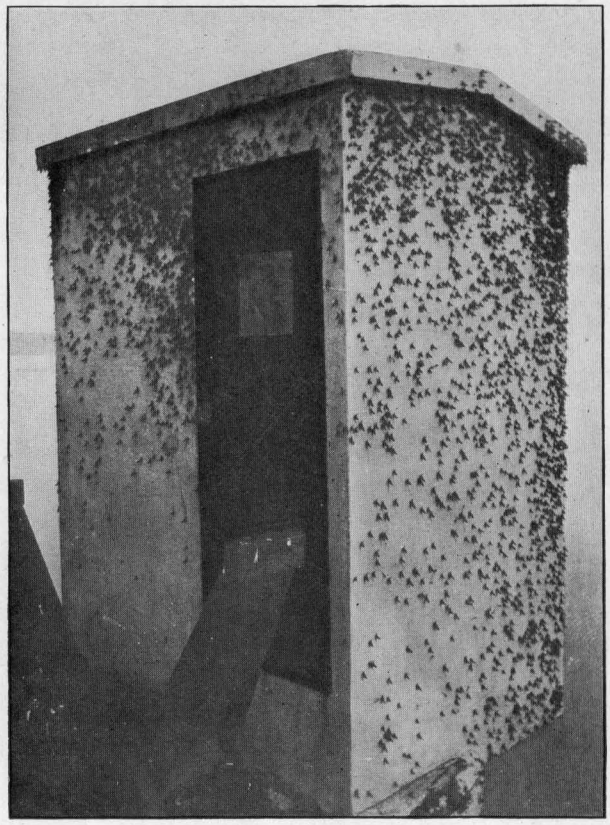

FIG. 1.

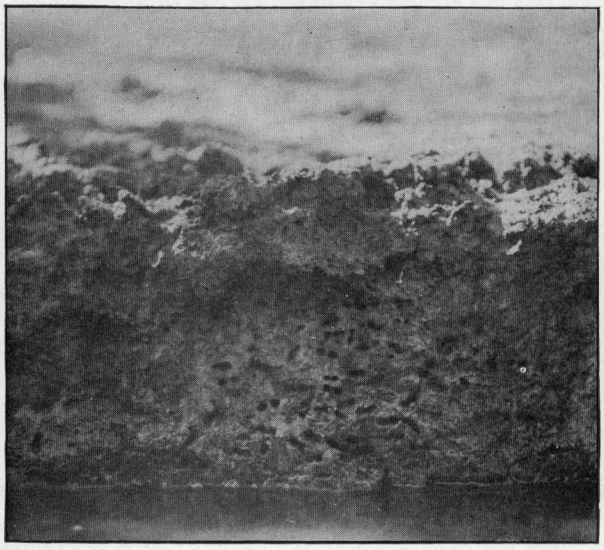

FIG. 2.

BURROWING MAYFLIES OF OUR LARGER LAKES AND STREAMS.

By James G. Needham,

Professor of Limnology, Cornell University.

INTRODUCTION.

In the beds of all our larger lakes and streams there exists a vast animal population, dependent, directly or indirectly, upon the rich organic food substances that are bestowed by gravity upon the bottom. Many fishes wander about over the bottom foraging. Many mollusks, heavily armored and slow, go pushing their way and leaving trails through the bottom sand and sediment. And many smaller animals burrow, some by digging their way like moles, as do the young of mayflies and of gomphine dragonflies; some by "worming" their way through the soil, as do the larvæ of crane flies and many oligochætes.

Among the burrowers none are more abundant or more important than the young of the mayflies. Indeed, there are hardly any aquatic organisms of greater economic value, for they are among the principal herbivores of the waters, and they are all choice food for fishes.

How abundant they are in all our large lakes and streams is well attested by the vast hordes of adults that appear in the air at the times of their annual swarming. They issue from the water mainly at night. They fly away to the banks and settle upon the shore vegetation. They cover the sides of buildings. They fly heedlessly into the faces of pedestrians. They settle upon the stream-side willows until their accumulated weight bends, and often breaks, the boughs. In the streets of riparian cities they fly to lights at night and fall beneath them in heaps upon the ground. Their bodies, crushed under the wheels of cars, render the rails slippery, sometimes impeding traffic. They feed a host of carnivores, terrestrial, aerial, and aquatic; indeed, many birds and fishes gormandize rather shockingly during their swarming season. And when those that have escaped both foes and casualties have conveyed their eggs back into their native waters, their bodies fall at last upon the surface and drift about. After the surfeited fishes can eat no more, the mayflies are blown into windrows upon the shores; or they drift in long lines that trail at the edges of the current in streams; or they gather in great masses and welter in the eddies. Sometimes they stop the river steamers by clogging the machinery. No dweller by the shores needs to be convinced of their abundance.

That they abound also far out from the shore is well attested by certain observations made by Commissioner Smith on Lake Erie nine years ago and later communicated in a letter. Dr. Smith wrote that, while making a cruise on a lighthouse tender which was visiting gas buoys in all parts of the lake, "Many of these buoys, especially

those toward the middle of the lake, had enormous quantities of dead mayflies on their flat surfaces. In several cases the mayflies formed a solid cake 6 or 8 inches deep, the result of one season's accumulation."

That they are also of prime importance as food for fishes has long been known. The anglers found it out first and used the soft bodies of the larger mayflies successfully for bait. Indeed, in view of the lack of acquaintance with our mayfly species existing at the present day, the many common names for them that were used by fishermen of old seems surprising. Such old-time books for anglers as Ronald's Fly-Fisher's Entomology (1877) abundantly attest this.

Food studies have everywhere demonstrated how generally the nymphs of these big, burrowing mayflies are eaten by fishes. Forbes's report (1888*b*) was one of the most extensive. He found that these larvæ constitute nearly one-tenth of all the food taken by the fishes that he studied. He says (pp. 484-485.):

> From the order Neuroptera fishes draw a larger part of their food than from any other single group. In fact nearly a fifth of the entire amount of food consumed by all the adult fishes examined by me consisted of aquatic larvæ of this order, the greater part of them larvæ of dayflies (Ephemeridæ), principally of the genus Hexagenia. These neuropterous larvæ were eaten especially by the miller's thumb, the sheepshead, the white and striped bass, the common perch, 13 species of the darters, both the black bass, 7 of the sunfishes, the rock bass and the croppies, the pirate perch, the brook silversides, the sticklebacks, the mud minnow, the top minnows, the gizzard shad, the toothed herring, 12 species each of the true minnow family and of the suckers and buffalo, 5 catfishes, the dogfish, and the shovelfish—70 species out of the 87 which I have studied.
>
> Among the above I found them the most important food of the white bass, the toothed herring, the shovelfish (51 per cent), and the croppies; while they made a fourth or more of the alimentary contents of the sheepshead (46 per cent), the darters, the pirate perch, the common sunfishes (Lepomis and Chænobryttus), the rock bass, the little pickerel, and the common sucker (36 per cent). * * *
>
> The larvæ of Hexagenia, one of the commonest of the "river flies," was by far the most important insect of this group, this alone amounting to about half of all the Neuroptera eaten. They made nearly one-half of the food of the shovelfish, more than one-tenth that of the sunfishes, and the principal food resource of half-grown sheepshead; but were rarely taken by the sucker family, and made only 5 per cent of the food of the catfish group.

Forbes's studies were made on such material as happened to be at hand, without regard to times or seasons or conditions under which the fishes he studied had obtained their food. Subsequent studies of the food of the shovel-nosed sturgeon have made it necessary to qualify his statement as regards that fish. Wagner (1908, p. 28) says:

> The food of Polyodon consists, in Lake Pepin, entirely of plankton material, in largest part of entomostraca, but not unmixed with algæ. There is one seeming, but only seeming, exception to this. Occasionally one finds the specimens of a morning's catch largely gorged with larvæ of Ephemerids. But in every such case it was found that ephemerid imagines appeared in vast numbers the same evening. It appears plain, therefore, that the larvæ taken by Polyodon were captured on their journey to the surface of the water.

Wagner (1908, p. 31) adds concerning the valuable rock sturgeon: "The food of this fish in Lake Pepin, in the summer at least, consists entirely of the larvæ of the Ephemerids;" but he does not specify what sort of mayflies.

Pearse (1915) records that 7 of the 16 species of small shore fishes studied by him at Madison, Wis., had eaten mayflies, the percentages of this sort of food averaging as high as 58.3 per cent in the largemouth black bass and 40 per cent in the bluegill sunfish. In regularity of consumption and in amount consumed the young of mayflies were second only to midge larvæ. But Pearse also fails to specify the kinds of mayflies

eaten, which omission, in view of the very great diversity in size, form, and habits of different mayflies, detracts much from the value of his report.

Materials for the present paper have been accumulated in the course of recent work done by various representatives of the Bureau of Fisheries in the Mississippi River. The most important part consists of field notes and specimens collected by Emerson Stringham in the vicinity of the big dam at Keokuk, Iowa. This includes material for the life history of a species of Pentagenia, a genus whose immature stages have not hitherto been made known. An extensive collection of aquatic-insect larvæ made by Dr. A. D. Howard in the course of a mussel-bed examination in Andalusia Chute, just above Fairport, Iowa, contains a considerable series of mayfly nymphs, mostly belonging to the group here treated. H. E. Schradieck collected adult mayflies on the grounds of the biological station at Fairport, Iowa, during the summer of 1916 and sent them to me. These adults are of the same species as are the immature stages from the mussel beds; thus they furnish additional evidence as to the mayfly population of the river. A. F. Shira, director of the station, sent me also the mayfly material from nine stomachs of the river herring (*Pomolobus chrysochloris*) collected by various persons. To this I have added data of my own, gathered during residence upon the shores of Lakes Michigan and Ontario and elsewhere.

MISSISSIPPI RIVER COLLECTIONS.

Since the pioneer work of Benjamin D. Walsh (1862, 1863, 1864) at Rock Island, Ill., the mayflies of the Mississippi have received little attention. Garman (1890) published a few observations on the habits of the adult and on the food[a] of the nymph of *Hexagenia bilineata* in the backwaters of the Mississippi bottom lands.

But it has remained for the collections above mentioned, made by Emerson Stringham, H. E. Schradieck, and Dr. A. D. Howard, to add material data. Mr. Stringham's collections, made by the waterside and along the Keokuk Dam, include adults, subimagos, and nymphs taken at transformation. Mr. Schradieck's collections, made from the walls of the biological laboratory at Fairport, Iowa, consist of adults that have flown from the river and alighted on the building. Dr. Howard's collections, made with a dredge from the bed of the river in Andalusia Chute just above Fairport, are all nymphs. These three collections supplement each other remarkably well and give a better picture of the mayfly life of the river than we have had hitherto.

Mr. Stringham's collections were made between the middle of June and the middle half of September, 1916 (save for a few adults of an undetermined species of Heptagenia taken on May 29 and a single nymph of Siplonurus taken on June 7, and neither again recorded). They relate mainly to two species: *Hexagenia bilineata* Say (Pl. LXXI) and *Pentagenia quadripunctata* Walsh (Pl. LXXIII, fig. 15). Mr. Stringham's notes were accompanied by specimens adequate for determination of the species. His record of the occurrence of these two species about the big dam is as follows:

HEXAGENIA BILINEATA.

JUNE 7.—One grown nymph collected.

JULY 12.—Yesterday I observed that a large, grayish-brown mayfly with two caudal setæ was very abundant about the dam. Still more abundant to-day.

[a] "The food consists of earth richly charged with dead organic matter and with unicellular plants and animals. Such protozoans as Euglena are quite common in it. A large part of the contents of the digestive tube is sand, which seems to be taken incidentally" (loc. cit., p. 180).

JULY 13.—The species collected yesterday is much more abundant to-day. They swarmed all over me while I was on the dam. Every shaded place was covered with them.

JULY 14.—Took photographs [see Pl. LXX, fig. 1] at about 5.30 a. m. of the gauge house on the dam between gates 29 and 30, covered with mayflies of which I collected specimens yesterday. In the lake above the dam there is a mass of cast skins, irregularly distributed, though the adults are distributed along the dam very generally. Have not seen this species mating.

From Keokuk to Montrose, Iowa, along the railroad track, the air was full of mayflies, all apparently the same species. The same conditions reported from Fort Madison.

JULY 15, 6.30 a. m.—Only a few mayflies on the dam to-day—comparatively few.

JULY 17.—Mr. Howland (assistant general manager, Mississippi River Power Co.) tells me that he saw a pile of mayflies in Nauvoo, Ill., this morning that was about 6 feet in diameter and 18 to 20 inches deep. When I crossed the dam to-night at about 6.45 p. m. they were quite thick and were coupling and mating while flying. Above the chutes of the lock there is an enormous floating mass consisting mainly of mixed ephemerid adults, cast skins, and duckweed.

JULY 18, 5.30 a. m.—As abundant as ever on the dam to-day. A little later.—They are more abundant than ever this morning.

JULY 22.—Still a scattering of these on the dam this morning.

JULY 26.—Still a couple of thousand on the dam. Many on train arriving from the north; so it is evident they are still coming out on the lake.

JULY 28.—Crossed the dam early this morning and was surprised to find thousands, perhaps millions, of the mayflies in the air. I believe that these are nearly as common as ever. The north end of the power house (see Bureau of Fisheries Doc. No. 805, Pl. III) is blackened with them. Workman tells me this lot has been here about two days. Night Lock Master Raber tells me the present lot started last night. Collected some in process of transformation and some apparently just ready to transform.

JULY 30.—Large mass of dead adults above the locks; smell offensive on the lee side. Very few on dam this evening (6.15 p. m.), less than a hundred, I think.

AUGUST 1 AND 2.—A few, scattering, on the dam.

AUGUST 5.—None on the dam to-day.

AUGUST 8, 11 a. m.—A scattering of large, brown ones on the dam this morning—quite a number, in fact, for the late forenoon. The shady side of the poles had a dozen or two each; some posts had more.

AUGUST 10.—A good many, but no great masses like those of last month. Collected a few at Fort Madison to-day.

AUGUST 12.—Collected some in Burlington, Iowa.

AUGUST 14.—As many on the dam as on the 10th; possibly more.

AUGUST 15 AND 16.—Mayflies still on the dam.

AUGUST 18.—Only a few dozen about the dam this morning.

AUGUST 19.—A hundred or more mayflies on the dam.

AUGUST 21.—Noticed only one live mayfly.

AUGUST 23.—Again abundant on dam. Many on the gauge house; some on power-house walls; the horizontal portions of the dam thick with them, so that at each step one or more are crushed. Heretofore they have been mostly confined to upright surfaces. Not very active; few on the wing, doubtless because of cold.

