

MORPHOLOGY AND TAXONOMY OF
EPHEMEROPTERA EGGS

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ABSTRACT

MORPHOLOGY AND TAXONOMY OF EPHEMEROPTERA EGGS

by Richard W. Koss

Mayfly eggs possess four main morphological features which may be used for taxonomic purposes: chorionic sculpturing, polar cap(s), accessory attachment structures, and micropylar devices. A new and simple technique is described for observing these structures.

A detailed morphological description of the egg is presented, including terminology for the parts of the micropylar device.

The eggs were found useful for generic or specific determinations for the Heptageniidae, Leptophlebiidae, Caenidae, Ephemeridae, and Polymitarcidae; and of doubtful value for the Ephemerellidae, Tricorythidae, and Potamanthidae. Their value in taxonomy is not now assessible for the Siphonuridae, Baetidae, and Ametropodidae.

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By

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INTRODUCTION

At the present time it is impossible or at least very difficult to determine most female mayflies to species when taken without males, and in many cases it is equally as difficult to identify them to genus. This difficulty develops from the lack of characters, especially genital differences as found in males. Likewise, specific identification of immatures is frequently difficult or impossible because they have not yet been reared through to adult, or because sound characters have not yet been found. Therefore, I undertook this study in an attempt to discover characters for separating and identifying immature and adult female Ephemeroptera. The eggs possess sound morphological characters which are far more dependable than body coloration. However, since closely related species often possess very similar or non-distinguishable eggs, one should not necessarily conclude that two groups of specimens are of the same species if the eggs are the same. On the other hand, if the eggs are distinctly different they will serve to separate females of closely allied species. Distinct polymorphism has been noted only within one species, Caenis simulans McDunnough, and this may be a case of sibling species. The study of eggs will also aid in the association and identification of undescribed adults and immatures. The contribution of eggs to insect taxonomy has been shown, among others, by the following: Onsager and Mulkern (1963), Orthoptera; Ross and Horsfall (1965), Culicidae; Knight, Nebeker, and Gaufin (1965 a & b), Plecoptera; Degrange (1960) Ephemeroptera; Southwood (1956), Heteroptera.

Detailed study of mayfly eggs began in Europe with Burmeister's (1848) discussion and illustration of the egg and embryo of Ephoron virgo (Olivier). He at first considered the polar cap to be a local thickening of the chorion, and later thought it might be the corpus luteum; he did not mention the micropyle. Leuckart (1855, pp. 200-203, pl. x) described the polar cap of Ephoron virgo as being a mass of spermatozoa attached to the micropylar apparatus (Figs. 72-75). Citing Swammerdam (1737), Leuckart supports his theory by the absence of this "mass of spermatozoa" on eggs in the ovaries; he also presents a direct comparison of what he saw (the polar cap) to spermatozoa. Grenacher (1868) and Palmen (1884), however, found the same structure on eggs taken from immature Potamanthus sp. Although classifying the caps with micropylar apparatuses, Grenacher did call them "polar caps"; Palmen correctly referred to their function of attachment. Grenacher felt that he discovered a simple pore-like micropyle connected externally to a shallow depression, and sometimes bearing the internal micropylar canal. He found these at the poles of the egg, and unfortunately he observed that portion of the chorion which supports the cap. Grenacher also noticed some threads attached to the chorion and terminated by spherical knobs; he correctly surmised that these were attachment structures. Bengtsson (1913) studied the eggs of 28 palearctic species, and believed that he found the micropyle on three of these: Ephemerella lactata Bengtss., Chitonophora aurivilii Bengtss., and Caenis horaria (L.). Like Grenacher, Bengtsson actually observed that portion of the chorion which supports the cap.

Morgan's (1913) discussion and illustration of thirteen species of mayfly eggs was the first major morphological study to occur in

North America. She did, however, continue the use of the term "micropylar apparatus" for "polar cap". The only other major North American study was that of Smith (1935) who illustrated fifty-one and discussed one hundred and thirty species of mayfly eggs. Unfortunately he frequently misinterpreted the chorionic sculpturing, thus negating many of his conclusions concerning the chorion. He did, however, quite accurately interpret those accessory attachment structures which he found; he referred to polar caps correctly, but did not mention the micropyle. Aside from the above studies, observations on mayfly eggs in North America have been at a minimum. Occasionally workers have had a passive interest in mayfly eggs, but they have never produced a study of more than two or three species, and none has observed the micropyles.

Degrange (1956, 1960) studied European fauna, and was the first to actually find and describe the micropyles on the eggs of mayflies. Previous to Degrange, all workers looked at the polar cap and polar areas in their search for the micropyle; Degrange found it to be lateral in position. Degrange (1956) first published a description of four types of micropyles on twenty-four species of mayfly eggs, and later (1960) published a paper on the reproduction of mayflies. A section of the latter was devoted to descriptions of eggs of 51 species and it illustrated thirty-four species. Degrange used fresh and hatched eggs whenever possible.

TECHNIQUES

Standard resin mounts are unsatisfactory for studying the chorionic sculpturing of the eggs, because the contents are opaque and form a background of "bubbles" which conceals the surface details (Figs. 12, 30, 31, 61). Reflected light, rather than transmitted light, was tried without success. Because of this "contents" problem, most of the earlier workers experienced difficulties and included the egg contents on their drawings.

Many clearing techniques were tried, and when effective they rendered the eggs too fragile for handling and for transferring to a slide. A General Biological Supply House product, CMC-S, has proved to be the most efficient mounting media. Since CMC-S contains a red stain and a clearing agent, eggs mounted in it will clear to a certain degree and be stained in the same process. CMC-S is, however, a water base mounting media, making it necessary to ring the coverslip with asphalt or any other suitable ringing compound.

It is possible to obtain fully developed eggs from final instar immatures, and in many cases this was necessary. Since the adult life is so short, and given over entirely to mating and egg laying, there is no time in the adult life for egg maturation; therefore it is accomplished during the immature stages.

Adults are best preserved in 70% Ethyl alcohol when collected, and immatures are best preserved in 95% ETOH when collected, and transferred to 70% ETOH a week later. Eggs removed from specimens preserved

in 70% ETOH and collected within five to ten years of slide mounting were usually clear enough for study within a week. Specimens remaining in preservative for a longer period of time (especially if in 95% ETOH) usually required three to four weeks for sufficient clearing; however, frequently the shape of the egg was distorted. A specimen collected in 1924 yielded eggs which were distorted, but which did clear well enough for observation of the chorion.

The specimens were initially soaked in water for a few minutes to rinse off the preservative. The eggs were then removed from the abdomen into a water-filled cell on a spot plate where they remained for 10-20 minutes before slide mounting. This waterbath cleanses the eggs of alcohol, which is not miscible with CMC-S. It is of utmost importance to keep the number of eggs per slide to a minimum. Large numbers of eggs on a slide prevent the mounting media from clearing the eggs quickly or effectively enough for observation and photography.

Where possible, two slides were made from the eggs of a single specimen. I have kept one set of these slides, and the other set, together with the specimens used, remains in the Entomology Museum of Michigan State University.

For many species, duplicate slides were made from specimens collected in different localities in order to determine variation in details. No significant variation in egg characters was found to occur between individuals of a given species, with the possible exception of Caenis simulans (as presently understood). Within a species, any structural variations of the eggs can usually be readily detected on the one or two slides made from the eggs of a single specimen.

Because it is nearly impossible to interpret most details at lower magnifications, a magnification of 1000x or greater, on a phase contrast microscope, is recommended. In the present study, a phase microscope was used with magnifications of 125x, 500x, and 1250x (oil immersion) for examining the eggs. With few exceptions magnifications of 400x and 1000x (oil immersion) were used for photography. When viewing and photographing details in relief (tangential view) ordinary bright field lighting was superior to phase lighting. All photographs were made with an Exakta IIa 35mm camera, using Kodak Panatomic-X film.

MORPHOLOGY

The shape or form of the egg varies from ovoid to nearly rectangular, excluding the polar caps. However, the presence or absence of polar caps is mentioned under the heading "FORM" since they do contribute to the general appearance of the egg.

Length and width dimensions of mayfly eggs have been given in past literature (Morgan, 1913; Smith, 1935; Degrange, 1960), and they range from 150-200 μ in length by 90-150 μ in width. The eggs of larger mayflies (e.g. Ephoron, Hexagenia) are 250-300 μ long by 150-200 μ wide. Length and width dimensions are not given in this study because it was found that pressure of the coverslip was so great that measurements were at least fifty microns greater than those cited in the literature. A further check was made on the accuracy of measurements by measuring eggs placed in a welled slide. These measurements agreed with measurements given in the literature because the coverslip was not in contact with the eggs. With the use of slide mounts for the study of the eggs, it is apparent that length and width measurements would be too variable and inaccurate to include as morphological characters.

Mayfly eggs possess four main morphological features which may be used for taxonomic purposes: chorionic sculpturing, polar cap(s), accessory attachment structures, and micropylar devices.

Chorionic sculpturing is often an excellent specific characteristic. Sculpturing may be tuberculate, peglike, netlike, rugous, punctate, or maculate. Tubercles are considered to be small bumps or

protuberances which, at first glance, appear simply as maculations; whereas peg-like structures are longer, more definite projections, and are considered to be adhesive in function. When the sculpturing is netlike, it is referred to as the reticulation. There are two types of reticulation, one formed by raised ridges (Fig. 67), and the other by depressed furrows (Fig. 47), which are collectively termed the strands. Therefore, the mesh, the areas between the strands, may be either raised or depressed surfaces. Thus, when discussing a netlike sculpturing, a net, its fibers, and spaces will correspond respectively to the reticulation, its ridges or furrows (strands), and mesh. The size of the mesh of the reticulation has been found to be of value in discerning taxa. The mesh has been consistently measured across its greatest inside dimension (excluding the strands), and this measurement is given as the length of the mesh (Fig. 47). A large-mesh reticulation (Fig. 67) would be readily visible under lower magnifications (125x), whereas under the same magnification, a small-mesh reticulation (Figs. 31, 32, 63), if apparent at all, would be difficult to discern. Structures are discussed with chorionic sculpturing when it is uncertain whether or not they play a role in attachment.

To insure survival and aid dispersal, mayfly eggs must have a means for attaching to submerged objects and the substrate. This is especially important in lotic waters wherein maximum dispersal is probably attained when some eggs adhere to submerged surfaces soon after deposition, while others move further downstream. Attachment structures thus prevent most eggs from being washed downstream, as well as prevent them from being carried to an environment unsuitable for development. Lentic species have eggs that are equally equipped with attachment

structures, and here the lake currents must serve to disperse the eggs away from the oviposition site and bring them in contact with submerged objects to which they adhere. Concerning the eggs of Hexagenia limbata (Serville) s. l., Hunt (1953) states:

Laboratory experiments showed that in still water individual eggs sank at an average rate of 1 foot in 80 seconds, and small clumps of eggs settled 1 foot in about sixty seconds. Two to three minutes were required for eggs to settle one foot when the water was agitated. Application of these results to natural water indicates that more than six minutes would be required for eggs to reach bottom in still water five feet deep. It is quite probable that at times wave action and currents serve to distribute eggs widely before they eventually come to rest.

Also, Hunt (1953) relied on the adhesiveness of the eggs when he collected them with glass plates submerged in water three feet deep.

Attachment structures consist of three basic types: polar caps, accessory attachment structures, and an external adhesive layer.

Polar caps are attachment structures which are found at one or both poles or ends of many mayfly eggs. Most polar caps appear to be solid structures prior to their release into the water (Figs. 43, 52, 54). Upon entering the water the caps swell and expose the many threads with terminal knobs which function in attachment or anchorage of the egg (Fig. 41). Cap morphology varies from this "solid structure" type in Caenis (Caenidae), Ephoron (Polymitarcidae) and the interpunctatum species group of Stenonema (Heptageniidae). In Caenis the cap is composed of long, knob-terminated, spirally arranged threads which are coiled at the poles of the egg when the egg has not been in water. The cap may appear as a solid structure (Figs. 54, 56) or as a loose coil. When in water, the cap uncoils (Fig. 55) and the threads unspiral or separate (Fig. 57) in order to serve as an attachment device.

The interpunctatum species group in the genus Stenonema possesses caps which are merely very loose coils of thread encircling each pole of the egg (Fig. 16), and which uncoil upon contact with water.

The cap of Ephoron is unique in that it is a solid structure type which is divided into a cluster of cylinder-like structures (Figs. 72-75). Each cylinder, according to Degrange (1960), is composed of many threads with terminal knobs. The effect of water is uncertain, but it probably causes the cap to swell and expand as in Ephemerella (Fig. 41).

The accessory attachment structures are located on the lateral surfaces of the eggs. These are highly variable structures which may be in the form of sucker-like discs or plates (Figs. 24, 25, 45, 47); coiled or uncoiled threads, which are frequently appended with terminal knobs (Figs. 1, 10, 39, 40); or variously shaped adhesive projections (Figs. 30, 36). The coiled threads uncoil or spring out upon contact with water and become entangled with submerged objects such as algae or twigs. The knobs aid entanglement, but probably will also catch in small cracks or crevices. When coiled, the terminal knob frequently covers the coil of thread making it difficult to see, and chorionic sculpturing underneath the structure is usually much finer or absent.

Some eggs do not have polar caps or accessory attachment structures, the method of attachment being an adhesive layer which coats the egg and swells upon contact with water. Since this adhesive coating is often difficult to distinguish, it is not always possible to state that it is present or absent. It is discussed only when noticeable, and one should not necessarily assume its absence if it is not discussed or if it cannot be found.

The micropylar device is the structure which allows the sperm to enter the egg; and it is lateral in position, variable in number, and usually composed of three parts: the micropyle, the actual opening in the chorion which allows the sperm entrance; the sperm guide, an external depression in the chorion which usually lacks chorionic sculpturing, and which leads to and presumably aids in funneling sperm to the micropyle; and the micropylar canal, an internal tube leading from the micropyle into the egg (Figs. 4, 49, 53). One of the supplementary structures, the micropylar canal, has been noted in past literature (Korschelt, 1884; Johannsen & Butt, 1941). The other, the sperm guide, is apparently a term new to literature. Degrange (1956, 1960) used the term micropyle for what I refer to as the micropylar device.

In discussing the sperm guide and micropylar canal the terms "proximal" and "distal" are used with the micropyle being the point of reference--thus distal to or proximal to the micropyle.

The presence of two or more micropylar devices is most common, and often it is difficult to count them exactly. Occasionally two micropylar devices will overlap, usually the micropyle of one being situated in the sperm guide of another. These are always atypical, and are not morphological features of any particular species or group of species.

The absence or modification of the sperm guide or micropylar canal results in three basic types of micropylar devices: a funnel-shaped sperm guide with micropylar canal short or lacking (Figs. 24, 27, 77, 79); an oval-shaped sperm guide with the micropylar canal situated to one side (Figs. 4, 49); and an elongate sperm guide, when present, followed by a more conspicuous micropylar canal (Figs. 15, 53, 71).

In most cases the type of micropylar device remains constant within a family, and although useful for family determinations, it is seldom of value for generic and specific determinations.

In funnel-shaped micropylar devices (Figs. 24, 27, 77, 79) the micropyle is situated at the base and near the center of a funnel-shaped sperm guide. In the Leptophlebiidae the micropyle is in a plane parallel to that of the chorion (Figs. 24, 27), and the presence or absence of the micropylar canal cannot be ascertained (Degrange, 1960, has noted its presence by studying hatched eggs). In Tortopus (Polymitarcidae), however, the plane of the micropyle intersects that of the chorion, and here a short micropylar canal can be seen internal to the opening (Figs. 77, 79). These are the only groups known to have this type of micropylar device.

A more common micropylar device is that in which the micropyle is at one side of an oval-shaped sperm guide, and is followed by a micropylar canal of variable lengths (Figs. 4, 16, 49, 60). This micropylar device is found in the Ephemerellidae, Potamanthidae, Siphonuridae, Tricorythidae, Baetidae (Degrange, 1960), Oligoneuriidae (Degrange, 1960), most Heptageniidae, and in Ephoron of the family Polymitarcidae. In Ephoron virgo (Olivier), Degrange (1956, 1960) described a micropylar device consisting of a "half-skullcap" ("demi-callote") followed by a canal, and established this as a separate type. In the two North American species of Ephoron, the micropylar device is different from E. virgo. The proximal portion of the micropylar canal is expanded, and it forms the "half-skullcap" (Fig. 75) described by Degrange; however, a typical oval-shaped sperm guide is also present,

and for this reason I include Ephoron with other groups having an oval-shaped sperm guide.

The third micropylar device, basically a conspicuous micropylar canal, is found in Caenis, Ephemeridae, and some Stenonema. The sperm guide may be present or absent. When present, it is either an elongate depression, usually free of chorionic sculpturing (Figs. 53, 62), or an elongate channel in the ridges of the reticulation (Fig. 71).

Dimensions (in microns) are given for most of the structures described above. When over five microns, the dimensions are rounded off to the nearest whole number. However, when under five microns, or over five microns and with a narrow range, the measurements are expressed to the nearest tenth.

Occasionally such inexact terms as "usually" are used in the keys or descriptions to note variations. The variation, however, can be noted among the eggs from a single specimen, and by examining many of the eggs upon a slide, one can determine that condition which is most common.

Table one presents a summary of the morphological features found on the eggs discussed in this study. The taxa have not been arranged according to presently conceived phylogenetic relationships (Edmunds, 1962), nor is the arrangement an attempt at a new concept of relationships. Rather it is arranged first by type of micropylar device, and second by type of accessory attachment structures. This is done so that one can more readily determine which features are common to which taxa.

