

December 1974

Ephemeroptera eggs and their contribution to phylogenetic studies of the order¹

RICHARD W. KOSS²

Meadowbrook Acres, Palmer, Mass, U.S.A.

AND

GEORGE F. EDMUNDS, JR.³

Department of Biology, University of Utah, Salt Lake City, Utah, U.S.A.

Eggs of representative genera of all families of Ephemeroptera except the Palingeniidae were studied. Their external morphology is reviewed, and hypotheses have been proposed to explain the evolution of several chorionic features and types of attachment structure.

The archetypal Ephemeroptera egg is considered to have been round, with a smooth chorion, non-fibrous adhesive layer, funnellform micropyle, and a suprachorionic sperm guide. Subsequent evolution resulted in several different micropyles and many different chorionic sculpturings and attachment structures.

Data obtained from studying the egg stage are utilized as aids to understanding the phylogeny of the Ephemeroptera. The proposed classification divides the order into 21 families arranged into 6 superfamilies.

CONTENTS

Introduction	268
Techniques	269
Morphology	270
Attachment structures	270
Micropyles	274
Chorion and chorionic sculpturing	276
Comparative evaluation of data	276
Attachment structures	277
Micropyles	280
Chorionic sculpturing	282
Intrafamilial phylogenetic relationships	282
Interfamilial phylogenetic relationships	289

¹ A dissertation submitted in 1969 by the senior author to the faculty of the Biology Department, University of Utah, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The research was funded by National Science Foundation grants to the junior author.

² Department of Geography and Environmental Engineering, 513 Ames Hall, The Johns Hopkins University, Baltimore, Maryland 21218. Reprint requests should be addressed to the junior author, c/o Univ. of Utah.

³ Department of Biology, University of Utah, Salt Lake City, Utah 84112.

Systematics	293
List of species studied	293
Heptagenioidea	296
Siphonuridae	296
Siphlaenigmatidae	304
Baetidae	305
Metretopodidae	307
Oligoneuriidae	308
Heptageniidae	309
Ametropodidae	320
Leptophlebioidea	320
Leptophlebiidae	320
Ephemerelloidea	321
Ephemerellidae	322
Tricorythidae	322
Ephemeroidea	323
Behningiidae	323
Potamanthidae	324
Euthyplociidae	325
Ephemeridae	326
Pentageniidae	336
Polymitarcidae	337
Palingeniidae	339
Caenoidea	340
Neoephemeridae	340
Caenidae	341
Prosopistomatoidea	342
Baetiscidae	342
Prosopistomatidae	342
Acknowledgements	342
References	343

INTRODUCTION

The most complete and informative studies on the external morphology of Ephemeroptera eggs are those by Bengtsson (1913), Morgan (1913), Smith (1935), Degrange (1960), and Koss (1968). The contributions of the former studies have been reviewed by Koss (1968). Previous descriptions of Ephemeroptera eggs are compiled in this paper following the respective familial discussions.

The object of this study was to describe eggs of as many mayfly genera as possible, and to utilize the egg characters for phylogenetic purposes. When attempting to reconstruct the phylogeny of any group, it is desirable to have as many different sets of data as possible. The Ephemeroptera may be uniquely suited for phylogenetic study because detailed studies have been made of the external and internal anatomy of the nymphal and adult stages of a large number of genera from all parts of the world. Approximately 75% of these genera have one or more species with adults reared from nymphs (Edmunds, 1965; Edmunds & Allen, 1966). This study, together with those of Degrange (1960) and Koss (1968), indicates that characters from the eggs may be nearly as valuable for taxonomic and phylogenetic analyses as those from the adult and nymph. The data provide for further testing of the numerous hypotheses involved in proposed phylogenies, and suggests revision of some of the present concepts of ephemeropteran phylogeny.

Throughout the course of this study a considerable amount of unpublished data on the internal and external anatomy of nymphal and adult stages were available through visits to our laboratory by Vladimir Landa (Institute of

Entomology, Prague, Czechoslovakia) and Edgar F. Riek (Commonwealth Scientific and Industrial Research Organization, Canberra, Australia). In addition, during the course of this study, Steven L. Jensen and William P. McCafferty were engaged in revision studies of the Heptageniidae and Ephemeridae, respectively, at the University of Utah. Discussions with these students of the Ephemeroptera contributed substantially to the analysis of the data.

Cobben (1968) wisely states: "It is unrealistic to assume a constant pattern of egg-structure within a given taxonomic group." This fact may seem unfortunate for taxonomists who prefer distinct character gaps for "pigeon-holing" their taxonomic entities; but it is valuable for the phylogenist because he is mostly concerned with filling in the gaps in order to determine anagenetic and cladogenetic evolutionary sequences for the various character stages of organisms. Character-states at the generic and familial levels tend to form a continuum from primitive to advanced states which frequently do not coincide to the generic or familial limits. The apomorphic characters are most useful in clustering species into distinguishable groups (Throckmorton, 1969) and plesiomorphic characters are more useful in determining the origin of the various taxa. If the sequence of character-states can be established with reasonable certainty for a variety of characters, the sequence of branching and amount of divergence can be hypothesized with reasonable certainty.

We use the terms "primitive" and "recent" solely for indication of relative chronology of branching sequences. Although any extant taxon is definitely recent and not primitive in the absolute sense, it is primitive or recent according to whether it evolved from the ancestral stock either early or late in time.