AUGUST 27.—Did not see any mayflies when crossing the dam yesterday or early this morning.

AUGUST 29.—Have not seen any more living ones.

SEPTEMBER 2.—Some of the trolley poles on the dam, of which there are about 40, had 200 or 300 of large, brown mayflies; nearly all of them had some; few compared with earlier flights.

SEPTEMBER 15, 8 a. m.—Noticed about two dozen clinging to floor of dam.

[Observations discontinued.]

Thus Mr. Stringham's records show that during the summer of 1916, at least, July was the month of the principal flights of this species; that emergence was in waves; that successive waves reached their height at about the 13th, 18th, and 23d of the month, with falling away in numbers on intervening dates; that subsequent smaller waves culminated on the 10th and the 23d of August, separated by intervals of entire

absence of adults; and that belated reappearances occurred on the 2d and 15th of September. It is not likely that the first great wave arose on the 12th of July with such suddenness as Mr. Stringham's notes indicate; it is more likely that a few adults appeared earlier but were unnoticed.

Mr. Stringham noted the difference in behavior of the adult mayflies accompanying changes of temperature, adults when it is warm being able to cling to vertical surfaces, when it is cool (as on Aug. 23, minimum temperature 58° F., mean 70° F., some 15° lower than during preceding waves of emergence) lying flat upon horizontal surfaces only. That the adults adjust themselves, also, in relation to light (Krecker, 1915) and to wind is well known. Desiring to know whether waves of emergence are influenced by local meteorological conditions, I requested data from Fred Z. Gosewisch, in charge of the Keokuk station of the U. S. Weather Bureau. He very courteously sent me rather full data sheets covering temperature, precipitation, sunshine, winds, etc., and I have studied these carefully in relation to the facts furnished by Mr. Stringham, but I have not been able to trace any relation between emergence and meteorological conditions other than that which goes with the progress of the season. The mean daily temperature at Keokuk for the month of June is 72.5° F.; for July, 77° F.; for August, 74.6° F.; for September, 66.4° F. Emergence mainly occurs at the hottest part of the season, but belated transformations trail along into the comparatively cool weather of early autumn.

PENTAGENIA QUADRIPUNCTATA.[a]

JUNE 25.—They are transforming among the timbers of the boom above the lock. At 7.30 p. m. saw one leave cast (skin), and I took the insect and the cast. Took another just before it left the cast, but it struggled nearly free in the formaldehyde.[b] Saw more of these this evening than I have heretofore seen this year.

JUNE 27.—These are becoming more common. On a window sill over the water outside the compressor room, eastward of the lock, within an area of 1½ square meters, I counted 31 of them at 6.15 a. m. Other windows similarly covered. At 9.30 a. m., on the entrance door of the power house (area about 3 square meters), there were 53 of them. They were much thicker on this black iron door than on the dirty white concrete all about.

JUNE 29.—Less abundant.

JULY 1.—To-night large numbers about the power house; also about the dam.

JULY 4.—On door of power house and on adjoining walls.

JULY 11.—[No notes, but there is a vial containing a single nymph.]

AUGUST 12.—In Burlington, Iowa, yesterday and to-day, large, yellow mayflies; not very abundant.

AUGUST 23.—Scattering on dam and on power house.

AUGUST 31.—Collected a solitary live one at 7 p. m.

SEPTEMBER 2.—A few present.

SEPTEMBER 7.—One on Fisheries launch *No. 27* (ran from Fairport to Fort Madison, Iowa). Did not see any live ones about Keokuk yesterday or to-day.

These less continuous observations on Pentagenia seem to show that it appears commonly about a fortnight earlier in the season than Hexagenia, and in smaller swarms, and that it continues to appear in dwindling numbers through the season. On July 4, Mr. Stringham wrote:

Entrance door to power house had about 200 mayflies on it this morning. The adjoining walls were likewise covered. There appeared to be seven or eight different species, but the most common

[a] Again from Mr. Stringham's field notes.

[b] This specimen served for certain determination of the nymph, and for the life history which appears on a subsequent page.

was a small one having brownish-gray wings, light-brown body, reddish antennæ, and only two caudal setæ.

Accompanying this is a vial of the same date containing specimens of *Pentagenia quadripunctata*, *Potamanthus flaveola*, and *Chirotenetes siccus*. The commonest form was the subimago of the last named. This note has been quoted in full to call the attention of collectors to the diversity of appearance that may be presented by the different forms of a single species. Males and females differ strikingly in size of eyes, in length of legs and of tails, and in size and color; and each sex when adult may differ strikingly from its own antecedent subimago stage—the first winged stage that is assumed on leaving the water. These differences are shown side by side for *Chirotenetes siccus* in Plate LXXXII.

A single entry from Mr. Stringham's notes (August 6), the only one applying to *Polymitarcys albus* Say, is quoted subsequently under the account of thats pecies, page 286.

Henry E. Schradieck, while engaged in other work at the Fairport biological laboratory, at my request collected from the outside of the walls of the building, as he had opportunity, samples of the winged mayflies that settled there and kindly sent them to me in alcohol. The building is some 500 feet from the river and much nearer to the fish-ponds of the station, and these collections include a mixture of forms from both of these sources. Doubtless, Bætis, Callibætis, and Cænis came from the ponds, or from slack-water shoals, rather than from the open river. The other river species in the order of their abundance were: *Chirotenetes siccus*, best flyer of them all, July; *Hexagenia bilineata*, July to October; *Polymitarcys albus*, September 6 to 11; *Pentagenia vittigera*, August 25; and *Heptagenia* sp., July.

Dr. A. D. Howard's collections of nymphs were made with a fine-meshed dredging net that was drawn on lines at 25-foot intervals from the bank to the 100-foot line and from there on at 100-foot intervals. It covered several square miles of stream bed, and, although made primarily as a mussel survey, it furnishes much more comprehensive data of the insect life of the river bed under flowing water than we have hitherto possessed.

Dr. Howard's data will be published elsewhere; but it may not be out of place here to mention some facts concerning the river mayflies as evidenced by his insect collections that were sent me for determination.

In this collection of over 600 specimens, sent in vials under 102 entry numbers, more than 75 per cent was composed of the following eight species of insect larvæ, in the proportions indicated:

	Specimens.	Times occurring.		Specimens.	Times occurring.
Dragonflies:			Mayflies:		
Gomphus plagiatus	190	57	Hexagenia bilineata	38	12
Gomphus externus	67	37	Chirotenetes siccus	29	15
Stoneflies:			Polymitarcys albus	13	8
Acroneuria ruralis[a]	81	28	Pentagenia quadripunctata	5	1
Acroneuria abnormis	21	12			

[a] The *rupinsulensis* of Walsh is a synonym of this species.

The only other specimens sent in any considerable numbers were caddisworms of the genus Hydropsyche, of which 49 specimens were sent under 15 separate numbers.

The mayflies are the chief herbivores among the insects of the stream bed. That they are not more numerous there is doubtless due to the remarkable abundance of carnivorous dragonflies and stoneflies always associated with them. In this population both pursued and pursuers fall into two principal ecological groups, according as they burrow in the sand and gravel of the stream bed or live in the water above it. The mayflies of the genera Hexagenia and Pentagenia and the dragonflies of the genus Gomphus are all true burrowers, possessed of flattened and more or less shovel-like, digging, front feet (see Pls. LXXII and LXXIV), have the hind legs appressed to the body and adapted for pushing, and have the front of the head sloping forward and somewhat pointed. There are also many special adaptations to burrowing, among which none is more remarkable than the development in these mayflies upon the front of the mandibles of a pair of long, strong, upcurving, and pointed tusks that are driven forward into the soil and upon which the roof of the burrow is lifted, opening a subterranean passageway.

When a burrowing mayfly nymph is thrown out upon the surface of the sand, it digs in again more quickly than a mole. A few thrusts of the tusks forward, a few tosses of its head upward, a few side sweeps with its broad front feet, and it disappears from view beneath the sand.

The mayflies of the genera Polymitarcys and Chirotenetes and the stoneflies of the genus Acroneuria live above the stream bed and do not burrow. They prefer the shelter of stones or of timbers but occur occasionally in more open places. In Dr. Howard's collections these two mayflies are more frequently associated with one another than with any other species, and neither is once taken in association with either of the burrowing mayflies named above.

Polymitarcys and Chirotenetes have little more in common, however, than a habitat. They are very different in form and also in manner of life. Polymitarcys is a bottom sprawler, depressed, flat, hairy, protectively colored, and inactive. Chirotenetes is an agile swimmer and an artful dodger, with body compressed, smooth, and of beautiful stream-line form. It gathers its food from the passing current by means of plancton-retaining fringes of hairs that margin the fore legs (Clemens, 1917). Polymitarcys is a member of the subfamily Ephemerinæ and has for its nearest allies the burrowing mayflies above discussed. Its mandibles are tusked (Pl. LXXVIII, fig. 41), but the tusks are not upcurving and are not used for burrowing; they are laid out flat upon the bottom as are also those of the allied Euthyplocia (Pl. LXXIX, fig. 48). Chirotenetes is a member of the subfamily Bætinæ, a group in which there are no burrowers. This is the only member of the group that appears abundantly in the collections from the Mississippi River, and, beyond the figures of Plate LXXXII illustrating *Chirotenetes siccus*, the group receives no further treatment in this paper.

In January A. F. Shira, director of the Fairport station, sent me the insect contents of nine stomachs of river herring that had been collected during the two preceding seasons and observed to contain mayflies, so far as determinable, as indicated in the following table:

FOOD OF NINE SPECIMENS OF RIVER-HERRING (POMOLOBUS CHRYSOCHLORIS).

No.	Date.	Locality.	Collector.	Pentagenia nymphs.	Hexagenia.			Heptagenia.	Miscellaneous.[b]
					Nymphs.	Adults or subimagos.[a]	Eggs.		
1	May 23, 1916	Keokuk, near dam	Parker	2			(c)	2	(d)
2	June 4, 1915	Keokuk		2	3		(c)		(d)
3	June 11, 1916	do			2			1	
4	June 21, 1915	do		3	3				
5	July 2, 1916	do							(e)
6	July 4, 1915	do	Stringham		Many.	Many.	(c)		
7	July 14, 1916	Lake Cooper above depot	do	1	1	200	(c)		(e)
8	do	do	do		3	100	(c)		(f)
9	Sept. 8, 1916	Keokuk, above dam				[g] 100	(c)		(a, h)

[a] Approximate only; many badly disintegrated.
[b] The fishes named below were not sent me, having been previously determined.
[c] Occurring in large numbers.
[d] A damselfly nymph of the genus Argia.
[e] 1 Hiodon and 4 undetermined fishes.
[f] 2 Hiodon, 4 Dorosoma, 10 undetermined fishes.
[g] Of recognizable specimens all were females.
[h] 20 caddisflies of the family Leptoceridæ.

Evidently, during the season of flight of Hexagenia, this fish gorges itself with adults. Earlier it eats the nymphs. The eggs found might about equally well be obtained from nymph or adult, since they are matured, so far as external aspect is concerned, during the nymphal period.

SYSTEMATIC ACCOUNT OF THE GROUP.

The burrowing mayflies and their allies comprising the subfamily Ephemerinæ include in North America half a dozen genera of rather large species. Among these are the largest of our mayflies, the "brown drakes" of the genus Hexagenia, which by reason of their enormous swarms are known to everyone; the "yellow drakes" of the genus Pentagenia; the beautiful "mackerels" of the genus Ephemera, with ornate color patterns on both wings and body, and most graceful and lively nuptial flight; and several genera of smaller and less familiar mayflies. These will be characterized and illustrated and an account of their habits so far as known will be given in the following pages.

The group of the burrowing mayflies may be distinguished from other groups, and the genera of the group may be distinguished from each other in both adult and larval stages as follows:

KEY TO THE SUBFAMILIES OF EPHEMERIDA.

A. Adults.

1. Basal fork of the cubital vein[a] strongly unilateral; cubital and first anal veins strongly divergent at base ..... EPHEMERINÆ.
   Basal fork of the cubital vein symmetrical, or nearly so; cubital and first anal veins at base parallel or very slightly divergent ..... [b] BÆTINÆ and HEPTAGENINÆ.

B. Nymphs.

1. Mandibles with a prominent, tusklike, external branch projecting forward from the mouth and visible from above ..... EPHEMERINÆ.
   Mandibles not "tusked" ..... [b] BÆTINÆ and HEPTAGENINÆ.

[a] The terminology of the venation of the wings is illustrated and explained in Plate LXXXI, figure 55.
[b] Not here treated.

KEY TO THE NORTH AMERICAN GENERA OF THE SUBFAMILY EPHEMERINÆ.

A. Adults.

1. The posterior fork of the median vein in the fore wing very deep, almost reaching the base of the wing; two long simple intercalary veins between the first and second anal veins..... CAMPSURUS.
   The posterior fork of the median vein not extending more than three-fourths the distance to the base of the wing..... 2.
2. Between the first and second anal veins is a bunch of three or four long, straight, intercalary veins conjoined basally before their attachment to principal veins; the second anal vein is nearly straight, and unbranched ..... POLYMITARCYS.
   Between the first and second anal veins are only shorter, sinuate, and sometimes forking intercalary veins, that are attached directly to the first anal vein; the second anal vein is sinuate and often branched..... 3.
3. The posterior fork of the median vein extends two-thirds to three-fourths the distance to the base of the wing; vein Cu_2 not more strongly curved at the base than is the first anal vein. . EUTHYPLOCIA.
   The posterior fork of the median vein less deep, not longer than its stem; vein Cu_2 more strongly curved at its base than is the first anal vein..... 4.
4. The third anal vein not forked, but attached to the hind margin of the wing by a series of cross veins; forceps of the male 4-jointed..... 5.
   The third anal vein ends in a single fork and is not attached to the hind margin of the wing, though a few isolated intercalated veinlets lie between; male forceps 3-jointed..... POTAMANTHUS.
5. Tails 3 in male and female; fore wings with a definite and beautiful pattern of spots. . EPHEMERA.
   Tails 2 in the male; fore wings diffusely marked or plain..... 6.
6. Tails 3 in the female; mature color predominantly yellowish ..... PENTAGENIA.
   Tails 2 in the female; mature color predominantly brownish ..... HEXAGENIA.