Table one.--A summary of the morphological features found on the eggs discussed in this study. The taxa have not been arranged phylogenetically, but are arranged first by type of micropylar device, and second by type of accessory attachment structures.

FAMILY	CHORION	ACCESSORY ATTACHMENT STRUCTURES	POLAR CAPS	SPERM GUIDE
LEPTOPHLEBIIDAE	Variable	Variable; <u>Thraulodes</u> only one with threads (& terminal knobs)	Absent	Funnel-shaped
POLYMITARCIDAE <u>Tortopus</u>	Punctate	Absent	Absent	Funnel-shaped
POLYMITARCIDAE <u>Ephoron</u>	Large-mesh reticulation or smooth	Absent	One	Oval-shaped
EPHEMERELLIDAE Sg. <u>Eurylophella</u>	Large-mesh reticulation--furrows	Sucker-like plates?	Absent	Oval-shaped
EPHEMERELLIDAE Other Subgenera	Small-mesh reticulation--ridges	Coiled threads with terminal knobs	One	Oval-shaped
POTAMANTHIDAE	Maculate	Coiled threads with terminal knobs	Two	Oval-shaped
TRICORYTHIDAE	Overlapping plates	Paired threads without terminal knobs	One	Oval-shaped
SIPHONURIDAE	Maculate	Coiled threads without terminal knobs	Absent	Oval-shaped
AMETROPODIDAE	Tuberculate	Coiled threads without terminal knobs	Absent	Micropylar Device unknown
HEPTAGENIIDAE <u>Arthroplea</u> <u>Epeorus</u> <u>Heptagenia</u> <u>Rhythrogena</u>	Variable	Variable	Absent	Oval-shaped
HEPTAGENIIDAE <u>Stenonema</u> , <u>interpunctatum</u> group	Sparsely tuberculate	Coiled threads without terminal knobs	Two-six	Oval-shaped
HEPTAGENIIDAE <u>Stenonema</u> except <u>interpunctatum</u> grp.	Sparsely tuberculate, tubercles often in a reticular arrangement	Absent	Absent	Elongate
EPHEMERIDAE <u>Ephemera</u>	Small-mesh reticulation or punctate	Absent	Absent	Elongate or absent
EPHEMERIDAE <u>Hexagenia</u>	Large-mesh reticulation	Absent	Absent	Elongate
CAENIDAE <u>C. anceps</u>	Smooth	Absent	One	Absent
CAENIDAE other species of <u>Caenis</u>	Variable	Absent	Two	Elongate or absent

LIST OF SPECIES STUDIED

This study treats the following sixty-one species, which are distributed in twenty-three genera or subgenera and ten families.

Siphonuridae

Siphonurus alternatus (Say)

Siphonurus mirus Eaton

Heptageniidae

Arthroplea bipunctata McDunnough

Epeorus (Iron) suffusus McDunnough

Heptagenia diabasia Burks

Heptagenia hebe McDunnough

Heptagenia junco McDunnough

Heptagenia pulla (Clemens)

Rhithrogena impersonata (McDunnough)

Rhithrogena sanguinea Ide

Stenonema canadense (Walker)

Stenonema femoratum (Say)

Stenonema frontale (Banks)

Stenonema fuscum (Clemens)

Stenonema heterotarsale McDunnough

Stenonema lepton Burks

Stenonema minnetonka Daggy

Stenonema nepotellum (McDunnough)

Stenonema rubromaculatum (Clemens)

Stenonema tripunctatum (Banks)

Stenonema vicarium (Walker)

Ametropodidae

Siphloplecton basale (Walker)

Leptophlebiidae

Habrophlebia vibrans Needham ?

Habrophlebiodes americana (Banks)

Leptophlebia sp.

Paraleptophlebia adoptiva (McDunnough)

Paraleptophlebia debilis (Walker)

Paraleptophlebia mollis (Eaton)

Thraulodes speciosus Traver

Ephemerellidae

Ephemerella (Ephemerella) dorothea Needham

Ephemerella (Ephemerella) excrucians Walsh

Ephemerella (Ephemerella) inconstans Traver

Ephemerella (Ephemerella) invaria (Walker)

Ephemerella (Ephemerella) subvaria McDunnough

Ephemerella (Serratella) deficiens Morgan

Ephemerella (Drunella) cornuta Morgan

Ephemerella (Drunella) lata Morgan

Ephemerella (Drunella) walkeri Eaton

Ephemerella (Eurylophella) prudentialis McDunnough

Ephemerella (Eurylophella) temporalis McDunnough

Tricorythidae

Tricorythodes atratus (McDunnough)

Tricorythodes explicatus (Eaton)

Tricorythodes fallax Traver

Tricorythodes stygiatus McDunnough

Caenidae

Caenis anceps Traver

Caenis forcipata McDunnough

Caenis jocosa McDunnough

Caenis simulans McDunnough

Potamanthidae

Potamanthus myops (Walsh)

Potamanthus neglectus Traver

Ephemeridae

Ephemera guttulata Pictet

Ephemera simulans Walker

Ephemera varia Eaton

Hexagenia limbata occulta (Walker)

Hexagenia limbata venusta Eaton

Hexagenia munda munda Eaton

Hexagenia rigida McDunnough

Polymitarcidae

Ephoron album (Say)

Ephoron leukon Williamson

Tortopus sp. no. 1, Alabama

Tortopus sp. no. 2, Texas

TAXONOMY

Key to Families

1. With one or more polar caps (Figs. 16, 43, 52, 54).....2
Without polar caps (Figs. 9, 15, 37, 76).....8
- 2(1). With two or more polar caps (Figs. 16, 54, 59).....3
With one polar cap (Figs. 43, 52, 56, 72).....5
- 3(2). Sperm guide oval (Figs. 16, 60).....4
Sperm guide elongate or absent (Figs. 53, 56, 58).....
.....most CAENIDAE
- 4(3). Polar caps a loose coil of thread encircling the poles
(may be more than one coil or cap per pole) (Fig. 16);
accessory attachment structures, if present, are
coiled threads without terminal knobs.....
.....Stenonema, interpunctatum group, HEPTAGENIIDAE
Polar caps appearing as a solid structure (Fig. 59);
accessory attachment structures are coiled threads
with terminal knobs (Figs. 59, 60).....POTAMANTHIDAE
- 5(2). Chorion composed of many irregular, usually hexagonal-
shaped, overlapping plates (Figs. 50-52); accessory
attachment structures are paired, uncoiled threads
without terminal knobs.....TRICORYTHIDAE

- Chorion not as above; if accessory attachment structures
are thread-like, they occur singly, coiled, and with
terminal knobs (Figs. 42, 44).....6
- 6(5). Sperm guide lacking (Fig. 56); chorionic sculpturing
absent except under the cap.....Caenis anceps, CAENIDAE
Sperm guide oval (Figs. 43, 44, 73, 75); chorionic
sculpturing present on entire egg, or if absent,
cap as in Figs. 72-75.....7
- 7(6). Preserved cap appearing as a single solid structure
(Fig. 43); accessory attachment structures present,
in the form of coiled threads with terminal knobs
(Figs. 40, 42); chorion with small-mesh (3.1μ or less)
reticulation of irregular polygons (Fig. 44); micro-
pylar device located in the middle half of the egg
(Fig. 43).....most EPHEMERELLIDAE
Polar cap appearing as a cluster of cylinders (Figs. 72-
75); accessory attachment structures absent; chorion
smooth or with a large-mesh reticulation ($11-27\mu$)
(Fig. 72); micropylar device located at the capped
end of the egg (Figs. 72, 73, 75)...Ephoron, POLYMITARCIDAE
- 8(1). With a large-mesh reticulation (greater than 10μ in
length) (Figs. 17-20, 47, 67-71).....9
With a small-mesh reticulation (less than 5μ in length)
(Figs. 31, 32, 63), or reticulation absent.....11

- 9(8). Strands of reticulation are furrows, the mesh being a raised surface (Figs. 45, 46, 47); sperm guide oval (Figs. 47, 48, 49).....
Ephemerella (Eurylophella), EPHEMERELLIDAE
 Strands of reticulation are ridges (Figs. 67-71), or tubercles (Figs. 15, 17-20), the mesh being a depressed surface; sperm guide elongate (Figs. 15, 67, 71).....10
- 10(9). Strands of reticulation are ridges (Figs. 67-71); sperm guide an elongate channel in the ridges of the reticulation (Figs. 67-71).....Hexagenia, EPHEMERIDAE
 Strands of reticulation are tubercles (Figs. 15, 17-20); sperm guide elongate, but not in ridges or reticulation (Figs. 15, 17-20).....some Stenonema, HEPTAGENIIDAE
- 11(10). Chorion densely tuberculate (Fig. 3); accessory attachment structures are coiled threads often in linear groupings surrounding one or both poles of the egg (Fig. 3).....AMETROPODIDAE
 Chorion not tuberculate, or sparsely tuberculate (Figs. 7, 21); coiled threads, if present, never arranged in linear groupings as described above.....12
- 12(11). Chorion completely covered with coiled, thread-like attachment structures (Fig. 1).....SIPHONURIDAE
 Coiled threads never as dense as in Fig. one.....13

- 13(12). Sperm guide funnel-shaped (Figs. 23, 24, 27, 32, 77, 79)....14
 Sperm guide oval (Figs. 4, 13), elongate (Figs. 21, 62,
 66), or absent (Fig. 63).....15
- 14(13). Egg nearly circular, surrounded by an adhesive layer
 composed of many threads with terminal knobs (visible
 under 1250x) (Figs. 76, 80, 81); accessory attachment
 structures lacking; plane of micropyle at an angle to
 that of chorion, thus the micropylar canal is
 apparent (Fig. 79).....Tortopus, POLYMITARCIDAE
- Egg ovoid, without an adhesive layer as described above;
 accessory attachment structures often present in
 various forms [coiled threads (Fig. 39), peg-like
 structures (Figs. 30-36), sucker-like discs (Figs.
 23-26)]; plane of micropyle parallel to that of the
 chorion, thus micropylar canal is absent or not
 apparent.....LEPTOPHLEBIIDAE
- 15(13). Sperm guide oval (Figs. 4, 5, 6, 8, 11, 13).....
 most HEPTAGENIIDAE
- Sperm guide elongate or absent (Figs. 21, 61-64, 66).....16
- 16(15). Chorion reticulate or punctate (Figs. 61-66).....
 Ephemera, EPHEMERIDAE
- Chorion sparsely covered with small tubercles (Fig. 21).
 some Stenonema, HEPTAGENIIDAE

SIPHILONURIDAE

Genus Siphonurus Eaton

(Figs. 1, 2)

FORM. Ovoid, without polar caps.

CHORION. (Fig. 2). Covered with many small dark round maculae, 2.3 μ or less in diameter.

ATTACHMENT STRUCTURES. The entire surface of the egg is covered with groups of threads arranged in coils and lacking terminal knobs. Eggs of S. mirus Eaton laid in a two dram vial of water were held together and to the side of the vial by a thick gelatinous mass, visible to the naked eye. When this is magnified one can see a very dense network formed by an infinite number of small, entwined threads. The female continually extruded the eggs until spent; they did not exit as a single ball or mass, and therefore I am not certain that all the eggs would remain together when laid in a stream.

Degrange (1960), in discussing the attachment structures of S. aestivalis Eaton and S. lacustris Eaton, described a nipple-like structure covering each of the coils. When in water each nipple swells into a cluster of tenuous filaments making a projection on the surface of the rest of the adhesive layer. I could not find these structures on North American Siphonurus eggs.

MICROPYLAR DEVICE. Only one found, on an egg of S. mirus, and it agrees in form with those described by Degrange. Sperm guide oval, 18 μ long by 15 μ wide; micropylar canal 11.5 μ long.

Although eggs of S. alternatus (Say), S. mirus Eaton, S. quebecensis (Prov.), and S. rapidus McD. were available, only the

first two cleared well enough for study. The diameter of the maculations is the only character that will separate the two species: $.8\mu$ or less in S. alternatus, $.8-2.3\mu$ in S. mirus.

HEPTAGENIIDAE

With the exception of the genus Stenonema, an oval-shaped sperm guide and lack of polar caps are the only characters typical of the family. Within Stenonema, the interpunctatum group possesses an oval sperm guide and two polar caps; the other species groups have an elongate sperm guide and no polar caps. The attachment structures vary from peglike in Rhithrogena, to coiled threads in Heptagenia, to an adhesive layer in most Stenonema. Two or more micropylar devices are present in all species studied.

Key to Genera

1. Chorionic sculpturing and accessory attachment structures
 - absent.....2
 - Chorionic sculpturing and or accessory attachment structures present (Figs. 4-21).....3
2. Sperm guide elongate or lacking (Fig. 22).....some Stenonema
 Sperm guide oval.....Epeorus
3. Chorionic sculpturing a series of longitudinal ridges
 (Fig. 5).....Arthroplea
 Chorionic sculpturing not as above.....4
4. Chorionic sculpturing consists of peg-like structures
 (Figs. 12, 13).....Rhithrogena
 Chorionic sculpturing not as above.....5

5. Sperm guide elongate (Figs. 15, 17-21), or absent...some Stenonema
 Sperm guide oval (Figs. 4, 6-9, 11, 16).....6
6. With two to six polar caps, each in the form of a loose coil
 of thread (Fig. 16).....some Stenonema
 Polar caps lacking (Figs. 7, 9).....Heptagenia

Arthroplea bipunctata McDunnough

(Fig. 5)

FORM. Oval, strongly tapered at each pole; without caps.

CHORION. Sculpturing a series of longitudinal ridges, 2-4 μ wide. The chorion must be much more fragile than that of other mayfly eggs, because several slides yielded no eggs without a cracked or broken chorion.

ATTACHMENT STRUCTURES. Since no accessory attachment structures were found, attachment must occur by means of an adhesive layer (although this was not observed).

MICROPYLAR DEVICE. Sperm guide oval, 9.5-11.5 μ long, by 5.5-7.5 μ wide; micropylar canal 7.5-9.5 μ long. Although averaging five, as many as ten have been found scattered throughout the mid-region of the egg.

Epeorus (Iron) suffusus McDunnough

FORM. Ovoid, without polar caps.

CHORION. Smooth, with no sculpturing.

ATTACHMENT STRUCTURES. None found.

MICROPYLAR DEVICE. Sperm guide oval, 11-16 μ long by 8-11 μ wide; micropylar canal 7-13 μ long.

Degrange (1960) studied E. assimilis Eaton and E. alpicola Eaton and likewise found a smooth chorion and a lack of attachment structures.

Genus Heptagenia Walsh

(Figs. 4, 6-11)

The eggs of H. hebe McDunnough, H. rusticalis McD., H. lucidipennis (Clemens), H. aphrodite McD., H. maculipennis Walsh, H. elegantula (Eaton), H. marginalis (Banks), H. pulla (Clemens), and H. flavescens (Walsh) were studied by Smith (1935). The eggs of H. coerulans (Rostock), H. lateralis (Curt.), and H. sulphurea (Muller) were studied by Degrange (1960).

All known Heptagenia eggs are ovoid and lack polar caps. The chorion is covered with many unevenly scattered tubercles (Fig. 6) which vary in diameter. On the eggs of this study, there are areas in which the tubercles have been replaced by ring-like markings (Figs. 6, 8), and the size and abundance of these areas vary among the species. Obscure maculations form a background to the obvious pattern presented by the tubercles and ring-like markings. Heptagenia eggs characteristically have attachment structures in the form of threads (Figs. 9, 10) ($.5\mu$ in diameter except in H. pulla) which are often so tightly coiled that they appear as large maculations (Fig. 8). Palmen (1884), Smith (1935), and Degrange (1960) correctly reported terminal knobs for these threads. The threads are usually concentrated at one or both poles, but may also be found on the lateral surfaces of the egg.

Key to Species

1. Tubercles usually less than 1μ in diameter (Figs. 9-11);
 attachment threads mostly restricted to the poles of the
 egg (Figs. 9, 10).....pulla
- Tubercles greater than 1μ in diameter (Figs. 4, 6-8);
 attachment structures not restricted to the poles of the
 egg (Figs. 7, 8).....2
2. Ring-like markings not abundant, occurring singly or in
 small groups of 2-6 (Fig. 4).....diabasia
- Ring-like markings abundant, concentrated into large groups
 and frequently covering up to 1/5 or more of a given
 surface (Figs. 6-8).....hebe and juno

Heptagenia diabasia Burks

(Fig. 4)

CHORION. Tubercles $1.2-1.5\mu$ in diameter; ring-like markings
 not abundant, usually isolated or in groups of about 2-6.

ATTACHMENT STRUCTURES. Coiled threads concentrated at the poles,
 but also occurring in the mid-region of the egg.

MICROPYLAR DEVICE. Sperm guide oval, with a rim $1.2-1.5\mu$ wide.
 Inside dimensions of sperm guide are $11-15\mu$ long by $7-10\mu$ wide;
 micropylar canal $6-14\mu$ long.

Heptagenia hebe McDunnough and Heptagenia juno McDunnough

(Figs. 6-8)

CHORION. Tubercles $1.2-2.3\mu$ in diameter; ringlike markings
 abundant, covering as much as 1/2 of a given surface, concentrated

in large groups or occurring singly.

ATTACHMENT STRUCTURES. Coiled threads scattered about the surface of the egg, not restricted to poles.

MICROPYLAR DEVICE. Sperm guide oval, $8.5-12\mu$ long by $6-8.5\mu$ wide; micropylar canal $8-17\mu$ long.

Heptagenia pulla (Clemens)

(Figs. 9-11)

CHORION. Tubercles usually less than 1μ in diameter. Ring-like markings much less abundant than in other species, but will occur in large concentrations.