For any pair of character-states, plesiomorphic refers to the ancestral condition and apomorphic to the derived condition, and thus the terms are only relative. A character state is either plesiomorphic or apomorphic only in relation to some other character state.

TECHNIQUES

The techniques used in this study are essentially those described by Koss (1968). Two slides were usually made from the eggs of a single specimen. The senior author has retained one set of these slides, and the other set, together with the specimens used, remains in the Entomology Museum of the University of Utah. The collection localities of all materials studied is available free on request from the Department of Biology, University of Utah, Salt Lake City, Utah, 84112, U.S.A. and will be sent with reprints to all institutions with active Ephemeroptera collections. When more than one undetermined species in a single genus is described, the undetermined species are listed in the text together with a University of Utah slide number (e.g. UU140-1) to facilitate location in the future of specimens and egg slides.

A Carl Zeiss Photomicroscope equipped with phase-contrast and Nomarski interference-contrast attachments (magnification range of $\times 160$ to $\times 1600$) was used for observation and photography. In the figure legends "P.C." is used to indicate use of phase contrast for the respective photograph; "I.C." indicates use of interference contrast. Interference contrast presents the image in relief,

and photographs of this image also show relief. When viewing such illustrations (e.g. Plate 1: figs 7, 9; Plate 3: fig. 28 and Plate 15: fig. 172) it must be remembered that light is directed from the upper left. If the visual image does not coincide with the caption or labels (e.g. structures stated to be ridges appear to be furrows) it may be helpful first to invert the page.

MORPHOLOGY

Mayfly eggs possess three major types of external morphological features which are useful for taxonomic and phylogenetic purposes: attachment structures, micropyles and chorionic sculpturing. Koss (1968) has discussed these features and the terminology applied to them. From new data we have modified and elaborated on earlier concepts and definitions, but the earlier paper should be consulted for an understanding of mayfly egg structures.

For convenience in discussion, we have categorized the various character states of attachment structures, micropyles and chorionic sculpturings. However, because many character states have evolved into other character states, it is obvious that many intermediate conditions and relatively continuous character gradients exist among living mayflies that make some such categorizations difficult.

Attachment structures

Koss (1968) arranged attachment structures into three groups and considered two of these (polar caps and accessory attachment structures) as separate features of the eggs, thus making four types of morphological features found on the eggs rather than three. It seems now preferable to refer to all attachment structures collectively as one type of external morphological feature found on mayfly eggs. Such a decision is necessary because polar caps, adhesive layers and "accessory attachment structures" (Koss, 1968) all constitute attachment structures, and new data have eliminated any possibility of a clear cut distinction between polar caps and certain other attachment structures.

Attachment structures can be conveniently, but not absolutely, categorized according to the following outline:

- I. Non-fibrous attachment structures
 - A. Sucker-like discs or plates
 - B. Adhesive projections
 - C. Non-fibrous adhesive layers
- II. Fibrous attachment structures
 - A. Non-coiled types
 1. Fibrous adhesive layers
 2. Non-coiled attachment threads
 - a. Lateral threads
 - b. Type I polar caps
 - c. Type II polar caps

- B. Coiled types
 - 1. Fiber-coils
 - a. Without terminal fiber clusters
 - b. With terminal fiber clusters
 - c. With terminal knobs
 - 2. Collectively coiled attachment threads
 - a. Type III polar caps
 - 3. Individually coiled attachment threads
 - a. Knobless coiled threads
 - (1) Lateral threads
 - (2) Type IV polar caps
 - b. Knob-terminated coiled threads
 - (1) Lateral threads
 - (2) Type V polar caps

An adhesive layer is a compact mass of material surrounding the egg, and it may appear granular, fibrous or undifferentiated (no recognizable structure under the light microscope). All adhesive layers are suprachorionic, as suggested by Cobben (1968); and in a study of micropylar morphology, Koss (1970) pointed out that the adhesive material must be deposited by the same follicle cells that secrete the chorion. Since all other attachment structures have a distinct morphology and are actually attached to the chorion it follows that they too are formed by the follicle cells.

Non-fibrous attachment structures

Non-fibrous adhesive layers are somewhat common on Ephemeroptera eggs and very likely represent the most plesiomorphic type of attachment structure in the order. They appear granular (as in *Ephemerella simulans* Walker, Ephemeridae) or undifferentiated (Plate 14: figs 157, 169). Other non-fibrous attachment structures are relatively uncommon on mayfly eggs; adhesive projections and sucker-like discs or plates occur primarily in the Leptophlebiidae and in all known members of the subgenus *Eurylophella* of *Ephemerella* (Ephemerellidae) (see Plate 11: figs 122-4, and Koss, 1968).

Fibrous attachment structures

Fibrous attachment structures are those formed by a loose collection of monofilamentous "fibers" (Plate 6: figs 72, 73) or a tight spiraling of those fibers into polyfilamentous "threads" (Plate 1: fig. 51).