B. Nymphs.

1. Unknown (tropical and subtropical) ..... CAMPSURUS.
   Mandibular tusks shorter than the head, only their tips visible from above..... POTAMANTHUS.
   Mandibular tusks longer than the head and very conspicuous..... 2.
2. Front of head rounded; legs decreasing in length posteriorly; fore legs longest..... 3.
   Labrum wider than long; tusks hairy almost to tips ..... EUTHYPLOCIA.
3. Front of head produced forward and conspicuously lobed; legs increasing in length posteriorly.... 4.
   Labrum longer than wide; tusks hairy only at enlarged base..... POLYMITARCYS.
4. Frontal prominence semicircular, shelflike..... HEXAGENIA.
   Frontal prominence bifid at its tip ..... 5.
5. Both mandibular tusk and frontal prominence denticulate externally..... PENTAGENIA.
   Mandibular tusk and frontal prominence smooth externally ..... EPHEMERA.

SINGLE DISTINCTIVE CHARACTERS OF OUR GENERA OF EPHEMERINÆ.

So well marked are these genera that they may be recognized at a glance by the following characters:

Adults.

EPHEMERA alone has the fore wings ornamented with a pattern of transverse spots.

HEXAGENIA alone has a border of brown on the front of the fore wing and another on the outer margin of the hind wing.

PENTAGENIA alone has the transverse row of four dots on the veins, as shown in Plate LXXIII, figure 15, and a single conspicuous dorsal stripe laid lengthwise of the body.

CAMPSURUS alone has the middle and hind legs aborted, also the greater depth of the posterior fork of the median vein, almost reaching the wing base.

POTAMANTHUS is the smallest (expanse of wings about three-fourths of an inch), and it alone has the wings wholly transparent (the two following white-winged genera have gray or purplish margined fore wings).

POLYMITARCYS alone has three or four long, straight, intercalary veins between the first and second anal veins, joined together basally before their attachment to these veins.

EUTHYPLOCIA alone lacks all the preceding characters.

Nymphs.

EPHEMERA alone has a frontal prominence divided by a deep, round notch into two smooth spines.

HEXAGENIA alone has a rounded, shelflike, frontal prominence on the head.

PENTAGENIA alone has numerous brown denticles on margins of frontal prominence, antennal basal folds, tusks, and front tibiæ.

These three are the true burrowers, having upturning tusks, front feet flattened for digging, more or less cylindric bodies, and erect gills.

CAMPSURUS nymph is unknown.

POTAMANTHUS alone has the tusks shorter than the head.

POLYMITARCYS alone has long, smooth tusks as long as the head and hairy only at their dilated bases.

EUTHYPLOCIA alone has the enormous tusks, hairy almost to the tip and beset also externally with brownish prickles.

These last three are the sprawlers, having tusks horizontally extended, elongate fore legs, and laterally extended gills.

HEXAGENIA, the Brown Drakes.

This genus includes the largest of our mayflies, measuring often an inch and a half in expanse of wings and nearly an inch in length of body, to which the long tails may add 2 inches of length; all this without counting the very long fore legs which are usually extended forward. The fore wings are marked with a brownish band along the front border, and there is usually a narrower border of brown around the outer margin of the hind wings. This color varies from a faint, brownish tinge in newly emerged individuals and in pale varieties to dark brown, almost black, in older ones or in other varieties; and when these bands are darker, then the cross veins of the middle area of both wings become bordered with brown. The body is brown above, yellowish beneath; there is a paler longitudinal middorsal stripe upon the thorax, dividing the brown into two broad stripes, as in the typical *H. bilineata* Say; and there are interrupted yellowish rings upon the abdomen, all of which pale markings tend to become obscured in the darker specimens.

Hexagenia bilineata is the name I apply to all the variants of the species that occupies the beds of our larger lakes and streams. The color differences appear to be only differences of degree. Even the differences of the male genitalia—usually our ultimate criteria of species—are intergradient.

Walsh (1863) thought there were two good species in the Mississippi River at Rock Island. He said (p. 199):

> Nothing is easier than to distinguish the living specimens of these insects [*H. bilineata* and *H. limbata=variabilis* Eaton] by the color of the eyes. In the former the upper half of the eyes is cinnamon brown, in the latter bright, greenish yellow; in both the lower half of the eyes is black. The dried specimens, especially those of the male, are very difficult to distinguish. * * * In the middle of July, when on the shallow area of the Mississippi known as "the slough" at Rock Island, *H. bilineata* appears in prodigious swarms, so that the bushes absolutely bend down with their weight. * * * I am sure that in the thousands of individuals, both male and female, which blackened the bushes there was not one with the upper surface of the eyes yellow or yellowish; the only variation I noticed from the normal color was that one male had the eyes a shade or two paler than the rest on their upper surface.

I have not had the privilege of studying the Hexagenias of the Mississippi River alive, but I am unconvinced by this emphatic opinion and by the long table of other

color differences that he gives on the following page (1863, p. 200); for I fear Walsh did not take into account the color differences due to age, and, though he examined thousands of specimens at a time, these thousands may well have been all of practically the same age—all of one day's brood.

Several forms have been named upon the basis of slight and inconstant color differences. Dr. Hagen (1890) thought to reduce the species to two in number because of differences he found in the form of the penes of the male, whether gently curved and finger-form (*bilineata*) or hooked and pointed (*limbata* Pictet = *variabilis* Eaton). I thought for a long time I could recognize males of these two species; and in my earlier papers I have treated *variabilis* as a distinct species, but a careful study of more material has shown intergradients and additional forms. Four of the more typical forms of male appendages are shown in Plate LXXXI, figures 61, 62, 63, and 64. In a general way it may be stated that the long, straightish penis goes with the lighter coloration of wings and body and with northward distribution; but there are exceptions to this also. A separation of species on such characters as these should not be made without a careful study of at least two things:

1. *Changes of form due to age.*—A casual examination of the subimago, when the penis of the adult is clearly outlined within that of the subimago, shows that there will be a considerable change of form at the final molting. Figure 65 of Plate LXXXI shows this condition. The inclosed penis, it may be seen, will be of the form shown in figure 62 of the same plate.

2. *Changes due to functional activity.*—There is a relatively immense sperm mass gathered at the outlet of the vasa deferentia of the newly issued adult male, whose presence there may have something to do with the prominences of the penes and whose discharge may allow for much retraction.

A good many names have been applied to the different forms of this genus, but after a careful study of a good bit of material from many localities I am unable to recognize more than two good and distinct species in the eastern United States—a lowland species from lakes and rivers, *Hexagenia bilineata* Say, and an upland bog-stream species, *H. recurvata* Morgan.[a]

The former is, of all our mayflies, the most important, the most abundant, the most observed, the most characteristic of the river fauna. The adult male is figured on Plate LXXI. The female would be similar, larger in size, with shorter fore legs and much shorter tails. The nymph is figured on Plate LXXII. I have examined nymphs and exuviæ from many lake and river localities and have been unable to find any constant differences between them to indicate more than a single species.

The material for this species that I have studied is as follows:

Mississippi River material, as stated in detail in preceding pages, including adults from Emerson Stringham collected about and above the Big Dam, on dates ranging from July 12 to September 15, showing several great swarms in July and several reappearances in dwindling numbers to the end of the season; adults collected by H. E. Schradieck on the outer walls of the biological laboratory at Fairport, Iowa, July 12 (when

[a] With this species we are not here concerned. It is still insufficiently described, but its determination is made possible by the figures of the genitalia that were published by Miss Morgan in the Annals of the Entomological Society of America, volume 6, page 395, 1913. Figures 8 and 12 of Plate LXXII herewith show that its nymph is readily distinguished from the lowland form by the relatively greater length of the mandibular tusks and by the unbranched condition of the rudimentary first gill. This is an early season species that swarms in May and then disappears, none being seen after early summer.

most abundant) and 25, and August 16; nymphs collected by Dr. A. D. Howard from the stream bed of Andalusia Chute just above Fairport, showing 12 occurrences in 102 collections; fragments of hundreds of adults (mostly females) from the full stomachs of the river herring, *Pomolobus chrysochloris*, sent by Director Shira. With these were a few nymphs that were probably taken when on their way to the surface to transform; and many nymphs taken from the stomachs of the shovelfish, *Polyodon spathula*, at Lake Pepin, and sent me by Dr. George Wagner, of the University of Wisconsin. These were doubtless taken while on their way to the surface, for they were eaten just before the swarms of adults appeared and at no other times (Wagner, 1908). The particular specimens sent me bear date of June 21, 1904.

Other material made up of that collected by Prof. J. H. Comstock at Peoria, Ill., on July 17, 1887, and at Kidders Ferry on Cayuga Lake, N. Y., on July 17, 1886; by Prof. T. L. Hankinson at Walnut Lake, Mich., in June and July, 1906; by Prof. C. Betten at Buffalo, N. Y., on the 18th, the 24th, and the 31st of July, 1906, and in Storm Lake, Iowa, in June, 1902; by Prof. C. C. Adams at Ann Arbor, Mich., in June, July, and August, 1904; by Prof. George D. Shafer at Lansing, Mich., on August 16, 1906; by E. B. Williamson at Howe, Ind., on September 14, 1916; by Prof. C. R. Crosby at Columbia, Mo., on June 16, 1905; and by myself in Lake Michigan, at Lake Forest, Ill., Walnut Lake, Mich., and Cayuga Lake, Ithaca, N. Y., July and August of several years.

HABITS.—This species, though found in a wide variety of situations, prefers shoal waters whose beds are covered with soft ooze, rich in organic materials. There the burrowing is easy and food is abundant. Figure 2 of Plate LXX shows a soft-mud bank left bare by the receding stream. A portion of the mud has fallen into an undercutting current, and in the portion that remains undisturbed a section is exposed, perforated in all directions by the many burrows of the Hexagenia nymphs. Miss Morgan (1913, p. 99) has thus described the burrowing of the upland species which she studied:

> The sloping banks were mined by Hexagenia nymphs, the open burrows showing only 2 or 3 inches apart. Most of the burrows were apparent by their round openings; from some, hairy caudal setæ protruded at full length. When a nymph was pulled out it speedily began to burrow again, placing the fore legs together with the bladelike tarsi held vertically. It next pressed them forward and outward, at the same time wedging the head between them in the cavity thus made. This movement was followed by a sudden lurch of the body forward, accompanied by wriggling of the abdomen. During these motions the second pair of legs was folded close up to the body, while the third pair was held outstretched, ready to brace against the mud. These motions, rapidly repeated, enabled the nymph to bury itself in a surprisingly short time. Some of the soft ooze taken from where the burrows were most numerous was later examined in the laboratory and found to be packed with diatoms. Stomachs of two of the nymphs were found full of silt and diatoms, showing that the nymphs had found plentiful forage as they burrowed.

The length of nymphal life is unknown, possibly two years, if one may judge by the half-grown nymphs one finds in midsummer. Transformation occurs at the surface of the water and usually at night. The grown nymph swims up and floats. A rent appears in the skin of its back. The subimago suddenly emerges from this rent, its wings expanding full size almost instantly. It stands a moment on the surface and then rises and flies away to the shore. It settles on any convenient support, often alongside countless others of its kind, as figure 1 of Plate LXX testifies, and remains quiescent for about 24 hours, when it molts again and becomes fully adult. Probably on the evening of the day following its final molt (I do not know that this has been determined in

any case) it flies forth over the waters with myriads of its kind, all together making a great company, filling the air and forming one of the great swarms that have been so often described and that are so well known on every stream side.

Mating occurs in the air during flight, and almost at once thereafter the female seeks the surface of the water. She flies hither and yon, dipping the surface, and then falling flat upon it with wings outspread. Her eggs are liberated in the water, just when and how has not been actually observed; but I have seen many playing above the surface of the water, egg-laden, and I have picked many from the surface, all of which have been spent females with eggs all gone.

When gravid females are injured, as by squeezing the thorax or snipping off the head, they at once extrude their eggs in two long, yellow packets of extraordinary size (similar to those of Polymitarcys, Pl. LXXVII, fig. 36). If these be placed in water, the masses crumble and the eggs tend apart in falling; thus they become disturbed on the bottom. The egg coat, which is slightly adhesive, quickly gathers a protective covering of silt and becomes well-nigh invisible.

The eggs of a single female will usually number above 8,000. The body of the female mayfly has become hardly more than a scaffolding for carrying this mass of eggs. Her mouth parts are atrophied; her alimentary canal is an air reservoir; her muscles are nearly all muscles of flight; her chief appendages are outriggers for control of flight; and her body is filled with eggs from end to end, even up into the rear of the head. To produce this great mass of eggs and to get them fertilized and back safely into the water, is her great end in life.

The habits of the young nymphs that hatch from these eggs have not been observed. Doubtless they have many enemies, such as the predacious burrowing gomphine dragonfly nymphs. They have also parasites. I found a large nematode worm filling the body cavity of one Mississippi River specimen, and most of the nymphs have their gills thickly beset with the cysts of some parasite unknown to me.

The grown nymph of *Hexagenia bilineata* may briefly be described as follows:

Length, 28 mm.; tails, 12 mm. additional; antennæ, 6 mm. Body pale, becoming purplish brown on abdomen and on gills, bare and shining on top of thorax, hairy around all margins. Frontal prominence of head shelflike, elliptical in outline when viewed from above, marked with a median dark dot, its margin fringed with pale hairs. There is a densely hairy circular ridge or fold surrounding the bases of the antennæ externally. The long, strong mandibular tusks are bare and shining brown in color at their extreme tips, but bear a marginal line of hairs externally, the fringe becoming longer and denser toward the base.

Prothorax with its side margins widened by a fringe of long, horizontally extended hairs. Fore legs stout and twisted. Femur ovoid, with a small lobe beside the apical articulation, hairy in longitudinal patches, the brushes short on the sides and very long on the edges. Tibiæ greatly dilated apically and further widened by marginal fringes of hairs, with a single, large apical tooth and that close beside the base of the short cylindric tarsal joint. Claw very short and stout, not more than twice as long as wide. Middle and hind legs slender, similar, each with a pincherlike prolongation of the apex of the tibia inferiorly, beside the base of the tarsus, the prolongation bearing an obliquely placed comb of short, stiff hairs. All expanded margins of all the legs bear dense brushes of yellow hairs.

The hind wings of Keokuk nymphs show a distinct outer border of brown.

Abdomen purplish brown above, darker on the middle segments, on each of which is included a pair of oblique, pale marks that are divergent at the rear. Gill on abdominal segment 1 rudimentary, tuning-fork shaped; on 2 to 7 large, composed of nearly equal lanceolate, long-tapering divisions that are broadly margined with whitish respiratory filaments. Tails stout, tapering broadly, fringed each side with tawny hairs, the very slender tips bare.

PENTAGENIA, the Yellow Drakes.

This is another genus of very large mayflies. These are almost as large as the brown drakes but have shorter legs and tails. The prevailing color is yellowish, but there is a wide dorsal band of obscure brownish laid upon the body its entire length; the wings are only tinged with yellowish along the front border.