ATTACHMENT STRUCTURES. Coiled threads mostly restricted to the poles, very few occurring in the mid-region; threads much thicker (1.5μ) than those on other species ($.5\mu$).

MICROPYLAR DEVICE. Sperm guide oval, $12-21\mu$ long by $10-16\mu$ wide; micropylar canal present but rarely distinguishable, 9μ long.

Genus Rhithrogena Eaton

(Figs. 12, 13)

FORM. Ovoid, without polar caps.

CHORION AND ATTACHMENT STRUCTURES. The chorion is covered with short peglike structures ($3.5-5\mu$ long) which undoubtedly serve for attachment as do those of some Leptophlebiidae.

MICROPYLAR DEVICE. Sperm guide oval, $11-17\mu$ long by $8-10\mu$ wide; micropylar canal $11-17\mu$ long. The sperm guide possesses a thick rim, and the measurements given are inside dimensions.

Characters could not be found to separate the eggs of R. impersonata (McDunnough) and R. sanguinea Ide.

Genus Stenonema Traver

(Figs. 14-22)

Smith (1935) and Spieth (1947) correctly noted that there are two types of eggs in the genus: the interpunctatum group with a coiled thread at each pole, and the other species groups lacking threads and possessing a gelatinous coat that swells when the egg is deposited in water.

With the exception of the interpunctatum group, the eggs of Stenonema (species groups as given by Burks, 1953) can be readily recognized by the type of micropylar device. The sperm guide (usually absent in S. vicarium) is an elongate depression in which the sculpturing persists (Fig. 20), and which often possesses a proximal "hood" (Figs. 15, 17). Eggs in water are needed, but I think this hood is formed by the adhesive layer--thus the distal portion of the sperm guide is without an adhesive layer covering it. The distal end of the sperm guide fades and is often obscure; therefore it is frequently difficult to measure its length accurately. The micropylar canal tapers distally, and it frequently has a terminal appendage (Fig. 14) which may or may not have an apical "brush". I am unable to make any decisions concerning the function and nature of this appendage, and have not included it in length measurements of the micropylar canal.

The chorion of the tripunctatum, pulchellum, and terminatum species groups is sparsely covered with short, irregularly-shaped tubercles, many of which are often arranged in a reticular pattern of large, irregular-polygonal mesh. The chorion of the vicarium group is smooth. The only attachment structure is an adhesive layer which presents a striated appearance in preserved material.

The eggs of the interpunctatum group possess two to six polar caps, each formed by a single thread coiled about the pole (Fig. 16). The micropylar device, with an oval sperm guide, is typical of the family. The chorion is sparsely covered with tubercles which are not as irregular in shape as those of the other species groups.

Because Stenonema is a large genus, and its species often vary considerably in their own external morphology, the keys and descriptions for the species are given with a certain amount of reservation. Enough material of wide distribution was not available, and therefore the reliability of the keys and descriptions is not known. Although these must serve at best as a foundation for future studies of the genus, I am quite sure that characters used to distinguish the genus from other genera in the family are reliable.

Key to species

1. With two to six polar caps (Fig. 16).....canadense
 Without polar caps.....2
2. Chorion smooth, without sculpturing (Fig. 22).....3
 Chorionic sculpturing in the form of short tubercles, often
 with a reticular pattern of arrangement (Figs. 15, 17-21).....4
3. Sperm guide usually lacking; micropylar canal 8-15 μ long;
 egg nearly circular in form.....vicarium
 Sperm guide present, elongate (Fig. 22); micropylar canal
 13-18 μ long; egg ovoid in form.....fuscum
4. Tubercles not in a reticular pattern (Fig. 21).....femoratum
 Tubercles arranged in a reticular pattern (Figs. 15, 17-20).....5

5. Micropylar canal usually 12-14 μ long.....6
 Micropylar canal usually 5-12 μ long.....7
6. Sperm guide with basal hood (Fig. 15).....nepotellum
 Sperm guide without basal hood (Figs. 19, 20).....tripunctatum
7. Micropylar canal 10-12 μ long; sperm guide with basal hood
 7-23 μ long (Fig. 17).....lepton
 Micropylar canal 5-9 μ long; sperm guide with short basal
 hood (3-6 μ long) or hood absent (Fig. 18).....rubromaculatum

CANADENSE Group

Stenonema canadense (Walker)

(Fig. 16)

FORM. Ovoid, with two-six polar caps.

CHORION. Sparsely covered with short tubercles ranging from
 1-4 μ in diameter.

ATTACHMENT STRUCTURES. Each of the two polar caps (Fig. 16)
 is formed by a single thread coiled about the pole, which, according
 to Smith (1935), can be outstretched to a length of two inches or
 more. Smith noted that the thread is attached at a small protuberance
 on the chorion. Smith also noted the presence of smaller coils of
 thread which are usually located near the margins of the caps.

A specimen from Maine, tentatively determined as S. canadense,
 yielded eggs with two and occasionally three coils of threads arranged
 on one or both poles.

MICROPYLAR DEVICE. Sperm guide oval, 13-17 μ long by 11-13 μ
 wide; micropylar canal 17-25 μ long.

Eggs of S. frontale (Banks), S. heterotarsale McDunnough and S. minnetonka Daggy did not differ from S. canadense in details of the cap (one per pole) and micropylar device; the chorion could not be satisfactorily observed.

PULCHELLUM Group

Stenonema nepotellum (McDunnough)

(Fig. 15)

FORM. Ovoid, tapered towards the poles; without polar caps.

CHORION. Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (19-27 μ long).

MICROPYLAR DEVICE. Sperm guide elongate (42-61 μ long), tapering distally, and with a proximal hood 12-20 μ long; micropylar canal 12-14 μ long.

Stenonema rubromaculatum (Clemens)

(Figs. 14, 18)

Like S. nepotellum except the sperm guide does not taper distally, the proximal hood is short (3-6 μ long) or lacking, and the micropylar canal is 5-9 μ long.

TERMINATUM Group

Stenonema leptum Burks

(Fig. 17)

FORM. Ovoid, tapered toward poles; without polar caps.

CHORION. Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (23-31 μ long).

MICROPYLAR DEVICE. Sperm guide elongate (31-54 μ long), not tapering distally, and with a proximal hood (7-23 μ long); micropylar canal 10-12 μ long.

TRIPUNCTATUM Group

Stenonema femoratum (Say)

(Fig. 21)

FORM. Ovoid, not tapered at poles; without polar caps.

CHORION. Tubercles randomly scattered, having no particular pattern of arrangement.

MICROPYLAR DEVICE. Sperm guide elongate (35-54 μ long), tapering distally, and without a proximal hood; micropylar canal 10-11 μ long.

Stenonema tripunctatum (Banks)

(Figs. 19, 20)

FORM. Ovoid, slightly tapered towards poles; without polar caps.

CHORION. Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (17-23 μ long).

MICROPYLAR DEVICE. Sperm guide elongate (38-54 μ long), tapering distally, and without a proximal hood; micropylar canal 12-14 μ long.

VICARIUM Group

Stenonema fuscum (Clemens)

(Fig. 22)

FORM. Ovoid, without polar caps.

CHORION. Smooth, sculpturing absent.

MICROPYLAR DEVICE. Sperm guide elongate (50-62 μ long), not tapering distally, and with a basal hood (5-17 μ long); micropylar canal 13-18 μ long.

Stenonema vicarium (Walker)

Like S. fuscum except nearly circular in form, sperm guide usually lacking, and micropylar canal 8-15 μ long.

AMETROPODIDAE

Siphloplecton basale (Walker)

(Fig. 3)

FORM. Distorted, without polar caps. The only material available was collected in 1950, and preserved in 85% Ethyl Alcohol. I could not determine if the distortion of these eggs is natural or due to preservation. Smith (1935) indicates that the eggs of S. basale (Walker), S. signatum (Traver), and S. speciosum Traver are ovoid.

CHORION. Tuberculate; tubercles 2 μ or less in height, 2-3.5 μ wide.

ATTACHMENT STRUCTURES. Coiled threads without terminal knobs occurring singly, or in linear groupings which often encircle one or both poles of the egg. When single, the diameter of the coil is approximately one half that of the coils occurring in linear groupings.

MICROPYLAR DEVICE. Unknown.

LEPTOPHLEBIIDAE

There is such a wide diversity of chorionic sculpturing and attachment structures within this family, that it is impossible to use these features for recognition of the family. However, the type

of micropylar device, the lack of polar caps, and the ovoid form (except the nearly rectangular eggs of Thraulodes speciosus) are constant features characteristic of the family.

There are two or three micropylar devices present, and these are located about the equatorial region of the egg. The micropyle is situated at the base and near center of a funnel-shaped sperm guide; the micropylar canal is apparently lacking. Measurements have been given for the diameter of the top rim of the funnel (which is at the surface of the egg) and for the diameter of the micropyle.

Key to Genera and species

1. Surface of egg evenly covered with coiled thread-like attachment structures (Fig. 39).....Thraulodes speciosus
Egg without thread-like attachment structures arranged like those in Fig. 39.....2
2. Chorionic sculpturing a series of longitudinal ridges or bands (Figs. 27-29).....Habrophlebia vibrans ?
Chorionic sculpturing never in the form of longitudinal ridges, but may be raised sucker-like discs, tubercles, peg-like projections or a reticulation (Figs. 23-26, 32-38)...3
3. Chorionic sculpturing in the form of tubercles or raised sucker-like discs (Figs. 23-26, 37, 38).....5
Chorionic sculpturing reticulate or peg-like, or both (Figs. 30-36).....4

4. Chorionic sculpturing a small-mesh reticulation (Figs. 31, 32); attachment structures are stout (3.5-5.5 μ wide) peg-like translucent projections which are frequently clumped in groups of two to six or more, and which do not "mushroom" when in water (Figs. 30, 32).....Leptophlebia sp.

Chorionic reticulation absent; attachment structures are slender (1.1-1.5 μ wide) peg-like projections which are evenly scattered about the surface of the egg, and which develop a mushroom shape when in water (and occasionally, to some extent in alcohol) (Figs. 33-36).....
.....Paraleptophlebia adoptiva and P. mollis

5. Raised surfaces are sucker-like discs averaging 5.4-6.9 μ in diameter (Figs. 23-26).....Habrophlebiodes americana

Raised surfaces are tubercles only, not sucker-like discs, averaging 2.3-3.8 μ in diameter (Figs. 37, 38).....
.....Paraleptophlebia debilis

Habrophlebia vibrans Needham ?

(Figs. 27-29)

CHORION. Chorionic sculpturing a series of wide (11.5-13.5 μ), elevated, longitudinal bands which are occasionally branched, and are separated by a space of 7-10 μ . On the lateral margins of the bands many small fingerlike projections occur (.7-3.1 μ long), the purpose of which is unknown. With the use of a Carl Zeiss Photomicroscope equipped with the Nomarski interference-contrast attachment (shows relief), it was determined that the longitudinal bands consist of three ridges, one median and two lateral (Figs. 27, 28).

ATTACHMENT STRUCTURES. Degrange described attachment structures as being refractive granular masses (20-28 μ in diameter) located in the middle and posterior regions of the egg. No such structures could be found in the available material. The longitudinal ridges, as well as their lateral projections, most likely have something to do with attachment--no other structures could be found, and fresh material was unavailable.

MICROPYLAR DEVICE (Figs. 27, 29). Sperm guide funnel-shaped, rim 8-13 μ in diameter; micropyle 1.5-2 μ in diameter.

The determination of this species is questionable, since it is based upon a single female collected in New York state.

Habrophlebiodes americana (Banks)

(Figs. 23-26)

CHORION. Reticulation absent. However, there is an apparent reticulation which is not readily discernible, and which should not be confused with a true reticulation. This pseudo-reticulation is composed of six-sided mesh (occasionally five or seven sided) including a distinct light spot at the joints of the strands (Fig. 26). The spots are .8-1.2 μ in diameter, whereas the strands are mere lines the width being immeasurable even under oil immersion (1250x). It appears that this pseudo-reticulation is formed by the close fitting nature of the circular attachment structures described below.

ATTACHMENT STRUCTURES. (Fig. 25). Sucker-like plates which are usually circular in form, but often vary from an irregular circle to nearly a rectangle. The outside dimensions of the raised portion of the plates (Fig. 25) range from 4.6-9.2 μ , the average being between

5.4-6.9 μ . The width (thickness) and height of the rim of the sucker-like plates both range between 1.5-2.3 μ .

Nothing is known about the adhesive nature of these eggs, but it is suspected that these plates act as suckers, aided by an adhesive substance coating the egg.

MICROPYLAR DEVICE. (Figs. 23, 24). Sperm guide funnel-shaped, inserted among the closely spaced plates. Although the micropyle is nearly a perfect circle (1.5-2.3 μ in diameter), the rim of the sperm guide is a very irregularly shaped polygon (3.8-6.2 μ long).

Leptophlebia sp.

(Figs. 30-32)

NUMBER. 3,700 according to Morgan (1913).

CHORION. (Fig. 32). The chorion bears a small-mesh (3.8 μ or less in length), irregular polygonal reticulation formed by ridges .5-1.5 μ in thickness. Morgan (1913) described in L. cupida (Say) the presence of irregularly scattered pits and bosses, but did not describe the actual reticular pattern.

ATTACHMENT STRUCTURES. (Figs. 30, 32). Both Morgan (1913) and Smith [1935, L. austrina (Traver), L. cupida (Say), L. grandis (Traver), and L. nebulosa (Walker)] noted the presence of stout peg-like projections, Smith correctly noting that they are translucent. They occur singly or in groups of two to six or more, are 5.5-10 μ long by 3.5-5.5 μ wide, and are found scattered over the entire surface. Smith remarks that when "in water these projections stand out at right angles to the surface of the egg and adhere even to glass."

MICROPYLAR DEVICE. (Figs. 31, 32). Sperm guide funnel-shaped, rim 5.8μ in diameter; micropyle ovoid, $1.5-2.7\mu$ long.

The egg of L. marginata (L.), described and figured by Degrange, is very similar to the one described above, except the peg-like projections are not grouped. Smith describes L. johnsoni as being unlike the other four Leptophlebia studied by him, its egg having "a reticular pattern of sinuous ridges, and translucent projections stand up like fence posts wherever these ridges branch."

Genus Paraleptophlebia Lestage

(Figs. 33-38)

Smith (1935) states that P. adoptiva (McD.), P. debilis (Walker), P. moerens (McD.), P. mollis (Eaton) and P. memorialis (Eaton) [as P. pallipes (Hagen)] "all have ellipsoid eggs, .18-.20mm by .10mm. In preserved material the chorion is thickly covered with many small bosses and by focusing carefully, a few small finger-like projections may be seen." His techniques apparently did not allow him to observe that his "bosses" were actually end views of the projections. He believed that these bosses must spring out when in water to form the narrow projections (cilia) described by Morgan (1913). Three of his species were studied herein, and two (P. adoptiva and P. mollis) possess peg-like (fingerlike) projections, the third (P. debilis) possesses small tubercles (bosses). Both Morgan (1913, Leptophlebia sp.?) and Degrange [1960, P. submarginata (Steph.)] record similar projections. The micropyles are all typical of the family, and no generic characters could be found to separate Paraleptophlebia from the other genera of Leptophlebiidae.

Paraleptophlebia adoptiva (McDunnough)and P. mollis (Eaton)

(Figs. 33-36)

CHORION AND ATTACHMENT STRUCTURES. The entire surface of the egg is covered with short peg-like projections (Figs. 33, 34), doubtlessly adhesive in nature. When eggs are laid in water, the ends of these projections swell, and the projections become "mushroom" shaped (Figs. 35, 36), thus forming a greater surface area for adhesion. The projections are $3.1-3.8\mu$ long (including the cap when formed) by $1.1-1.5\mu$ wide (not the cap). The cap itself is up to 3.8μ wide. It may be possible to obtain larger measurements for the projections if the eggs are allowed to remain in water for more than five minutes.

MICROPYLAR DEVICE. (Figs. 33, 34). Sperm guide funnel-shaped, rim 5.8μ in diameter; micropyle $1.9-3.1\mu$ in diameter.

Paraleptophlebia debilis (Walker)

(Figs. 37, 38)

CHORION. Covered with many small circular tubercles $2.3-3.8\mu$ in diameter. Much smaller tubercles, 1.5μ or less in diameter, occur intermittently among the larger ones. Relatively wide striations weave among the tubercles.

ATTACHMENT STRUCTURES. None, unless the tubercles described above act as adhesive devices.

MICROPYLAR DEVICE (Figs. 37, 38). Sperm guide funnel-shaped, rim $5.4-6.9\mu$ in diameter; micropyle 1.5μ in diameter.

Thraulodes speciosus Traver

(Fig. 39)

FORM. Nearly rectangular.

CHORION. Covered with irregular circular maculations .8-3.1 μ in diameter.

ATTACHMENT STRUCTURES. Threadlike attachment structures, covering a circular area of 8.5-10.7 μ in diameter when coiled, are evenly distributed over the chorion. No uncoiled threads could be found; however, it appears that they are terminated by very small knobs. An adhesive layer is also apparent.

MICROPYLAR DEVICE. Typical of the family, except the micropyle (1.5 μ in diameter) sits at the bottom of a funnel-shaped sperm guide which is much deeper than in other Leptophlebiids. Only one per egg, the micropylar device is most commonly found very close to one of the coiled threads.

