

TAXONOMIC STUDIES ON THE EPHEMEROPTERA

IV. THE GENUS STENONEMA

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The genus *Stenonema* is abundant and ecologically widely distributed in North America east of the Rocky Mountains. The flattish nymphs of one or more species are to be found in most permanent bodies of water in which currents are set up either by wind action or by gravity. For a number of years I have been accumulating material for a generic revision. The taxonomy of the group is involved and it is apparent that considerable rearing of imagoes from their respective nymphs must be undertaken before some of the problems can be solved. *Stenonema* does, however, consist of three distinct complexes or groups of species. For two of these, i. e., *tripunctatum* and *interpunctatum*, enough data have been accumulated by various investigators as well as by the author that a rather clear picture can be presented at this time. The third complex, *pulchellum*, consists of numerous closely related species and subspecies and presents many puzzling questions. To solve the problems presented in the last named complex, imagoes must be reared from various parts of the geographical ranges of the sundry species, a type of investigation which proceeds slowly and demands the co-operation of numerous students of the ephemeroptera. I hope that this preliminary paper may stimulate such endeavors and that eventually we shall be able to compose a complete picture of the taxonomy of the group from its entire range. The present work is restricted to a general discussion and delimitation of the genus plus taxonomic revision of the *tripunctatum* and the *interpunctatum* complexes.

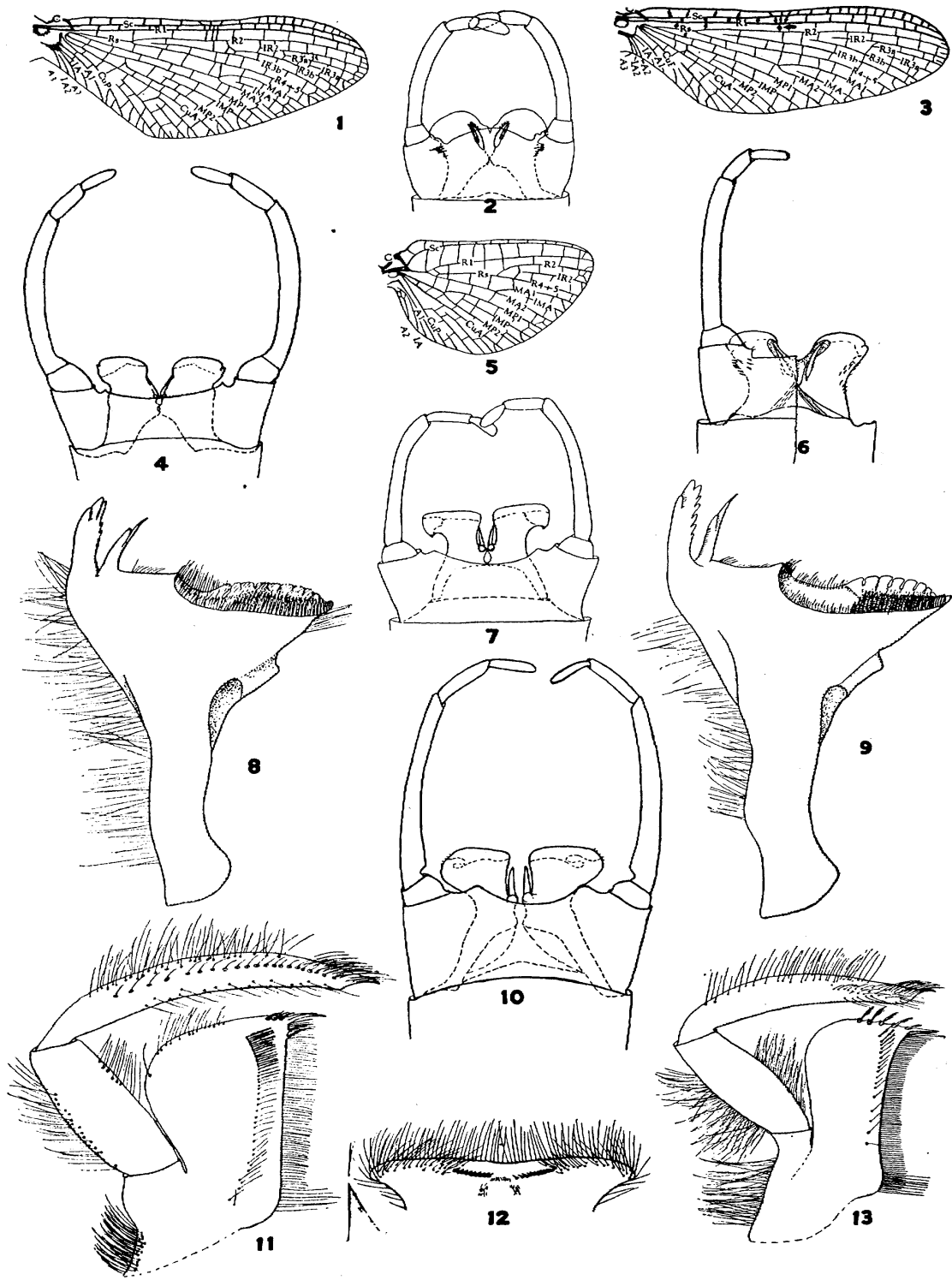
In preparation for this paper I have seen the collections and types for the genus which are deposited in the British Museum (Natural History) Collection, the Canadian National Collection, the Cornell University Collection, the Illinois Natural History Survey Collection, the Museum of Comparative Zoology Collection as well as those in the American Museum of Natural History Collection and, of course, in my own personal collection. I wish to thank the various officers and scholars of the above institutions for courtesies extended to me. Special thanks are due the American Museum of Natural History, and particularly the late Dr. Frank E. Lutz, for research facilities. Dr. Mont A. Cazier suggested the utilization of the statistical techniques that have been applied to the *interpunctatum* complex. His aid and advice, as well as that of Miss Annette Bacon, have been invaluable. Any errors in the use of these techniques or of interpretation should, however, be charged solely to the author. Finally, I should like to say that detailed distributional records have not been given at this time for two reasons: (1) Because they are as yet incomplete, and (2) in order to save printing space. I do, however, have detailed records of emergence dates, localities, etc., in note form.

Genus *Stenonema* Traver

Imago.—Compound eyes of male moderately large; separated dorsally by about the diameter of a laterally situated ocellus; eye of female flattened and separated by distance greater than diameter of eye; the posterior margin of the female head weakly excavated. Pronotum strongly excavated posteromedially; lateral lobes reflexed. Fore leg of male as long as or longer than body. Tibia one and a quarter to one and one-third times as long as femur; fore tarsi approximately one and one-third times as long as tibia. First fore tarsal joint typically about one-half as long as second. In some individuals of *S. interpunctatum heterotarsale*, however, it is almost as long as second joint. Third segment subequal to second; fourth shorter than third but longer than first; fifth slightly shorter than first. Ranked in descending length, the tarsal segments of male are 2, 3, 4, 1, 5. Fore leg of female shorter than body; fore tibia subequal to femur; tarsus shorter than tibia; first tarsal joint one-half to three-quarters as long as second; third subequal to second; fifth subequal to third but longer than first, and fourth shorter than fifth. Ranked in descending length, the fore tarsal segments of female are 2, 3, 5, 1, 4. The femur of the metathoracic leg of both sexes is subequal to or slightly longer than the tibia; the tarsus about one-half of the tibia. Metathoracic fifth tarsal joint longest; in the *interpunctatum* and *tripunctatum* complexes the first joint is subequal to the second; the third is subequal to the first and the fourth is shortest. Thus the arrangement in descending lengths is 5, 2, 1, 3, 4. Species of the *pulchellum* complex are similar except 2 is subequal to 1 so that the arrangement is 5, 1, 2, 3, 4. Claws dissimilar on all tarsi. Typical Heptagenine venation in fore wing (figs. 1 and 3). Basal cross veins well developed. Stigmatic veins normally showing no anastomosing but may be slightly aslant. Cross veins of bullar area may or may not be crowded. Typical Heptagenine venation in hind wing (fig. 5). Between the CuA and CuP a pair of elongated marginal intercalaries. Sometimes an elongated marginal veinlet in front of the normal pair and another behind gives the appearance of two pairs of intercalaries in the cubital area of the hind wing. Male genitalia (figs. 2, 4, 6, 7 and 10) with four-jointed forceps; penes deeply divided with a strong spine on the inner side of each division. Members of the *interpunctatum* complex with penes shaped as in figs. 2, 4 and 6; in all others shaped somewhat as in figs. 7 and 10. Posterior margin of styliger plate straight or slightly convex in the *interpunctatum* complex; slightly excavated in all others. Subanal plate of female well developed, extending at least as far as tip of dorsum of abdomen; may be slightly excavated on distal margin. Median pseudocercus completely absent.

EXPLANATION OF PLATE I

1. Fore wing of *S. femoratum tripunctatum*. 2. Male genitalia of *S. interpunctatum interpunctatum*. 3. Fore wing of *S. interpunctatum interpunctatum*.
4. Male genitalia of *S. carolina*. 5. Hind wing of *S. femoratum tripunctatum*.
6. Male genitalia of *S. gildersleevei*. 7. Male genitalia of *S. pulchellum*.
8. Mandible of *S. rubromaculatum*. 9. Mandible of *S. interpunctatum interpunctatum*.
10. Male genitalia of *S. femoratum femoratum*. 11. Maxilla of *S. femoratum femoratum*.
12. Labrum of *S. interpunctatum frontale*. 13. Maxilla of *S. ithaca*.



Nymph.—Moderately flattened Heptagenine type. Head large, flattened, and wider than long with posterior margin slightly excavated. Mouthparts completely ventral; labrum (fig. 12) broad with smooth front margin; mandibles (figs. 8 and 9) slender, incisors moderately large with inner member somewhat smaller than outer; inner incisors asymmetrical, right one (fig. 17) possessing a sharp, sturdy spur which is not developed on the left member. Lacinia mobilis (fig. 18) a large, slender seta found only on left mandible and often it may be broken. Maxillae (figs. 11, 13 and 14) with two-jointed palp, the distal segment of which is sparsely setose except on outer distal surface where a denser mass of simple, long, slender setae are found. Galea-lacinia widest distally; inner lacinial edge with dense stockade of simple setae; lateral to lacinial edge is row of somewhat evenly spaced plumose setae; distal lacinial dentes slender; distal margin of galea with a variable number of heavy setae that vary from hemiplumose spines (*ithaca*) to sturdy combs (*interpunctata*). Hypopharynx (fig. 21) with wing-like superlinguae. Labium (fig. 15) typically heptagenine.

Prothorax with lateral extensions that do not extend back past the anterior margin of the mesothorax. Legs flattened and tarsal claws with or without pectinations.

Gills carried dorsally and not utilized as an adhesive organ; gills one to six (figs. 20, 22, 23 and 25) double; seventh gill (figs. 16, 24 and 27) single, slender and lanceolate, lacking fibrillar portion. Tracheal branches may or may not be present in this seventh gill. Posterior lateral abdominal spines variable. Pseudocercus and two lateral cerci present.

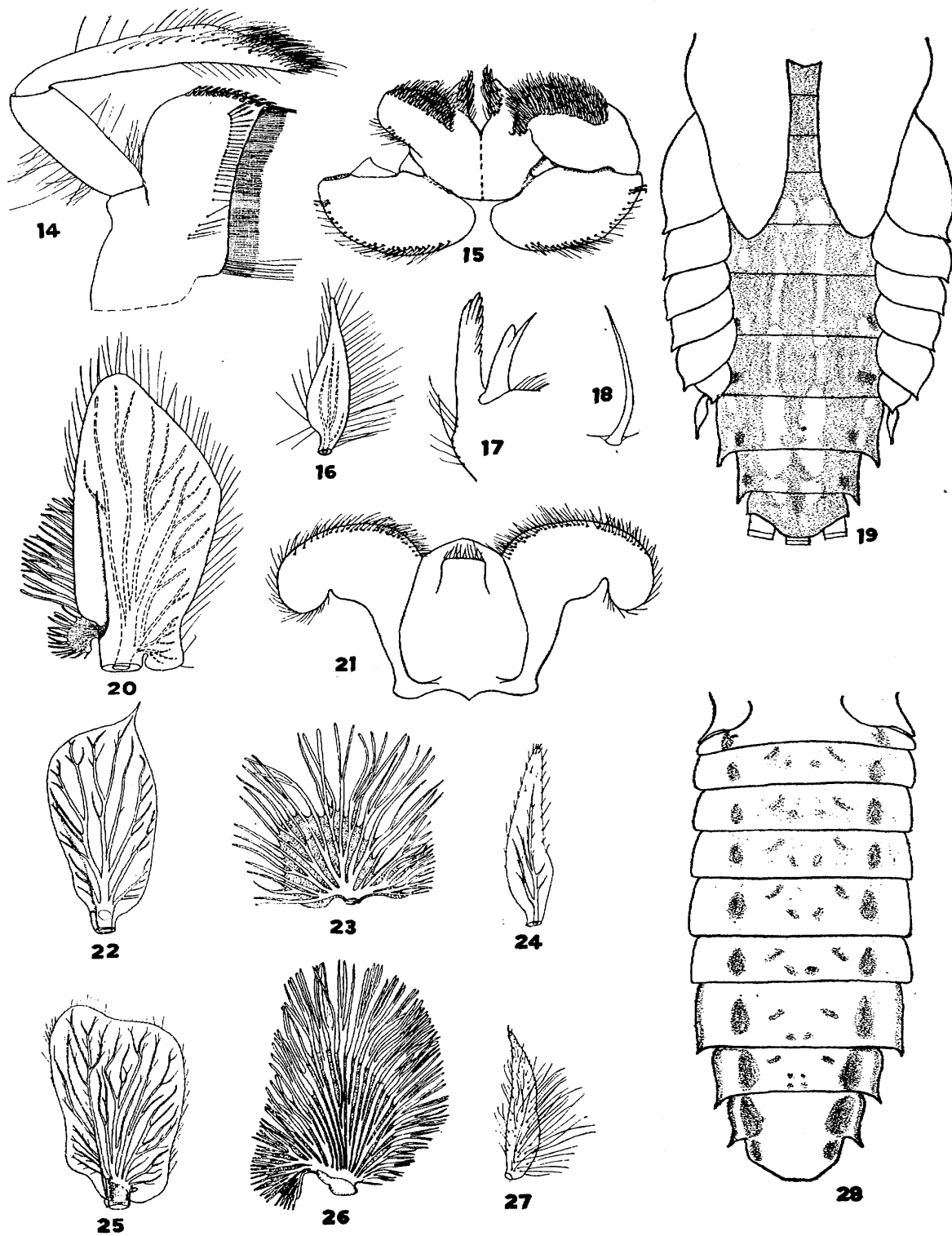
Genotype.—*Stenonema tripunctatum* (in *Heptagenia*) Banks.