There is, I think, a single species of this genus in the Mississippi River, though Walsh described two. I call them all, therefore, by the name he first used, *Pentagenia vittigera;* for *Pentagenia quadripunctata*, the form with four dots on the veins of each fore wing (figured on Pl. LXXIII herewith), appears to be only a variant. The conspicuousness of these dots is exaggerated in the figure; in a series of specimens some will be found in which one can hardly tell whether the dots are present or absent.

This genus is very insufficiently known. Nothing has been published hitherto concerning it except bare and incomplete descriptions of the adult. Mr. Stringham's brief notes, cited in the preceding pages, are the first that deal with habits; and his care in collecting subimagos, together with their cast nymphal skins, make it possible to identify with certainty the immature stages. The nymph is described below and is figured on Plate LXXIV.

My specimens of Pentagenia are all from the Mississippi River. (It is reported in Banks's Catalogue elsewhere only from Kansas.) The dates of adults range from June 16 to September 7, with maximum occurrence in late June. Transformation was observed by Mr. Stringham at 7.30 p. m. on June 25. Mr. Schradieck's imagos from Fairport, Iowa, bear date of August 16. Dr. A. D. Howard encountered the nymph in the bed of Andalusia Chute only once. There is a single nymph sent me besides, bearing the label H. McAdams, Keokuk.

The nymph of Pentagenia is similar to that of Hexagenia but is more yellow and more hairy, and a glance at the denticulations of the front of the head is sufficient for certain identification. It may be described as follows:

Length, 24 mm.; tails, 6 mm. additional; antennæ, 4 mm.

Color pale yellowish, deepening to brownish posteriorly on the dorsum, whitish below. The head in front, the legs exteriorly, and the lateral lobes of the abdomen are densely clothed with shining, golden hairs. Eyes and ocelli black.

The diffuse brown of the thoracic dorsum becomes a broad definite longitudinal stripe on the abdomen, nearly as wide as the segments. On each segment a pair of obliquely placed pale dashes is included in the brown.

Antennæ wholly pale and naked. Head with a strongly chitinized, two-toothed, frontal prominence, and a ridge bearing two unequal denticles above the base of each antenna. Cheeks and outer edges of palpi densely clothed with brushes of yellow hair.

Mandibular tusks very strong, bare and upcurving in their apical third, dilated basally and bearing an external carina that is edged with irregular, brown denticles. This portion of the tusk is hairy within, and at the base externally.

Top of head and thorax smooth, shining, save for some short, yellowish pubescence about the wing roots.

Legs short and heavy, hairy on front and rear margins, especially the front legs. Front femora flattened and quadrangular, with an expanded inferior lobe beside the knee joint that bears an immense brush of stiff, yellow hairs. Front tibia dilated apically and bearing a similar inferior lobe that is densely clothed with shorter, stouter bristles; bearing also an external denticulate-margined ridge of increasing prominence distally where it ends in a strong and conspicuous brown tooth. Just beyond this, at the apex of the tibia, another similar tooth lies against the base of the short cylindric tarsal

segment. There is an angulate line of long, thin hairs extending across the tibia near its base on the inner side. These hairs are outspread, fanlike beneath the mouth, meeting from the two sides, and may serve as a sort of table to hold up the food convenient to the jaws. The front tarsus is hardly longer than the tibia is wide; its claw, a third as long, is short and thick and curved and abruptly tapering. Middle and hind legs are more slender and less hairy; third tarsi are longer, with claws of equal length, more slender and tapering.

The wings of the nymph show four round, black spots at the points where dots will appear in the wing of the adult (see Pl. LXXIII, fig. 15), and two additional larger pigment spots that do not reappear in the adult—one on the posterior fork of the median vein and one on the rear end of the humeral cross vein.

The abdomen is nearly cylindrical, nearly covered above by the bushy, purplish gills. The lateral margins of segments 3 to 7 just outside the gill bases are expanded with bluntly rounded, lateral lobes that are densely clothed externally with golden-yellow hairs. These lobes increase in size to the fourth segment and then diminish in size posteriorly. The two divisions of the gill are unequal, the posterior being reduced in length, especially on the anterior gill-bearing segments. The tails are rather short and stout and thickly fringed with hairs.

EPHEMERA, the Mackerels.

This is a genus of beautiful mayflies, somewhat smaller in size than the two preceding, with relatively longer fore legs and tails. The cross veins of the front and middle portions of both wings are bordered with brown, and on the middle of the fore wing the brown is confluent in a series of spots arranged in a beautiful pattern. (See Pl. LXXV.) By this pattern our adult mackerels may all be easily recognized.

The mackerels are lacustrine rather than fluviatile in habitat, especially *E. simulans*. The shores of the Great Lakes swarm with this species during early July, and on the Finger Lakes of New York they are only a little less abundant.

The poorly differentiated species, *E. varia* Eaton, seems to prefer the little lakes and ponds and the muddy pools of stream beds.

I have already published a description and figures of the nymph of *E. varia* (1901, p. 429). Miss Morgan has also figured it (1913, Pl. XLIV, fig. 8) and has added the following interesting notes on the habits of the species at Ithaca (p. 100):

> No Ephemera nymphs were found in lower Fall Creek up to this time, that cleaner portion being nearly devoid of mud. On the first of July, however, the water in Beebe Lake was allowed to run off, bringing into the Lower Creek large quantities of mud. Three days later the shores below the dam were again examined. Tracks similar to those made by earthworms covered the bottom near the shore line. Nymphs were crawling over the surface and setæ could be seen projecting from many burrows. From an area of about 10 square feet 30 nymphs were removed.

From this it appears that this species seeks out the muddy pools in even so turbulent and rocky a stream as is Fall Creek.

E. varia is but doubtfully distinct from *E. simulans*. The wings of the typical form are less suffused with brown; the tip of the penis is a little more squarely truncated, and the proportionate length of the segments composing the forceps is slightly different; but none of these differences is either very tangible or very constant. I present new figures of the adult of *E. varia* on Plate LXXV, of its nymph on Plate LXXVI, and of the male genitalia of the three nominal species of the northern United States (these two and the very distinct *E. guttulata*) on Plate LXXXI, figures 58–60.

Concerning the habitat and habits of the beautiful, but rare, broader-winged species *E. guttulata* Pictet no information is available. I have not seen that species alive, and the only specimen I possess is a fine male that was collected for me.

So, again, in this genus there is a single species commonly occurring in the larger lakes and streams; and to that species mainly the following remarks will apply.

I have observed *Ephemera simulans* during several seasons at each of two places on the Great Lakes—at Lake Forest, Ill., on the shore of Lake Michigan, and at "Afterglow," my summer home near North Fair Haven, N. Y., on the shore of Lake Ontario. In both of these places the lake bed is sandy and not muddy. In neither place have I seen Hexagenia at all. Ephemera is the dominant form and the sole representative of the group here discussed, and it is associated in its swarming with several mayflies of other subfamilies and with a number of exceedingly abundant caddisflies.

The swarms of *Ephemera simulans* arise less suddenly than do those of Hexagenia and decline more steadily after a single maximum that is reached about the first week in July. For many days together the herbage of the shores and the trees upon the bluffs are thickly besprinkled with adults for more than a stone's throw inland from the shore. Then, after sundown, when they rise to enter upon their nuptial flight, the air is darkened with the clouds of them that extend in an unbroken line along the margin of the water. At Lake Forest, with an on-shore breeze their cast skins accumulate beside the piers in great floating masses, acres in total area and several inches deep, each cubic inch of these masses representing scores of individuals. At "Afterglow" the little hop hornbeam trees that cling to the front of the bluff are constantly aflutter with the mackerels that can not find resting places without disturbing one another; and if one shake such a tree, a perfect cloud of them will rise in the air

The smallest lake at which I have studied *E. simulans* is Walnut Lake in Michigan. It is there, where the numbers are not so great and where the evening swarms are less rough-and-tumble, that I have seen their mating flight at its best. I have described this (1908*b*, p. 261) as follows:

> After sundown the beautiful mayfly, *Ephemera simulans*, appears in companies of males over the edge of the water. The flight of one of these companies is a most delightful performance to witness, it is so light and graceful, and appears, withal, so exhilarating. Yet it is all up and down in vertical lines. With upturned head each individual flies rapidly upward, mounting quickly to a height of 10 or 15 meters; then spreading its wings out horizontally it falls upon them, with long fore legs extended forward and longer tails extended backward full length, rudderlike, keeping it always head to wind. Thus it descends, floating on the air, yet not drifting, until at the lower level of the swarm (4 or 5 meters above the water), it lifts its head and rises rapidly again in flight. And the whole company flying and falling thus, weaving up and down in vertical lines, and passing and repassing each other, create a scene of great animation.

My material in this genus comes from a good many sources, none of it, however, from the Mississippi River, though doubtless the genus will yet be found in many places in that stream.

Typical specimens of *E. simulans* come from Dr. C. C. Adams, collected at Portage Lake, Washington County, Mich., on May 30 (these bear the earliest date of all); from Prof. J. H. Comstock, collected on Cayuga Lake on the 1st and 6th of July; from Dr. C. Betten, collected at Buffalo, N. Y., on Lake Erie on the 11th of July; and from Walnut Lake, Mich., Lake Forest, Ill., and North Fair Haven, N. Y., on numerous dates in the fore part of July, collected by myself.

Typical specimens of *E. varia* Eaton are from Three Mile Island, Lake Winnepesaukee, N. H., collected by J. H. Emerton on July 10, 1906; from Lansing, Mich., collected by George D. Shafer; from Gloversville, N. Y., collected by Dr. C. P. Alexander

on July 26; and from many places in the Adirondacks and about Ithaca, collected by myself. Miss Morgan gives the date of the first appearance at Ithaca as June 14.

Of *E. guttulata* the sole specimen I have seen comes from Sport Island in the Sacandaga River, N. Y., and was collected by Dr. C. P. Alexander.

I have reared the nymphs of both *E. simulans* and *E. varia* several times, and have been unable to find any differences between them except a slight, somewhat intangible and apparently not quite constant difference in the shape of the notch that divides the frontal prominence into two points. This notch is in *E. simulans* typically a complete half circle, while in *E. varia* it is somewhat more widely open and forms but a segment (somewhat less than half) of a larger circle. Aside from this, the following description will apply to either species:

Length when grown, 18 mm.; tails, 8 mm. additional; antennæ, 4.5 mm.

Color yellowish; abdomen with a pair of longitudinal brown streaks laid on the yellow which they divide.

Antennæ slender, twice the length of the mandibular tusks, thinly hairy above on basal half and naked thereafter to slender flexuous tips. The frontal prominence ends in a sharp tooth at either side, the two separated by a rounded notch in front. Mandibular tusks long, slender, upcurved, brown in color, and nearly naked. Maxillary palpi long, slender, thinly hairy, yellow.

Legs moderately stout and somewhat flattened and twisted, clothed with tawny yellowish hairs on all exposed edges. All femora oval, fore tibia moderately flattened, widened from base outward only to midway its length, then parallel sided with an obtuse, bristle-covered, apical angle, but with no accessory apical tooth. Tarsus more than twice as long as wide and more than half as long as the tibia. Hind tibia prolonged beside the tarsus into a forcepslike joint, which is nearly wanting on the more normal middle legs.

Wing cover of the grown nymph shows a transverse series of spots, which are those of the adult more closely grouped.

Gills mainly yellowish, purplish only along the main axis. On segment 1, a bifurcated rudiment; on segments 2 to 7, large, bushy, the two divisions of about equal size. Tails thinly margined with tawny hairs.

POLYMITARCYS, the Trailers.

These are mayflies of medium size, having broad, white wings. The fore wings bear a border of dull, purplish color along their entire front margin. The legs are rather short, except the fore legs of the male, which are very long. The tails are very long.

There is a single known North American species, *P. albus* Say. An adult female with protruding egg masses is shown in Plate LXXVII. The nymph is shown in Plate LXXVIII.

The best account of the species is that given by W. E. Howard (in Needham et al., 1905, pp. 60–62), who studied it at Ottawa, Ill., from which account we quote a portion:

Nymphs of *P. albus* are abundant in both the Illinois and Fox Rivers at Ottawa. These rivers flow at this place over bottoms of solid sandstone, with bars of loose sand accumulated in the eddies. The streams are swift in the main currents, and the nymphs of this species are to be found under flat stones at the edge of swift water when about ready to transform. It was from two such situations that most of my collections were made, from which I succeeded in breeding a single specimen. I have seen the subimagos emerge and arise from the surface of the water in great numbers, but always just far enough out from the shore, so that the nymph skins were immediately swept into the current, where they disappeared before they could be procured. The difficulty in collecting the skins from the natural breeding places is further heightened by the emergence occurring during the evening twilight. All emerge from the nymph skin at the surface of the water and leave the skin afloat.

This is a midsummer species in northern Illinois. My bred specimen is dated June 22. None of the imagos in my collections shows an earlier date than this, but I have nymphs which are evidently

near to transforming which were collected the first week in June. Imagos and subimagos of the collections are scattered all through July, but August 5 shows them most abundant. At about this date they were observed in swarms. By the end of August they are much less numerous, and I have no collections which are as late as September.

The subimago stage lasts 24 hours, and when the final emergence takes place the subimago alights on some object near the edge of the stream, where it transforms in less than a minute. The skin of the subimago remains attached to the bases of the setæ of the imago and in this manner is carried out over the stream by the flying insect, where it is finally released after some minutes.

Miss Morgan found this species in Fall Creek at Ithaca on June 20, the earliest date on record. I have received specimens from points on the Susquehanna River and from Corning on the Chemung River in southern New York, those from the latter place bearing date of August 20. Say found it swarming on Lake of the Woods, United States, Canadian boundary.

Mr. Stringham's single entry concerning this species is as follows:

August 6.—Small, white mayflies have been common for at least a week or two about the river, though I have never seen any of them on the dam. Collected a few this evening at 6.45. In the morning there are many dead ones, but I never saw a live one in the day.

His specimens bear date of August 5 and 6, and those of Mr. Schradieck from Fairport, Iowa, bear the later date. So far as scattered records at present indicate, this species comes on slowly and reaches its maximum of swarming in early August.

The species is probably much more widespread than present records indicate. Usually it is not abundant; it is pale and inconspicuous in coloration; it is quiescent in habits; it is crepuscular in flight; it is rarely noticed.

The nymph does not burrow, but lies flat upon the bottom, with its legs and tusks and tails outspread upon the sand. It is protectively colored (see Pl. LXXVIII, fig. 39) and very inconspicuous. As noted before, it is an associate of Chirotenetes, and, like that species, its front tarsi bear two lines of long setæ within, the hairs of the two lines diverging and extending forward when the legs are outspread. Observations are lacking on this species, but it seems probable that it also uses these fringes as strainers to gather plankton and other food out of the passing current.