EPHEMERELLIDAE

A single polar cap, coiled threads with terminal knobs, ovoid form, and an ovoid sperm guide will serve to distinguish the Ephemerellidae [except E. Ephemerella maculata Traver (described by Smith, 1935) and the subgenus Eurylophella] from other North American families of Ephemeroptera. Smith (1935) has studied twenty-five species, representing all of the North American subgenera. He indicated that only E. maculata and the subgenus Eurylophella are atypical, having a nearly rectangular form and lacking the coiled threads and polar cap typical of the rest of the family. However, Eurylophella does have a micropylar device typical of the family; that of E.

maculata is unknown. The eggs studied by Degrange are also typical of the family.

The eggs of the subgenera other than Eurylophella all possess one polar cap (Fig. 43) which swells and separates when in water, revealing a thick mass of short threads with terminal knobs (Fig. 41). The accessory attachment structures are coiled threads with terminal knobs; the latter being a fibrillous disc with the thread attached at the center (Fig. 40).

The micropylar devices of all subgenera consist of an oval sperm guide, a micropyle, and an elongate micropylar canal; and they vary considerably in their dimensions. In all cases there is more than one micropylar device present, and these are usually located in the middle half of the egg.

Key to Subgenera

1. Polar cap and knob-terminated coiled threads present (Figs. 40-44).....2
- Polar cap and knob-terminated coiled threads absent
(Fig. 47).....Eurylophella

2. Oval areas, in which the reticulation is finer or absent, usually numbering six or less on a given surface, and providing the attachment point for the coiled threads (Fig. 44).....Drunella and Ephemerella
- Oval areas usually numbering 45 or more; coiled threads not as frequent as, and not always attached in the oval areas (Fig. 42).....E. (Serratella) deficiens

Subgenera Ephemerella Walsh and Drunella Needham

Five species of Ephemerella (E. dorothea, E. excrucians, E. inconstans, E. invaria, and E. subvaria) and three of Drunella (E. cornuta, E. lata, and E. walkeri) were studied and found indistinguishable even at the subgeneric level; one species of the subgenus Serratella (E. deficiens) was found to be separable from the eight species of Ephemerella and Drunella. Smith (1935) likewise found most species of Ephemerellidae to be inseparable.

Ephemerella (Drunella) cornuta Morgan

(Figs. 43, 44)

The egg of this species is typical of those of the eight species of the subgenera Ephemerella and Drunella studied, and will suffice as a description for both subgenera.

FORM. Ovoid, with one polar cap.

CHORION. Finely reticulated with an irregular polygonal mesh measuring up to 3.1μ in length. Oval areas with reticulation much finer or absent, scattered about on the chorion; usually numbering less than six, and never more than twelve, on a given surface.

ATTACHMENT STRUCTURES. (Figs. 40, 43, 44). Two types: a single polar cap; and several coiled threads with terminal knobs, each thread being attached in one of the oval areas described above.

MICROPYLAR DEVICE. (Fig. 44). Sperm guide oval, $20-22\mu$ long by $17-18\mu$ wide; micropylar canal $3-5\mu$ long.

Ephemerella (Serratella) deficiens Morgan

(Figs. 40, 42)

FORM. Ovoid, with a single polar cap.

CHORION. (Fig. 42). Finely reticulated with an irregular polygonal mesh measuring up to 3.1μ in length. Scattered about on the surface are many oval areas completely void of the reticulation. There are forty-five or more of these areas on a given surface, and this feature will distinguish E. deficiens from the species of the subgenera Ephemerella and Drunella mentioned above. The boundaries of these areas are difficult to distinguish, but the diameters range between $8-19\mu$.

ATTACHMENT STRUCTURES. (Figs. 40, 42). Two types: a single polar cap; and several coiled threads with terminal knobs, the threads not as frequent as, and not always attached in, the oval areas described above.

MICROPYLAR DEVICE. Sperm guide oval, 19μ long, 11.5μ wide; micropylar canal $6.2-7.7\mu$ long.

Subgenus Eurylophella Tiensuu

(Figs. 45-49)

The lack of polar caps and coiled threads, and the presence of a rectangular form and a large-mesh reticulation formed by furrows serve to separate eggs of the subgenus Eurylophella from all other known eggs of the Ephemerellidae. The chorion of Eurylophella eggs is covered with irregularly shaped polygonal plates whose edges are raised (Figs. 45, 46, 47) and whose length varies from $15-31\mu$. This results in a large-mesh reticulation formed by furrows (spaces between the

raised edges of the plates) 1.9-5.4 μ wide, rather than ridges as stated by Smith (1935). When eggs are laid in water, the edges of these plates swell inwardly and upwardly to form sucker-like structures (Fig. 45), which undoubtedly serve, together with an adhesive layer, for the attachment of the egg. Many variously shaped granules and clear spots can be found on the sucker-like plates (Figs. 47-49).

The micropylar device is typical of the family (Figs. 47-49); sperm guide oval, 15-19 μ long by 13-17 μ wide; micropylar canal 23-38 μ long.

The only character found to separate the eggs of E. prudentalis McDunnough and E. temporalis McD. is the presence of many clear spots on the plates of E. temporalis (Fig. 49), and the reduction or absence of these in E. prudentalis (Figs. 47, 48).

TRICORYTHIDAE

Genus Tricorythodes Ulmer

(Figs. 50-52)

NUMBER. 750, according to Morgan (1913).

FORM. Ovoid, with one polar cap which tapers to a nipple-like point.

CHORION. Morgan (1913) described the egg of T. allectus (Needham) to be bright green with a yellowish cap and "with a prominent shingle-like surface". Smith (1935) disagreed with Morgan believing the chorion to be "sculptured, not with 'shingles' as figured by Morgan (1913), but with a reticular pattern having the ridges interrupted in such a way that the egg appears to be covered with overlapping shingles or scales."

The surface of the egg actually does have a shingle-like surface (Fig. 50), and is not like the reticular pattern described and figured by Smith. These overlapping "shingles" or plates are mostly hexagonal and 15-19 μ across. There is a curved band of small, circular-mesh reticulation across the middle of each plate.

ATTACHMENT STRUCTURES (Fig. 52). In addition to the polar cap, there are a few pairs of relatively thick threads which are attached between the plates, and are not coiled.

MICROPYLAR DEVICE. (Figs. 51, 52). Sperm guide oval, 15-23 μ long by 13-17 μ wide; micropylar canal difficult to see, but at least 9 μ long; only one per egg, and located near the uncapped pole.

Characters could not be found to separate the eggs of T. atratus McD., T. explicatus (Eaton), T. fallax Traver and T. stygiatus McD.

CAENIDAE

Genus Caenis Stephens

(Figs. 53-58)

Smith (1935) studied eggs of C. amica Hagen, C. jocosa McD., C. hilaris (Say), C. perpusilla (from India), and C. simulans McD.; and Degrange (1960) studied eggs of C. horaria (L.), C. macrura Steph., C. moesta Bengtsson, C. robusta Eaton, and C. sp.

The two polar caps and the micropylar device are the two distinctive features of Caenis eggs. Most Caenis eggs have two polar caps; however, C. sp., described by Degrange, and C. anceps Traver possess only one. The polar caps, unlike the polar caps of other mayfly eggs, are composed of a long mass of tightly cohering, spirally arranged threads with variously sized terminal knobs (Figs. 54-57) (according to

Smith, 1935, C. perpusilla has only four threads). Upon contact with water the threads uncoil (Fig. 55) and unspiral (Fig. 57) in order to become entangled with submerged surfaces (Fig. 57).

The micropylar device may lack the sperm guide and consist simply of an elongate micropylar canal (Fig. 56); the distinctive feature, however, is that the canal is the most evident part of the micropylar device (Figs. 53, 58). Unlike most other mayfly eggs, only one micropyle occurs on Caenis eggs except in C. horaria, where Degrange states there are two present.

Smith (1935) observed a smooth chorion and two polar caps on the five species of Caenis eggs which he studied. I observed the eggs of two of these (C. jocosa and C. simulans) and found their chorion to be definitely sculptured.

Key to species

1. With one polar cap (Fig. 56); chorion mostly smooth, sculpturing absent except under the cap.....anceps
 With two polar caps (Figs. 54, 55); the entire chorion
 reticulate or finely punctate (Figs. 53, 58).....2
2. Chorion finely punctate, the punctures up to .5 μ in diameter
 (Fig. 58).....forcipata
 Chorion finely reticulate with irregularly-shaped polygonal
 mesh up to 1.2 μ in length (Fig. 53).....jocosa

Caenis anceps Traver

(Fig. 56)

FORM. Ovoid, with one polar cap.

CHORION. Smooth, except for the area under the cap which is coarsely and unevenly sculptured.

ATTACHMENT STRUCTURES. The single polar cap is large, like C. sp. described by Degrange, and unlike the cap of other Caenis species, it encircles approximately one-fourth of the egg.

MICROPYLAR DEVICE. Sperm guide lacking; micropylar canal (23.1-29.2 μ long) gradually expands distally (3.1 μ in outside diameter at micropyle, 3.8-4.2 μ in outside diameter at distal end).

Caenis forcipata McDunnough

(Figs. 54, 57, 58)

FORM. Ovoid, with two polar caps.

CHORION. (Fig. 58). Very finely punctate, the punctures approximately .5 μ in diameter.

ATTACHMENT STRUCTURES. Two polar caps.

MICROPYLAR DEVICE. (Fig. 58). Sperm guide elongate, flame-shaped, 15-30 μ long; micropylar canal (22-27 μ long, 3.1-3.8 μ in outside diameter at micropyle) mostly parallel-sided, expanding suddenly at the distal end (5.4-6.9 μ in outside diameter). The expansion is a flaring, not a flange as in C. jocosa (Fig. 53).

Caenis jocosa McDunnough

(Figs. 53, 55)

FORM. Ovoid, with two polar caps.

CHORION. (Fig. 53). Finely reticulated, the mesh measuring up to 1.2 μ in length.

ATTACHMENT STRUCTURES. Two polar caps.

MICROPYLAR DEVICE. (Fig. 53). Sperm guide elongate, flame-shaped, 8-22 μ long; micropylar canal (15-24 μ long, 2.3-3.1 μ in outside diameter at micropyle) parallel-sided or gradually expanding, often with an abrupt flange-like expansion at the distal end (4.6-6.9 μ in outside diameter).

Caenis simulans McDunnough

C. simulans, as presently understood, can be broken into three separate groups based upon differences in the eggs. These are from Utah, from Michigan and New York, and from Michigan and Ontario. I am not yet prepared to say which one is (or that all are) the true C. simulans.

POTAMANTHIDAE

Genus Potamanthus Pictet

(Figs. 59, 60)

Ide (1935) and Smith (1935) examined eggs of P. rufous Argo, and Degrange (1960) has examined those of P. luteus (L.).

FORM. (Fig. 59, distorted by preservative). Ovoid, with two polar caps.

CHORION. (Fig. 60). Covered with many dark maculations.

ATTACHMENT STRUCTURES. Scattered about the surface are 6-12 coiled threads with terminal knobs (Figs. 59, 60), the center of which is marked by a cluster of maculations. The coiled threads and the two polar caps are the only attachment structures. Ide's (1935) illustration of an egg of P. rufous shows the swelled caps which are characteristic of eggs laid in water.

MICROPYLAR DEVICE. (Fig. 60). Sperm guide nearly circular, 11-23 μ in diameter; micropylar canal 4-15 μ long. The sperm guide is clear of maculations, and is marked by a dark ring around its border. Usually two in number, occasionally more, they are scattered in the equatorial region.

Characters could not be found to separate the eggs of P. myops (Walsh) and P. neglectus Traver.

EPHEMERIDAE

Similar to Caenidae, the micropylar canal is the most evident part of the micropylar device on Ephemera and Hexagenia eggs. The sperm guide, when present, is somewhat variable and will serve to distinguish the two genera. The eggs are not equipped with accessory attachment structures or polar caps, their only method of attachment being an adhesive layer coating the eggs. Hunt (1951, 1953) relied on the adhesiveness of Hexagenia limbata s.l. eggs when he collected them with submerged glass plates. Eggs of Pentagenia were not studied.

Key to Genera

Chorion with a large-mesh reticulation (mesh 13-31 μ long) (Figs. 67-71); sperm guide always present as an elongate channel in the ridges of the reticulation (Figs. 67-71).....Hexagenia

Chorion with a small-mesh reticulation (mesh 1.5-3.1 μ long) (Figs. 63-66), or punctate (Figs. 61, 62); sperm guide, when present, simply an elongate depression devoid of sculpturing (Figs. 62, 66).....Ephemera

Genus Ephemera Linnaeus

Smith (1935) states that the eggs of E. blanda Traver, E. simulans Walker, and E. varia Eaton "are all plain ellipsoid...and they have no chorionic patterns or appendages. When they are laid in...water, the eggs scatter over the bottom but they are held together in small bunches by a more or less stringy gelatinous material."

Degrange (1960) states that the exochorion of E. danica Müll. and E. vulgata L. is very finely reticulated with an irregular polygonal mesh, and that the exochorion of E. glaucops Pictet is finely granulated. He mentions the presence of an adhesive substance which is finely granular; and describes a micropylar device which lacks a sperm guide, and in which the canal partially projects beyond the micropyle and above the surface of the chorion.

Two of the three species studied by Smith were also examined in the present study (E. simulans and E. varia). In both of these species, and also in E. guttulata Pictet, the eggs have distinct chorionic sculpturings, and are ovoid in form. Eggs of E. simulans, when broken, best showed the finely granular adhesive substance observed by Degrange (Fig. 65). Eggs of E. varia that had been in water for twelve hours readily adhered to the glass vial in which they were laid, and displayed the same adhesive substance. Here, however, the granulations were not so closely spaced as in preserved material, for the adhesive layer swells when in water (and was probably also stretched when the eggs were removed from the vial).

Although the micropylar device is similar to that described by Degrange, the micropylar canal is divided into two parts (Fig. 64):

a proximal part with thick parallel walls, and a distal part with much thinner walls which taper inwardly from the proximal part (except in E. guttulata). In E. simulans and E. varia, the proximal part projects beyond the micropyle and above the surface of the chorion, and resembles a pincer-like structure (Figs. 63, 66). In E. guttulata and E. varia a sperm guide is present as an elongate depression devoid of sculpturing (Figs. 62, 66). Two or more micropyles may be present, and they are found scattered in the equatorial region of the egg.

Key to species

1. Chorion finely punctate (Figs. 61, 62).....guttulata
 Chorion reticulate (Figs. 63, 66).....2
2. Micropylar device without a sperm guide (Figs. 63, 64)....simulans
 Micropylar device with an elongate sperm guide (Fig. 66).....varia

Ephemera guttulata Pictet

(Figs. 61, 62)

CHORION. Very finely punctate, punctures less than .7 μ in diameter.

MICROPYLAR DEVICE. (Fig. 62). Sperm guide elongate (19-30 μ long), without definite boundaries; micropylar canal 26-54 μ long. The thick walls of the proximal part of the micropylar canal do not project above the chorion as in E. simulans and E. varia, and project only slightly beyond the micropyle; the distal portion of the canal tapers only slightly or not at all. Usually one micropylar device per egg, occasionally two.

Ephemera simulans Walker

(Figs. 63-65)

CHORION. (Figs. 63, 64). Reticulated with a very small, irregular, polygonal mesh 1.5-3.1 μ long. In preserved material the granular adhesive layer often appears to be the exochorion. However, eggs laid in water show that this granular layer is the adhesive layer, thus it is not to be confused with the reticulated exochorion (Fig. 65).

MICROPYLAR DEVICE. (Figs. 63, 64). Sperm guide lacking; micropylar canal 18-38 μ long. Proximal part of micropylar canal (8-23 μ long) with a very short section projecting beyond the micropyle and above the chorion, resembling a pincer-like structure; distal part of canal (10-15 μ long) tapering inwardly from the proximal part.

Ephemera varia Eaton

(Fig. 66)

The eggs of this species resemble those of E. simulans except that the micropylar device is much longer (50-55 μ long) due to the presence of a sperm guide.

Genus Hexagenia Walsh

(Figs. 67-71)

The chorionic sculpturing, the type of micropylar device, and the shape of the egg serve as diagnostic features to distinguish Hexagenia eggs from other Ephemeroptera eggs.

Smith (1935) has studied eggs of ten of the fourteen species and subspecies of Hexagenia in North America, and has found that all but H. recurvata Morgan (which is sparsely covered with small nodules)

have a reticulation of large, irregular, polygonal mesh formed by ridges which may be either straight or sinuous. Smith states that the ridges of H. munda elegans Traver, H. limbata venusta Eaton, and H. rigida McD. are sinuous; those of H. munda orlando Traver and H. munda marilandica Traver vary (may be straight or sinuous or mixture of both); and the ridges of H. atrocaudata McD., H. bilineata (Say), H. limbata occulta (Walker), H. limbata viridescens (Walker), H. munda affiliata McD., and H. munda elegans Traver are straight. The observations of the present study are in agreement with Smith.

The sperm guide makes its way to the micropyle as an elongate channel in the ridges of the reticulation (Figs. 67-71); its proximal portion may vary in width from one species to another, and it may expand laterally as a depression in the chorion. The micropylar canal is the longest observed on any mayfly eggs, and together with the sperm guide its length may equal the width of the egg.

Hexagenia eggs are more nearly rectangular than most Ephemeroptera eggs.

Hunt (1951, 1953) has recorded observations on the number of eggs produced, and found that the number of eggs was positively correlated with body length. The total number of eggs varied between 2,260 and 7,684, and the body length varied between 19.9mm and 30.3mm. An average sized female (24-25 mm) produced about 4,000 eggs.