Non-coiled types occur as fibrous adhesive layers, lateral threads and polar caps, and they do not display any type of coiling arrangement of the fibers or threads. A fibrous adhesive layer is a relatively uniform, compact mass of fibers completely covering the egg. They are typical of eggs of *Tortopus* (Polymitarcidae, Plate 19: fig. 210) and *Neoephemerella* (Neoephemeridae, Plate 19: fig. 215). The Behningiidae are exceptional in that fibrous adhesive material is localized in several massive accumulations at the polar and equatorial regions of the egg (Plate 12: figs 138, 139). Non-coiled attachment threads usually occur in compact polar masses (Type I and II polar caps, see below) which do not reveal their multi-threaded nature until the egg is deposited in water (Plate 11: fig. 129; Plate 12: figs 131, 133). Only rarely do the threads occur singly or in

groups of two or three (in lateral positions only, Plate 12: fig. 135), and they usually lack terminal knobs or else they bear very minute ones.

Coiled fibrous attachment structures are the most common attachment structures on mayfly eggs, and there are several different types. The most plesiomorphic is the "fiber-coil" (Plate 6: figs 72, 73), a coil of many loosely-arranged fibers which may or may not terminate in a relatively compact "fiber cluster" (Plate 6: fig. 74). Fiber-coils are known only to occur in a uniform layer covering the entire egg (Plate 2: fig. 21; Plate 5: fig. 58). The terminal fiber clusters on these structures vary in degree of apical expansion and subapical compaction, and their origin seems to represent an important step in the evolution of knob-terminated coiled threads (see below and section on intrafamilial relationships). Terminal fiber clusters are entirely lacking on fiber coils in the Siphlaenigmatidae and *Metamonius*-complex (Siphonuridae), and they are present only on some coils of the *Siphonurus*-complex (Siphonuridae) and *Chromarcys*, *Oligoneuria* and *Elassoneuria* (Oligoneuriidae) (Plate 6: fig. 74); distinct terminal knobs occur on fiber-coils in *Homoeoneuria*, *Oligoneuriella* and *Lachlania* (Oligoneuriidae) (Plate 7: figs 77, 78).

Coiled attachment threads constitute the remaining types of coiled fibrous attachment structures. Although in some species coiled attachment threads, like fiber-coils, are uniformly distributed over the entire surface of the egg, their distribution is more commonly scattered or restricted. They are considered to be apomorphic attachment structures derived from fiber-coils.

Attachment threads are coiled either individually or collectively. When a group of attachment threads are coiled together as a single coiled unit (Plate 13: figs 149, 150; Plate 19: figs 207, 213), they are said to be collectively coiled. Collectively coiled threads are known only to occur at the polar regions of the eggs on which they are found and they are always in the form of a polar cap (Type III, see below).

When a single thread is in a coiled position before the egg has contacted water, it is referred to as an individually coiled attachment thread (Plate 15: fig. 50; Plate 10: fig. 114; Plate 11: fig. 130). On eggs of *Stenonema interpunctatum* species-group (Type IV polar cap) and *Arthroplea congener* Bengtsson (Heptageniidae) the coiled threads lack terminal knobs. In other mayflies with individually coiled threads each thread is terminated by a distinct fibrous knob (Plate 5: figs 50; Plate 7: fig. 80; Plate 8: fig. 91; Plate 10: fig. 114; Plate 11: fig. 130). This common type of attachment structure is called a "knob-terminated coiled thread" (KCT). Knob-terminated coiled threads may occur in a uniform layer covering nearly the entire egg (Plate 4: fig. 40; Plate 9: fig. 98), be sparsely scattered over the egg surface (Plate 9: fig. 103), concentrated at one or both poles (Type V polar cap, see below, Plate 8: fig. 94), or arranged in some other particular configuration.

Polar caps

Koss (1968) discussed several types of polar caps and their functional morphology. Although he defined polar caps as being "attachment structures which are found at one or both poles" of the egg, reference was mainly to those relatively solid appearing structures found on eggs of *Ephemerella* (except the subgenus *Eurylophella*), *Ephoron* and *Caenis* (Plate 11: fig. 129; Plate 18: fig. 204; Plate 20: fig. 220). However, the study of eggs of many

additional genera has revealed other types of polar caps, including an interesting type formed by relatively dense concentrations of knob-terminated coiled threads at one or both poles of the egg. Polar concentrations of KCTs as dense as those on eggs of *Analetris* (Siphonuridae) (Plate 3: figs 34, 35) give the egg an obvious "capped" appearance. However, eggs with sparse and intermediate densities of knob-terminated coiled threads (Plate 8: figs 89 and 97, respectively) approach the appearance of being "capped" and show the impossibility of completely separating the eggs into those "with" and those "without" polar caps. Nevertheless, the term "polar cap" has utility in describing those eggs with an obvious capped appearance. The most workable definition of a polar cap may be the following: any polar concentration of attachment structures which covers or obscures a considerable amount of the polar chorion (Plate 8: fig. 94), or gives the egg a rather obvious two or three part appearance (Plate 3: fig. 34; Plate 11: figs 116, 129, Plate 12: fig. 133; Plate 13: figs 142, 145). Eggs approaching the appearance of being capped by polar concentrations of coiled attachment threads will be described accordingly.

Attachment threads evolved at least into the following five different polar cap configurations as a result of their reduction in number or disappearance from the equatorial and lateral regions of the egg, and their survival or increase in number, at one or both polar regions.