REMARKS

This genus was erected by Traver (1933) to include certain American species that Eaton had placed in *Heptagenia*, *Ecdyonurus* and genus incerti. Some investigators had considered these species to be members of the genus *Heptagenia* (Banks, Needham, and Clemens) while McDunnough and others had placed them in *Ecdyonurus*. Ulmer (1939 and 1940) considers *Stenonema* to be a synonym of *Heptagenia*. He concludes this from the factual basis that his *Heptagenia nasuta* adults from Borneo have fore tarsal segments similar to those of *Stenonema* while the genitalia are similar to certain species that are included in *Heptagenia*. If we follow Ulmer, *Heptagenia* contains a large number of species, some of which obviously are phylogenetically quite widely diverse. The genus becomes large and unwieldy with the resultant

EXPLANATION OF PLATE II

14. Maxilla of *S. interpunctatum interpunctatum*. 15. Labium of *S. interpunctatum canadense*. 16. Seventh gill of *S. femoratum tripunctatum*. 17. Detail of right incisors of *S. fuscum*. 18. Lacinia mobilis of *S. pulchellum*. 19. Dorsal view of nymphal abdomen of *S. interpunctatum frontale*. 20. Third gill of *S. femoratum femoratum*. 21. Hypopharynx of *S. fuscum*. 22. Dorsal gill lamella of *S. interpunctatum*. 23. Ventral gill lamella of *S. interpunctatum*. 24. Seventh gill of *S. interpunctatum interpunctatum*. 25. Dorsal gill of lamella of *S. ithaca*. 26. Ventral gill lamella of *S. ithaca*. 27. Seventh gill of *S. pulchellum*. 28. Ventral view of nymphal abdomen of *S. interpunctatum frontale*.



obscuring of phylogenetic relationships. Further, if we accept Ulmer's definition of the genus *Heptagenia*, we must either (1) synonymize the genus *Ecdyonurus* as it is now delimited into the genus *Heptagenia*, or (2) divide *Stenonema* as defined by Traver between *Heptagenia* and *Ecdyonurus*. The reasons for these alternatives are as follows: The only way imagoes of *Heptagenia* (in Ulmer's sense) and *Ecdyonurus* can be separated is that in the latter the first segment of the metatarsus is longer than the second, while in the former the second metatarsal segment is longer than the first. On this basis the *pulchellum* complex would belong to *Ecdyonurus* and the *interpunctatum* and *tripunctatum* complexes to *Heptagenia*. Such a procedure would be unwarranted since we have adequate evidence from both nymphal and adult material that these three complexes are monophyletic in origin. The alternative is to fuse *Ecdyonurus*, *Stenonema*, and *Heptagenia* into a single huge genus, which would further complicate the problem of elucidating phylogenetic relationships.

The answer to the question of generic delimitation is always a difficult one for taxonomists, especially in groups such as the heptageniids where the genera appear to be closely related. The following basic factors appear pertinent to any decision that may be reached concerning *Stenonema*, *Ecdyonurus* and *Heptagenia*:

1. We assume tacitly, upon the basis of morphological evidence primarily, that all species that belong to the family Heptageniidae are of monophyletic origin. From this ancestral stock various stocks have differentiated and some of these in their turn have further differentiated, and so on.

2. Since the various species that belong to each family or to each genus have descended from a single ancestral stock, we should expect the species to have many characters that are common to all and only a few that are different. Thus the set of characters found to be possessed by any single species of the family overlaps in large part the set of characters of any other species. Conversely the characters that differentiate them from another are few in number. Further, the differences between the various species or genera within a family tend to be restricted to a given set of structures. Thus, in Heptageniidae the tarsal lengths, the penes, and certain mouthparts (but not the forceps or the abdominal gills) have apparently undergone repeated modification. To put it another way, certain characters within any given stock seem to be highly susceptible to modification and to have independently become modified many times within a stock. Other characters, and by far the greater number, remain stable and are thus similar in all individuals of the stock. Such a view has received additional support from the accumulated evidence on the mutations of such organisms as *Drosophila* where the various species have many homologous mutations.

3. We also should, to the best of our ability, be sure that all of the species included in any given genus belong to the same phylogenetic substock.

It is obvious from what has been outlined above that all categories above the species are human concepts. True, such a category as the genus should always and usually does represent a monophyletic group, but the pertinent thing is that it does not exist in nature but merely as

a concept in the human mind. An author, in establishing a genus, although he may not say it in so many words, arbitrarily chooses a locus in the phylogenetic descent of a stock and says that all species which have differentiated since this locus shall belong to the genus. His choice of a locus is naturally determined by the material at hand, namely the specimens and sundry information known about the various species. Obviously various workers may choose different loci on the phylogenetic stem. Such things as the number of species, the apparent

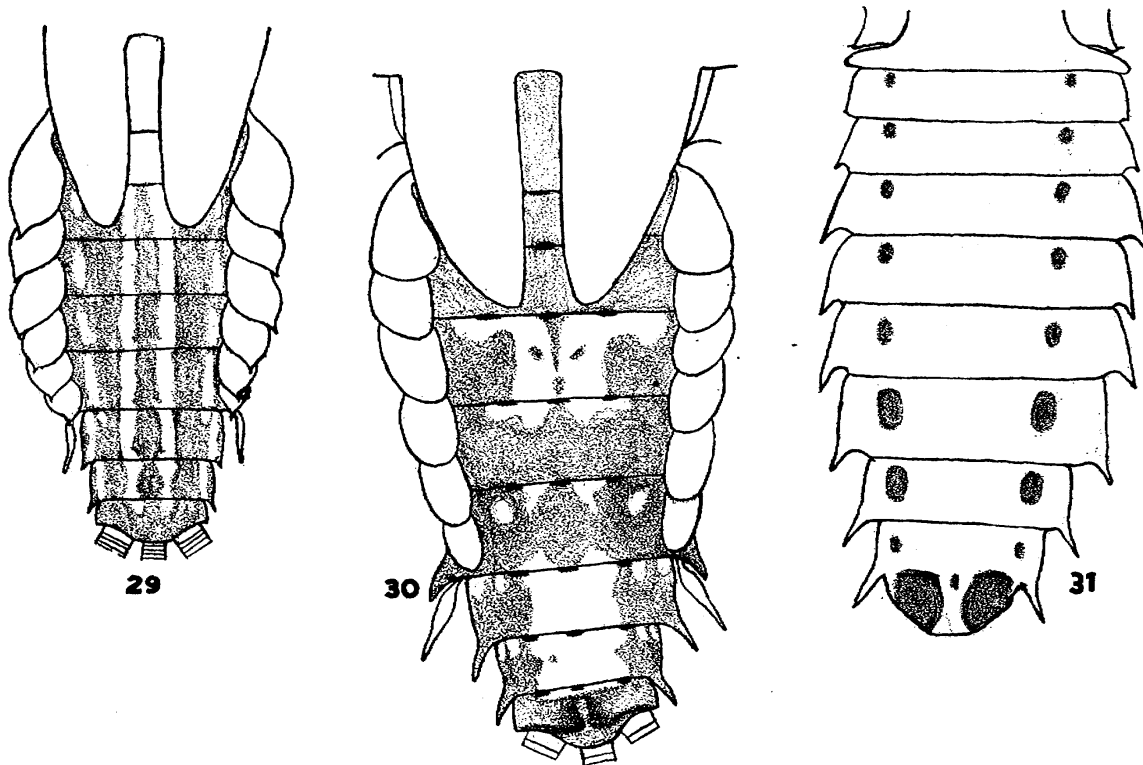


FIG. 29. Dorsal view of nymphal abdomen of *S. interpunctatum canadense*.
 FIG. 30. Dorsal view of nymphal abdomen of *S. femoratum tripunctatum*.
 FIG. 31. Ventral view of nymphal abdomen of *S. femoratum tripunctatum*.

homogeneity or non-homogeneity of the various species, the completeness of the information about the species, their geographical distribution, etc., will all play a part in the investigator's decision. All of these various principles have, of course, been offered time and time again by various writers and are in no sense original. I have restated them merely as a basis for the discussion of the present problem, i. e., the validity or non-validity of the genus *Stenonema*.

As defined by Traver and redefined above, the genus *Stenonema* consists of a moderate number of species that all live within a clearly delimited geographical area. All of these species have a common set of characters which they display during the various stages of their life cycles that distinguish them from other known species. The genus as defined is not unwieldy; it helps to elucidate the phylogeny within the family to which it belongs, and from all present information contains a group of species which are monophyletic in origin.

Finally, it should be noted that Ulmer (1939) added to the difficulties of the nomenclature of the wing venation by misinterpreting the cubital venation of all members of the family Heptageniidae (Ecdyonuridae of Ulmer). Needham, Traver, Hsu, etc. (1935), p. 120) state that in the hind wing "the cubital fork is extended to the wing base. Its intercalary is extended to the base also, so that the cubital triad has come to appear as three complete, subparallel, independent veins." Ulmer does not agree with this interpretation and maintains that in most heptageniids the cubital is represented by a single vein. After much study I am forced to conclude that I can not agree with either point of view. Careful comparison of the venation of the fore and hind wings shows that in generalized genera such as *Siphonurus* and in those genera of the family Heptageniidae that I have studied (*Stenonema*, *Heptagenia*, *Iron*, *Ironopsis*, *Cinygmula*, *Paegnoides*, and *Thalerosphyrus*) the cubitals of the hind wing consist of two veins, a high or convex anterior CuA and a low or concave posterior CuP. Between these two veins detached marginal veinlets may be found as in *Stenonema*, or may be absent as in *Paegnoides*. Note that I have used the terminology advanced by Lameere (1922). This has been done because I am convinced that confusion will always exist about ephemerid venation until Lameere's views and nomenclature are utilized. As a concrete example, if either Needham and Traver or Ulmer had followed Lameere, they would not have faced the difficulties they did in interpreting the cubital veins of the hind wings of the heptageniids and other generalized forms.

BIOLOGY

The flattish nymphs of *Stenonema* are negatively phototactic and positively thigmotactic. They are normally to be found during the day time on the under sides of stones, boards, shells, etc. Although some, such as *Stenonema tripunctatum* and *S. interpunctatum*, are found in lakes, they all seem (at least during the warmer months of the year) to demand a habitat in which currents exist, due either to gravity as in streams or to winds as in lakes. So far as known, they do not live in bodies of waters which are almost, if not completely, devoid of currents, i. e., small ponds, etc. None of them, however, can ever tolerate the torrents. Thus they are normally found in regions of moderate currents.

In lakes the nymphs are found during the summer months in shallow waters and usually close to the shore. In large rivers they are congregated in areas such as rapids and falls and are almost, if not completely, lacking in the intervening quiet waters. During the colder months of the year, the nymphs (both lake and stream forms) are found in the deeper regions. In the case of the lakes that completely freeze over, the nymphs then live in an area where no currents are found.

The nymph feeds by sweeping, scraping and tearing detritus, diatoms, algae, etc., from the substratum. This is accomplished by highly efficient mouthparts.

So far as is known, no species has an egg which undergoes a diapause. The embryonic development proceeds continuously from the time the egg is deposited. Ide (1935a, p. 63) has, however, ascertained that the eggs of three females of *S. interpunctatum canadense*, all deposited at the same time and maintained under identical conditions, continued to

hatch over a period of six weeks. Further the rate of embryonic development seems dependent upon the temperature of the water, being slowed down during periods of lower temperatures. In any case the individuals overwinter as nymphs. Ide (1935b) has studied the nymphal development of *S. interpunctatum canadense*, *S. femoratum tripunctatum* and *S. fuscum*. He studied *canadense* most intensively and although unable to ascertain exactly how many instars it passed through (he identified thirty-five with certainty), it appears that it must shed its cuticula between forty and forty-five times during nymphal development.