Key to species and subspecies

1. Ridges of reticulation 2 μ wide and strongly sinuous (Fig.

68); portion of sperm guide proximal to micropyle enlarged and oval, the width usually being at least three times the diameter of the micropyle (Fig. 68).....rigida

Ridges of reticulation 2-3.5 μ wide, straight or only slightly sinuous (Figs. 67, 69-71); portion of sperm guide proximal to micropyle only slightly widened, not wider than twice the diameter of the micropyle (Figs. 69-71); or if the proximal portion of the sperm guide is enlarged and oval (Fig. 67), the width being at least three times the diameter of the micropyle, then the ridges are 3.5 μ wide (Fig. 67).....2

2. Ridges of reticulation 3.5 μ wide (Fig. 67); proximal portion of sperm guide enlarged and oval, the width usually being at least three times the diameter of the micropyle (Fig. 67).....munda munda

Ridges of reticulation 2 μ wide, (Figs. 69-71); proximal portion of sperm guide only slightly widened, usually not wider than twice the diameter of the micropyle (Fig. 71).....3

3. Ridges of reticulation straight or very slightly sinuous (Figs. 70, 71); micropylar canal usually longer than 67 μlimbata occulta

Ridges of reticulation definitely more strongly sinuous

(Fig. 69); micropylar canal usually less than 67 μ

.....limbata venusta

Hexagenia limbata occulta (Walker)

(Figs. 70, 71)

CHORION. Large mesh (13-31 μ long) reticulation formed by ridges (2 μ wide) which are straight or only faintly hinting at sinuosity.

MICROPYLAR DEVICE. (Figs. 70, 71). Sperm guide 42-67 μ long; micropylar canal 67-77 μ long. The sperm guide gradually widens as it approaches the micropyle, but its width is typically not greater than twice the diameter of the micropyle.

Hexagenia limbata venusta Eaton

(Fig. 69)

Egg as in H. l. occulta, except the chorionic ridges are definitely sinous, although not as strongly as in H. rigida; and the micropylar canal is 44-67 μ long.

Hexagenia munda munda Eaton

(Fig. 67)

CHORION. Large mesh (13-31 μ long) reticulation formed by straight or slightly sinuous ridges (3.5 μ wide).

MICROPYLAR DEVICE. Sperm guide elongate, 48-58 μ long; micropylar canal 58-67 μ long. The proximal portion of the sperm guide is an abruptly enlarged oval area, the width usually being at least three times as great as the diameter of the micropyle.

Hexagenia rigida McDunnough

(Fig. 68)

CHORION. Large-mesh (13-31 μ long) reticulation formed by ridges (2 μ wide) which are strongly sinuous. A single tubercle is found in the center of each mesh.

MICROPYLAR DEVICE. Sperm guide elongate, 48-62 μ long; micropylar canal 44-55 μ long; the proximal portion of the sperm guide is an abruptly enlarged oval area, usually at least three times as wide as the diameter of the micropyle.

POLYMITARCIDAE

The eggs of the two subfamilies of Polymitarciidae have no characters in common, and the strong differences in their eggs suggest that they are not closely related. Only one subfamily has polar caps; and strikingly different micropylar devices, chorionic sculpturings, and methods of attachment can be noticed between the two subfamilies. Such diverse differences have also been noted only with the genus Stenonema (Heptageniidae).

Key to Genera

Eggs with a polar cap (Figs. 72-75); micropylar device with an oval-shaped sperm guide and an elongate micropylar canal (Fig. 72, 73, 75); "sides" nearly parallel.....Ephoron

Eggs without a polar cap (Figs. 76-79); micropylar device with a funnel-shaped sperm guide and a short micropylar canal (Figs. 77-79); egg with the appearance of a sphere which has had one side pushed in (Fig. 78).....Tortopus

Genus Ephoron Williamson

(Figs. 72-75)

Smith (1935) studied what he thought to be E. album (Say) but actually looked at eggs of E. leukon Williamson as did Ide (1935). The egg of E. virgo (Olivier), studied by Degrange (1960), is similar to that of E. album in that it lacks reticulation.

As many as five micropylar devices have been found at the capped end of the egg. The sperm guide is oval, and the micropylar canal is proximally expanded forming the "half-skullcap" described by Degrange (1956, 1960) for E. virgo (Figs. 72, 73, 75).

The only attachment structure is a large polar cap which is composed of many tubular-shaped structures (Figs. 72-75). Each of these structures, according to Degrange (1960), is composed of many threads with terminal knobs. This grouping of the threads into tubular shaped structures is unique to Ephoron. The base of the cap is surrounded by a chorionic collar (Fig. 74), and this suggests that the cap is attached to the endochorion rather than the exochorion.

Key to Species

Chorion smooth, without reticulation.....album
 Chorion with a large-mesh (11-27 μ long) reticulation
 (Figs. 72, 73).....leukon

Ephoron album (Say)

(Figs. 74, 75)

NUMBER. Average of 908 eggs per specimen, according to Britt (1953).

FORM. Nearly rectangular, with one polar cap.

CHORION. Smooth, sculpturing absent.

MICROPYLAR DEVICE. (Fig. 75). Sperm guide oval, 7-10 μ in diameter; micropylar canal 13-21 μ long. With the polar cap at "north" position, the sperm guide may be east or west of the micropylar canal (Fig. 75), whereas in E. leukon, the sperm guide is to the east of the canal (Fig. 73).

Ephoron leukon Williamson

(Figs. 72, 73)

E. leukon differs from E. album by the possession of a chorionic

reticulation of large, irregular, polygonal (mostly hexagonal) mesh formed by ridges 3-8 μ in width. The length of the mesh ranges from 11-27 μ .

Genus Tortopus Needham & Murphy

(Figs. 76-81)

Two collections of females, each from different localities, appear to be different species; and this is supported by the eggs. Since they cannot be named they will be designated by numbers and place collected.

Key to Species

Chorionic punctures large, 3-6 μ in diameter (Figs. 76, 77, 79);
 adhesive layer composed of threads radiating from many small
 circular areas (Fig. 80); threads terminated by knobs with
 no particular pattern of arrangement.....Tortopus sp. no. 1 Alabama
 Chorionic punctures small, less than 1.2 μ in diameter; adhesive
 layer composed of a maze of threads, which lack any pattern
 of arrangement; threads bear knobs arranged in a "floral"
 type pattern (Fig. 81).....Tortopus sp. no. 2 Texas

Tortopus Sp. No. 1, Alabama

(Figs. 76-80)

FORM. (Fig. 78). The egg has the appearance of a sphere which has had one side pushed in. Smith (1935) observed that it probably aided storage of the eggs in the females' abdomen.

CHORION. (Figs. 76, 77, 79). Very evenly punctate with large, widely spaced circular punctures 3-6 μ in diameter.

ATTACHMENT STRUCTURES. (Figs. 76, 80). The egg is covered by an adhesive layer which, under 1,250 magnifications, is readily seen to be composed of a dense mat of threads, many of which are terminated by knobs. In most areas the threads are so numerous and intermingled that it is impossible to discern their terminus and/or point of attachment. However, in those areas where the threads are not so numerous, the attachment of the threads can be found to be like that shown in Figure 80. These threads radiate from a central area which has no definite border. Some of the radiating threads connect to other thread-radiating areas, and some are lost to the maze of threads with terminal knobs. It appears that the radiating areas are columns composed of threads perpendicular to the chorion and attached in the chorionic punctures; this is hypothesis, however, for nothing could be definitely decided about the actual nature of attachment of the threads to the chorion.

MICROPYLAR DEVICE. (Figs. 77, 79). Sperm guide funnel-shaped, rim 28-40 μ in diameter; the ovoid micropyle is followed by a short micropylar canal 3-10 μ long. Only one micropyle present per egg.

Tortopus sp. No. 2, Texas

(Fig. 81)

Differs from Tortopus sp. no. 1 in features of the chorion and attachment structures.

CHORION. Very evenly punctate with small, widely spaced circular punctures less than 1.2 μ in diameter.

ATTACHMENT STRUCTURES. The thread-radiating areas as in sp. no. 1 could not be found. There is, however, a peculiar arrangement

of the terminal knobs--many terminal knobs are grouped in a "floral" type arrangement (Fig. 81), rather than being independent of each other as in sp. no. 1.

SUMMARY

The object of this study was to aid taxonomy of adult and immature female Ephemeroptera by utilizing the morphological features found on the eggs. Below is a list of the major contributions of this study. Following this, is a list of suggestions for future studies.

Major contributions:

1. A simple technique for studying the eggs.
2. A detailed morphological discussion of the egg.
3. Generic keys are given for most of the genera of the Heptageniidae.
4. Slide mounting of the eggs is not necessary to separate the subgenus Eurylophella from the other subgenera of Ephemerella (Ephemerellidae).
5. The presence or absence of chorionic reticulation will separate the two North American species of Ephoron (Polymitarcidae).
6. Specific characters have been found on species of Leptophlebiidae, Caenidae, Hexagenia (Ephemeridae), and Tortopus (Polymitarcidae).

Suggestions for future studies:

1. Although the eggs of only a few species of Leptophlebiidae, Caenidae, Hexagenia and Tortopus were observed, they do

indicate that they are diverse enough so that further study will make them valuable for determinations at the specific level.

2. With a more inclusive study the females of the Heptageniidae may become determinable to the specific level.
3. Specific determinations within the Ephemerellidae, Tricorythidae, and Potamanthidae will prove difficult or impossible on the basis of the eggs. It is also doubtful that many of the subgenera of Ephemerella can be distinguished by the eggs.
4. Sufficient study has not yet been done on the eggs of Siphonuridae and Ametropodidae to assess their contribution to taxonomy.

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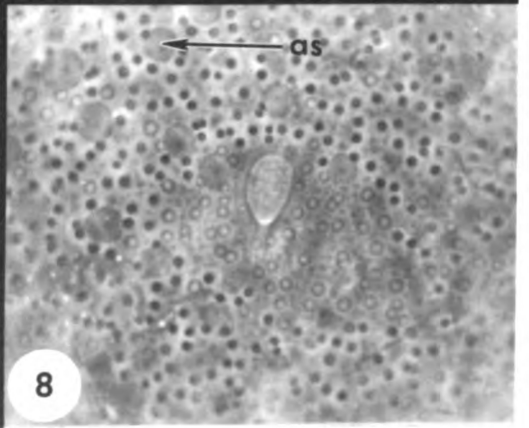
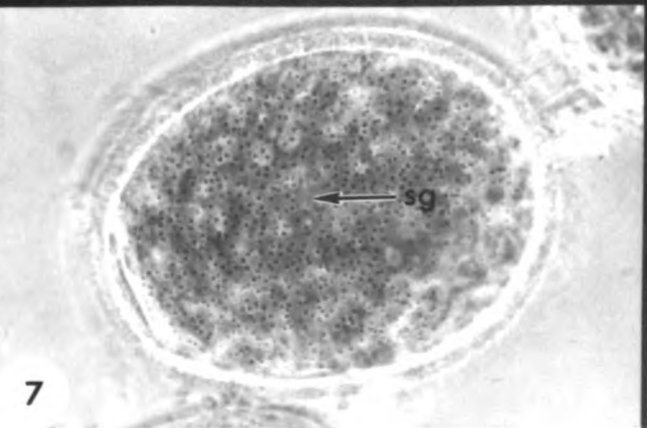
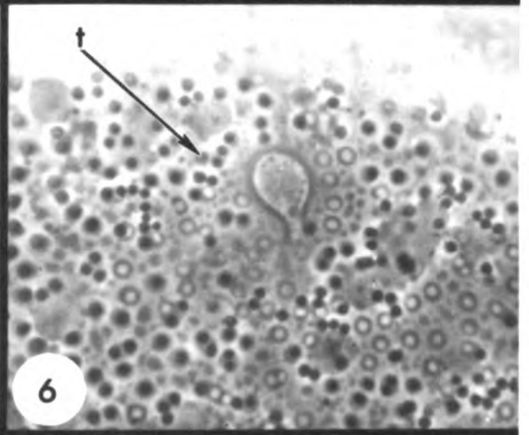
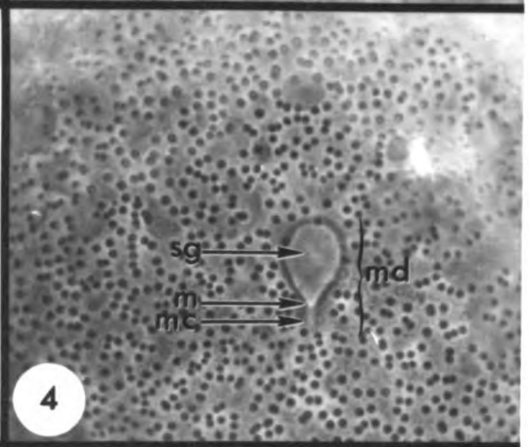
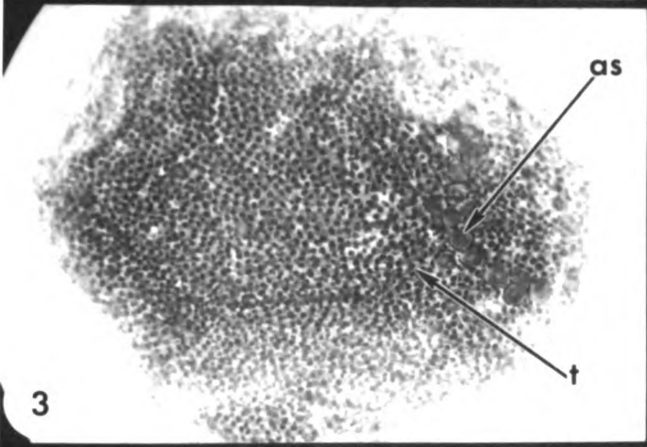
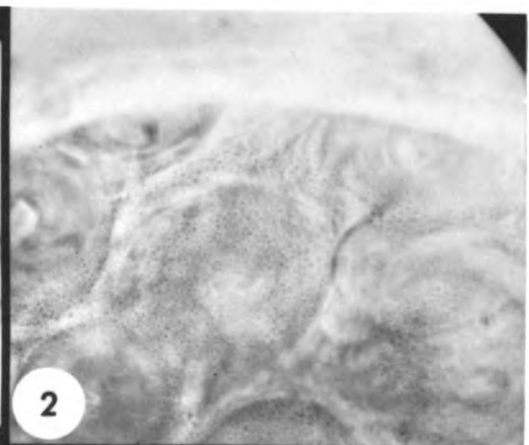
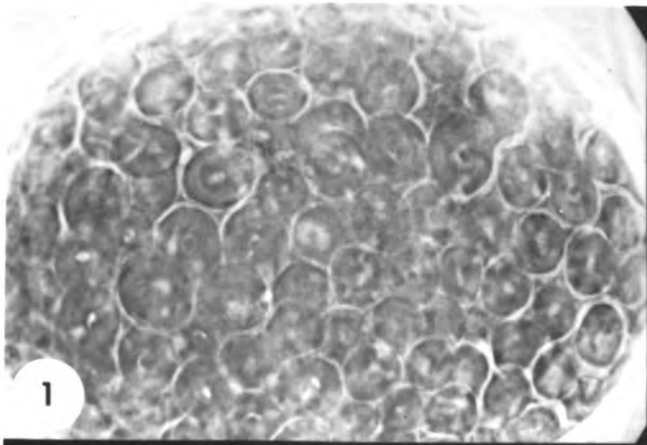
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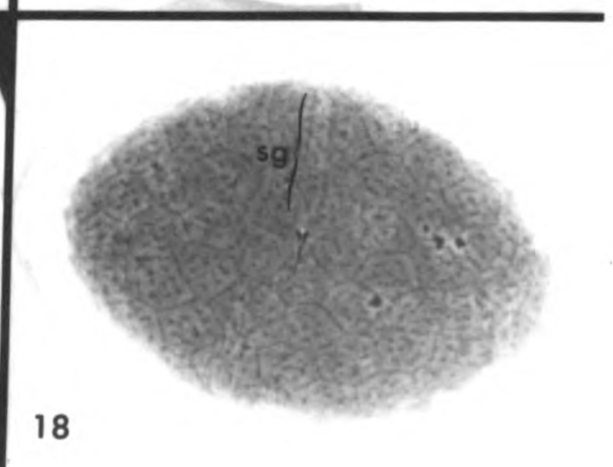
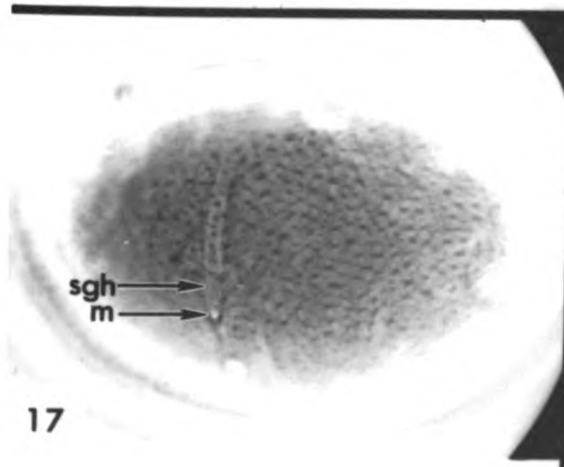
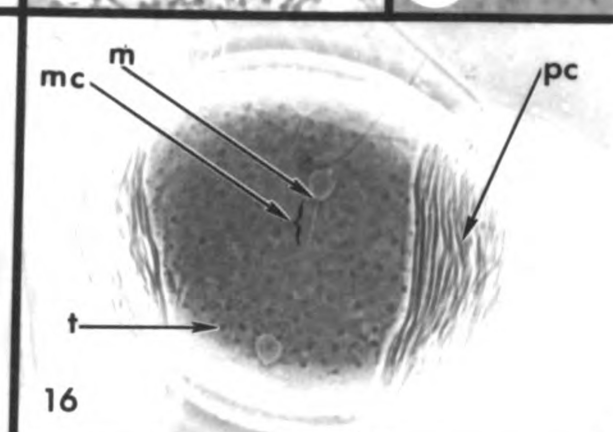
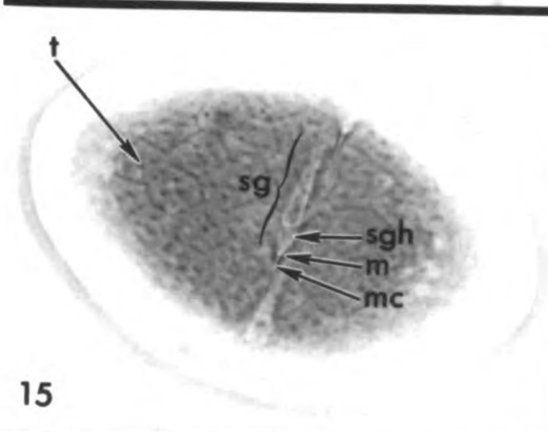
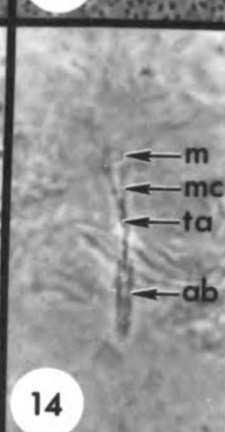
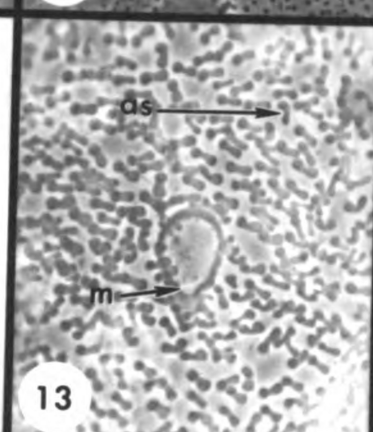
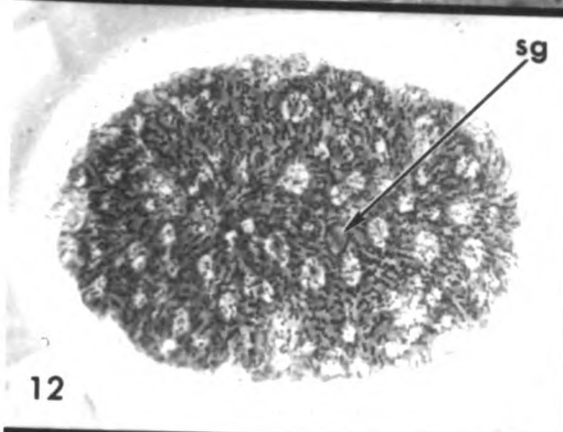
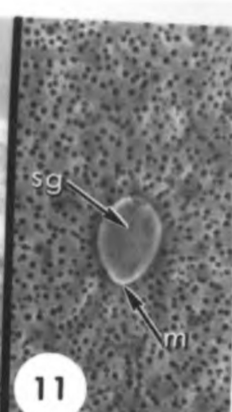
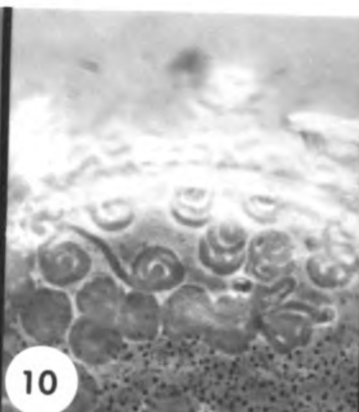
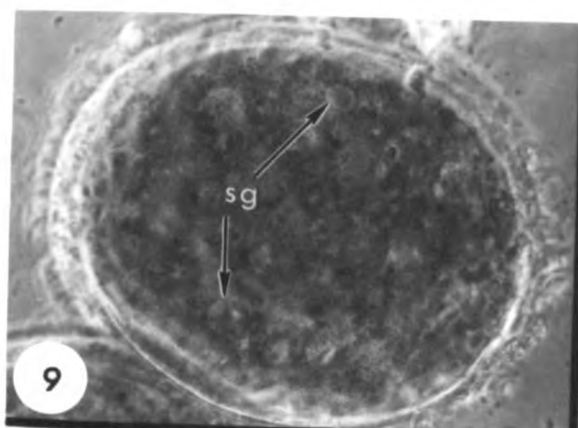
LIST OF ABBREVIATIONS