Type I. Non-coiled, single unit cap. This type of cap is formed by a countless number of short, non-coiled threads which are tightly compacted into a single unit prior to their contact with water (Plate 11: fig. 129; Plate 12: fig. 133; Plate 13: fig. 142). Upon entering the water the caps swell and expose the many threads which function in attachment or anchorage of the egg (Plate 12: fig. 131). Such caps are found in all Tricorythidae and Potamanthidae and in most Ephemerellidae; the caps on eggs of *Euthyplocia* (Euthyplociidae) also appear to be of this type.

Type II. Non-coiled, multi-unit cap. The composition of this cap is the same as Type I caps except the threads are compacted into several distinct units (Plate 18: figs 204, 206) rather than into a single unit. The cap is only known to occur in the genus *Ephoron* (Polymitarciidae).

Type III. Multi-threaded coiled cap. The Type III cap consists of many threads collectively coiled about the pole of the egg. Threads may be loosely coiled about the pole, or poles, as in *Campylocia* (Euthyplociidae), some Asthenopodinae and Campsurinae (Polymitarciidae) and *Potamanthellus* (Neophemeridae) (Plate 13: figs 149, 150; Plate 19: figs 207, 213, 216); or tightly coiled about the pole(s) as in the Caenidae (Plate 20: figs 217, 220). The polar cap on Ametropodidae eggs is not well understood, but it is tentatively assigned to this type.

Type IV. Single-threaded coiled cap. A single-threaded coiled cap is formed when one, two or three individually coiled attachment threads are situated at a pole of the egg. The only known occurrence of this type of polar cap is on eggs of the *Stenonema interpunctatum* species-group (Heptageniidae); in this group the threads are loosely coiled and occur at both poles.

Type V. KCT cap. When knob-terminated coiled threads are so densely concentrated at the polar regions as to give the egg an obvious "capped" appearance, the egg is said to possess a KCT cap (Plate 3: figs 34, 35). This type of polar cap is found in some Siphonuridae and many Heptageniidae.

Micropyles

Koss (1968) erred in the use of the term "micropyle". In that treatise the micropyle was defined as "the actual opening in the chorion which allows the sperm entrance", but the discussion went on to restrict the use of the term "micropyle" to the junction or union of the sperm guide with the micropylar canal. Further, the entire structure (sperm guide, micropylar canal and "micropyle" [the junction]) was called a "micropylar device", a term suggesting a structure with several parts functioning together as a whole. However, scientists generally agree that the micropyle is an opening in the investing membranes of an egg through which sperm passes in the process of fertilization. Thus the micropyle is the entire structure, not part of the structure as termed by Koss (1968). It is superfluous to introduce a new term synonymous with micropyle, so use of the term "micropylar device" is discontinued.

The terms used by Koss (1968) are redefined. The *micropyle* is the structure which allows sperm to enter the egg, and, on Ephemeroptera eggs, it normally consists of two parts: a sperm guide and a micropylar canal. In discussing the sperm guide and micropylar canal, the terms "proximal" and "distal" are used, with the junction of the guide and canal being the point of reference. For convenience this junction will be called the *micropylar opening*.

The *sperm guide* is a chorionic depression and/or a suprachorionic void or depression that leads to and presumably aids in directing sperm to the micropylar canal. A *chorionic sperm guide* (Plate 8: fig. 93; Plate 9: figs 102-106) is an external depression in the chorion and it usually lacks sculpturing and attachment structures. A *suprachorionic sperm guide* (Plate 14: figs 155-157) is a void or depression in a layer of attachment structures (e.g. an adhesive layer). A *suprachorionic-chorionic sperm guide* (Plate 16: figs 179, 181, 182) consists of a void in a layer of attachment structures, combined with a depression in the chorion (or an elongate groove in the ridges of the reticulation, as in some Ephemeridae). Sperm guides are almost always of a nearly constant shape for any one species. Dimensions given for sperm guides are inside dimensions, especially when a thickened rim occurs; the dimensions include, however, any inner flange that may be formed by an adhesive layer (Plate 10: fig. 113).

The *micropylar canal* is a tunnel-like passage leading from the sperm guide, through the chorion, and into the egg; it may terminate at the inner surface of the chorion, or continue into the egg for a short distance (see broken piece of chorion, fig. 49 of Koss, 1968). Usually no attempt has been made herein to distinguish between micropylar canals which just penetrate the chorion and those that extend below it into the interior of the egg. The micropylar canal is essentially a cylindrical or sometimes conical tube (e.g. *Ephemera*). Since it is usually seen in optical cross-section, however, the micropylar canal is described, for the sake of convenience, as having either parallel or approximating walls.

Unless otherwise stated, micropylar canals are measured via a surface view of the chorion. If a micropylar canal is curved in a surface view, its length is taken as a straight line measurement from the proximal end to the distal end of the micropylar canal (Plate 7: fig. 88). Thus, the length measured is not always the true length (i.e. length of passage), but it is the most accessible measurement.

The *angle of the micropylar canal to the sperm guide* is the estimated obtuse angle between the micropylar canal and the only sperm guide axis which intersects the micropylar opening (almost always the long axis of the sperm guide), as seen in a surface view of the chorion (Plate 7: fig. 88). The *angle of the micropylar canal to the chorion* is an estimation of whether the micropylar canal is perpendicular to or acutely angled with a plane tangent to the chorion at the micropylar opening.