The nymph, when ready to emerge, comes to the surface. Apparently some individuals may adhere to some object and partially crawl out of the water, while others emerge without any support. In the latter instances, the emerging subimago utilizes the nymphal exuvia as a raft. So far as is known, none emerges under the water as is found in the genera *Iron* (Ide, 1930) and *Ecdyonurus* (Kimmins, 1941).

After emergence, shedding of the subimaginal pellicle and the nuptial dance, all of which follow the standard ephemerid pattern, the female then deposits her eggs. These are extruded a few at a time from the oviducal openings as the female flies back and forth over the body of water into which she oviposits. Now and then she comes very close to the surface and depresses the abdomen in such a way that it touches the water and the eggs are loosened and washed off. This procedure is repeated many times.

Two types of eggs are found in the genus. The primitive *interpunctatum* complex has ellipsoid eggs with a coiled thread at each pole. In the *tripunctatum* and *pulchellum* complexes, the eggs are ellipsoid but lack the threads and have a gelatinous coat that swells when the egg is deposited in the water.

In the northern part of the range there is normally only one generation a year. Ide (1935a, p. 36) has shown, however, that under abnormal conditions there may be two generations each year. Further south in the range, there seems to be in some species at least two generations per year. Our information on this point is meager.

TAXONOMIC CHARACTERS

As with many ephemerids, imaginal coloration is of considerable importance in this genus. Its coloration conforms with the widespread tendency that has been set forth earlier (Spieth, 1938), namely, that those species which emerge during the spring and early summer are more darkly pigmented than are close relatives that emerge during the summer and early fall. In species of *Stenonema* which emerge over a comparatively long period of time, i. e., *tripunctatum*, the early individuals are much darker than are those that emerge later. In such species a few dark individuals, however, can be observed sometimes in the later part of the season. Whenever this occurs, it is apparently due to the fact that a smallish, spring-fed, cool stream is tributary to a larger, warm body of water. Thus the individuals that matured in the small, cold streams are exposed to the same factors as the dark forms that emerged much earlier from more normal streams in the same vicinity.

The color pattern itself is helpful but often the presence of the generalized melanistic coloration may obscure the pattern. In the wings,

pigmentation (in the form of dashes and infuscations around the cross veins) is of some aid. Color, however, is always variable no matter where or when found.

Structurally the arrangement of the cross veins, particularly the crowding or non-crowding in the region of the bulla, the length of the fore and hind tarsal segments, the ratio of the first to second fore tarsal joint, the ratio of the first tarsal joint to the fore wing length, the shape and spination of the genitalia as well as the size of the individuals, are of value. These are highly variable even to the point of varying between the two sides of the body in the case of bilateral structures, while wing length and body length show great seasonal variation. The paucity of reliable imaginal characters is one of the reasons why so much difficulty has been experienced in the taxonomy of the genus.

In the nymph, the mouthparts, especially the maxillae, the abdominal gills, the posterolateral spines of the abdominal segments, and the tarsal claws, are structural characters that are of considerable value. Again, however, we must depend primarily upon color pattern and coloration. As in the adult this must be employed with caution. Finally geographical origin and emergence time are helpful factors that can be utilized.

***Stenonema tripunctatum* complex**

This complex consists of one species, *S. femoratum*, represented by three subspecies, i. e., *femoratum* Say, *tripunctatum* Banks, and *scitulum* Traver. All of them are restricted mainly to the Mississippi and St. Lawrence drainages although both *femoratum* and *tripunctatum* are found east and south of these two river systems. In the Mississippi drainage and the western part of the St. Lawrence system they, especially *tripunctatum* and *femoratum*, occupy the ecological and to a great extent the seasonal niche that *Stenonema vicarium* and its relatives fill in the eastern part of North America.

Taxonomically the imagoes of these subspecies are difficult to handle because practically all the structural characters and the color pattern are similar intersubspecifically, and extremely variable intrasubspecifically. If it were not for the characters of the wings, all subspecies would unquestionably be merged into one. In addition geographical ranges and emergence periods of the three broadly overlap.

On the basis of present information the complex is represented in Canada, Minnesota, Wisconsin and Michigan solely by *tripunctatum*. In Illinois, Indiana, Ohio, and New York both *femoratum* and *tripunctatum* are present and I have seen intergrades from all these states except Illinois. Both of these subspecies extend further south and also intergrade where they are found together, i. e., Georgia, Oklahoma, and North Carolina. However, in part of this area the picture is further confused by the presence of the third subspecies *scitulum*. It is separated from *femoratum* by emerging after the *femoratum* emergence period, but does intergrade with *tripunctatum*. Thus intergrades of *scitulum* and *tripunctatum* are known from Texas, Alabama, Kansas, Oklahoma, West Virginia, Illinois, Indiana and Ohio. Our knowledge is as yet quite incomplete as to the exact ranges of these three subspecies.

In general, *femoratum* is an early spring form that occupies the area east of the Mississippi, south of the Great Lakes, and west of the Hudson River, and extends into the southern Piedmont; *tripunctatum* occupies the upper and middle Mississippi and St. Lawrence drainages and follows *femoratum* in emergence time; *scitulum* is restricted to Oklahoma, Kansas, Missouri, Illinois and Indiana, emerging from early summer to late fall. *S. femoratum scitulum* and *S. femoratum femoratum* both prefer streams, perhaps exclusively, while *tripunctatum* prefers lakes but also lives abundantly in streams.

Perhaps the last extensive glaciation is responsible for this confused picture. Unquestionably during that period *femoratum* was unable to live in much of the area which it now occupies. In the unglaciated parts of southeastern North America there probably dwelt at that time, especially in the uplands, the *femoratum femoratum* stock. This stock varied from very darkly pigmented early spring emergents to much lighter *tripunctatum*-like late season individuals. Westwardly, this stock was replaced geographically by a *femoratum scitulum* stock, early emergents (seasonally) and lighter colored than the corresponding individuals of *femoratum femoratum*. With the retreat of the glacier, large areas were opened to colonization. We have considerable evidence, especially in *Hexagenia*, that the south central and southwestern populations of ephemerids moved into this area which was exposed by the retreating glacier much faster than did the southeastern stocks. Probably it was mostly a question of drainage patterns which naturally determined the availability of routes of migration. It should be recalled that a river formed by the Wabash, lower Ohio and Mississippi formed an important, perhaps the main stream that drained the water from the glacier. When these two stocks moved back into the exposed region, the *scitulum* stock advanced most rapidly and the *femoratum* stock more slowly. From these immigrating stocks developed *tripunctatum*, but primarily *tripunctatum* seems to be derived from *scitulum*. Thus in the original territories *scitulum* and *femoratum* are still found, and both intergrade with *tripunctatum* but *tripunctatum* being primarily derived from *scitulum* shows greater similarity to that stock.

The complex is characterized as follows:

Eggs.—Ellipsoid without chorionic markings or threads, but with a gelatinous adhesive covering that swells into a thick coat upon contact with the water.

Nymph.—Sturdy, flattened stonemids; galear portion of maxilla with two or three finely dissected setae on distal margin; second segment of maxillary palpus as in fig. 11; dorsal lamellae of gills 1–6 (fig. 20) elongate and rounded distally; 7th gill (Fig. 16) relatively sturdy, hairy and with a single trachea which may branch once; abdomen (fig. 30) with posterolateral spines on 3–9, slender 8th one longest, 9th similar in shape to 8th but shorter; spines on 3–7 stubby.

Imago.—Sturdy stonemids which range in color from deep raw umber to pale creamy white; mesothoracic cross veins of costa, subcosta and radius always crowded in region of bulla, often margined with dark pigment; no transverse dashes of color in wings; genitalia (fig. 10) L-shaped; abdominal tergites 2–8 with three transverse dark dashes on posterior margin.

Stenonema femoratum femoratum Say

Baetis femorata Say, Western Quart. Reporter 2 (11): 162, 1823. Leconte, Complete Writ. T. Say 1: 171, 1857.

Ecdyonurus femoratus Say. McDunnough, Canad. Ent. 57: 190, 1925.

Stenonema femoratum Say. Travel, Biol. Mayflies, p. 311, 1935.

Subspecific Characteristics; Male imago.—General coloration raw umber; head and thorax raw umber with yellowish and fuscous markings; mesoscutum yellow; coxae raw umber; meso- and metafemora yellow, fore femora darker; all femora with medial and distal dark bands; all tibia with proximal darker band; longitudinal wing veins dark, immaculate and fine; mesothoracic cross veins a translucent burnt umber, robust and heavily margined with raw umber; mesothoracic cross veins at bullar region crowded in first six spaces (from costal margin to the M A), with the raw umber infuscations fusing to form a vertical streak in wing membrane; pterostigma burnt umber fading to pale raw umber distally; metathoracic wing with fine cross veins and raw umber apical cloud. Abdominal tergites 2–8 with three transverse black dashes, a median and a lateral on each side, on posterior edge; stigmal spots usually robust; tergites 2–7 yellowish brown, darker distally and laterally; 8, 9, and 10 much darker; sternites yellow, much lighter than tergites, unmarked except for faint ganglionic spots and the outer edge of 10th sternite; genitalia as in fig. 10; cerci smoky yellow, annulate with alternate segmental bands darker and broader; fore wing length 10–13 mm.

Female imago.—Similar to male except for dimorphic differences; fore wing length, 13–17 mm.

Variations in imagoes.—Specimens of *femoratum* which emerge very early in the spring display less variation than those which appear later. The general intensity of the coloration in this subspecies is relatively constant and variability is restricted mainly to the abdominal stigmal markings which vary in all degrees from large, robust ones to complete absence. Likewise the crowding of the cross veins in the bullar area, the amount of infuscation along the cross veins and finally the size of the apical cloud of the hind wing are subject to fluctuation. *S. femoratum* shows intergradation with *tripunctatum* which lives in the same area but emerges later, and thus some specimens may be placed either as dark *tripunctatum* or light *femoratum*.

Nymph.—Differs from all other known members of the *tripunctatum* complex in having the anterior margin of the head emarginate; abdominal sternites typically without the round dark spots that are characteristic of *tripunctatum*; abdominal tergal pattern as in *tripunctatum* but often much obscured even to the extent of lacking the characteristic light areas, especially the one on segments 7, 8, 9, and 10, and thus the entire dorsum appears uniform.

Variations in nymph.—The early spring emergents, i. e., the typical *femoratum*, have the dorsal abdominal pattern obscured and the ventral spots absent or present only on the posterior segments. As the season advances the mature nymphs appear more like the typical clear-cut *tripunctatum* pattern. Examples showing various degrees of intergradation between typical nymphs of *femoratum* and *tripunctatum* have been found.

Holotype.—The type material, which has subsequently been destroyed, was collected by Thomas Say at Cincinnati, Ohio, about the middle of May.

Known distribution.—Illinois, Indiana, Ohio, New York, and Georgia.

Remarks.—This robust, dark, early spring subspecies can be distinguished by the infuscation along the cross veins of the fore wing and the crowding and number of the cross veins in the bullar area from the fore margin to MA₁. This, combined with the infuscation, creates a dark band in the fore wing. The sturdy, chunky nymph is identifiable by the emarginate front edge of the head, the lack of ventral abdominal spots and the obscured dorsal pattern. The nymph appears to be a denizen of small, cool streams which probably accounts for the fact that Say found it to be scarce at Cincinnati. There exists the possibility that the differences between *femoratum* and *tripunctatum* are due to environmental rather than genetic influences. This subspecies has been associated sometimes with *pudica* Hagen. Actually there is no close relationship here; the resemblances are purely superficial. *S. pudica* is really a close relative of *Stenonema vicarium* which in turn belongs to the pulchellum complex.

Say's specimen, as McDunnough has suggested, was probably an imago. If individuals are studied in the clear daylight by means of a hand lens, the wings often, as Say indicates, appear milky. Under a binocular with strong light, this appearance disappears. In reading and checking any original description, it is always helpful to try to utilize the same magnification and lighting that the original investigator used.

***Stenonema femoratum tripunctatum* Banks**

Heptagenia tripunctata Banks, Canad. Ent. 42: 199, 1910. Clemens, Canad. Ent. 45: 255, figs., 1913.

Ecdyonurus tripunctatus Banks. McDunnough, Canad. Ent. 65: 59, 1933.

Stenonema tripunctatum Banks. Traver, Biol. Mayflies, p. 332, 1935.

Stenonema birdi Traver, Biol. Mayflies, p. 306, 1935.

Subspecific Characteristics; Male imago.—General coloration highly variable, ranging from raw umber to creamy white; except for wings the color pattern and all structures are similar in all respects to *femoratum*, from which it varies only in the reduced intensity and tone of coloration. Mesothoracic wings with cross veins slightly, if at all, infuscated, with the bullar region having only those cross veins in the costal, subcostal and radial areas crowded and with the general intensity of coloration paler than in *femoratum*. Otherwise, wing as in *femoratum*. Metathoracic wings without apical cloud and with all veins pale or almost so; fore wing length, 10–13 mm.

Female imago.—Similar to male except for dimorphic differences; fore wing length, 13–17 mm.