The full grown nymph may be briefly characterized as follows:

Length, 15 mm.; tails, 7 mm. additional; antennæ, 4 mm.

Body depressed, widest across the thin, flaring, lateral margins of the prothorax, smooth. Color brownish, with faint marmorate markings on thorax, and a line of pale elongate spots laid upon and crossing the sutures between the abdominal segments; gills pale.

Head broadly rounded. Antennæ pale, bare. Mandibular tusk much shorter than the antennæ, swollen at the base beneath the head, where clothed externally with many prickles and a few hairs, the tips long and slender and bare, very gently incurved.

Prothorax widest across the front, where the thin, lateral margin is most expanded, and ends in a sharp angle directed forward just outside the rear of the head.

Legs long, especially the fore legs, pale, but ringed and banded with brown and hairy along the edges; femora moderately flattened, twice banded; fore tibia and tarsus elongate and double fringed internally with long hairs; the long, straight, apical tibial spur is closely applied beneath the basal fourth of the tarsus, and a similar shorter spur at the tip of the tarsus is extended beside the sharply decurved claw.

Abdomen depressed and with gills widely extended laterally. The gill on segment 1 is an erect, simple, hairy rudiment, on 2 to 7 double, composed of flattened tapering filaments. The lateral margins of the segments are rounded in front and angulate at the rear beside the gill bases. Tails rather stout, segments ringed with short, pale bristles.

EUTHYPLOCIA, the Flounders.

This is a large, white-winged species, similar in aspect to Polymitarcys, but the dark, front border of the fore wings is more diffuse, showing a tinge of sepia or even roseate warmth of color, and the wing tips are hooked and so strongly corrugated lengthwise that the venation of the tips is difficult of examination. This is a tropical American genus likely to be taken only on our southern border. The type species *E. hecuba* Hagen is from Vera Cruz.

The unidentified nymph of which I present a figure in Plate LXXIX, was collected by E. B. Williamson in Gualan, Guatemala. It appears to differ specifically from the unidentified nymph that was figured by Eaton on plate 29 of his monograph (1883–1886); however, that description was drawn from a cast skin; this, from a good alcoholic specimen.

There are no other data accompanying these specimens.

This nymph is remarkable for its flatness and for the extraordinary length of its tusks and antennæ. This species may be briefly described as follows:

Euthyplocia sp.

Length, 29 mm.; tail, 12 mm. additional; antennæ, 15 mm. Color grayish brown, including the gills; antennal legs and setæ yellow. Head and body depressed, widest across the prothorax.

Head short and thick, depressed, wider than long, bare and shinning above, hairy about the mouth. Antennæ very long, slender, flexuous, and bare. Mandibular tusks very long, sickle-shaped. Stout to near the tip when suddenly narrowed to bare brown points, hairy on both inner and outer margins, the outer margin and dorsal surface beset as well with brownish prickles.

Prothorax broadly depressed with flaring parallel side margins; anterior angles more broadly rounded and incurved to a low, obtuse tooth at rear of head each side. Mesothorax with a low, thin, lateral lobe each side above the base of the middle leg, at front of segment, and strongly tapering rearward.

Legs strong, thickly fringed with hairs in all exposed lateral margins, femora flattened and marked above with scarlike, longitudinal, bare areas. Fore tibia longer than its femur and prolonged still further by a long, straight spine that lies closely beneath the tarsus for more than half its length. Tarsus similarly prolonged in a spur beneath the short, tapering claw. Middle and hind legs smaller, with only short apical prolongation of tibiæ. Wing cases uniformly purplish brown.

Abdomen long, depressed, slowly tapering posteriorly, bordered by the wide fringe of the extended gills. A pale middorsal line emerges conspicuously on the posterior segments. The lateral margins also are pale, and there are obscure, paired, pale dots in the brown of the sides. Gills on segment 1 erect, simple rudiments; on segments 2 to 7 double, long, flattened, and copiously fringed with filaments. Tails very long, flexuous, and nearly bare.

POTAMANTHUS, the Spinners.

This genus includes the smallest and daintiest of our Ephemerinæ. They are white, faintly tinged with yellow in one species, *P. flaveola* Walsh, and with green in the male of the other, *P. diaphanus* Needham. They have an expanse of wings of something less than an inch, with white tails of the same length. There are minute fuscous markings on the tips of the segments of the fore legs of the male and on the middle cross veins of the fore wings of the female of *P. flaveola* that are entirely wanting in *P. diaphanus*. Only these two American species are known.

The former (Pl. LXXX) is the species occurring in the Mississippi River. I have specimens of it also from Lansing, Mich., and from Ithaca, N. Y. Miss Morgan (1913) has published an excellent figure of the nymph, copied herewith on Plate LXXXI as figure 56. She says that "in Fall Creek Potamanthus crawls upon silt-covered stones and muddy bottoms." Eaton (1883–1886) says of the European *P. luteus*: "The nymph harbors

under stones in gently flowing water at the borders of rapids." The other published observations on the habits of the group are those of Betten (in Needham, 1908*a*, p. 194), as follows:

Returning on the boat from Buffalo I happened to look up, and saw a swarm about 20 feet above the water. I was able to take a few, but most of them were out of reach from the upper deck. It was too dark for me to see the manner of their flight. I returned next evening for further observation, but a strong wind prevented. I found the cast skins, however, belonging to this species floating upon the water and drifting upon the shore.

The eggs of females of *P. diaphanus* in alcohol hang in rounded, globular masses beneath the tip of the abdomen.

My material in this genus all bears dates in the month of July: *P. flaveola*, July 1 and 12 at Keokuk (Schradieck's Fairport specimens have only the month specified); and *P. diaphanus*, collected in the Niagara River near Buffalo, July 31, 1906.

The full grown nymph (Pl. LXXXI, fig. 56) may be briefly described as follows:

Length, 13 mm.; tails, 4 mm. additional; antennæ, 1 mm., their tips much surpassing the tips of the mandibular tusks.

Body elongate and depressed. Prothorax wider than the head, with broadly rounded, flaring, lateral margins. Fore legs longer than the others; fore tibia much longer than femur, beset with long hairs internally and bearing a stout, straight, apical spur about half as long as the tarsus. Middle legs shorter and more slender than are the hind legs. Abdomen regularly tapering posteriorly; gills rudimentary on the first segment, well developed and about equal in size on segments 2 to 7. The two divisions of each deeply fimbriate. Tails densely hairy along the middle portion, but bare at tips.

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EXPLANATIONS OF PLATES.

PLATE LXX.

Hexagenia bilineata Say.

Fig. 1. The mayflies on the gauge house on the big dam at Keokuk, Iowa, at 5.30 a. m. July 14, 1916. They were about equally numerous all along the dam, which is nearly a mile in length. Photo by Emerson Stringham.

Fig. 2. The burrows of the mayfly nymphs in a mud bank of the Okaw River near Sullivan, Ill. Burrows exposed by lowering of water in the stream and by undercutting of the current giving a vertical section. Photo by Prof. T. L. Hankinson.

PLATE LXXI.

Hexagenia bilineata Say; adult.

Fig. 3. The adult male (segmentation of the tails omitted, as in all the similar figures following).

Fig. 4. The legs of one side, fore, middle, and hind from left to right, as in the following plates.

Fig. 5. The end of the abdomen of the male from beneath, showing forceps, penes, and base of tails; middle tail rudimentary.

PLATE LXXII.

Hexagenia nymphs.

Fig. 6. The nymph of *H. bilineata* Say; dorsal view. The hind feet are turned forward for comparison with the other feet, and the gills on the right are moved aside to show the markings on the abdomen. The 3-branched, rudimentary gills on the first abdominal segment are abnormal. (See fig. 13.)

Fig. 7. Portion of head of same, more enlarged.

Fig. 8. Comparable portion of head of *H. recurvata* Morgan.

Figs. 9, 10, 11. Fore, middle, and hind legs, respectively, of *H. bilineata* Say; the front leg adapted for shoveling, the hind leg for pushing.

Fig. 12. The unbranched rudimentary first gill of *H. recurvata* Morgan.

Fig. 13. The normal bifid rudimentary first gill of *H. bilineata* Say.

Fig. 14. The functional second gill of same, showing its fringes of respiratory filaments.

PLATE LXXIII.

Pentagenia vittigera Walsh; adult.

Fig. 15. Adult male of the *quadripunctata* form.

Fig. 16. Legs of one side.

Fig. 17. End of abdomen of male from beneath.

Fig. 18. End of abdomen of female from beneath.

PLATE LXXIV.

Pentagenia vittigera Walsh; nymph.

Fig. 19. The nymph from above, with the gills on the right pushed aside to show the markings of the abdomen.

Fig. 20. Head of same from above, more enlarged.

Fig. 21. Mandible of same, showing serrated tusk.

Figs. 22, 23, 24. Fore, middle, and hind legs, respectively.

Fig. 25. A rudimentary gill of the first abdominal segment.

Fig. 26. A functional gill of the second abdominal segment.

PLATE LXXV.

Ephemera varia Eaton; adult.

Fig. 27. The adult male.
Fig. 28. The legs of one side of the same.
Fig. 29. The end of abdomen of the same from beneath.

PLATE LXXVI.

Ephemera varia Eaton; nymph.

Fig. 30. The nymph from above, gills on the right turned aside to show normal color pattern.
Fig. 31. Head of same, more enlarged.
Figs. 32, 33, 34. First, middle, and hind legs, respectively.
Fig. 35. A gill from the second abdominal segment.

PLATE LXXVII.

Polymitarcys albus Say; adult.

Fig. 36. Adult female, hovering with egg packets extruding.
Fig. 37. The legs of one side, adult male.
Fig. 38. End of abdomen of male from below, showing strongly divaricate penis tips.

PLATE LXXVIII.

Polymitarcys albus Say; nymph.

Fig. 39. The nymph from above.
Fig. 40. Head of the same, more enlarged.
Fig. 41. Mandible of the same.
Fig. 42. Maxilla of the same.
Fig. 43. Labium of the same.
Fig. 44. Fore leg of the same.
Fig. 45. A gill of the second abdominal segment.

PLATE LXXIX.

Euthyplocia sp.? nymph.

Fig. 46. The nymph from above.
Fig. 47. Head of the same, more enlarged.
Fig. 48. Mandible of the same, hairs of the tusk omitted.
Fig. 49. Maxilla of the same.
Fig. 50. Labium of the same.
Fig. 51. A gill of the second abdominal segment.

PLATE LXXX.

Potamanthus flaveola Walsh; adult.

Fig. 52. The adult female.
Fig. 53. The legs of one side of the adult male.
Fig. 54. The ventral aspect of the male genitalia, showing the form of forceps and penes.

PLATE LXXXI.

Miscellaneous (figs. 55, 56, and 57 by Dr. Anna H. Morgan).

Fig. 55. The venation of the wings of *Ephemera*.

Vein designations are those used in accompanying key; the six principal veins are: *C.* costa, *Sc.* subcosta, *R.* radius, *M.* media, *Cu.* cubitus, *A.* anal vein.

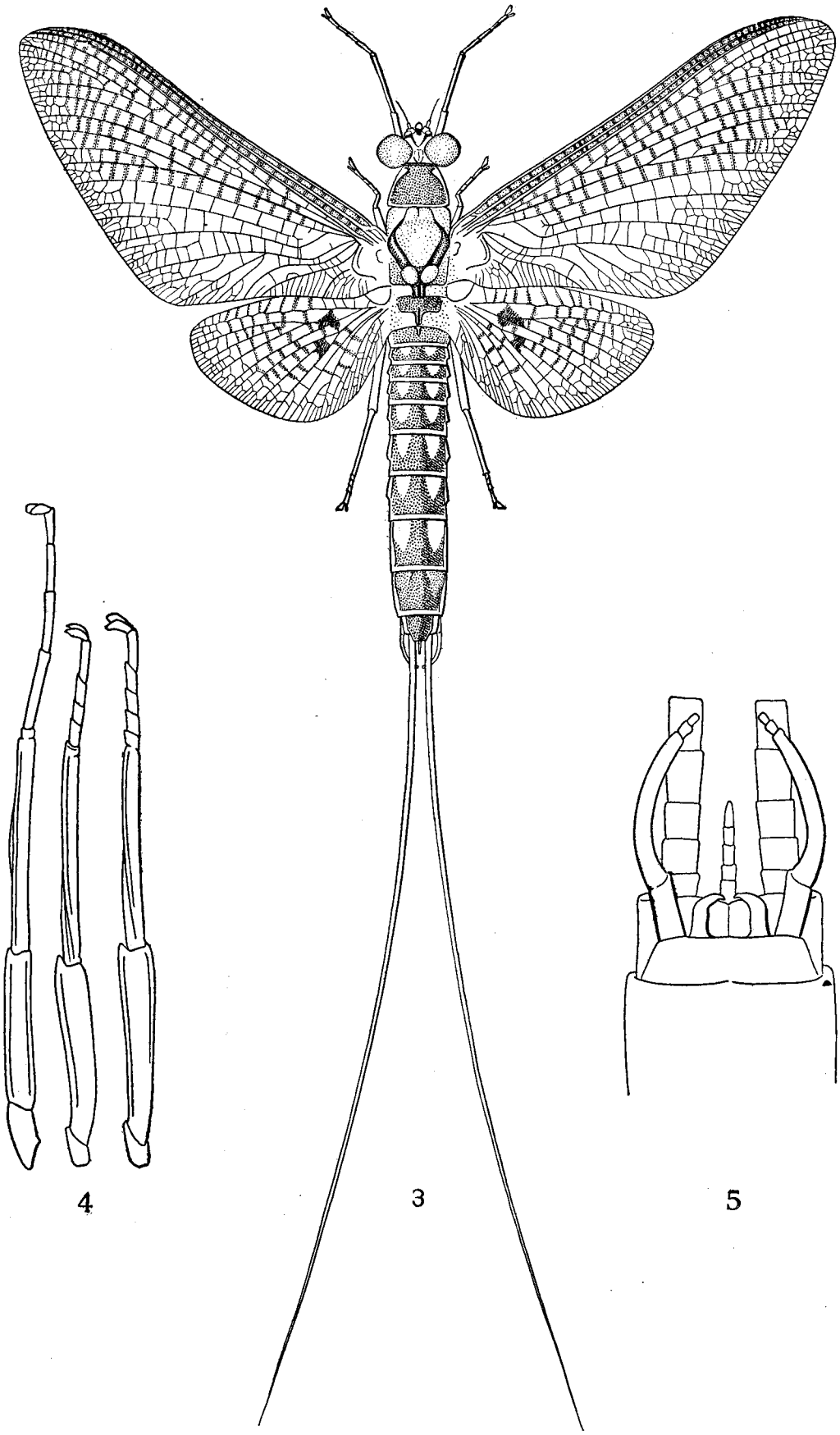
Branches of veins are marked with small numerals, in order from the front. The posterior fork of the median vein is the one in which veins M_3 and M_4 unite. R_5 is the radial sector; 1 is the principal accessory vein. The third anal vein is the forked vein behind the second anal.