The sperm guide and micropylar canal are usually quite distinguishable from each other, and a point of junction may be readily identified as the micropylar opening. However, on the eggs of some Oniscigastrinae and Leptophlebiidae, the boundary which separates the two parts is not exact. Instead, the sperm guide seems to blend into the micropylar canal with no obvious change in shape, and thus the proximal boundary of the sperm guide cannot be distinguished from the proximal boundary of the micropylar canal. Plate 2: fig. 17; Plate 11: fig. 126, and Plate 21: fig. 227 illustrate micropyles in which naming of parts is difficult. A comparison of those figures with Plate 2: figs 18, 19; Plate 11: fig. 125, and Plate 21: fig. 228 facilitates the estimation of homologous structures. In the latter group of figures, the outer (perpendicular) part of the micropyle is distinguishable as a chorionic sperm guide, and it is possible to locate the position of the micropylar opening. A comparison of Plate 21: figs 227 and 228 shows that most of the outer (perpendicular) portion of the micropyle in Plate 2: fig. 17; Plate 11: fig. 126, and Plate 21: fig. 227 may be homologous with the sperm guide on micropyles shown in Plate 11: fig. 125, and Plate 21: fig. 228. Notice, however, that in *Habroleptoides* (Plate 11: fig. 125) only a section of the perpendicular portion has actually developed the appearance of a true sperm guide. In light of the above data, we restrict the term "sperm guide" to those instances in which such a structure is recognizable by its own distinctness. In those cases where a sperm guide is not readily distinguishable from the micropylar canal (Plate 2: figs 17; Plate 11: fig. 126; Plate 21: fig. 227), the micropyle is considered to consist of a micropylar canal only, although it is realized that part of the canal is probably homologous with the sperm guide.

Koss (1968) and Degrange (1956, 1960) have previously described the basic types of micropyles found on mayfly eggs, but it would be more convenient to have a descriptive name for each type of micropyle instead of referring to these structures by terms applicable to only one of their respective parts.

In all three types, the sperm guide may be suprachorionic, chorionic, or both. Eggs of *Analetris* and *Rallidens* (Siphonuridae) are the only Ephemeroptera eggs known to have micropylar structures which project above the chorion, a feature common on certain Heteroptera eggs (Southwood, 1956; Cobben, 1968).

The following terms and definitions are proposed.

Type I. A funnellform micropyle (Plate 1: figs 11, 16; Plate 2: figs 17, 18; Plate 11: figs 125, 126; Plate 21: figs 227, 228) is one in which at least part of the structure is perpendicular to the chorion. The micropylar canal either issues from the base and near the center of a funnel-shaped sperm guide, and is perpendicular to or acutely angled with the chorion; or else the sperm guide is lacking or not readily discernible, and a portion of the micropylar canal is definitely perpendicular or nearly so to the chorion at least throughout most of

the chorion's depth (Plate 2: fig. 17; Plate 11: fig. 125; Plate 21: fig. 227). The latter feature distinguishes funnellform micropyles lacking sperm guides from linear (Type II) micropyles lacking sperm guides since in the latter case the micropylar canals are always acutely angled with the chorion. The funnellform type is considered the most plesiomorphic. It corresponds with type 2 of Degrange (1960) and has been found in the Ameletopsinae, Oniscigastriinae, Acanthametropodinae and Rallidentinae (Siphonuridae), Leptophlebiidae, Behningiidae, Campsurinae (Polymitarciidae), and *Campylocia* (Euthyplociidae).

Type II. A linear micropyle (Plate 15: fig. 166; Plate 16: fig. 179; Plate 20: fig. 221) is one in which the micropylar canal is acutely angled with the chorion, and the sperm guide is either lacking or is elongate and narrow; in both cases the micropyle appears as a linear structure. This is a heterogeneous group of independently evolved, similar appearing micropyles. It corresponds to type 3 of Degrange (1960), and has been found in Baetidae (according to Degrange), Ephemeridae and Caenoidea.

Type III. A tageniform micropyle (Gk., *tagenon*, frying pan) (Plate 7: fig. 88; Plate 8: fig. 93; Plate 13: fig. 143) has the micropylar canal situated at one side of an oval-shaped sperm guide. Although considered to be of polyphyletic origin, this type is remarkably consistent in form. It corresponds with types 1 and 4 of Degrange (1960), is the most common type, and has been found in all families except Leptophlebiidae, Behningiidae, and Euthyplociidae. The micropyles of Ametropodidae, Palingeniidae and Baetiscidae are unknown.

Chorion and chorionic sculpturing

Hinton (1963) and Cobben (1968) suggest avoiding the terms endo- and exochorion until the various chorionic layers can be homologized, because varying numbers of chorionic layers above two have been found (e.g. Beament, 1946, found seven layers on eggs of the hemipteran *Rhodnius*). They recommend referring to these layers topographically, and their suggestion has been followed herein. In this study, there has been no attempt to study the different layers of the chorion; reference is always to the outer surface of the outer layer except where otherwise noted.

Koss (1968) discussed chorionic sculpturing (reticulation, tubercles, etc.); with one exception, the terminology and measurements used in that paper are used here. Terms for the dimensions of tubercles, peglike structures or other structures projecting from the chorion were not always the same in the Koss paper, but have been standardized here. The distance from the base of a structure to its apex is its height. If the structure is cylindrical or nearly so, then the term "diameter" is employed; otherwise, length and width are used for the remaining linear dimensions (see Plate 21: figs 225, 226).