Variations in imagoes.—The amount of color variation is large. The early spring forms are dark and only by drawing an arbitrary line can they be separated from *femoratum*. Late summer specimens are extremely pale, lacking all dark tints except for the pterostigmal area of the fore wing and the medial dashes on the posterior margins of the abdominal tergites. Such specimens often lack the lateral abdominal

dashes which, with the medial one, give the characteristic *tripunctatum* appearance to members of the complex. Small individuals also have relatively large compound eyes, and in the smaller males the eyes more nearly approximate each other dorsally than in the larger individuals.

Nymph.—Similar to *femoratum*; the head is not emarginate on anterior margin, but may have three small, pale spots on fore edge; abdominal tergal pattern (fig. 30) never obscured; abdominal sternites 2-8 (fig. 31) with a lateral pair of brown spots on each segment; sternite 1 lacks the brown spots and sternite 9 has two pairs, an anterior and a posterior pair. These spots increase in size progressively from segments 2-7; those on the 8th sternite are slightly smaller than on the 7th; the anterior pair on the 9th is much smaller while the posterior pair is the largest of all. A small median dash may be present between this last pair.

Type.—Milwaukee Co., Wis., 22.VII.1908, S. Graenicher collector, in Mus. Comp. Zool.

Known distribution.—Ontario and Quebec, New York, Wisconsin, Minnesota, Ohio, Michigan, Indiana, Illinois, Pennsylvania, Missouri, Oklahoma, Kansas, Texas, Alabama, Georgia, and North Carolina.

Remarks.—This is one of the most variable subspecies of the genus insofar as coloration of the imago is concerned. The nymph, however, seems rather constant. It lives in the quieter waters of streams of various sizes and seems particularly well suited to the lakes of the glaciated areas. The three dark dashes on the abdomen, the crowding of the cross veins in the first three areas of the bullar region, and the lack of the dark cloud in the apex of the hind wing will separate the subspecies from all others. *S. birdi* Traver represents a dark *tripunctatum*. It is interesting to note that *S. femoratum tripunctatum* has not been found in southeastern New York or in those states that lie east of the Hudson River.

Stenonema femoratum scitulum Traver

Stenonema scitulum Traver, Biol. Mayflies, p. 330, 1935.

Subspecific Characteristics; Male imago.—Differs from *tripunctatum* only in the small size and the presence of the brown cloud in the apex of the metathoracic wing; the compound eyes appear relatively large and nearly contiguous; length of fore wing, 8-10 mm.

Female imago.—Similar to male except for dimorphic differences; length of fore wing, 9-11 mm.

Variations in imagoes.—The color variation of this subspecies parallels that of *tripunctatum* except that no individual is as dark as the extremes of *tripunctatum*. The amount of apical infuscation varies considerably but is always present in both sexes.

Nymph.—Unknown; unquestionably close to *tripunctatum*.

Type.—Latimer Co., Oklahoma, 10.VI.31 (R. D. Bird), No. 1343.1 in Cornell Univ. Coll.

Known distribution.—Kansas, Oklahoma, Missouri, Illinois and Indiana.

Remarks.—Except for the dark tip of the hind wing, individuals in this subspecies would invariably be considered as small specimens of *tripunctatum*. In fact, individuals that have lost the hind wings cannot

be placed with certainty, although the small size is a dubious criterion. The comparatively large size of the male's compound eyes is not reliable since small individuals of *tripunctatum* also show this character. Likewise I have specimens of *tripunctatum* that occasionally display a small amount of infuscation in the apex of the hind wing.

Information now available indicates that *scitulum* nymphs are stream dwellers that emerge from June to September. Probably it commences its emergence later than does *tripunctatum* and continues later in the season, but there is a considerable period when they are both emerging at the same time.

Stenonema interpunctatum complex

This complex consists of the species *gildersleevei*, *carolina* and *interpunctatum*. *S. gildersleevei* and *carolina* occupy relatively small geographical areas, i. e., the uplands and hill country of the eastern United States. Individuals of *gildersleevei* and *carolina* are relatively uniform and, upon the basis of present information, these species display no subspeciation. *S. interpunctatum* in contrast occupies a wide area and is found in lakes and streams, both lowland and upland, and the individuals are highly variable. Numerous species have been described in the past but, employing numerous specimens as a basis, I have synonymized a number of these species and reduced the remainder to subspecific status. Due to a paucity of morphological characters, we are forced to rely mainly upon such characters as color for subspecific determinations. Genitalic as well as distinct, clear-cut color differences are available, however, for the separation of the three species. Within *interpunctatum*, degree of difference rather than absolute difference is the main delimiting criterion. No experimental evidence exists to indicate how much or how little coloration of the imaginal individuals of this genus is independent of the environment in which the nymph develops. Circumstantial evidence (Spieth, 1938) indicates, and such evidence is constantly accumulating, that the environment may play a part in determining the *degree* of coloration of the adult.

The complex is characterized as follows:

Egg.—Ellipsoid without chorionic markings but with a long terminal thread at each end which is coiled when oviposited, but which Morgan (1913) says uncoils in the water. In addition, there are several other shorter and finer chorionic threads.

Nymph.—Slender, appearing more delicate than the robust, chunky *femoratum* nymphs; galear portion of maxilla with nine or ten heavy setae that are comb-like on their distal ends; 2nd segment of maxillary palpus as in fig. 14; dorsal lamellae of gills 1-6 (fig. 22) pointed distally; tracheal distribution of these lamellae reminiscent of that found in *Heptagenia maculipennis*; 7th gill (fig. 16) sparsely setose, often with as many as three tracheal branches; no spines (figs. 19 and 29) on posterolateral corners of abdominal segments 1-6, very small spines on 7, and small slender spines, equal in length, on 8 and 9.

Imago.—Slender stenonemids that range in color from piceous brown with yellow tones to pale translucent whitish yellow, tinged with greenish; cross veins in the proximal regions of the costal and radial areas aslant, thickened and margined; in the bulla region of radial area

often a black dash connects the cross veins; genitalia (figs. 2, 4 and 6) not boot-shaped and, except for *carolina*, with a group of spines on lateral margin.

Remarks.—This complex, on the basis of the nymphal mouth parts, especially the maxillae, the nymphal gills, both shape and tracheation, the spination of the nymphal abdomen, the shape of the adult styliiger plated and the penes, is more closely related to *Heptagenia* and *Ecdyonurus* than is any other part of *Stenonema*.

Stenonema carolina Banks

Heptagenia carolina Banks, Proc. Acad. Nat. Sci. Phila. 66: 616, 1914.

Ecdyonurus carolina Banks. McDunnough, Trans. Roy. Soc. Canada 19: 207, 222, 1925.

Stenonema carolina Banks. Traver, Jour. Elisha Mitch. Sci. Soc. 48 (2): 197, 1933. Biol. Mayflies, p. 309, 1935. Jour. Elisha Mitch. Sci. Soc. 53 (1): 38, 1937.

Specific Characteristics; Male imago.—General color gallstone yellow, faintly tinged with green; no black marking on face; eyes small and relatively widely separated; vertex tinged with orange; prothorax with slender oblique black streak on each side; meso- and metathorax unmarked; thoracic femora with medial and distal black dashes, but medial dash is lacking on the metathoracic femur; first tarsal joint of fore leg slightly less than one-half of second; radial cross veins proximal to the bulla and costal cross veins proximal to stigmal area aslant and margined with black; radial cross veins in bullar area rather heavily margined, but only rarely fused to form a dash; wing membrane of stigmal area and adjacent wing tip tinged with tawny; marginal veinlets of wing tips not thickened. Posterior margin of abdominal segments black with pigmentation heavier on tergites than on sternites; genitalia as in fig. 4; forceps pale fuscous; cerci pale fuscous with joinings very narrowly black; fore wing length, 8–12 mm.

Female imago.—Similar to male except for dimorphic differences; fore wing length, 11–14 mm.

Variations in imagoes.—Considerable size difference (8–12 mm. wing length) exists in the males of this species. The difference appears to be seasonal since the small individuals were collected late in the summer (August). Early season specimens from New York are darker than normal due to a brownish coloration on the dorsal surface, which somewhat obscures the greenish tinge. Otherwise, the individuals of the species seem remarkably constant.

Holotype.—Black Mt., N. C., May, 1913 (north fork Swannanoa Riv.). Mus. Comp. Zool.

Known distribution.—The species is found in the upland waters of eastern North America. *S. carolina* has been reported from New York, West Virginia, Tennessee, North Carolina, and South Carolina. In Canada it has been taken at Covey Hill and Knowlton, Quebec, which are located on northern outliers of the Appalachian and Green Mountains. It is absent from the lowlands of the St. Lawrence River drainage. Eventually it will probably be reported, in addition to the above areas, from the uplands of Alabama, Georgia, Virginia, Pennsylvania, Connecticut, Massachusetts, Vermont, and possibly New Hampshire.

Remarks.—Imagoes of *carolina* can be distinguished from all other species and subspecies of the *interpunctatum* complex by the male penes, the clear greenish-yellow coloration, and the almost total lack of black markings. The nymphs, on the basis of present information, can be identified by the lack of the continuous dorsal, longitudinal, light abdominal stripes. Since the imagoes lack stigmal spots there is no indication of these showing through the nymphal cuticle as is the case in *frontale*. Living in a relatively small area that is ecologically rather uniform, this species exhibits the least variation of any of the *interpunctatum* complex.

***Stenonema gildersleevei* Traver**

Stenonema gildersleevei Traver, Biol. Mayflies, p. 315, fig. 92, 1935.

Specific Characteristics; Male imago.—General color yellow but darker dorsally, especially on abdomen; heavy black mark on clypeus under each antenna; black mark on carina at similar level, sometimes forming with lateral dashes a continuous transverse band; eyes normal for *interpunctatum* complex; vertex reddish-brown; prothorax with oblique black streaks; meso- and metathoracic scutella piceous; pterothoracic pleura unmarked except for a slight darkening before the mesothoracic coxae; pterosternum unmarked; all femora with medial and distal piceous areas; first tarsal joint of fore leg usually one-half of second; radial and costal cross veins proximal to bulla only slightly aslant, sometimes faintly thickened, but never margined; bullar area usually with 1-2 radial cross veins which are lightly margined but never joined to form dash; costal and subcostal membrane tinged with yellowish-green; veinlets of fore wing tip faintly thickened. Abdomen dorsally with yellow background; tergites heavily infuscated with piceous, especially along median line and posterior margins; as this infuscation fades out laterally, the combination with the yellow ground color creates a brownish color; the anteriolateral corners of the tergites lack the piceous infuscation and therefore appear yellow. Small submedian lighter areas are usually found in the deeply infuscated dorsal region. The posterior tergites are also much less infuscated than are the anterior ones. Sternites yellow with piceous infuscation along the median line, heaviest just behind the anterior margins of each sternite; ninth sternite usually tinged with red; genitalia (fig. 6) with penes longer than in *interpunctatum* and with reduced distolateral expansion; length of fore wing, 10.5-12 mm.

Female imago.—Similar to male except for dimorphic differences; length of fore wing, 12-15 mm.

Variations in imagoes.—Size variations in the species are small. The length of the male first fore tarsal joint when compared to the second is somewhat variable. Usually it is about one-half the length of the second, but in some individuals it is less than one-half and in others it is greater than half the length of the second. Thus measurements of 19 male fore legs show the ratio of the second tarsal/first tarsal to range from a minimum of 1.71 to a maximum of 2.30. Statistical analysis of this sample gives an arithmetical mean of 1.99 with a standard deviation of 0.17 and a V of 8.47. The estimated range for

this ratio is 1.48–2.50. The amount of melanistic pigmentation, especially of the abdomen, varies considerably. The abdominal tergites of some specimens are intensely and broadly blackened. These individuals have a complete frontoclypeal band, have the abdominal sternites considerably darkened and show no signs of abdominal stigmal spots due to the covering effect of the dorsal coloration. In others the black pigment of the abdominal tergites is much reduced and mainly concentrated near the medial line. In such specimens the clypeus has a dash under each antennae and a blackish mark on the carina, while the abdominal sternites may almost lack any dark colors and stigmal spots are visible, especially on segments 2–6.

Nymph.—Head without anterior light marginal area; abdomen with a narrow transverse piceous stripe on terminal edge of each tergite; medial part of tergites, especially the anterior ones, infuscated; a pair of submedial, light areas on each tergite, these tending to be oval and not linear, small on the anterior segments but longer posteriorly. These light areas give the abdomen the lined appearance typical of the *interpunctatum* complex, which is less evident than in *canadense* but more evident than in *carolina*. Sternites immaculate except for dark lateral dashes on segments 7–10.

Holotype.—Kirtland, O., August 31, 1930 (spring-fed stream of Gildersleeve Mt.), No. 1337.1 in Cornell Univ. Coll.

Known distribution.—The species has been collected in northern and southern New York and northeastern Ohio. The intensive collecting done by numerous Canadian entomologists has failed to discover any specimens of *gildersleevei* in Canada. It probably occupies a limited area in the northern Appalachians.