Fig. 56. The nymph of *Potamanthus flaveola* Walsh.
Fig. 57. An adult "Peg-leg," *Campsurus* sp.? (from Brazil), the extremely long tips of the tails omitted. Note the stubs of the vestigial middle and hind legs.
Fig. 58. Forceps and penes of *Ephemera guttulata* Pictet.
Fig. 59. Forceps and penes of *Ephemera simulans* Walker.
Fig. 60. Forceps and penes of *Ephemera varia* Eaton.
Fig. 61. Forceps and penis of *Hexagenia bilineata*, form *bilineata* Say.
Fig. 62. Forceps and penis of *Hexagenia bilineata*, form *falcata* n. nom.
Fig. 63. Forceps and penis of *Hexagenia bilineata*, form *variabilis* Eaton (syn., *limbata* Pictet).
Fig. 64. Forceps and penis of *Hexagenia bilineata*, form *munda* Eaton.
Fig. 65. Forceps and penis of *Hexagenia bilineata*, subimago, showing within the outline of the adult, form *falcata*.

PLATE LXXXII.

Chirotenetes siccus Walsh.

Fig. 66. The female subimago.
Fig. 67. Sketch of tails of male subimago to show their relative length.
Fig. 68. The female imago.
Fig. 69. Sketch of tails of male imago to show their relative length.
Fig. 70. Legs of one side of male imago.