- ab - apical brush of micropylar canal (Stenonema)
- al - adhesive layer
- as - accessory attachment structure
- dr - rim of raised disc
- f - furrows (strands of reticulation)
- l - length of mesh
- m - micropyle
- mc - micropylar canal
- md - micropylar device
- p - puncture
- pc - polar cap
- pr - pseudoreticulation (Habrophlebiodes americana)
- r - ridges (strands of reticulation)
- sg - sperm guide
- sgH - sperm guide hood (Stenonema)
- t - tubercle
- ta - terminal appendage of micropylar canal (Stenonema)

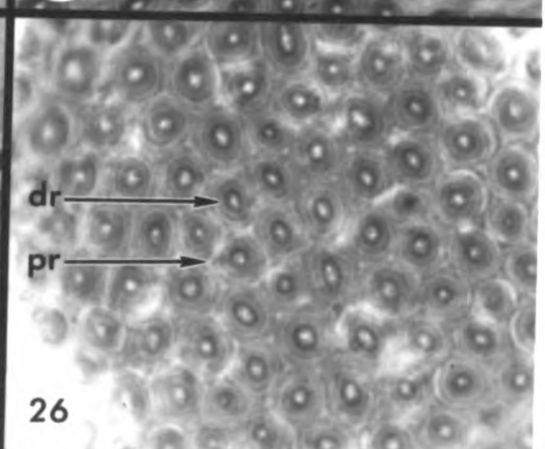
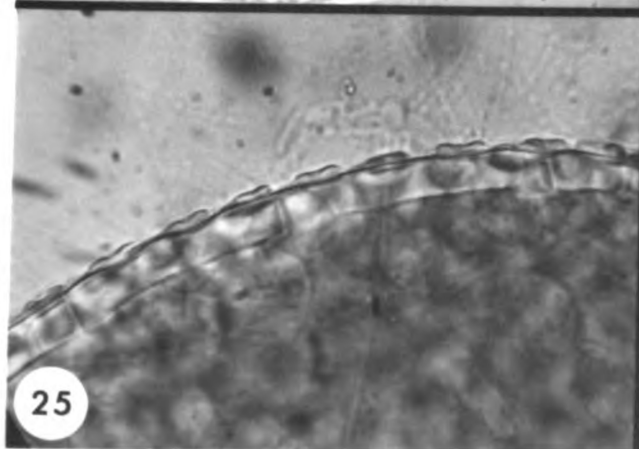
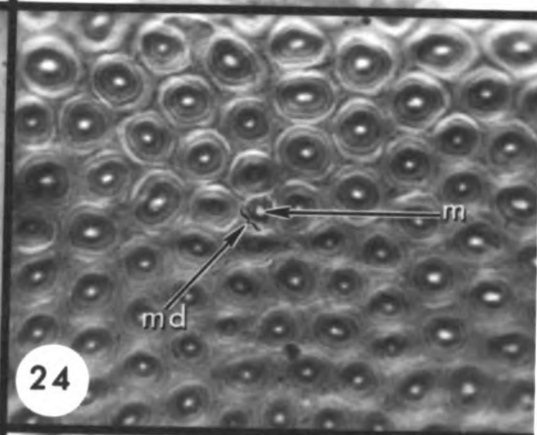
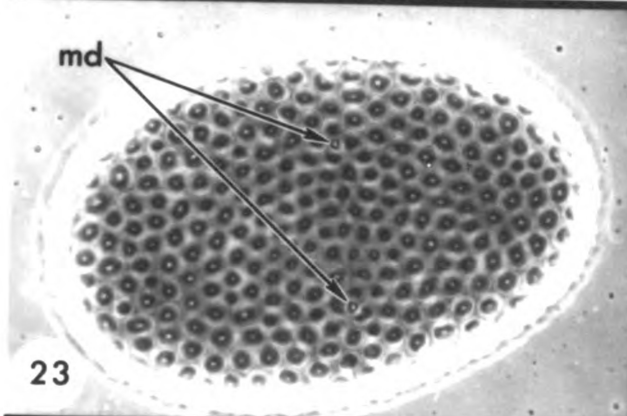
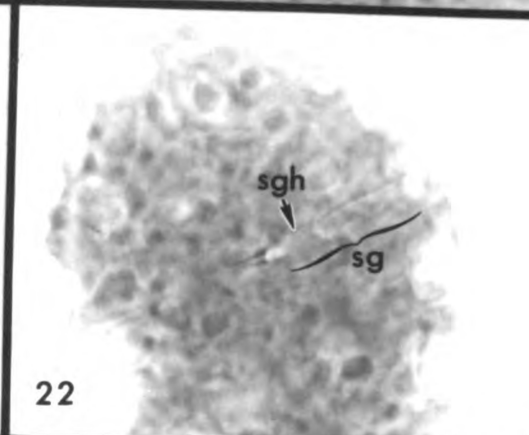
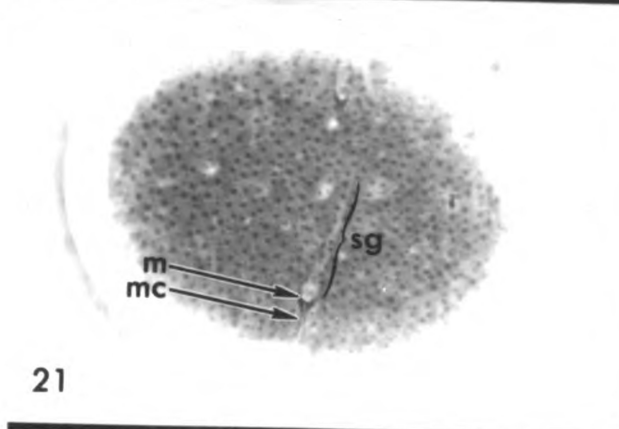
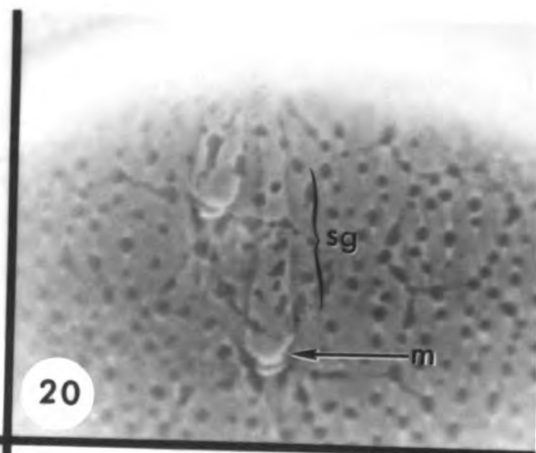
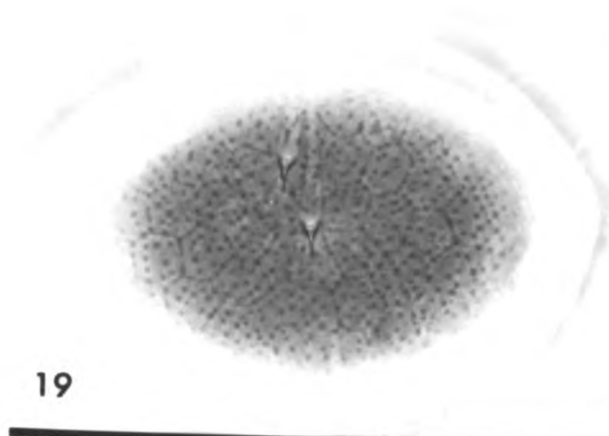
- Fig. 1. Siphonurus alternatus. Egg, covered with coiled thread-like attachment structures (300x).
- Fig. 2. Siphonurus alternatus. Chorionic maculations (938x).
- Fig. 3. Siphloplecton basale. Egg (300x).
- Fig. 4. Heptagenia diabasias. Micropylar Device (750x).
- Fig. 5. Arthroplea bipunctata. Egg (300x).
- Fig. 6. Heptagenia hebe. Micropylar device (938x).
- Fig. 7. Heptagenia juno. Egg (300x).
- Fig. 8. Heptagenia juno. Micropylar device (750x).



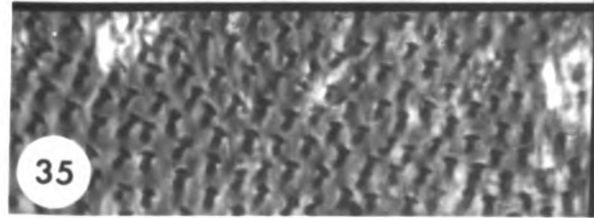
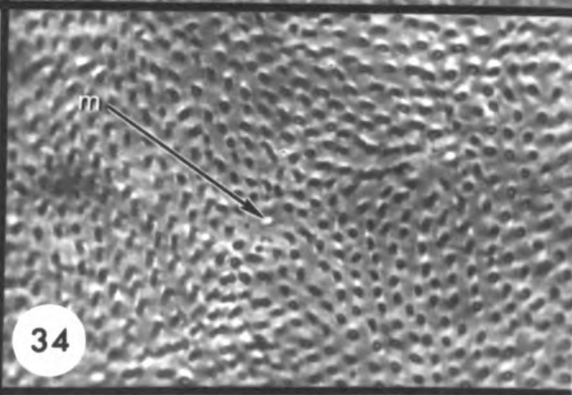
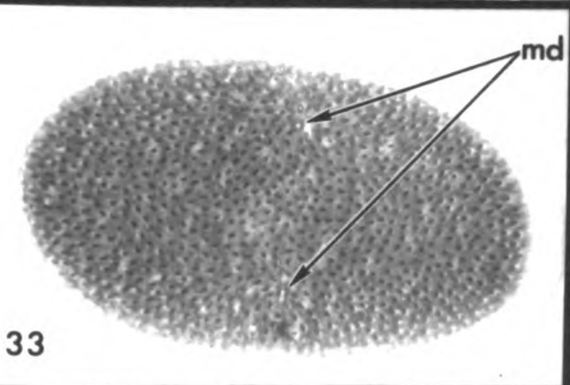
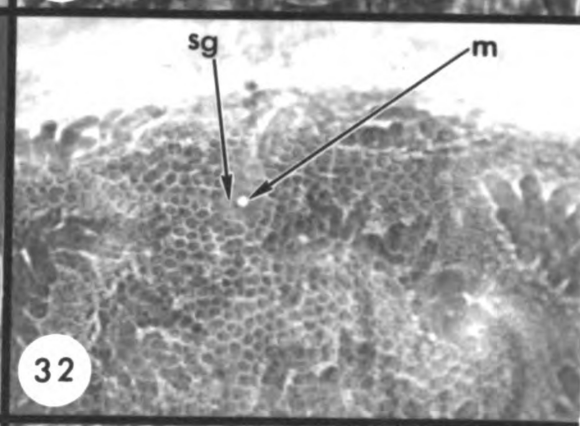
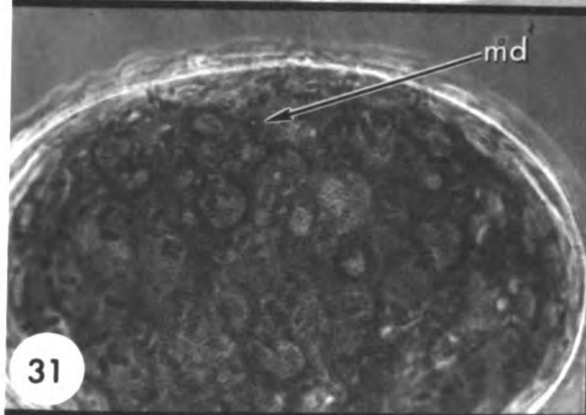
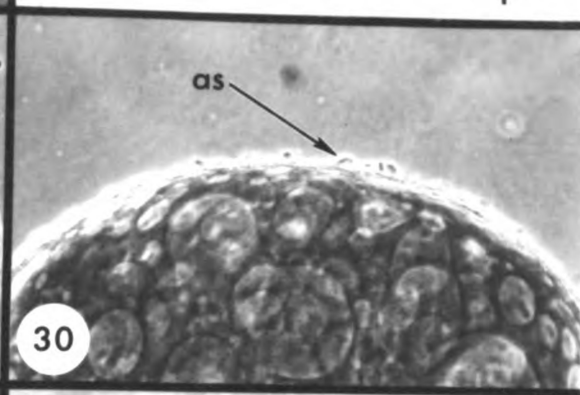
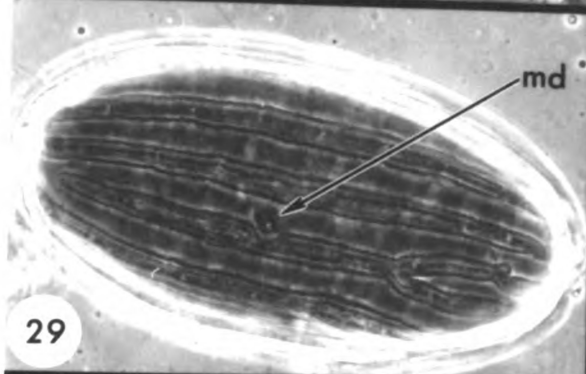
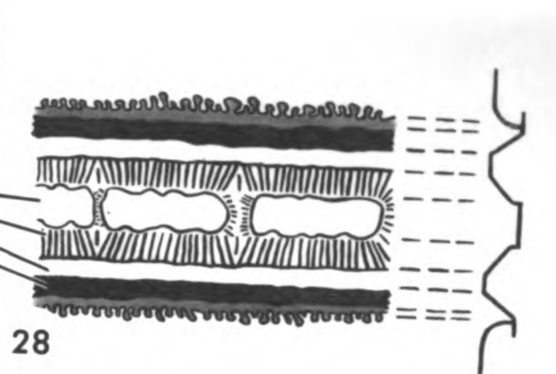
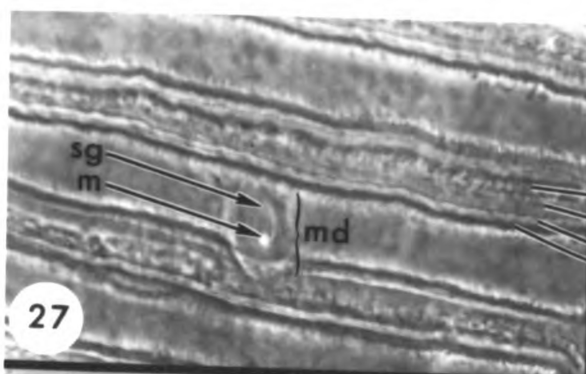
- Fig. 9. Heptagenia pulla. Egg (300x).
- Fig. 10. Heptagenia pulla. Coiled Attachment threads at pole (750x).
- Fig. 11. Heptagenia pulla. Micropylar device (750x).
- Fig. 12. Rhithrogena impersonata. Egg (300x).
- Fig. 13. Rhithrogena impersonata. Micropylar device (750x).
- Fig. 14. Stenonema rubromaculatum. Micropylar canal (750x).
- Fig. 15. Stenonema nepotellum. Egg (300x).
- Fig. 16. Stenonema canadense. Egg (300x).
- Fig. 17. Stenonema leptum. Egg (375x).
- Fig. 18. Stenonema rubromaculatum. Egg (300x).