Remarks.—Imagoes of *gildersleevei* can be readily distinguished by the male genitalia, the concentration of black pigments on the medio-dorsal part of the abdomen, and the unmarginated, almost vertical radial and costal cross veins. The yellowish ground color is also distinctive. Unquestionably it has been confused in the past with *canadense*. *S. canadense*, however, has the piceous pigments much more widely distributed, especially on the thorax, and the marginated, slanting cross veins plus the usually present bullar dash are distinctive characters for its separation from *gildersleevei*.

The type of *gildersleevei* was reared from the mature nymph which was found in a cold spring-fed stream. This holotype, plus the allotype and 8 paratypes all from the same locality, emerged in late August and early September. Traver also reared specimens at the same time from a nearby locality which she described as *ohioense*. She indicates (1935, pp. 316 and 322) that *ohioense* is rather closely related to *gildersleevei*. Study of the type of *ohioense* shows it to be a synonym of *canadense* and not closely related to *gildersleevei*.

Stenonema interpunctatum Say

This species consists of four subspecies, *interpunctatum* Say, *canadense* Walker, *frontale* Banks, and *heterotarsale* McD. *Stenonema candidum* Trav., *conjunctum* Trav., *major* Trav., *pallidum* Trav., and *proximum* Trav. have been described as species of the *interpunctatum* complex, but are synonyms of the four subspecies listed above. Traver

(Biol. of Mayflies, p. 316) synonymized *Stenonema affine* Traver with *heterotarsale* McD. Study of numerous individuals from a large number of localities, including all the types except that of *interpunctatum* s. str. which is nonexistent, has made it possible to modify the taxonomy of this complex.

Geographically *interpunctatum* is the most widespread species of *Stenonema* and apparently is found throughout the entire range of the genus. The nymph lives in streams, or in bodies of water where stream conditions are simulated, but it can not tolerate swift currents. It seems to be more hardy and adaptable than are most species of the genus.

The emerging imagoes become smaller in size and lighter in color as the season progresses, thus paralleling the condition found in *S. tripunctatum*. This phenomenon of size and pigment reduction as the season progresses is apparent only in areas which are ecologically uniform and in which only one subspecies is present. In areas where subspecies overlap and intergrade, the resultant mixed population may appear not to follow this pattern, especially so far as color is concerned. The picture is further complicated in such areas by seasonal and ecological isolation. Thus Ide (1935, p. 46) found that *heterotarsale* and *canadense*, both of which live in the Mad River, Ontario, overlap only slightly in their ecological and seasonal occurrence; *canadense* emerges earlier in the season and lives further up-stream, i. e., in colder water. Only at the upper range of *heterotarsale* and the lower limit of *canadense* do they overlap both in space and time. In regions where a large warm stream has numerous small spring-fed tributaries, it is to be expected that series can be collected which will show both subspecies to be plentiful at the same time, i. e., late emergents of the early form from the cool tributaries and early emergents of the late form from the warm stream.

Adequate sampling from such an area will always bring to light numerous intergrades. Sometimes the collection is complex, e. g., a series that I collected July 1 from the Lachine Rapids on the St. Lawrence River contains typical specimens of *canadense*, *frontale*, and *heterotarsale* and all intergrades between them; one specimen, except for the long first tarsal joint, can not be told from typical specimens of *interpunctatum* from southern Indiana.

The characters employed to separate these subspecies of *interpunctatum* deserve a word of comment. In the past, genitalic differences have been used but careful study of a series of genitalic preparations convince me that within the species any differences are either individual or caused by the technique used in the preparation of the specimen. Likewise, the length of the first tarsal segment has been used and is of considerable value but is highly variable. The ratio derived by dividing the length of the second segment of the male fore tarsus by the length of the first segment provides a character that can be handled statistically to good advantage. Likewise the ratio derived from the fore wing length divided by the first segment of the male fore tarsus is useful. Due to the paucity of such characters, coloration has been commonly utilized, especially the following: (1) the amount of black pigmentation on (a) the clypeus, (b) the prothorax, (c) the pterothoracic pleura, (d) the abdomen, especially the dorsum, and (f) the

cercal joinings; (2) the presence or absence of stigmal spots on the abdominal tergites, and (3) the bullar streak of the fore wings. All of these characters exhibit great variability—seasonally as well as individually. Size parallels coloration in variability. On the basis of present information, it can be said that in any given locality the early seasonal emergents are larger and darker than those that emerge later. Size and coloration thus display both seasonal and individual variation, and the latter type is of considerable magnitude.

Those species listed above which have been synonymized all appear to be color variants of the four subspecies that have been retained. The four subspecies, comprising the species, are distributed as follows: *interpunctatum s. str.* is found mainly in the lower and middle Mississippi and the Ohio River drainages; *canadense* in eastern Canada, in the northern tier of eastern and mid-western states, and extending southward along the eastern highlands; *frontale* in the eastern part of the United States, extending westward along the shores of the eastern Great Lakes. Finally, *heterotarsale* is centered around Lake Erie and Lake Ontario and extends westward into northern Indiana and Illinois.

Stenonema interpunctatum interpunctatum Say

Baetis interpunctata Say, Jour. Acad. Nat. Sci. Phila. 8: 41, 1839. Complete Writings of Thomas Say, 2: 411.

[nec] *Heptagenia interpunctata* Say. Eaton, Mono. Rec. Ephem., pt. 4: 267, 1885. Clemens, Canad. Ent., 56: 17, 1924.

Ecdyonurus interpunctatus Say. McDunnough, Canad. Ent., 65: 42-43, 1933.

Stenonema interpunctatum Say. Traver, Biol. Mayflies, pp. 317-318, 1935.

Stenonema affine Traver, J. Elisha Mitchell Sci. Soc. 48: 184, 1933.

Stenonema pallidum Traver, Biol. Mayflies, pp. 323-324, 1935.

Subspecific Characteristics; Male imago.—General color chrome yellow, faintly tinged with green; black dot on clypeus under each antenna; eyes normal in size; vertex reddish-brown; prothorax with oblique black streak on each side; pterothorax unmarked except for mesonotum which is normally pale chestnut; metathoracic femur with distal dark band but normally lacking medial; second tarsal/first tarsal ratio from .1.8 to 3.5 with about 2.6 as the most common; radial cross veins proximal to the bulla and costal cross veins proximal to the stigmal area aslant and margined; a black dash in radial area at level of bulla, often connecting two or more cross veins; wing membrane of costal and subcostal areas yellowish, with stigmal area and wing tip slightly darker; marginal veinlets of fore wing tip thickened; wing length varying from 5.8 to 10.1 mm. with about 8 mm. as the most common; abdominal tergites 1-8 pale translucent yellow; distal part of 8 and all of 9 and 10 ferruginous; all tergites with narrow piceous posterior margin; sternites unmarked; genitalia (fig. 2) cream colored; cerci pale with joinings faintly darkened.

Female imago.—Similar to male except for dimorphic differences.

Variations in imagoes.—The description given above is from a typical specimen collected at New Harmony, Indiana. Individuals that emerge in the early spring tend to be large and somewhat darkened due to the dorsum of the abdomen being infuscated with blackish while the metathoracic leg may have a dark medial band. Some individuals, irrespective of emergence time, show faint stigmal spots such as are

normally found in *frontale*. Measurement of 20 male fore legs gave an observed range for the second tarsal/first tarsal ratio of 2.15 to 3.5 with a mean of 2.63, a standard deviation of 0.28 and a coefficient of variation (v) of 10.65. The standard error of the mean is $\pm .063$. The distribution of the sample is positively skewed. The estimated range is 1.79 to 3.47. The forewing of 20 specimens gave an observed range of 6.6–9.05 mm. with a mean of 7.98 mm., a standard deviation of 0.72 and a coefficient of variation of 9.02; the standard error of the mean is $\pm .16$. The estimated range of the wing is 5.82–10.14 mm. The wing length, unlike the tarsal ratio, is influenced by seasonal variation.

Known distribution.—Mississippi River drainage, especially the middle and lower parts, and the Ohio River drainage.

Remarks.—The subspecies can be identified by the general yellow coloration, the lack of dark markings on the pterothoracic pleura, and the typically short first segment of the fore tarsus. As mentioned above, Say's description fits material that is possibly topotypical. Large specimens of *heterotarsale* may be confused easily with this subspecies and we may expect to find specimens of *heterotarsale* with fore wings that equal or exceed the longest wings of *interpunctatum*. The male second/first tarsal ratio and the dependent wing/tarsal ratio seem to be good criteria and the only fairly dependable ones available for separating some individuals of *heterotarsale* from *interpunctatum*. It is possible that specimens from the southeastern United States which have been considered as belonging to *interpunctatum* may belong to *frontale*. This also applies to Traver's *pallidum*. The reasons for such possible deductions are discussed below in the full discussion. In any instance, more specimens from such areas will be needed before a final decision can be drawn.

***Stenonema interpunctatum canadense* Wlk.**

Baetis canadensis Walker, List Neuropt. Ins. Brit. Mus., pt. 3: 569, 1853.

Ecdyurus canadensis Walker. Eaton, Revisional Mono. Rec. Ephemeroptera, part 4: 278, 1885.

Heptagenia canadensis Walker. Clemens, Canad. Ent. 45: 258, 1913.

Ecdyonurus canadensis Walker. McDunnough, Trans. Royal Soc. Canad., 19 (sec. 5): 222, 1925.

Stenonema canadense Walker. Traver, Biol. Mayflies, p. 307, 1935. Ide, Canad. Jour. Res., 12: 447–457, figs., 1935. Spieth, Ann. Ent. Soc. Amer., 33: 333, 1940.

Stenonema ohioense Traver, Biol. of Mayflies, p. 322, 1935.

Subspecific Characteristics; Male imago.—General coloration typically yellowish with enormous amount of piceous color, especially dorsally; superficially much like *S. gildersleevei* Trav. Differs from *interpunctatum* mainly in the increased amount of black infuscation. Clypeus with horizontal piceous band; eyes normal; vertex as in *interpunctatum*; prothorax with oblique bands and lateral markings; pterothorax with oblique, piceous pleural streaks from each wing base; mesonotum darker than in *interpunctatum* and with scutellum piceous; metascutellum dark; metathoracic femur with both distal and medial bands; first tarsal joint about as in *interpunctatum*; the second tarsal/first tarsal ratio varying from 1.6 to 3.1 with 2.3 as the most common; wings marked as in *interpunctatum* but more intensely; bullar area usually ferruginous.

Dorsum of abdomen broadly piceous with scimitar-shaped, paired, subdorsal pale streaks; areas that are not infuscated with piceous translucent to transparent and not colored with yellow as in *gildersleevei*; wing length varying from 6.6 to 12.1 mm. with about 9.3 mm. as the most common; sternites hyaline or semihyaline but often tinged with black; genitalia as in *interpunctatum*; cerci pale with dark joinings.

Female imago.—Similar to male except for dimorphic differences.

Variations in imagoes.—A large amount of variation exists in the amount of black infuscation which characterizes the subspecies. This can be attributed to three causes, but which is responsible in any particular individual it is impossible to say. These causes are: (1) individual variation; (2) seasonal variation, late seasonal emergents usually being much lighter in color; (3) interbreeding with lighter colored subspecies. The lightly infuscated individuals invariably display robust stigmal spots on the abdominal tergites. Apparently these are obfuscated in the darker individuals by the dark coloration of the tergites.

Measurement of 43 male fore legs gave an observed range for the second tarsal/first tarsal ratio of 2.00 to 3.00 with a mean of 2.34, a standard deviation of 0.257 and a V of 11.0. The standard error of the mean is $\pm .039$. The distribution of the sample is positively skewed. The estimated range is 1.57 to 3.10. The fore wing length of 26 male individuals ranges from 8.28 to 9.95 mm. with a mean of 8.96, a standard deviation of 0.389 and a V of 4.34. The standard error of the mean is $\pm .076$ and the estimated range is from 7.8–10.13 mm. Sometimes individuals are found that agree with *canadense* except for long first tarsal joints. These apparently are intergrades with *heterotarsale*.

Nymph.—Head without anterior light marginal area; abdomen (fig. 29) darker than thorax; four longitudinal abdominal streaks, two submedianly and the others near lateral margin; future stigmal dots of imago often visible; abdominal sternite with two light brown lateral streaks on white background; ninth sternite with lateral and posterior margins infused with same color.

Holotype.—Canada, in Walker Coll. in Brit. Mus. (Nat. Hist.). Nymph associated with imago by Clemens, 1913, at Go-Home-Bay, Georgian Bay, Ontario, Canada.

Known distribution.—Quebec, Ontario, Minnesota, Michigan, Illinois, Indiana, Ohio, New York, Connecticut, New Jersey, West Virginia, Tennessee, and North Carolina.

Remarks.—Clemens (1924) first indicated that this is a subspecies of *interpunctatum*. Superficially it is nearer to *S. gildersleevei* than is any other species of the complex. The genitalia, the color pattern, and the fore wing pattern are reliable means of separating the two. Typical specimens can not be confused with any of the other subspecies of *interpunctatum*. Lightly infuscated individuals, regardless of the cause, are extremely difficult to separate from *frontale*, or, if they also lack the stigmal spots, from *interpunctatum* and *heterotarsale*. Clemens (1913) reared and adequately described the nymph. It is typical of the *interpunctatum* complex. Upon the basis of my present information, I can not separate it from nymphs which I think belong to *interpunctatum*.