Fig. 71. End of abdomen of adult male from beneath.
Fig. 72. The nymph from the side. Note the plancton-gathering fringes of the fore legs.
Fig. 73. The tail fin of the nymph; outer tails fringed only on the inner side.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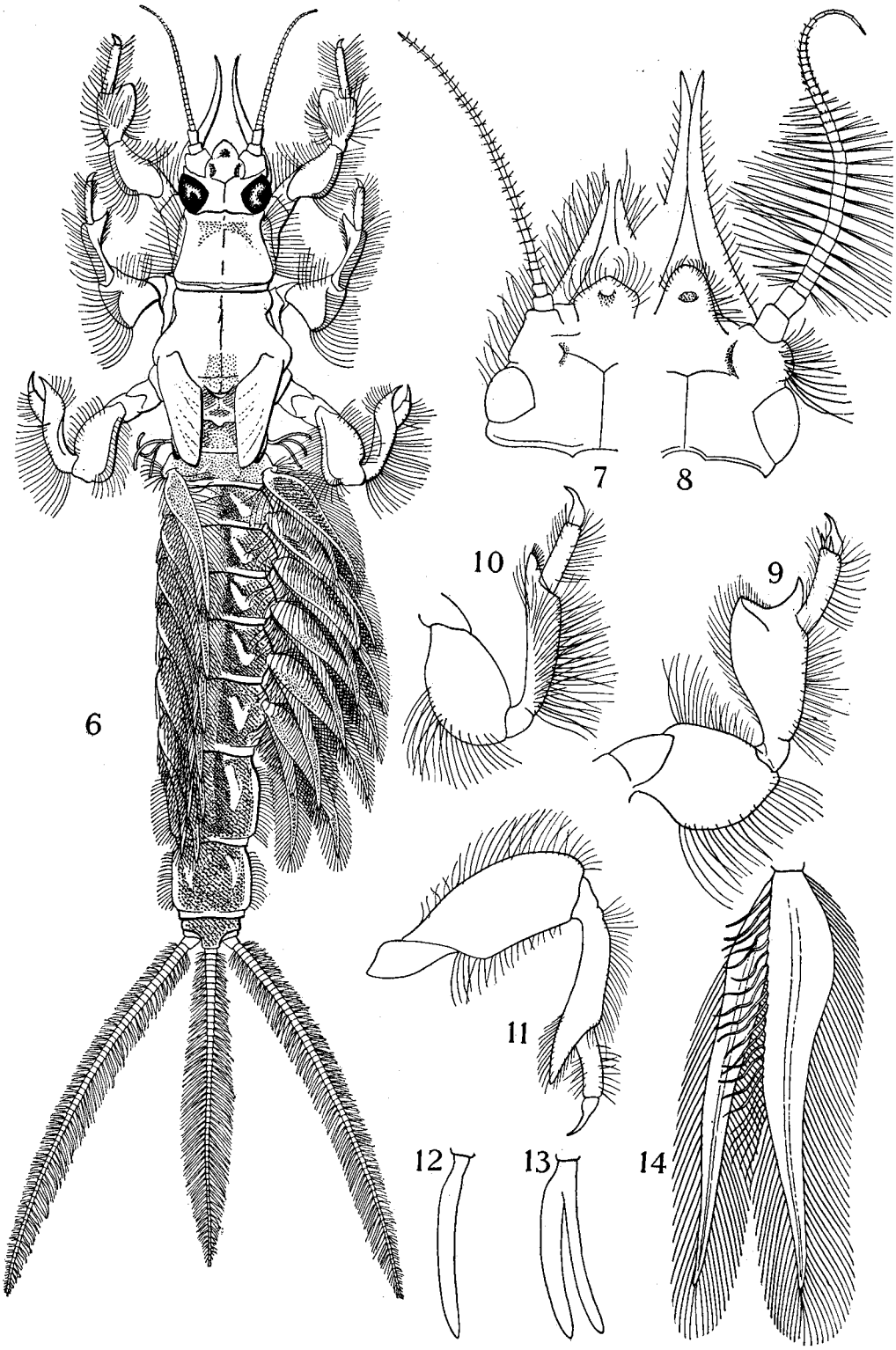
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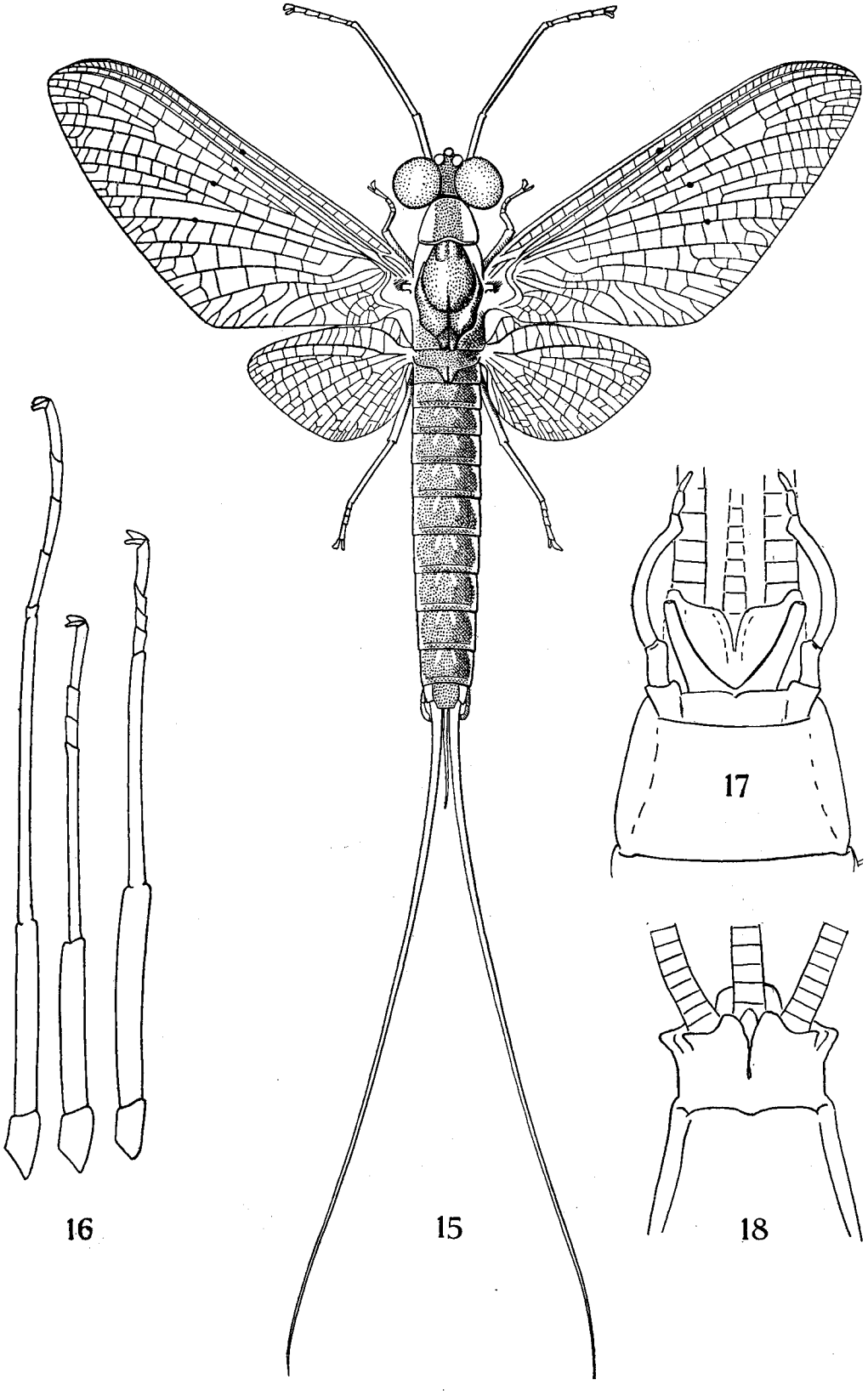
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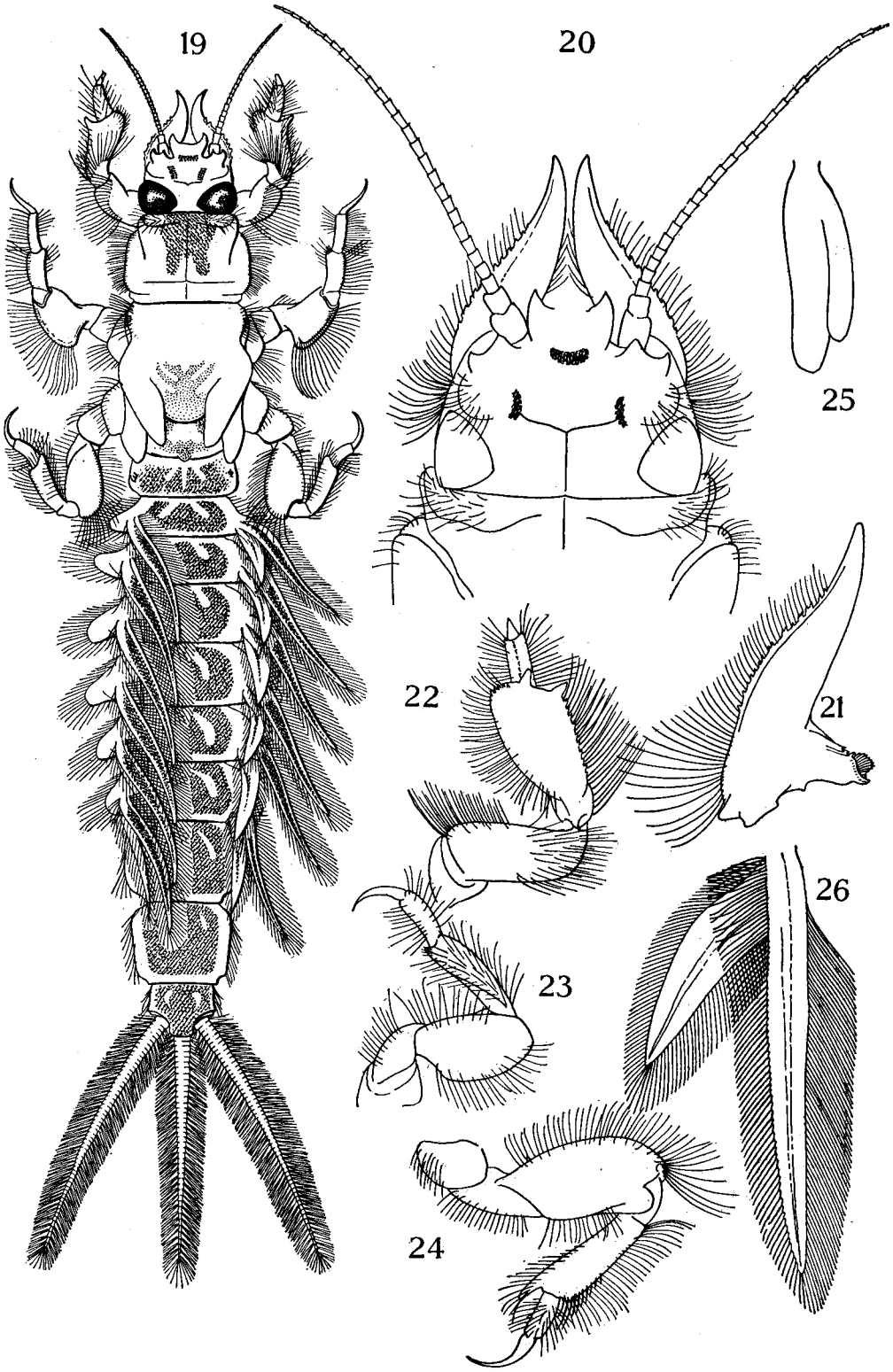
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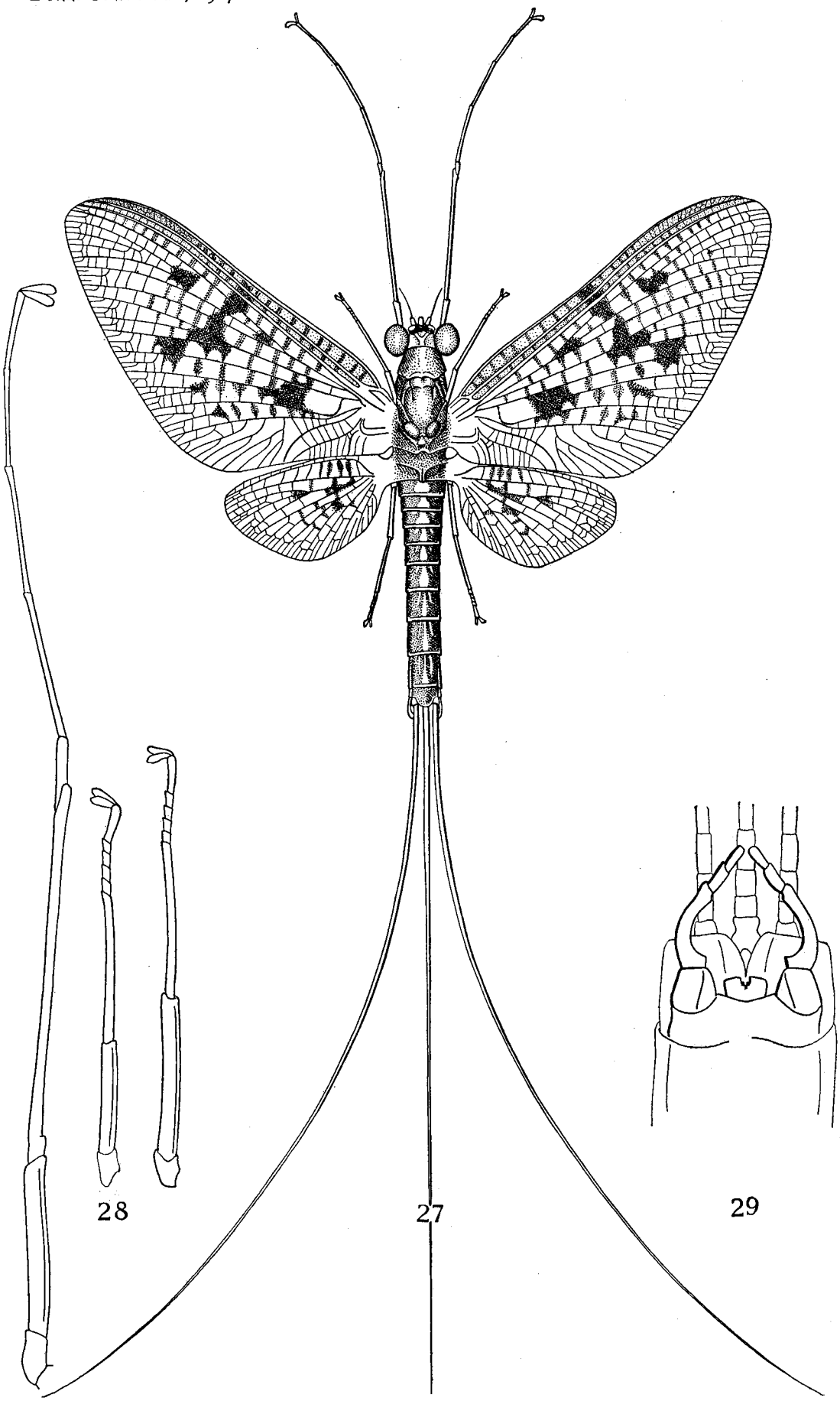
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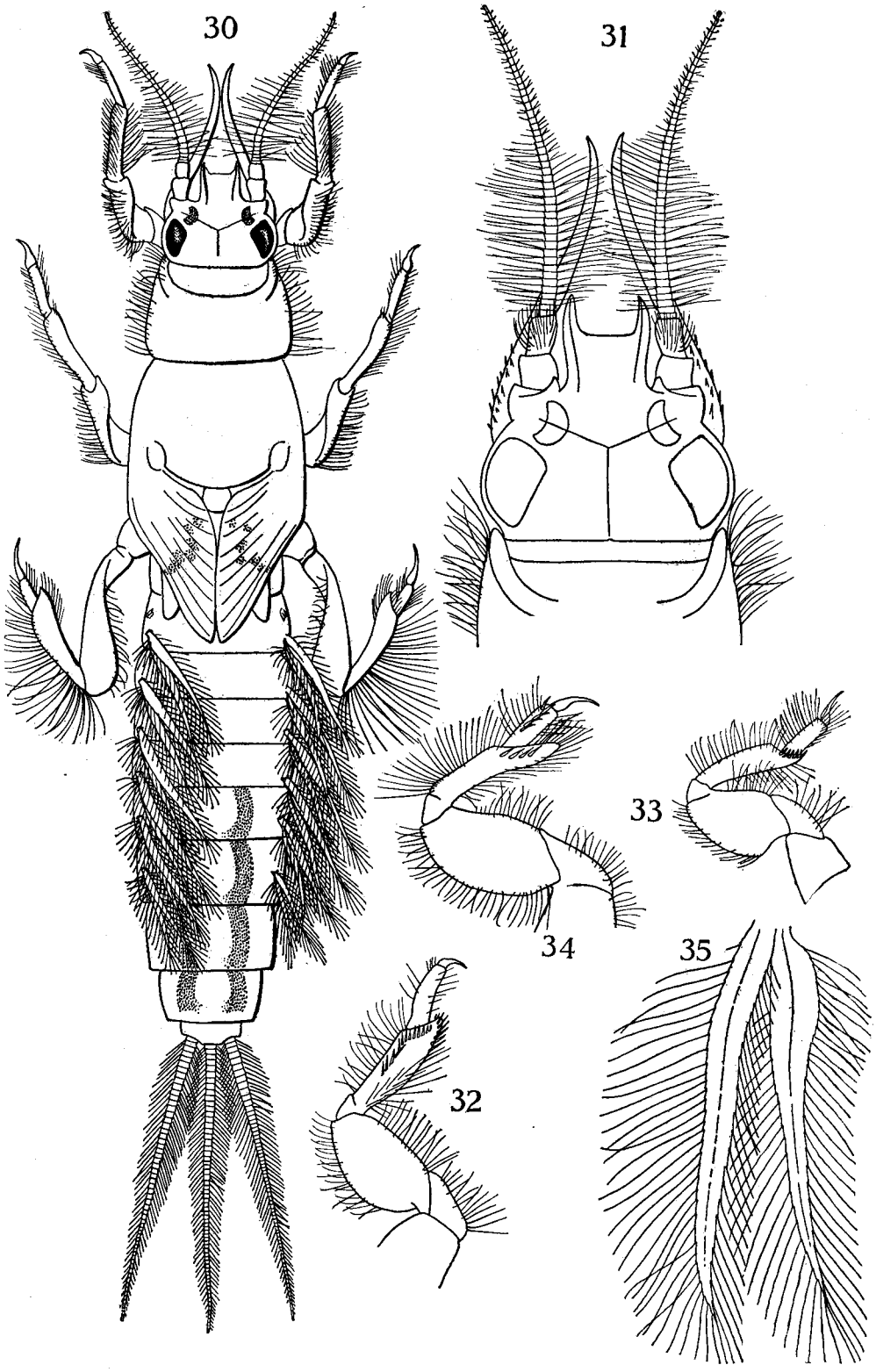
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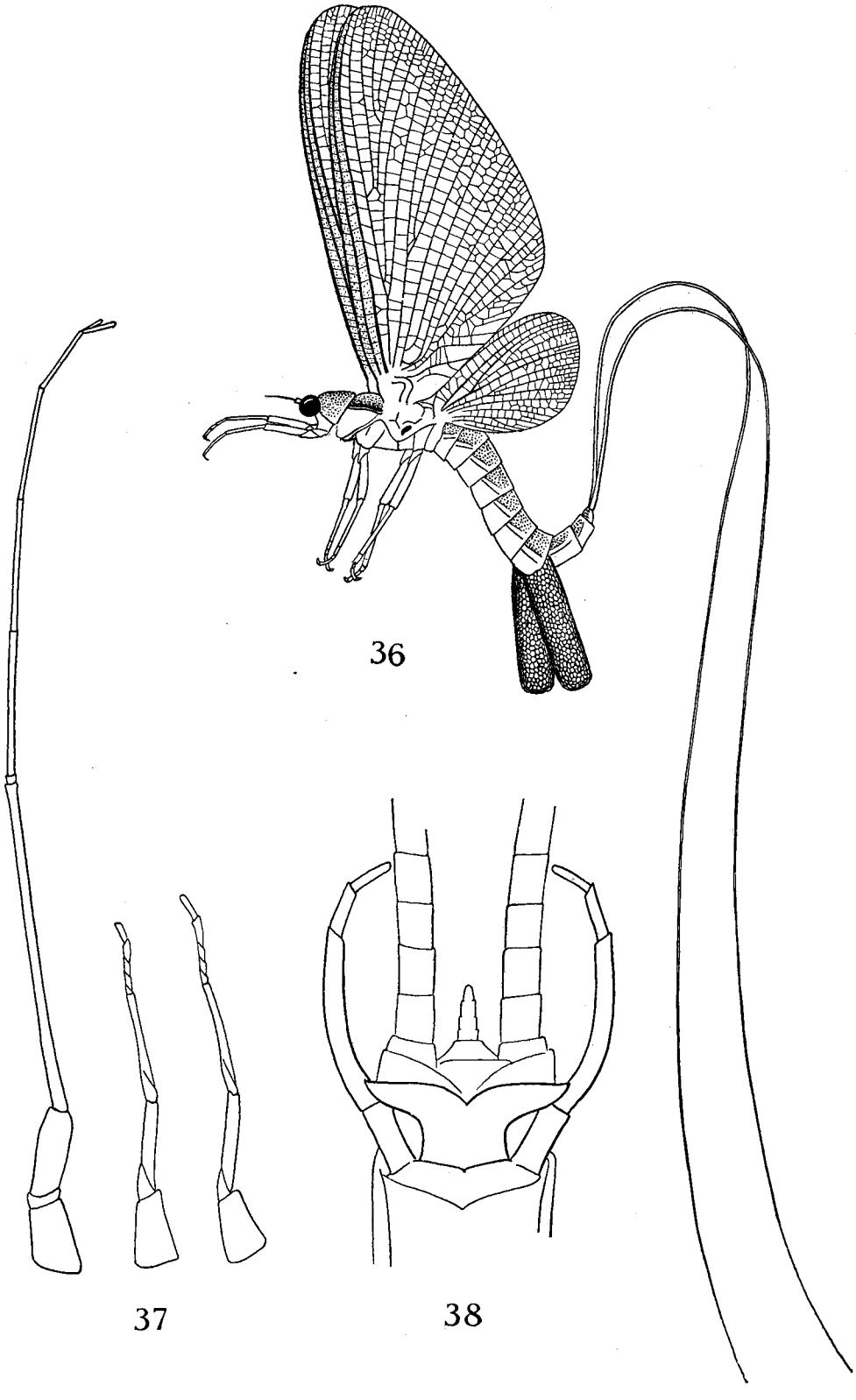
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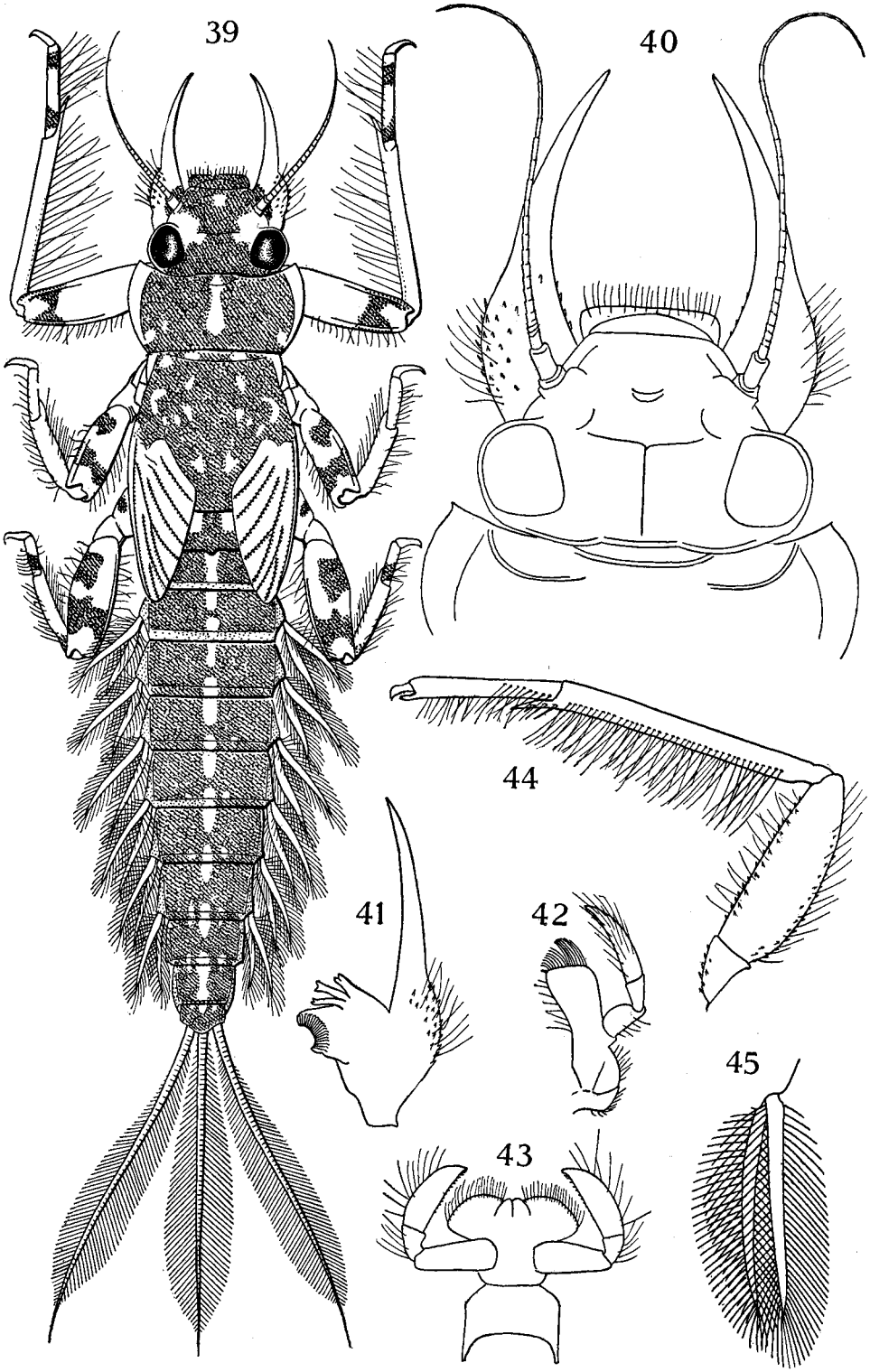
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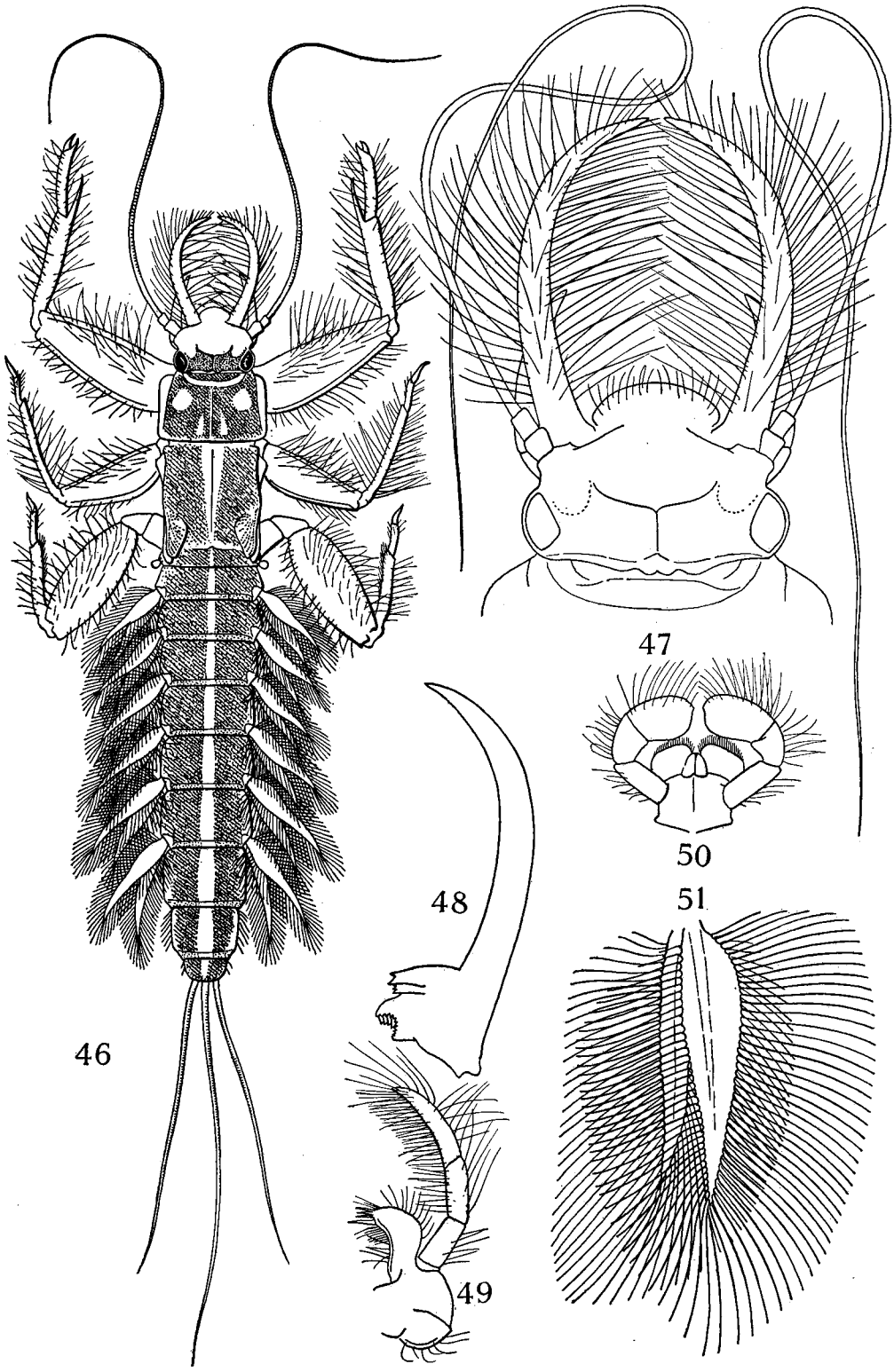
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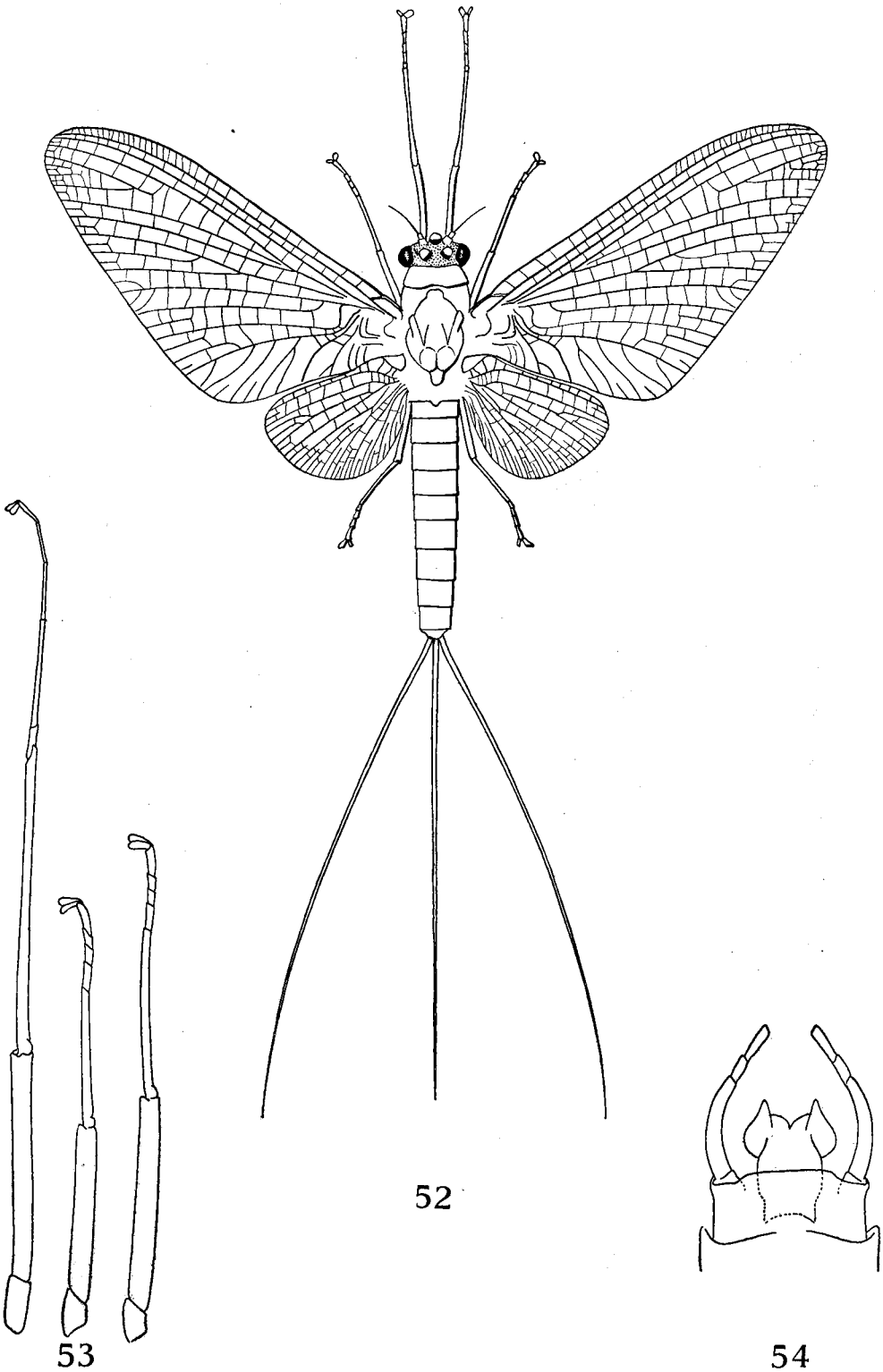
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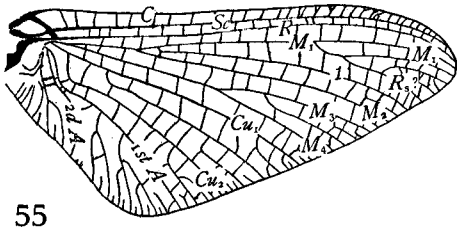