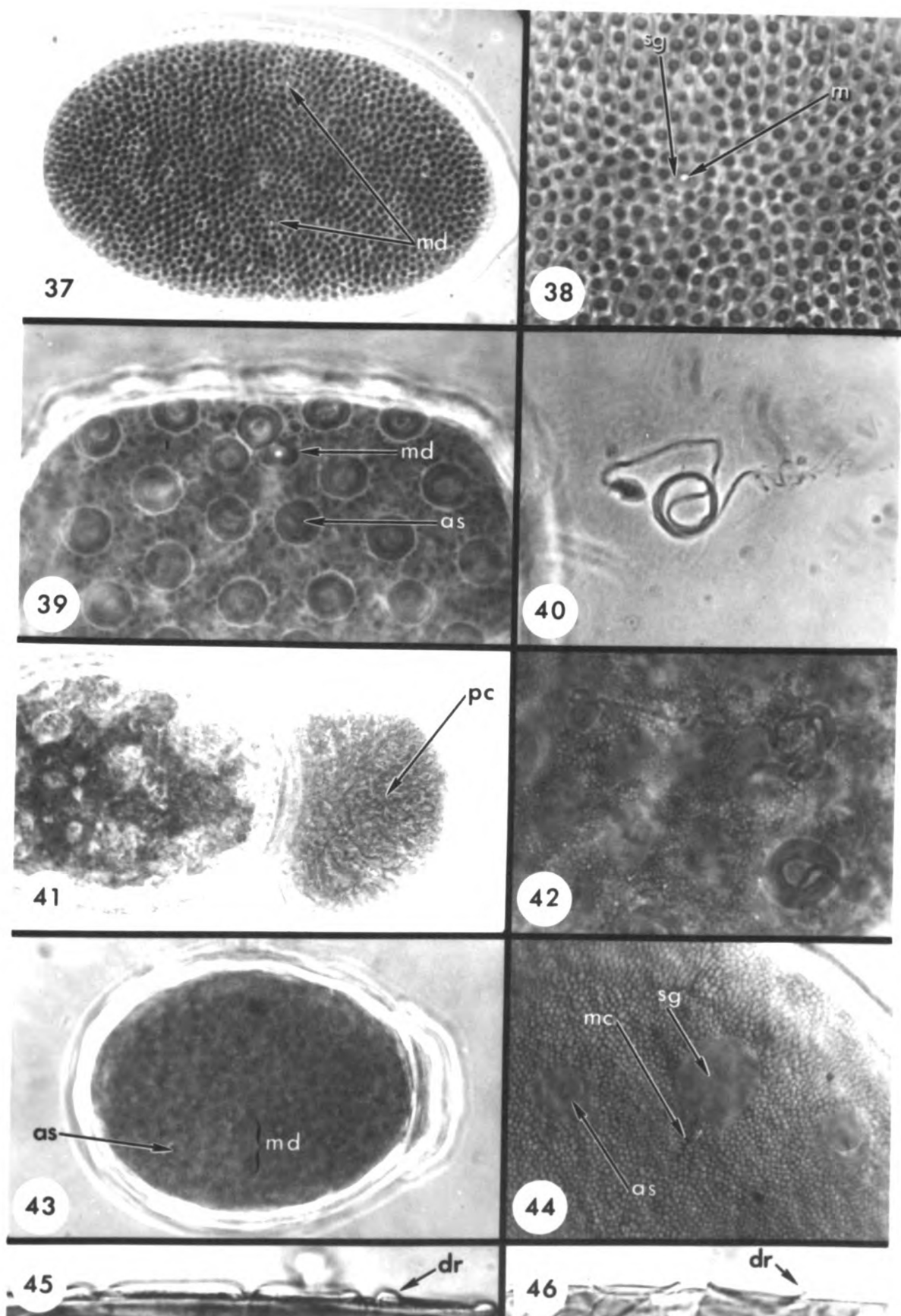
- Fig. 19. Stenonema tripunctatum. Egg (300x).
- Fig. 20. Stenonema tripunctatum. Micropylar device (750x).
- Fig. 21. Stenonema femoratum. Egg (300x).
- Fig. 22. Stenonema fuscum. Micropylar device (375x).
- Fig. 23. Habrophlebiodes americana. Egg (300x).
- Fig. 24. Habrophlebiodes americana. Micropylar device (750x).
- Fig. 25. Habrophlebiodes americana. Tangential view showing sucker-like discs in relief (750x).
- Fig. 26. Habrophlebiodes americana. Surface view showing pseudo-reticulation (750x).



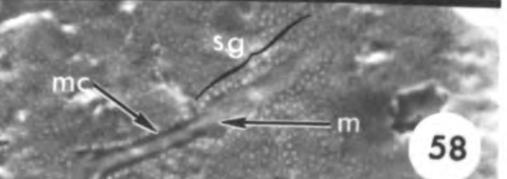
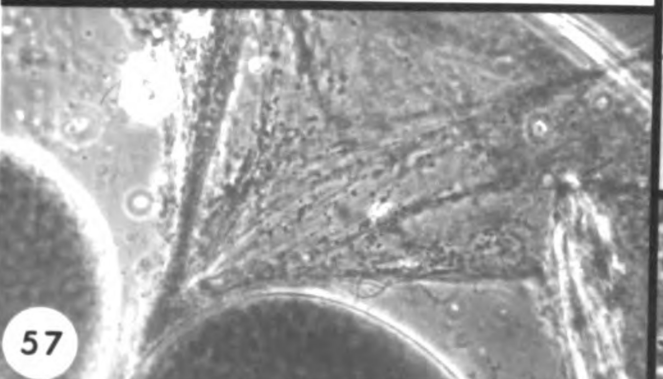
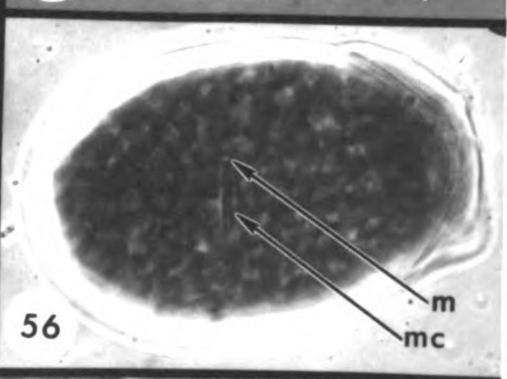
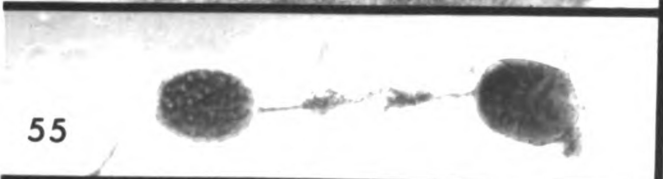
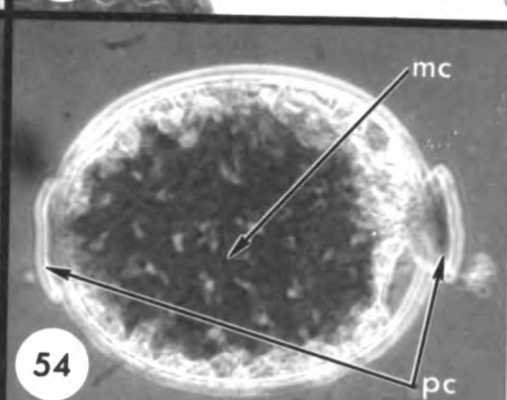
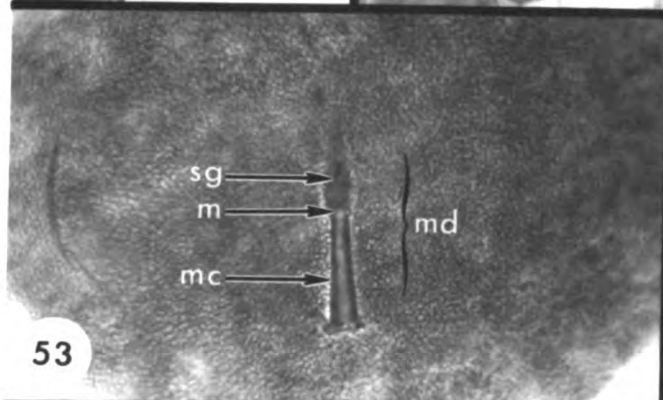
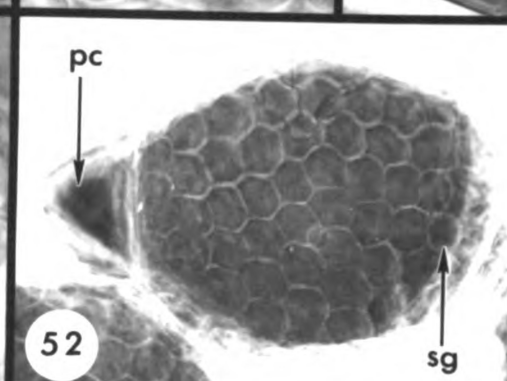
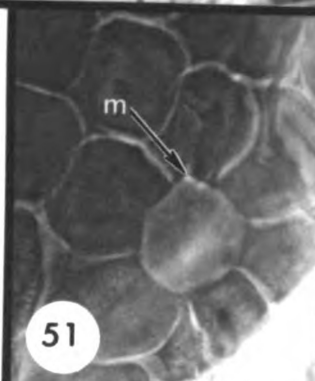
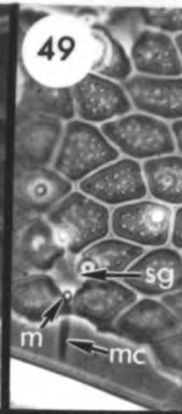
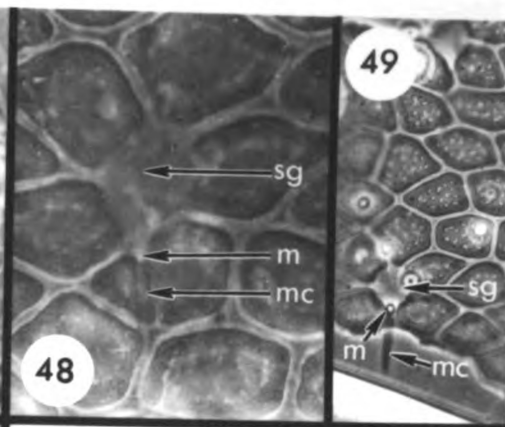
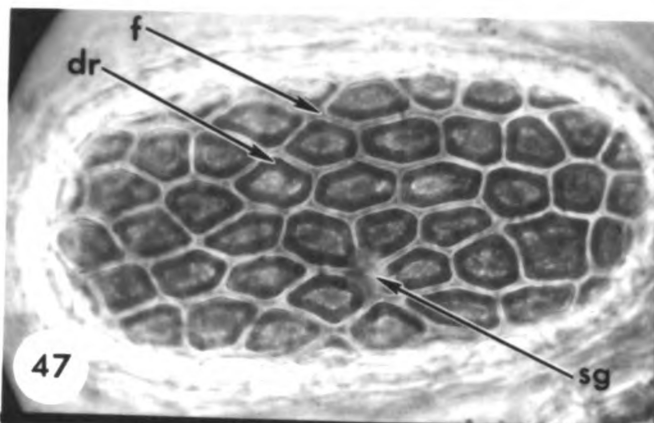
- Fig. 27. Habrophlebia vibrans? Micropylar device (750x).
- Fig. 28. Habrophlebia vibrans? Diagrammatic view and projected
cross-section of chorionic ridges.
- Fig. 29. Habrophlebia vibrans? Egg (300x).
- Fig. 30. Leptophlebia sp. Tangential view showing peg-like attachment
structures in relief (300x).
- Fig. 31. Leptophlebia sp. Egg (300x).
- Fig. 32. Leptophlebia sp. Micropylar device (750x).
- Fig. 33. Paraleptophlebia adoptiva. Egg (300x).
- Fig. 34. Paraleptophlebia mollis. Micropylar device (750x).
- Fig. 35. Paraleptophlebia mollis. Peg-like attachment structures.
Eggs laid in water, slide-mounted five minutes later
(750x).
- Fig. 36. Paraleptophlebia mollis. Same as Fig. 35, tangential view
(750x).