Stenonema interpunctatum frontale Banks

Heptagenia frontalis Banks, *Canad. Ent.*, 42: 199, 1910. Clemens, *Canad. Ent.*, 45: 259, fig. nymph, 1913.

Ecdyonurus frontalis Banks. McDunnough, *Canad. Ent.*, 62: 61, 1930. *Canad. Ent.*, 65: 43, 1933.

Stenonema frontale Banks. Traver, *Biol. Mayflies*, p. 312, fig., 1935.

Stenonema candidum Traver, *Biol. Mayflies*, p. 308, 1935.

Stenonema conjunctum Traver, *Biol. Mayflies*, pp. 309-310, 1935.

Stenonema majus Traver, *Biol. Mayflies*, p. 320, 1935.

Stenonema proximum Traver, *Biol. Mayflies*, p. 325, 1935.

Subspecific Characteristics; Male imago.—General color chrome yellow, faintly tinged with green; black dash on clypeus under each antennae and a spot on carina at the same level; eyes normal; vertex as in *interpunctatum*; prothorax with oblique band and black dot on posterolateral corner; pterothorax with oblique piceous pleural streaks from each wing base; mesonotum darker than in *interpunctatum* but lighter than in *canadense*; meso- and metascutella yellow; metathoracic femur with medial and distal bands; second tarsal/first tarsal ratio more variable than in *interpunctatum* or *canadense*, ranging from 1.2 to 3.5 with approximately 2.3 as the most common; wings as in *interpunctatum* except bullar dash is often restricted and does not join several cross veins; the wing length varies from 6.6-12.1 mm. with about 9.38 mm. as the most common. Abdomen as in *interpunctatum* except for heavier posterior black margins and the presence of prominent robust stigmal spots; genitalia as in *interpunctatum*; cercal joining darker than in *interpunctatum*.

Female imago.—Similar to male except for dimorphic differences.

Variations in imagoes.—Normal variation appears to be large and, especially where *frontale* intergrades with populations of *canadense* and *heterotarsale*, an extremely variable population is formed. Measurement of 56 male fore legs gave an observed range for the second tarsal/first tarsal ratio of 1.6-3.2, with a mean of 2.37, a standard deviation of 0.39 and a V of 16.60. The standard error of the mean is $\pm .052$. The distribution of the sample approaches that of normal but indicates considerable variability for this character of the subspecies. The estimated range is from 1.19-3.55. The fore wing of 42 males varies from 6.77-11.2 mm., with a mean of 9.38 mm. and a standard deviation of 0.92 and a V of 9.7. The standard error of the mean is $\pm .16$ and the estimated range is from 6.62-12.14 mm.

Nymph.—Often with a pale spot on anteromedial margin of head; dorsal abdominal color pattern (fig. 19) distinctive due to the reduction of the longitudinal light streaks that are present on the nymphal abdomens of the other subspecies. Sternites as in fig. 28.

Holotype.—Middlesex Falls, Mass., August. In Mus. Comp. Zool. Coll.

Known distribution.—Nova Scotia, Quebec, Ontario, New Hampshire, Vermont, Massachusetts, New York, and Ohio.

Remarks.—Typical specimens, either as nymphs or imagoes, of this subspecies are easily identified, the nymphs by the distinctive dorsal abdominal pattern and the adults by a combination of stigmal spots, thoracic coloration, and wing pattern. All degrees of intergradation exist between *frontale* and *canadense*, *frontale* and *heterotarsale*, and

frontale and *interpunctatum* in both the nymphal and the imaginal stages. The abdominal pattern of the nymph figured by Traver (1935, Pl. 24) is not typical for *frontale* and probably indicates *canadense* hybridization. The genitalic differences between *canadense* and *frontale* as given by Traver (1935, fig. 91) apparently are individual rather than specific or subspecific. *S. candidum* Trav., *conjunctum* Trav., *majus* Trav., and *proximum* Trav. are not quite typical examples of *frontale*. Actually, study of the types indicates that they represent intergrades (or environmental variants) of *frontale* with other subspecies. Since they are more nearly like *frontale*, I have synonymized them with it. *S. candidum* deserves mention in that the differences, given by Traver (1935), are restricted to the genitalia. According to the original description (Traver, 1935, p. 308) only three individuals of *candidum*, two males and one female, were known. At Cornell I found the male holotype from which the genitalia had been detached. Except for the penes it agreed in all respects with *frontale*. The mounted genitalia which merely bore the same data as the type, but no number or other identifying mark that would connect it with the holotype, agree with Traver's figure and certainly resemble those of *S. carolina*. Unfortunately the male paratype, except for a mounted wing and the nymphal skin, has been lost. These remaining parts bear facies of *S. frontale*. Perhaps one of two things has occurred: (1) either the genitalia attributed to the holotype are those of a specimen of *carolina*, or (2) the holotype was an aberration lacking the lateral genitalic spines. In any instance, I consider it to be a synonym of *frontale*.

***Stenonema interpunctatum heterotarsale* McD.**

Ecdyonurus heterotarsale McDunnough, Canad. Ent., 65: 42, 1933.

Stenonema heterotarsale McDunnough. Traver, Biol. Mayflies, p. 316, 1935.

Subspecific Characteristics; Male imago.—General coloration as in *interpunctatum*. Differs from *interpunctatum* in the lack of black markings and the greater length of the first fore tarsal joint. Clypeus unmarked; head otherwise as in *interpunctatum*; prothorax unmarked; pterothorax without black marks; mesonotum, metanotum, wings, and markings on legs as in *interpunctatum*. First segment of fore tarsus long; the second tarsal/first tarsal ratio ranging from 1.0–2.1 with 1.6 as the most common. Wing length varies from 5.0–10.2 mm. with about 7.5 mm. as the most common. Abdomen, including genitalia and cerci, as in *interpunctatum*.

Female imago.—Similar to male except for usual dimorphic differences.

Variations in imagoes.—Typical specimens as described are not very numerous. Only the size and long first tarsal joint seem relatively constant. Many individuals, although much lighter than those of *interpunctatum*, do have some dark markings. This is especially true of the clypeal marks, the oblique prothoracic marks, and stigmal marks. Measurement of 44 male fore legs gave an observed range for the second tarsal/first tarsal ratio of 1.15–1.95 with a mean of 1.57, a standard deviation of 0.18 and a V of 11.4. The standard error of the mean is $\pm .026$. The distribution of the sample approaches normal. The estimated range for this ratio is 1.03–2.10. The fore wing length of 22

individuals ranges from 6.18–9.22 mm. with a standard deviation of 0.87, a V of 11.57, and a mean of 7.59. The standard error of the mean is $\pm .187$ and the estimated range is 4.95–10.23 mm. Thus, both wing length and tarsal ratios may be expected broadly to overlap those of the other subspecies. Note that seasonal emergence plays a large role in wing length.

Nymph.—Undescribed, but probably close to *interpunctatum*.

Holotype.—Ottawa Golf Club, Quebec, 2.VII.24, No. 3527 Canadian Nat. Coll., Ottawa.

Known distribution.—Northern Ohio, northern Indiana, northern Illinois, Michigan, northwestern New York, Ontario, southwestern Quebec. This subspecies seems to be centered around Lake Erie and Lake Ontario.

Remarks.—*S. affine* Traver (1933) is probably a synonym of *interpunctatum* s. str. rather than of *heterotarsale* as she suggested (Traver, 1935). *S. heterotarsale* emerges on the average later in the summer than does any of the other subspecies of *interpunctatum*. It is possible that those specimens that have been placed in *heterotarsale* are merely late season individuals of *frontale*. Certainly size and fore tarsal segmental length are highly variable, and the casual student of ephemeroptera will find *heterotarsale* a rather exasperating subspecies to delimit.

DISCUSSION AND STATISTICS OF THE STENONEMA INTERPUNCTATUM COMPLEX

Study of all existing types and various collections (i. e., Cornell University, Museum of Comparative Zoology, Canadian National Collection, University of Michigan, Illinois Natural History Survey, American Museum of Natural History, plus my own collection) show the presently accepted species picture of the *interpunctatum* complex to be questionable. *Stenonema carolina* Banks and *S. gildersleevei* Traver are distinct species that can be definitely delimited and identified. The remaining nine species of the complex present a complicated and irritating problem. Comparison of numerous individuals with the holotypes shows that some specimens correspond closely with the types, but many individuals are clearly intermediate. Study of the available paratypes shows that many of them vary considerably from the holotypes. When confronted with a large series, especially from the areas around the Great Lakes, more "intermediate" than "typical" specimens are invariably found. All evidence indicates that some of the existing names need to be synonymized and the remainder reduced to subspecific status.

Such a revision seems rather drastic and I wished to study all available evidence before reaching a final decision. The following procedure was therefore undertaken. Utilizing my own collections and those of the American Museum of Natural History, all specimens of the complex, other than those of *S. carolina* and *S. gildersleevei*, were sorted according to geographical distribution and date of collection. Utilizing pinned adult males, those specimens that were relatively perfect were given individual numbers and then the following data were recorded in tabular form for each specimen: (a) length of first and second tarsal seg-

ments of fore leg, (b) coloration of thorax, (c) coloration of abdomen, (d) presence or absence of abdominal stigmal markings, (e) length of fore and hind wings, and (f) number of x-veins involved in the bullar dash or spot of the fore wing. For the coloration records, four arbitrary grades of ascending order of intensity, 0, 1, 2, and 3, were established. A low power binocular microscope was used for magnification. Tarsal segment measurements were made with 1.7x oculars and 2.3x objectives. Wing length measurements and all other data were recorded with 12.5x oculars and 1.0x objectives. An artificial light source (microscope lamp with "daylight" glass filter) was used to illuminate the specimens. Specimens preserved in alcohol were not used, although many were available, because the colors, especially those other than the melanins, fade rather rapidly and also because the male fore legs so often become detached. The information from series of individuals collected at the same place and time was then tabulated. Within the limits of availability, series were studied from the entire geographical range of the complex. Later, after these data had been studied, individual specimens or small series from what appeared to be critical areas were also studied and measured. In all, two hundred and one (201) specimens were so treated. Twelve (12) of these specimens were individuals of *S. gilderleevei* which were measured and utilized for comparative statistics.

The data thus assembled were subjected to statistical analysis. Not all of the characters could be subjected to the simple statistics employed, but they could be used in connection with those characters that were so analyzed. The arithmetic mean (M), the standard deviation (σ) and the coefficient of variation (V) were determined for the second/first tarsal segment ratio, the fore wing length, and the wing length/first tarsal segment ratio.^{1, 2} The two ratios gave pure numbers that are independent of the absolute size of the individuals. This is important because stonemids vary in size not only individually but also seasonally. In utilizing the data the assumption has been made that size, variation, both individual and seasonal, exert no effect on the ratios derived from the tarsal and wing measurements.

Since the coefficient of variation is a measure of relative variability, more weight has been given to it than to the absolute measurements. This will become more evident in the specific discussions below.

Note also that unless special mention is given whenever a series is considered, all the specimens taken at that particular place at that time have been utilized. Some individuals, however, lack legs (due to breakage subsequent to collection) while others possess wings that are unmeasurable, and therefore the total for the two series may vary for the different measurements.

Having determined the M and σ of each sample, an estimate was then made of the parameter of the particular population from which the

¹Since the cross hatched measuring scale was placed below the lens system of the ocular, by multiplying the wing length by 2.3 the resultant figure was of the same size units as those of the tarsal segments.

²The computations were accomplished with the aid of FORM FOR MEAN and STANDARD DEVIATION by Tryon and Searle, 1941, based on 1935 Form by R. C. and C. McC. Tryon.

sample was drawn. This was done by adding or subtracting three standard deviations from the mean (Tables I, II, and III). Finally, after the data had been analyzed and conclusions reached, a series of individuals typical for each of the four subspecies retained was selected and the statistics assembled. These series were treated similarly to the geographical series and will give at least the author's conception of the various subspecies which he considers valid.