COMPARATIVE EVALUATION OF DATA

Sufficient morphological data have been gathered to allow some estimations of the probable sequences involved in the evolution of several external features found on Ephemeroptera eggs.

Attachment structures

Evolution of knob-terminated coiled threads

The knob-terminated coiled thread is considered to be the most apomorphic fibrous attachment structure, and in this character state many fine fibers are tightly spiraled together to form a single thread (Plate 5: fig. 51) which is terminated by a distinct fibrous knob (Plate 5: fig. 50); each thread is coiled about its own base (Plate 5: fig. 50; Plate 11: fig. 130). Since threads do serve as attachment or “anchor” devices, it seems most probable that the apomorphic conditions would be the well-developed knob (or “anchor”) terminating an elongate thread (anchor line). The KCTs appear to have evolved from fibrous adhesive layers, the development of fiber-coils and terminal fiber-clusters being major achievements in that process.

Fiber-coils, the first major improvement over the fibrous adhesive layer, consist of many fibers loosely coiled together (Plate 5: figs 56, 57). They are known only to occur in a uniform layer covering the entire egg (Plate 2: fig. 21; Plate 5: fig. 58) and in their most plesiomorphic state, lack any terminal knob or terminal fiber-cluster development.

The origin of terminal fiber-clusters must have been an important step in the evolution of knob-terminated coiled threads. The fiber-clusters vary in their degree of development (i.e. their similarity to or development as terminal knobs), and they have been found only on fiber-coils, never on attachment threads. Terminal knobs subsequently evolved from terminal fiber-clusters (see Plate 6: fig. 74; Plate 7: figs 78, 77; Plate 5: fig. 50; Plate 7: figs 80 and 85, in that order), and the fibers in each fiber-coil became tightly spiraled together to form single coiled threads (Plate 5: figs 50, 51); the resultant structure was the knob-terminated coiled thread.

A variety of patterns evolved for the distribution of KCTs (see below), and thus they are not commonly found in a uniform layer covering the entire egg (the only distributional pattern known for fiber-coils).

The eggs of the Heptagenioidea reveal quite clearly the most probable sequence involved in the evolution of KCTs, and our data suggest numerous origins of KCTs from fiber-coils, even within the Heptagenioidea. Fiber-coils on the eggs of Siphlaenigmatidae and the *Metamonius*-complex (Siphonuridae) completely lack terminal knob or terminal fiber-cluster development. In the *Siphonurus*-complex (Siphonuridae), and *Chromarcys*, *Oligoneuria* and *Elassoneuria* (Oligoneuriidae) well-developed terminal fiber clusters exist on the fiber-coils (Plate 6: fig. 74). On fiber-coils in *Homoeoneuria*, *Oligoneuriella* and *Lachlania* (all Oligoneuriidae) there is sufficient subapical compaction plus apical expansion to call the structures terminal knobs (Plate 7: figs 77, 78). Distinct coiled threads terminated by well-developed terminal knobs occur on eggs of many Heptageniidae and Isonychiinae.

Evolution of polar caps

The different polar configurations of attachment threads evolved as a result of reduction in numbers or disappearance of such threads in the equatorial and lateral regions of the egg, and a survival or increase in numbers at one or both polar regions. There is little doubt that within each superfamily attachment

threads evolved from an adhesive layer state independently of the other superfamilies. This conclusion is suggested by the evidence from the hypothesized evolution of micropyles (see below) and the fact that a diversity of attachment structures is found within most superfamilies. Also, there remains little doubt that selection pressures several times independently favored the evolution of polar concentrations of attachment threads (polar caps). Such concentrations are found in all superfamilies except the Leptophlebioidea and Prosopistomatoidea.

Polar caps are quite obviously apomorphic attachment structures. Except for polar masses of fibrous adhesive material in the Behningiidae, all polar caps are formed by attachment threads, not the more plesiomorphic fiber-coils. The apparent survival advantage of having attachment structures concentrated at the poles lends support to the suggestion that polar concentrations of attachment structures are apomorphic to a complete coverage of the egg by the same. Polar concentrations of attachment threads seem more advantageous than lateral ones because anchorage at a pole would orient the elongate egg in a position of least resistance to water flow. Water currents are probably of little significance to the egg stage in those Ephemeroptera that lay their eggs in lakes and ponds.

Type I polar cap. The Ephemerellidae, Tricorythidae, Potamanthidae and possibly *Euthyplocia* (Euthyplociidae) possess the non-coiled, single unit type of polar cap. This cap consists of a solid-appearing mass of short threads terminated by small knobs. In addition to polar caps, the Ephemerellidae and Potamanthidae also possess well-developed knob-terminated coiled threads; the threads are relatively long and laterally distributed only. *Tricorythodes* eggs have long lateral threads, but they are not coiled or knob-terminated. Perhaps the relatively long, lateral threads serve to initially anchor the egg as it floats near an object. Once the egg itself contacts this substrate, the polar caps probably assume the role of permanent attachment. Laboratory studies of fresh eggs placed in simulated streams would contribute greatly to understanding the mode of operation of these and other attachment structures. The origin of the Type I polar cap is undoubtedly monophyletic concerning the Ephemerellidae and Tricorythidae, but perhaps of independent origin in the Potamanthidae. No intermediate forms are known which indicate the sequences in the evolution of this type of polar cap. Theorizing, however, the Type I polar cap probably evolved from a fibrous adhesive layer in accompaniment with the evolution of lateral attachment threads. Except for the retention of the few laterally distributed threads, lateral attachment structures most likely disappeared under selection pressures for permanent attachment to be of a polar nature.