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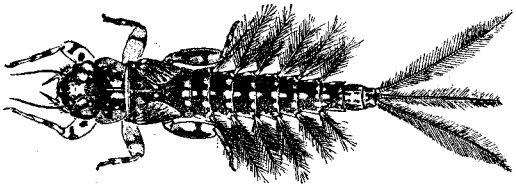

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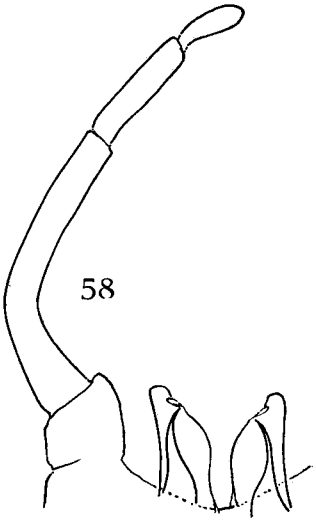

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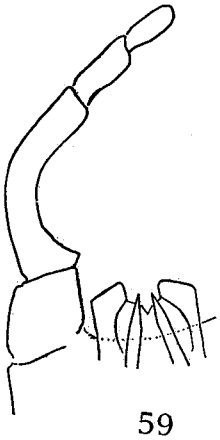

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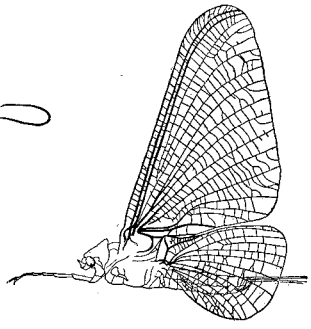

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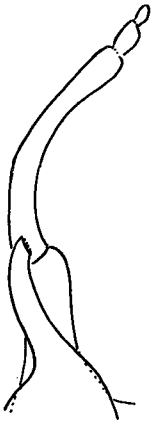

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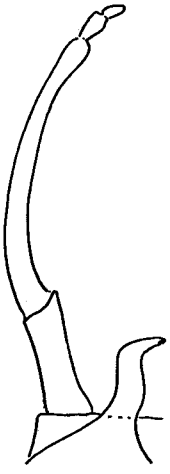

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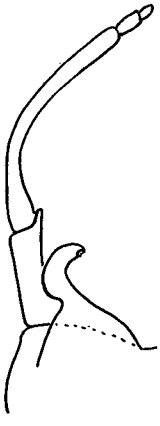

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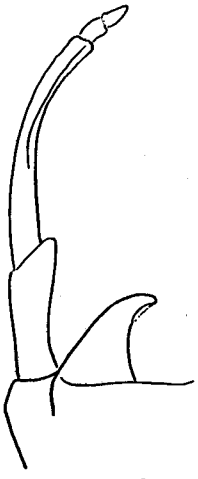

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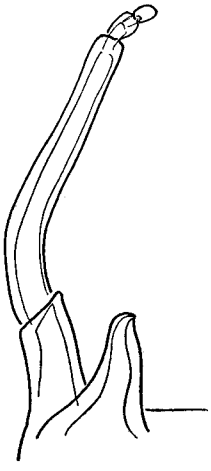

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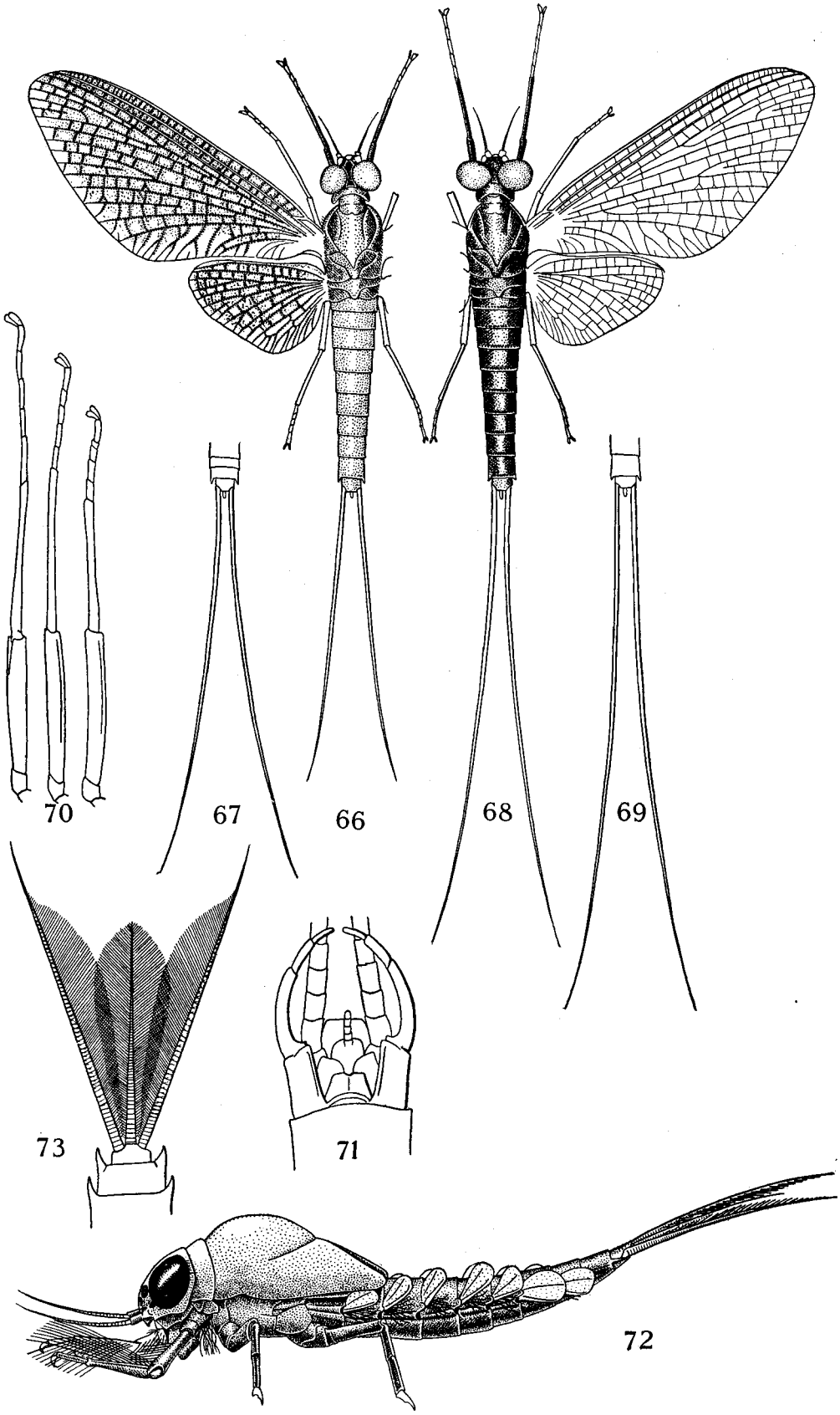
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