A series of specimens collected 26.VI.38 from Alymer, Quebec, omitting one specimen of *heterotarsale*, agree in all respects with the accepted definition of *canadense*. The ratio derived by dividing the length of the second tarsal segment of the ♂ fore leg by the first tarsal segment of the same leg (hereafter called, for convenience, the second tarsal/first tarsal ratio) gives for this series (Table I) a maximum of 3.00, a minimum of 2.00, a M of 2.35 and a V of 11.72. A small series combined from specimens collected at Louisville, Ky., and New Harmony, Ind., displays (Table I) a maximum of 2.71, minimum of 2.29, M of 2.52, and a V of 5.81. These specimens are all typical *interpunctatum*. From Lexington, N. Y., 11.VI.38, all individuals which agree with the delimitation of *frontale* show (Table I) a maximum of 2.71, a minimum of 1.82, a M of 2.29 and a V of 10.25. In comparison, a series collected at the Lachine Rapids, Montreal, Que., 1.VII.38, shows individuals ranging in color from very pale yellow to examples almost as dark as the darkest *canadense*. The tarsal ratio for the series varies from 2.83 to 1.14, with a M of 1.79 and a V of 20.90. Clearly this sample is more variable than the preceding three. If these specimens are sorted on the basis of thoracic coloration and those with grade 0 and 1 are separated from the darker grade 2 (there are no grade 3 specimens), then (Table I) the variability especially of the grades 0 and 1 specimens drops sharply to a V of 8.64 but that of the grade 2 specimens actually increases (21.80). Removal of one individual (No. 21) which has a dark thorax but a long first tarsal segment is sufficient to drop the V of the grade 2 specimens to 17.75. Sorting the specimens on the basis of the abdominal coloration gives a similar but reversed picture. The grade 2 individuals possess a V of 14.0 while the grades 0 and 1 have a V of 20.8. Removal of one specimen (No. 3) which has a light colored abdomen and a short first tarsal segment reduces this V from 20.8 to 11.7. Thus, two distinct populations seem involved in the series. Removal of the two intergrades leaves a light colored, long first tarsal joint group with a V equal to those of the "pure" series and a dark colored, short first tarsal joint group of slightly greater variability. The long first tarsal joint, light colored specimens represent *heterotarsale*, while the short first, tarsal joint, dark colored specimens are *canadense*. Ide (1935) found that both *heterotarsale* and *canadense* live in the same Ontario stream (Mad River) but the latter at higher elevations and the two populations only slightly overlap in space and emergence time at this particular locality. Evidence from localities other than the Lachine Rapids contributes additional information that *heterotarsale* intergrades not only with *canadense* but also with *interpunctatum*. Thus, from Orillia, Ont., 7.VII.38, a series of thirteen (13) individuals vary from light (Grade 0) to dark (Grade 2) and one of the intermediate specimens (thorax, Grade 1; abdomen, Grade 2) has a

TABLE I
RATIO OF $\frac{2\text{ND TARSAL SEGMENT}}{1\text{ST TARSAL SEGMENT}}$ OF ♂ FORE LEG

PART I. Arrangement by Locality

Locality and Date	Total Spec.	Observed Range		M	σ	V	Estimated Range		Notes
		Max.	Min.				Max.	Min.	
Lachine Rapids, Que., 1-VII-38	39	2.83	1.14	1.79	.376	20.90	2.92	0.66	All specimens
Same	21	2.00	1.43	1.64	.140	8.64	2.06	1.22	Spec. with Thorax 0 and 1
Same	18	2.83	1.14	1.95	.421	21.80	3.19	0.67	Spec. with Thorax 2
Same	16	2.83	1.60	1.98	.352	17.75	3.03	0.93	Spec. with Thorax 2; spec. 21 omitted
Same	29	2.83	1.14	1.65	.360	20.80	2.73	0.57	Spec. with Abdomen 0 and 1
Same	27	2.00	1.14	1.57	.185	11.70	2.12	1.02	Spec. with Abdomen 0 and 1; spec. 3 omitted
Same	10	2.57	1.75	2.01	.280	14.00	2.85	1.27	Spec. with Abdomen 2
Aylmer, Que., 26-VI-38	36	3.00	2.00	2.35	.278	11.72	3.18	1.52	All spec. have Abd. and Th. 2 or 3
Louisville, Ky., 22-VIII-40; New Harmony, Ind., 16- VI-36 and 30-V-40	14	2.71	2.29	2.52	.147	5.81	2.97	2.09	
Massey, Ont., 23-VI-36	10	1.87	1.50	1.66	.114	6.85	2.00	1.32	Th. and Abd. 0, but stigmal spots present
Sloatsburg, N. Y., 4-VI-33	20	3.25	1.67	2.53	.430	17.00	3.82	1.24	Th. and Abd. mostly 2; all with stigmal spots
Same	18	3.25	1.90	2.63	.332	12.60	3.62	1.63	Spec. 81 omitted; 81 has Th. and Abd. 0
Lexington, N. Y., 11-VI-38	20	2.71	1.82	2.29	.235	10.25	3.00	1.59	All spec. with stigmal spots
Bluffton, Ind., 20-VII-29	20	2.76	1.13	1.56	.416	26.70	2.80	0.32	
Same	15	1.66	1.13	1.35	.131	9.70	1.74	0.96	Spec. 136, 137, 151 omitted

PART II. Arrangement by Taxonomic Category

Category	Total Spec.	Observed Range		M	σ	V	Estimated Range		
		Max.	Min.				Max.	Min.	
<i>canadense</i>	43	3.00	2.00	2.340	.257	11.00	3.11	1.57	
<i>frontale</i>	56	3.20	1.60	2.370	.394	16.60	3.55	1.19	
<i>interpunctatum</i>	20	3.50	2.20	2.630	.280	10.65	3.47	1.79	
<i>heterotarsale</i>	44	1.90	1.10	1.57	.178	11.30	2.10	1.03	
<i>gildersleevei</i>	19	2.30	1.70	1.992	.169	8.50	2.50	1.48	

tarsal ratio of 1.67. One light specimen had a tarsal ratio of 2.00 for one leg and 1.80 for the other leg, and is typically *interpunctatum* in facies. Most of this series were dark (*canadense*) in appearance. As the season progresses *heterotarsale* becomes more numerous vis a vis *canadense* and *interpunctatum*. A series of eight specimens from Elkhart, Ind. (St. Joseph's River), 3.V.40, shows two individuals to have long first tarsal joints as well as typical *heterotarsale* coloration. The other six are definitely of the *interpunctatum-canadense* type (they could be either dark *interpunctatum* or light *canadense*) and have short first tarsal joints. A collection of six individuals from the same locality and the same area of the St. Joseph's River, but made 14.VIII.40, consists of one *interpunctatum* and five typical *heterotarsale*. A collection of eleven specimens from Montreal, Que., 5.IX.34, consists mostly of *heterotarsale* type individuals, but two specimens are decidedly of the *canadense* type and one of these has a *canadense* ratio (2.00) and the other a *heterotarsale* ratio (1.33 and 1.38). Finally, the most mixed series available is from Bluffton, Ind., 20.VII.29. Eighteen specimens vary in coloration from typical *heterotarsale* and *interpunctatum* to light *canadense*. The tarsal ratio of these (Table I) gives a V of 26.7 with a mean of 1.56. However, if specimens No. 136 and No. 139 (both light *canadense*) and No. 151 (typical *interpunctatum*) are omitted, then the remaining individuals have a tarsal ratio M of 1.35 with a V of 9.70. These individuals have *heterotarsale* tarsal ratios and are mostly pale colored, but several of them are atypical in having black marks on the thorax and all possess stigmal spots on the abdomen. As noted under the description of *heterotarsale*, many individuals do have piceous markings and the commonest seems to be the presence of pterothoracic streaks and abdominal stigmal spots. All specimens of a small collection of *heterotarsale* from Massey, Ont., 23.VI.36, show definite stigmal spots. Another collection of *heterotarsale* from Proctor, Minn., 20.VII.36 (unmeasured), is similar to the Massey series.

From the data given above, it is possible now to summarize tentatively the relationships of *interpunctatum*, *canadense*, and *heterotarsale*. *S. interpunctatum* dwells in the Mississippi drainage. In the St. Lawrence drainage *canadense* is to be found. Both have their emergence peaks in the early summer; the early emergents are larger and darker than the seasonally later ones and this is especially true of the coloration of *canadense*. Where the two populations meet, they probably intergrade, but it is impossible to tell a light *canadense* from a dark *interpunctatum*. Also in the area around the Great Lakes, northern Indiana, Illinois, Ohio, New York, and along the St. Lawrence, there is a third population, *heterotarsale*, that certainly intergrades with *canadense* and probably with *interpunctatum*. This population reaches its peak of emergence at the end of the *canadense-interpunctatum* season. This has been noted by Ide on the Mad River, Ont., and shows clearly in the present study. Just what has kept and is keeping the *heterotarsale* population from completely amalgamating with the *canadense-interpunctatum* populations, it is impossible to say. Obviously there must be a definite survival value attached to each of the populations or they would quickly fuse into one variable one. Even so, there must be in nature an immense number of intergrading individuals. From present

TABLE II
MALE FORE WING LENGTH
PART I. Arrangement by Locality

Locality and Date	Total Spec.	Observed Range		M	σ	V	Estimated Range		Notes
		Max.	Min.				Max.	Min.	
Lachine Rapids, Que., 1-VII-38	23	19.50	15.25	17.02	0.97	5.70	19.93	14.11	All specimens
Same	16	18.75	15.25	16.68	0.90	5.70	19.38	13.98	Spec. with 0 and 1 abdomens
Same	6	17.75	16.25	17.00	0.48	2.80	18.42	15.58	Spec. with 2 abdomens. N-1 for det. of V.
Aylmer, Que., 26-VI-38	23	20.50	18.00	19.27	0.62	3.21	21.13	17.41	All spec. have Abd. and Th. 2 or 3
Louisville, Ky., 22-VIII-40; New Harmony, Ind., 30-V- 40 and 16-VI-36	9	19.50	15.75	18.07	1.36	7.51	22.13	14.02	
As above except Louis- ville specimens omitted	6	19.50	18.00	18.97	0.55	2.90	20.63	17.32	
Sloatsburg, N. Y., 4-VI-33	12	24.00	19.50	21.46	1.40	6.51	25.66	17.26	Spec. 81 included; high V due to 83 and 87
Lexington, N. Y., 11-VI-38	12	22.00	19.50	20.83	0.88	4.19	23.45	18.21	
Bluffton, Ind., 20-VII-29	14	17.00	13.50	15.03	0.96	6.26	17.91	12.15	2 spec. have low tarsal ratio
Same	12	15.50	13.50	14.70	0.56	3.82	16.49	12.93	Spec. 136 and 139 omitted
Massey, Ont., 23-VI-36	5	17.50	19.00	18.32	0.57	3.10	20.03	16.61	N-1 used for determin- ing σ

PART II. Arrangement by Taxonomic Category

Category*	Total Spec.	Observed Range		M	σ	V	Estimated Range	
		Max.	Min.				Max.	Min.
<i>canadense</i>	26	9.95	8.28	8.96	0.39	4.34	10.13	7.79
<i>frontale</i>	42	11.20	6.77	9.38	0.92	9.70	11.20	6.77
<i>interpunctatum</i>	20	9.05	6.60	7.98	0.72	9.00	10.14	5.28
<i>heterotarsale</i>	22	9.22	6.18	7.59	0.87	11.57	10.23	4.95
<i>gildersleevei</i>	17	10.70	9.35	10.10	0.39	3.88	11.20	8.85

*These figures are given in actual mm. while the locality figures are in eye-piece cross-hatch units; 20 cross-hatch units=9.35 mm. The high V is due to seasonal variation except for *canadense* which is probably too low because most of the 26 specimens belong to the Aylmer series. *S. gildersleevei* is an early season species whose emergence period is short.

data, it is not known just what is the exact range of any one of these populations. Apparently *heterotarsale* is not present in southern Ohio, Indiana, or Illinois, although a series from Amity, Ind., 2.VI.40, appears to be typical *heterotarsale*. Individuals seen from southern Ohio, Indiana, and Illinois, and from Oklahoma, Missouri, and Kansas all belong to *interpunctatum*. With considerable certainty, it can be said that *heterotarsale* does not overlap the entire *interpunctatum* range.

It is probable, but not definitely known, that a similar but obverse relationship exists in the distribution of *heterotarsale* and *canadense*, i. e., that at the eastern and northern edges of the range *canadense* exists alone. There is, however, another population that meets with *canadense*, namely *frontale*. This seems to be the typical population of the lowlands of the Hudson River drainage and other eastern United States rivers. The holotype of this species was collected in the late summer (August). Emergents earlier in the season should be expected to be darker and probably larger. This is exactly what is found to be the case and these darker individuals are almost impossible to separate from *canadense* since the dark coloration tends to obscure the stigmal spots, etc., that differentiates *frontale* from *canadense*. As indicated above, a series from Lexington, N. Y., 11.VI.38, which appears to be relatively typical *frontale*, has a mean, a standard deviation and a coefficient of variation very close to those of *canadense* from Aylmer, Que. From Sloatsburg, N. Y., 4.VI.33, after a specimen of *heterotarsale* had been excluded, a series gave an M of 2.63 and a V of 12.60. These specimens have the facies of *canadense*. Thus, while it is possible to separate *frontale* from light colored *canadense*, it is impossible to tell typical *canadense* from dark *frontale*. Probably true *canadense* extends down the Appalachian highlands but is replaced in the lowlands by *frontale*.