Type II and Type IV polar caps. The Type II and IV polar caps are unique to *Ephoron* (Polymitarciidae) and the *Stenonema interpunctatum* species-group (Heptageniidae), respectively. Their evolutionary histories are unknown.

Type III polar caps. Long threads coiled about the poles (multithreaded coiled caps) have been found in *Ametropus*, Caenidae, Neoephemeridae, Polymitarciidae and *Campylocia* (Euthyplociidae). Caps of this type quite likely evolved independently in all of these taxa except Caenoidea and the survival advantage of having many threads "dangling" from each pole readily explains the many instances of convergent evolution assumed.

The polymitarcid genera show several different character states which may

have been involved in the evolution of the Type III polar cap. *Tortopus* eggs (Plate 19: fig. 210) possess a fibrous adhesive layer. Each *Povilla* egg (Plate 19: fig. 214) is enveloped in a mass of long, loosely-coiled threads, but it is obvious that an "adhesive layer" appearance is lacking. Eggs of *Campsurus* (Plate 19: fig. 207) and *Asthenopus* (Plate 19: fig. 211) possess perfectly formed polar caps which consist of long threads loosely coiled about the pole(s). Although *Campsurus* did not evolve from *Povilla*, it is probable that *Campsurus* eggs went through a *Povilla*-like stage (but not including the characteristic egg mass of *Povilla*) after the evolution of a C-shaped form. There is no reason why this sequence would not be equally applicable to the other groups possessing the Type III polar cap. Comparison of *Neoephemera*, *Potamanthellus* and *Caenis* eggs indicates that a similar sequence may have also occurred in the Caenoidea.

Type V polar caps. The Type V polar cap is known only to occur in the Heptagenioidea, and except for the Type III cap in Ametropodidae and the Type IV cap of *Stenonema interpunctatum* species-group, it is the only type found in that superfamily. Type V polar caps are formed by dense concentrations of knob-terminated coiled threads at one or both poles. Since KCTs are apomorphic to, and apparently derived from, a uniform layer of fiber-coils, then there is little doubt that restricted distributions of KCTs are apomorphic to a uniform covering of the egg by KCTs. In fact the data almost suggest that the evolution of knob-terminated coiled threads was accompanied by the gradual disappearance or reduction in numbers of fibrous attachment structures in the equatorial region and the concentration of these structures at one or both polar regions. The presence of knob-terminated coiled threads over the whole surface of the egg in some *Isonychia* and *Heptagenia* species makes it apparent that in most Heptagenioidea, knob-terminated coiled threads probably evolved prior to their concentration at the poles.

The most probable sequence involved in the evolution of Type V polar caps is illustrated by the following examples. In the *Siphonurus*-complex (Siphonuridae), Siphlaenigmatidae and Oligoneuriidae fiber-coils are distributed over the whole surface of the chorion, the proposed plesiomorphic condition. In the *Ameletus*-complex and *Analetris* (Siphonuridae), most Heptageniidae, and most of the remaining Heptagenioidea knob-terminated coiled threads are sparsely scattered or absent in the equatorial and lateral regions, but concentrated at one or both polar regions, the proposed apomorphic condition. Fiber-coils are absent in these groups. The Isonychiinae and *Heptagenia* (Heptageniidae) display an intermediate condition in that fully apomorphic, knob-terminated coiled threads cover the entire egg of some species in each group.

Knob-terminated coiled threads and their concentration at one or both poles are most likely cladogenetically evolved conditions within the Heptagenioidea (Plate 23: fig. 231). These conditions independently arose twice from the adhesive layer state—once in the Ameletopsinae and once in the Siphonurinae (and derived taxa). After plesiomorphic fiber-coils were developed in the ancestral Siphonurinae, the two apomorphic character states independently evolved in the Acanthametropodinae, Isonychiinae, the *Ameletus*-complex of the Siphonurinae, Rallidentinae, Baetidae, Metretopodidae, and Heptageniidae. The eggs in all of these groups are laid in lotic water (a few derived forms have subsequently invaded the pond habitat), and thus they would all have been

subject to the same selection pressures indicated earlier as important in directing the evolution and distribution of the knob-terminated coiled threads.

Micropyles

Evolution of sperm guides

Certain details of micropylar morphology indicate that in the Ephemeroptera suprachorionic layers must be deposited by the follicle cells after the same cells have deposited the chorion (Koss, 1970).

At some early stage in the evolution of insects, eggs undoubtedly lacked sperm guides, or similar structures, as well as suprachorionic layers deposited by the follicle cells prior to fertilization (e.g. adhesive layers in the Ephemeroptera). In order to allow sperm to reach the egg, the origin and evolution of suprachorionic sperm guides or the extension of micropylar canals to micropylar processes (as in the Heteroptera, Southwood, 1956; Cobben, 1968) necessarily coincided with the origin and evolution of any suprachorionic layers deposited prior to fertilization.