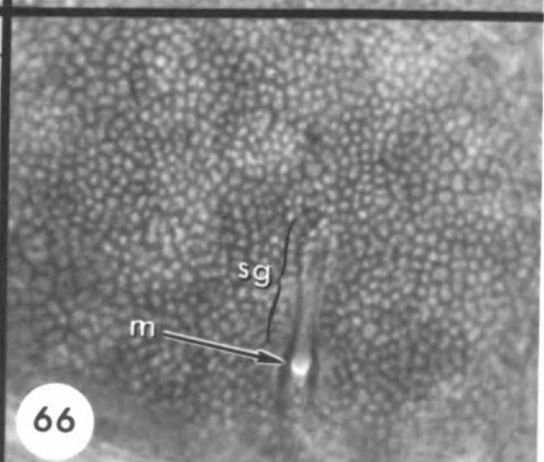
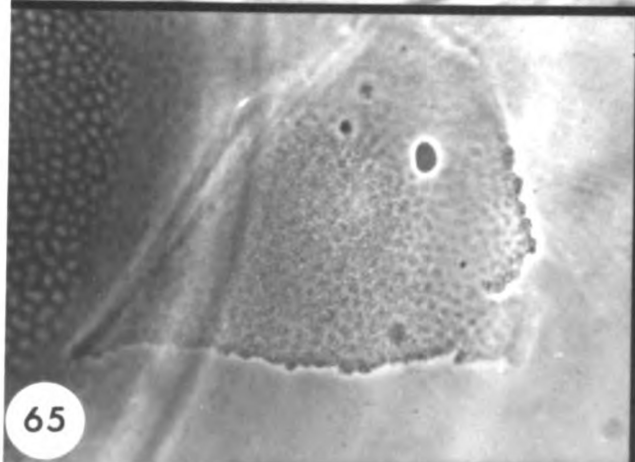
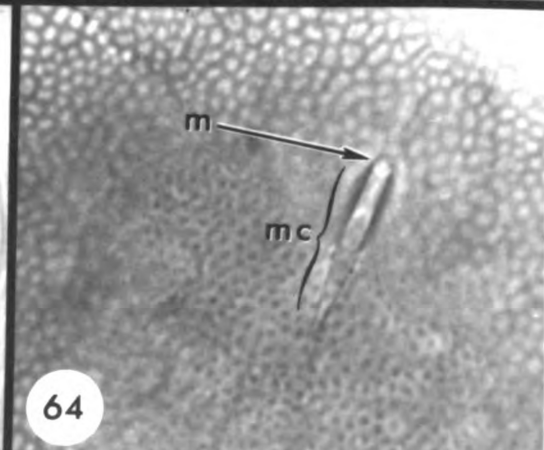
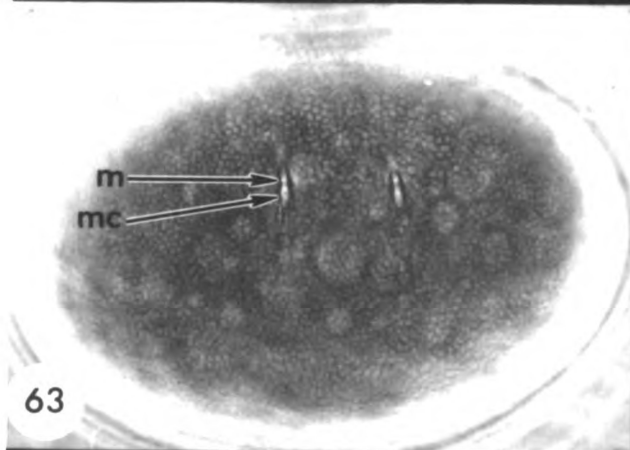
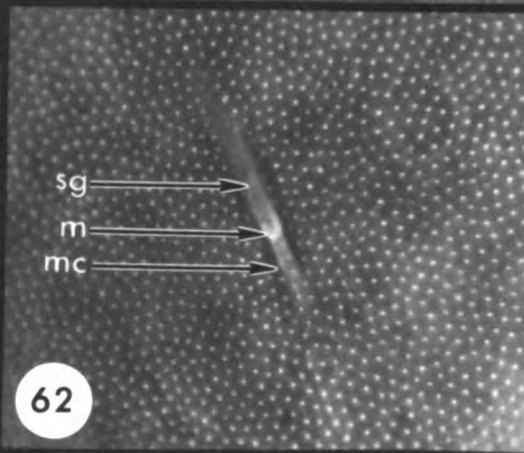
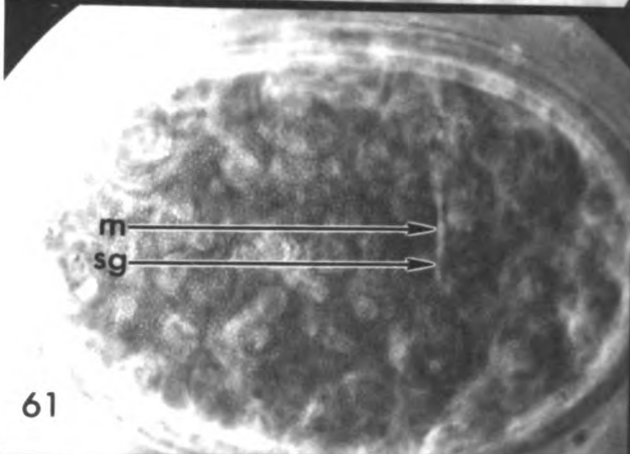
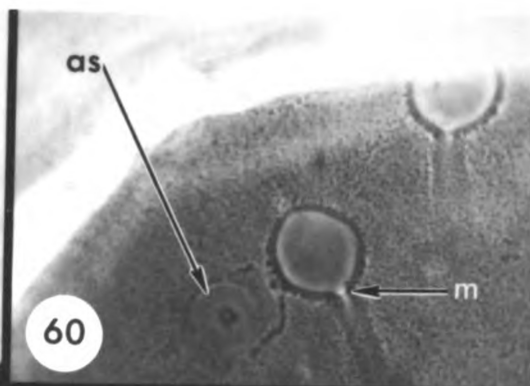
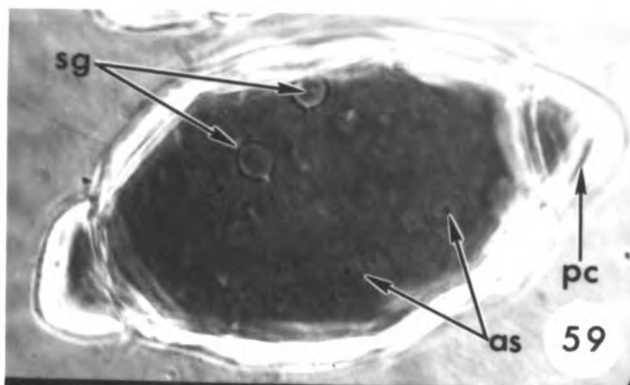
- Fig. 37. Paraleptophlebia debilis. Egg (300x).
- Fig. 38. Paraleptophlebia debilis. Micropylar device (750x).
- Fig. 39. Thraulodes speciosus. Egg (750x).
- Fig. 40. Ephemerella (Serratella) deficiens. Coiled thread-like attachment structure showing terminal knob; removed from egg (750x).
- Fig. 41. Ephemerella (Ephemerella) inconstans. Expanded polar cap. Eggs laid in water, removed to 70% ETOH 12 hours later (300x).
- Fig. 42. Ephemerella (Serratella) deficiens. Chorion and attachment structures (750x).
- Fig. 43. Ephemerella (Drunella) cornuta. Egg (300x).
- Fig. 44. Ephemerella (Drunella) cornuta. Micropylar device (750x).
- Fig. 45. Ephemerella (Eurylophella) prudentalis. Tangential view showing sucker-like plates. Eggs laid in water, removed to 70% ETOH 12 hours later (938x).
- Fig. 46. Ephemerella (Eurylophella) prudentalis. Same view as Fig. 45, eggs from preserved specimen (750x).



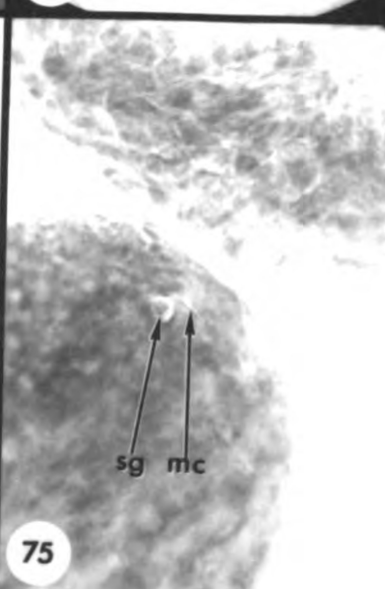
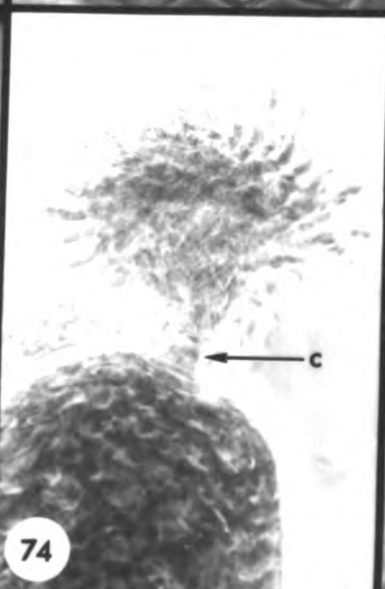
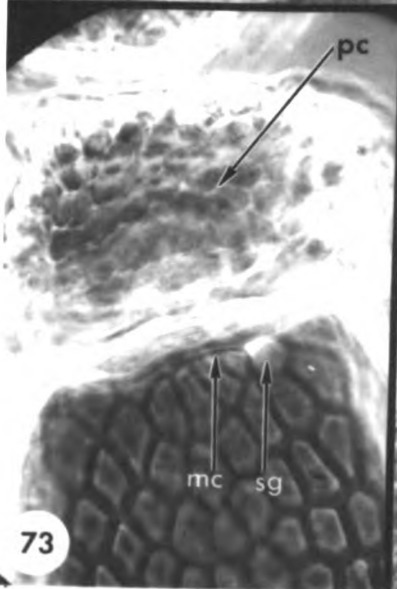
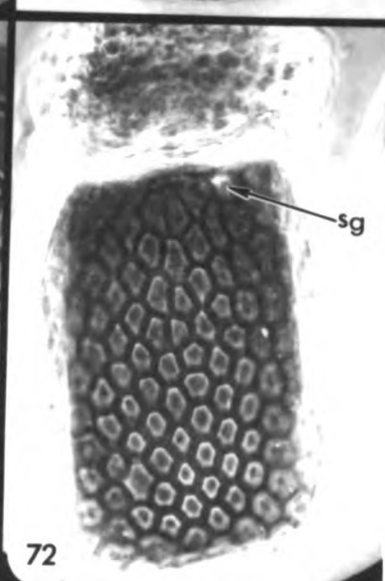
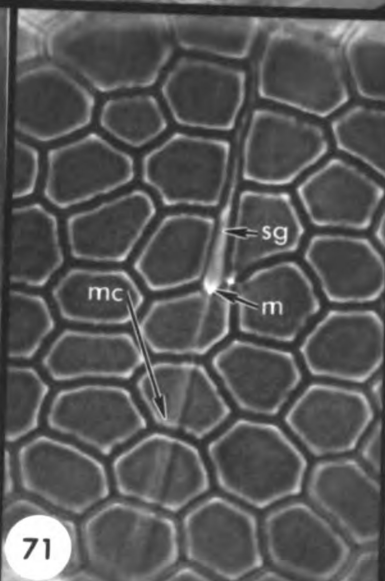
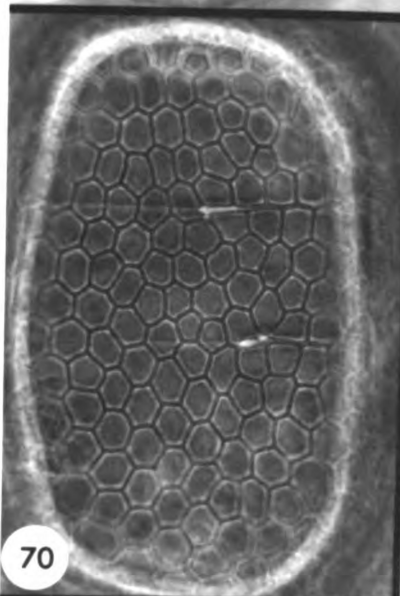
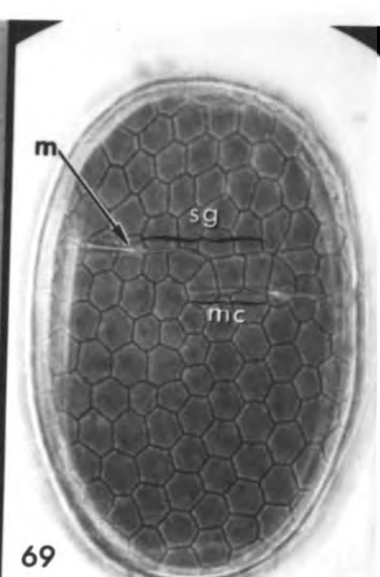
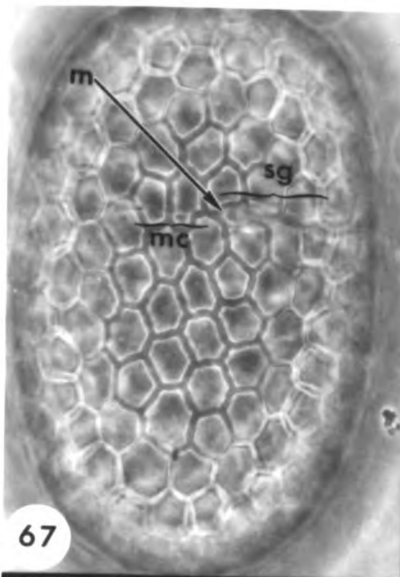
- Fig. 47. Ephemerella (Eurylophella) prudentialis. Egg. Laid in water, removed to 70% ETOH twelve hours later (375x).
- Fig. 48. Ephemerella (Eurylophella) prudentialis. Same as Fig. 47, micropylar device (750x).
- Fig. 49. Ephemerella (Eurylophella) temporalis. Chorion and micropylar device (375x).
- Fig. 50. Tricorythodes atratus. Tangential view (750x).
- Fig. 51. Tricorythodes atratus. Micropylar device (750x).
- Fig. 52. Tricorythodes atratus. Egg (300x).
- Fig. 53. Caenis jocosa. Micropylar device (750x).
- Fig. 54. Caenis forcipata. Egg (150x).
- Fig. 55. Caenis jocosa. Eggs with polar caps uncoiled (75x).
- Fig. 56. Caenis anceps. Egg (300x).
- Fig. 57. Caenis forcipata. Egg with threads of polar cap completely unraveled. Eggs laid in water, removed to 70% ETOH 12 hours later (300x).
- Fig. 58. Caenis forcipata. Micropylar device (750x).



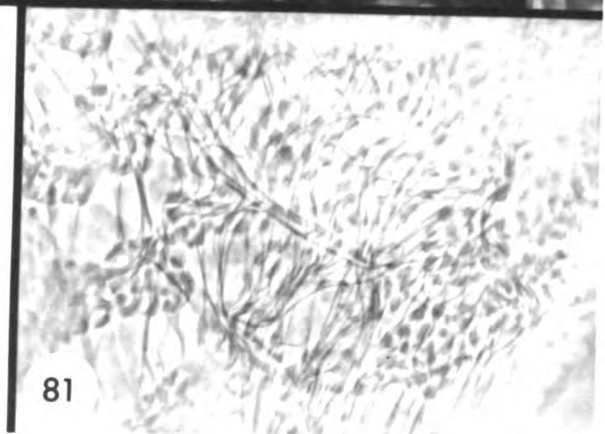
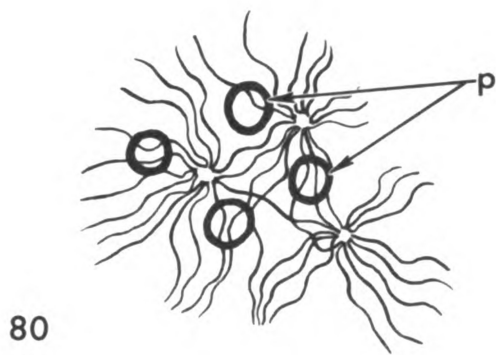
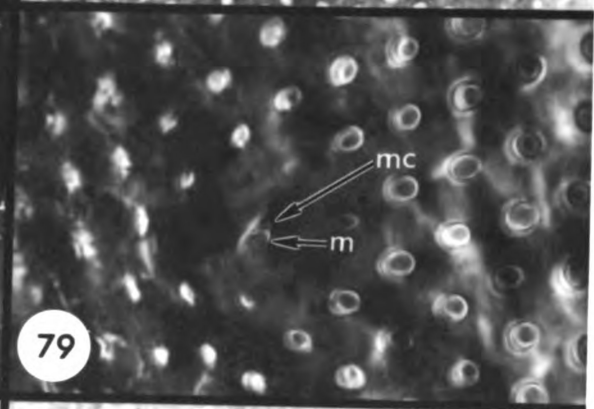
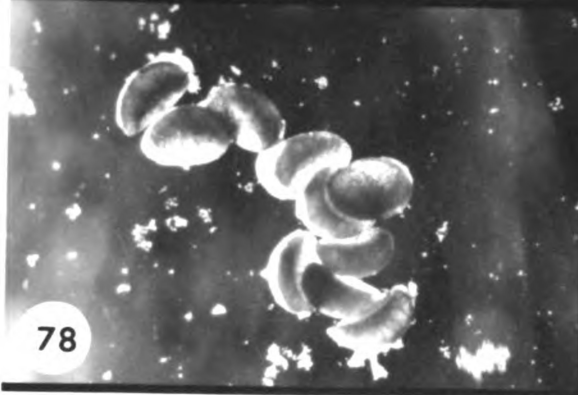
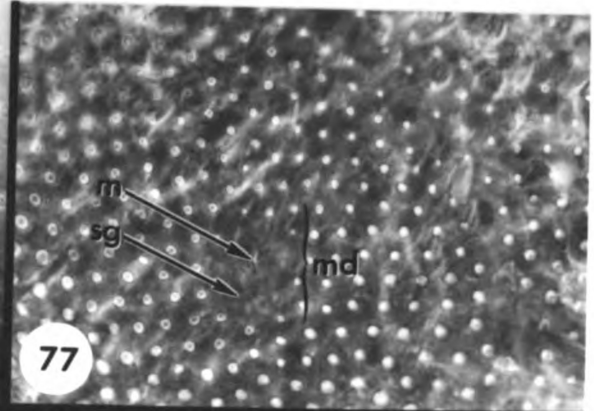
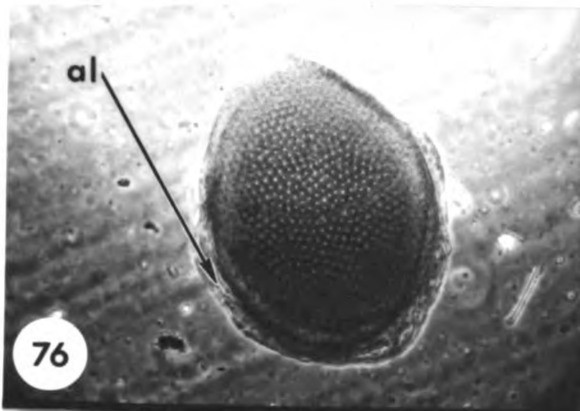
- Fig. 59. Potamanthus myops. Egg (300x).
- Fig. 60. Potamanthus myops. Micropylar device (750x).
- Fig. 61. Ephemera guttulata. Egg (300x).
- Fig. 62. Ephemere guttulata. Micropylar device (750x).
- Fig. 63. Ephemera simulans. Egg (300x).
- Fig. 64. Ephemera simulans. Micropylar canal (750x).
- Fig. 65. Ephemera simulans. Adhesive layer (750x).
- Fig. 66. Ephemera varia. Micropylar device (750x).



- Fig. 67. Hexagenia munda munda. Egg (267x).
- Fig. 68. Hexagenia rigida. Egg (267x).
- Fig. 69. Hexagenia limbata venusta. Egg (267x).
- Fig. 70. Hexagenia limbata occulta. Egg (267x).
- Fig. 71. Hexagenia limbata occulta. Micropylar device (667x).
- Fig. 72. Ephoron leukon. Egg (267x).
- Fig. 73. Ephoron leukon. Micropylar device (333x).
- Fig. 74. Ephoron album. Collar surrounding base of polar cap (267x).
- Fig. 75. Ephoron album. Micropylar device (333x).



- Fig. 76. Tortopus sp. no. 1, Alabama. Egg (94x).
- Fig. 77. Tortopus sp. no. 1, Alabama. Micropylar device (300x).
- Fig. 78. Tortopus sp. no. 1, Alabama. Stacked eggs (34x).
- Fig. 79. Tortopus sp. no. 1, Alabama. Micropylar device (750x).
- Fig. 80. Tortopus sp. no. 1, Alabama. Diagrammatic view of threads
composing the adhesive layer (viewed at 1250x).
- Fig. 81. Tortopus sp. no. 2, Texas. Adhesive layer (938x).



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