The general conclusions as listed above have been based not only on tarsal ratio but also on wing length and the ratio derived from the ♂ fore wing length/first tarsal segment of ♂ fore leg length (called wing/tarsal ratio for short). These statistics support the tarsal ratio but are also of interest in their own right. Wing length (Table II) shows much less variation than does tarsal ratio, and thus has a lower coefficient of variation. A typical *canadense* (Table II), Aylmer, Que., series, has a wing length V of 3.21; *frontale*, Lexington, N. Y., series, a V of 4.19; and *interpunctatum*, New Harmony, Ind. (Louisville, Ky., specimens excluded) a V of 2.90. The series from the Lachine Rapids, Montreal, Que., displays a high V of 5.70 and when the lightly pigmented specimens (abdomens 0 and 1) are separated from the dark (abdomens 2) the V remains high for the light, but drops to 2.8 for the darker individuals. This is exactly parallel to what happened with the tarsal ratio. Note should be given that specimen No. 3 had broken wings and could not be included in the wing measurements. The Bluffton, Ind., series also shows a high V which drops when two long winged individuals are omitted. One of these, No. 136, is a light *canadense* individual that was considered in the tarsal ratio discussion. The other one, No. 139, however, has a *heterotarsale* type tarsal ratio. The Sloatsburg, N. Y., series displays a high V due to two specimens with long wings (No. 83 and No. 87) but No. 81, which was responsible

for the high tarsal ratio V has a wing of average length. The combined New Harmony-Louisville series of *interpunctatum* shows clearly the effect of seasonal variation. The Louisville specimens were collected later in the season than were the New Harmony specimens; although the New Harmony individuals were collected in different years, it was

TABLE III
RATIO OF $\frac{\text{MALE FORE WING LENGTH}}{\text{1ST SEGMENT } \sigma \text{ FORE TARSUS}} *$
PART I. Arrangement by Locality

Locality and Date	Total Spec.	Observed Range		M	σ	V	Estimated Range		Notes
		Max.	Min.				Max.	Min.	
Lachine Rapids, Que., 1-VII-38	22	9.46	4.46	6.28	1.72	27.80	11.44	1.12	All specimens
Same	16	7.00	4.46	5.48	0.73	13.29	7.67	5.37	Spec. with 0 and 1 abdomens
Same	6	9.46	6.50	8.42	0.94	11.20	10.93	5.90	Spec. with 2 abd.; σ det. by N-1
Aylmer, Que., 26-VI-38	22	10.26	7.40	9.19	0.77	8.36	11.49	4.60	All spec. with thor. and abd. of 2 or 3
Louisville, Ky., 22-VII-40; New Harmony, Ind., 16-VI-36 and 30-V-40	9	11.70	9.25	10.57	0.75	7.10	12.82	8.37	σ det. by N-1
Sloatsburg, N. Y., 4-VI-33	12	11.19	6.50	9.26	1.37	14.95	13.37	5.15	
Lexington, N. Y., 11-VI-38	11	11.15	6.50	9.58	1.36	14.60	13.66	5.50	
Bluffton, Ind., 20-VII-29	9	11.20	3.06	6.41	2.75	42.70	14.86	2.04	See text

PART II. Arrangement by Taxonomic Category

Category	Total Spec.	Observed Range		M	σ	V	Estimated Range	
		Max.	Min.				Max.	Min.
<i>canadense</i>	26	10.25	7.00	9.08	0.82	9.02	11.54	6.62
<i>interpunctatum</i>	22	12.50	7.00	9.96	1.43	14.45	14.28	5.64
<i>frontale</i>	33	13.50	6.50	9.37	1.52	16.40	13.93	4.81
<i>heterotarsale</i>	21	6.50	3.50	5.48	0.88	16.14	8.13	2.82

*This ratio was determined by dividing the scale ratio of the wing by the scale ratio of the tarsal joint.

at approximately the same time seasonally. Combined, the V is high due to the small size of the late-season Louisville specimens, but as soon as the Louisville series is removed the V drops. Finally, the Massey specimens, although only five in number, give a V of 3.10.

The wing length/first segment of the σ fore tarsus ratio (called for brevity the wing length/tarsal ratio) presents a picture similar to that

shown by the wing and tarsi separately. The co-efficient of variation shows greater range (Table III) than do those of the other measurements, varying from 7.10 for the *interpunctatum* specimens from Louisville and New Harmony to 42.70 for the Bluffton series. Actually, the latter series when plotted shows three distinct groupings: (1) Five specimens which show a ratio of 3.66 to 4.76—all of these specimens have "0" abdomens and thoraces. (2) Three specimens with ratios of 7.85 to 8.57—all three of these specimens (No. 136, No. 139, and No. 151) were considered in Tables I and II. (3) Finally, specimen No. 136, the most darkly pigmented specimen of the whole series, has a ratio of 11.20.

To supplement the picture of each valid subspecies, a series of typical individuals of every subspecies has been selected, utilizing individuals from all parts of the range and all emergence dates available. The statistics for these are given in Tables I, II, and III. Note also that the estimated range for each character has been determined by adding or subtracting 3σ from the M. The coefficient of variability indicates that *canadense* is perhaps the least variable while *heterotarsale* and *frontale* are the most variable. The *canadense* figures are perhaps too low, due to the fact that the most of the specimens in the typical series of *canadense* came from the Aylmer series. The statistics for the other two subspecies are probably more reliable. As an added check to the validity of these findings, a number of specimens of *S. gildersleevei* have been measured and the statistics derived compared with those of the four subspecies. While they show less variability than any one of the four subspecies, the differences are not exceedingly great or beyond expectation since *S. gildersleevei* is a distinct, uniform appearing, geographically and ecologically restricted species.

In considering these series, the assumption has been made on the basis of coloration, size, markings, etc., that certain series, e. g., Aylmer, Lexington, Massey, and New Harmony represent samples drawn from populations that are sufficiently different to be allocated to different taxonomic populations. The same assumptions were made also for the series that was used to estimate the four subspecies. The statistics derived from these series show them all to have coefficients of variation that compare rather closely in magnitude and also compare closely with *Stenonema gildersleevei*, a distinct population for which ample and adequate evidence is available that it represents a different species. By utilizing the statistics derived from the two ratios and the wing length measurements, the question can now be studied as to whether, on the basis of these three characters at least, these various samples could have been derived from populations with the same means and variance, i. e., could they have come from one population? For this analysis, the following formulae were used:

1. $\sigma d = \frac{N_1}{N_2} \sigma^2 M_1 + \frac{N_2}{N_1} \sigma^2 M_2$ in which $\sigma M = \frac{\sigma}{\sqrt{N}}$
2. $D = M_1 - M_2$
3. $K = \frac{D}{\sigma d}$

The assumption is made that where $K < 2$, the difference is not significant, i. e., the two samples could be drawn from the same populations. If $K > 3$, the difference is significant, $K > 2.5$ probably significant and $K > 2$ possibly significant.

It can be seen (Table IV) that the Aylmer and Louisville plus New Harmony series are, on the basis of the tarsal ratio ($K=2.30$), possibly different, but that on the basis of wing length ($K=1.08$) the Aylmer and New Harmony series certainly do not have a significant K value. The

TABLE IV
VALUES FOR K

Locality and Date	2nd Tarsal Segment	Fore Wing	♂ Fore Wing Length
	1st Tarsal Segment		1st Seg. ♂ Fore Tarsus
Aylmer, Que., 26-VII-38..... Louisville, Ky., 22-VIII-40..... New Harmony, Ind., 16-VI-36... New Harmony, Ind., 30-V-40...}	2.30	1.08*	
Aylmer, Que., 26-VI-38 Lexington, N. Y., 11-VI-38	0.815	6.05	
Lexington, N. Y., 11-VI-38 Massey, Ont., 23-VI-36	8.17	6.68	
Lachine Rapids, Que., 1-VII-38 (spec. with abd. 0 and 1, No. 3 omitted); Same (spec. with abd. 2)	5.56	0.83†	
Taxonomic Category			
<i>frontale</i> <i>heterotarsale</i>	13.32	6.89	10.35
<i>frontale</i> <i>interpunctatum</i>	2.76	2.55	3.64
<i>frontale</i> <i>canadense</i>	0.48	1.52	1.34
<i>heterotarsale</i> <i>interpunctatum</i>	18.05	0.54	13.22
<i>heterotarsale</i> <i>canadense</i>	20.75	26.85	13.08
<i>interpunctatum</i> <i>canadense</i>	5.10	1.57	5.22

*Only New Harmony specimens involved (Louisville omitted), since seasonal variation of wing length would confuse picture.

†Specimen No. 3 included for wing measurements.

Aylmer and Lexington series have a significant K for wing length (6.05) but not for the tarsal ratio (0.815). With the Lexington and Massey series, the K is highly significant for both wing length and tarsal ratio. Most interesting is the Lachine Rapids series which, when divided on the basis of light abdominal coloration (0+1 for one series and 2 for the other) shows a significant K for the tarsal ratio but not for the wing length.

Turning to the various selected subspecies series, we find that only in the case of *frontale* and *canadense* is K of an insignificant value for all

three factors, i. e., tarsal ratio, wing/first tarsal ratio, and wing length. Obviously the two series studied could have come from the same population so far as these characters are concerned. For all the other pairs, at least one and more often all figures are significant, i. e., the samples could not have been drawn from the same population. It must be remembered that these figures apply only to certain characters and that there may be other characters which will clearly separate and distinguish the two populations under consideration.

On the basis of all the data available, there seem to be four distinct populations and the names *canadense*, *frontale*, *interpunctatum*, and *heterotarsale* legally and logically apply to these groups. All evidence, both qualitative and quantitative, indicate that these four populations are subspecies. Three of these subspecies (*canadense*, *frontale*, and *interpunctatum*) are definitely geographical subspecies, but the fourth (*heterotarsale*) may at present be separated from the other three ecologically rather than geographically, since it dwells in at least part of the range of all three other subspecies. *Canadense*, *frontale* and *interpunctatum* all reach the peak of their emergence in the late spring and early summer, while *heterotarsale* reaches its peak of emergence much later in the summer. Further, *heterotarsale* nymphs need a different type of environment than does *canadense*, e. g., *heterotarsale* lives in the lower reaches of a stream and *canadense* lives further up the stream. This indicates that there are considerable physiological differences between the nymphs of at least these two subspecies. Certainly there must be strong selective action being applied to keep these two subspecies distinct, or they long ago would have fused into one highly variable population. Probably this selective pressure is exerted upon the nymphal rather than the adult populations.

Just how the present distribution of the four subspecies arose is not completely clear, but at least part of the history since the Pleistocene glaciation can be hypothesized. At the time of the glaciation, probable *canadense* was the highland, cool stream form of the east with a closely related *frontale* population occupying the lowlands of the eastern coastal area. In the Mississippi Valley, an *interpunctatum* population emerging early in the summer dwelled in the southern lowlands with a *heterotarsale* population further to the north, a population that emerged later in the season than *interpunctatum*. When the glacier retreated, *canadense* moved north and also west along the Great Lakes, while *heterotarsale* also invaded the same area but at lower elevations. Thus, the present Great Lakes and their glacial predecessors served as a broad highway for the distribution of these two subspecies and, due to different ecological demands, they were able to live in the same geographical area and still maintain their integrity. The Atlantic coastal dwelling *frontale* stock was faced, when the glacial ice melted and the level of the ocean rose, with a much reduced territory while the "warm water" *interpunctatum* followed behind *heterotarsale* and eventually came into contact not only with *heterotarsale* but also with *canadense* which had geographically interdigitated with *heterotarsale*. In this area, there is the confusing picture resulting actually from the interbreeding of three populations. It is from this mixed population that

the greater majority of the species which have been synonymized have been derived, for with the exception of *pallidum*, the types of all these species were collected in this area.

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APES, GIANTS AND MAN, by FRANZ WEIDENREICH. Pages vii+122, 1946. The University of Chicago Press. Price \$2.50.

For many years our knowledge of the evolution of man was derived from the logical analysis of his relation to the other primates, supported by rather meager evidence from a few significant fossil remains. *Pithecanthropus erectus*, the ape-man of Java, was the one striking primitive ancestor, while Heidelberg man, Neanderthal man and Cro-Magnon man were transitional early human forms. The actual link with more primitive anthropoid stock was lacking and the precise relations of anthropoid and human ancestral lines was therefore uncertain. Well before the second World War the discovery of *Sinanthropus pekinensis* in China added considerably to our knowledge of the level of human evolution previously illustrated only by *Pithecanthropus*, but left the same gap between man and his anthropoid precursors.

Weidenreich's book discusses impressive additions to this fossil record which might have been made known earlier but for the intervention of the war. Java and China again are the sources of the important remains. *Gigantopithecus* from China and *Meganthropus* from Java fill the all-important gap as manlike creatures still more primitive than *Pithecanthropus* and *Sinanthropus*. They are interpreted as human remains, but of such primitive characteristics that they indicate the actual transition from the anthropoid ancestral line.

With these additions the author is enabled to offer a very convincing explanation of the evolution of the primates. As early as the Miocene the simiid stock apparently began its differentiation, giving rise to one line of descent represented by the fossil *Dryopithecus* which was possibly ancestral to the existing Simiidae and to another which produced the australopithecine forms and the human species. The gibbons probably diverged at an even earlier period. The combination of simiid and human characteristics in *Australopithecus* leads to the conclusion that these creatures were an isolated branch which became extinct without contributing to the formation of any existing species. In the human line of descent *Gigantopithecus*, *Meganthropus*, the pithecanthropine forms and the sequence of human remains form a sufficiently connected series to tax the debating capacity of the fundamentalists. They leave no reasonable doubt of the gradual transition already established, although they introduce another consideration in the apparent reduction of size as modern man has evolved.

The book is technical but not too technical. It arouses admiration even in a scientific mind of the detailed precision with which the physical anthropologists can interpret the meager remains of some of these early species and presents the results comparatively in a most clear and convincing form. It necessitates some revision of earlier concepts, particularly in the evolution of the brain, but even in such points it gives the impression of conservative judgment and dependability.

The author predicts a rich future in the pursuit of investigations in the Oriental region. We can only hope that he will not be impeded in the work now that the war is over and that before many more years have passed we may have other contributions from his pen.—A. W. L.