The presence of chorionic sperm guides is almost characteristically associated with a low number of attachment threads or other apomorphic attachment structures in the lateral regions of the egg, and a concentration of such structures at polar regions (a relatively apomorphic condition). The association is so repetitive as to suggest that chorionic sperm guides evolved from suprachorionic ones coincident with and as a direct result of the evolution and subsequent reduction in the distribution of such apomorphic attachment structures. This hypothesis is especially documented by micropylar features in the Heptagenioidea and Caenoidea, and the phenomenon undoubtedly occurred several times independently.

In the Heptagenioidea, it has already been shown that the *Siphonurus*-complex, Siphlaenigmatidae and the Oligoneuriidae are representative of the plesiomorphic end of a gradient leading to the development of knob-terminated coiled threads and the localization of these threads at the polar regions of the egg. The Isonychiinae and Heptageniidae, among others, are at the apomorphic end of this gradient. The evolution of tageniform micropyles with chorionic sperm guides from tageniform micropyles with suprachorionic sperm guides readily fits the same sequence. The *Siphonurus*-complex, Siphlaenigmatidae and the Oligoneuriidae have suprachorionic oval sperm guides, whereas the Isonychiinae and Heptageniidae, among others, have chorionic ones.

In the Caenoidea, *Neoephemera* eggs are undoubtedly the most plesiomorphic known for that superfamily. Although the micropyle could not be detected, the sperm guide most likely is suprachorionic since *Neoephemera* eggs are entirely enveloped by a dense fibrous adhesive layer. Other caenoids lack this adhesive layer, instead possessing one or two polar caps, and they either lack a sperm guide, or possess a chorionic one. It seems obvious that the replacement of an adhesive layer by polar caps has been coincident with and perhaps in some way responsible for the loss of the sperm guide in the suprachorionic material and its subsequent development in the chorion.

Although in most cases chorionic sperm guides probably evolved from suprachorionic ones, there are some examples of chorionic sperm guides having

possibly evolved without the prior development of suprachorionic layers. This seems to be the case in the Oniscigastrinae, and perhaps the Leptophlebiidae, and if true, then there could have been sequences wherein suprachorionic sperm guides existed intermediately between two separate occurrences of chorionic sperm guides; i.e. one occurrence being the time before suprachorionic layers evolved in the particular taxon, the other being after the evolution and scattered distribution of attachment threads in the taxon or its derivatives. Nevertheless, it still seems quite certain that of the existing taxa with chorionic sperm guides, most are related to some ancestral stock which originally had suprachorionic sperm guides.

Evolution of the different types of micropyles

The micropyles found on eggs of the Oniscigastrinae (Siphonuridae) suggest that the funnellform type is perhaps the most plesiomorphic. In *Oniscigaster* the micropyle is certainly funnellform, and it is nothing more than an undifferentiated micropylar canal (Plate 2: fig. 17; Plate 20: fig. 227). Proximally, the canal is nearly perpendicular to the chorion, but as the canal reaches the inner chorionic surface, it bends quite sharply and becomes acutely angled to the chorion. No sperm guide is distinguishable, although upon comparison with the micropyle of *Tasmanophlebia* (Plate 2: figs 18, 19; Plate 21: fig. 228) it is obvious that the sperm guide of *Tasmanophlebia* developed from the proximal portion of a micropylar canal similar to that of *Oniscigaster*. Thus, the proximal portion of the *Oniscigaster* micropylar canal (or micropyle) could be considered homologous to the sperm guide.

Two other types of micropyles seem evident upon examination of those in *Tasmanophlebia*. The micropyle of *T. sp. no. 1* (Plate 2: fig. 18; Plate 21: fig. 228) seems to have the potential of evolving into a tageniform type, whereas that of *T. sp. no. 2* (Plate 2: figs 19, 20) seems to be a rudimentary linear type. The extreme depth of the sperm guide is the only feature distinguishing the micropyle of *T. sp. no. 1* from typical tageniform types. Since the Oniscigastrinae micropyles show the possibility of the funnellform type giving rise to tageniform and linear types, and because the funnellform micropyle appears to be the least complex of the three types, it seems most logical to assume that the funnellform micropyle is plesiomorphic and ancestral to the tageniform and linear micropyles. The nearly exclusive occurrence of tageniform and linear micropyles in association with apomorphic attachment threads (e.g. in the Heptagenioidea and Caenoidea, respectively—see above), is further support for the hypothesis that they are the more apomorphic types of micropyles.

The relationship of the three micropyles is mostly cladogenetic since there are only scattered examples (in *Ephemera*) of linear micropyles having possibly given rise to tageniform ones; our data do not suggest that the reverse has ever occurred. The tageniform type is the most common.

The sperm guide of tageniform micropyles is usually chorionic and associated with the apomorphic conditions such as knob-terminated coiled threads and localization of these threads at the poles. When suprachorionic, it is most frequently situated among attachment structures more apomorphic than an adhesive layer (fiber-coils as in the Oligoneuriidae and *Siphonurus*-complex); only rarely does a tageniform micropyle have an adhesive layer sperm guide (e.g. in a few *Ephemera*, Plate 14: figs 155, 163, 164). Several

forms (e.g. *Coloburiscoides* and *Siphloplecton*) have micropyles that are suggestive of an intermediate step in the development of tageniform micropyles. In such cases, the micropylar opening is situated to the side of a weak, approximately ovoid, chorionic depression.

Tageniform micropyles seem to be of monophyletic origin within the Heptagenioidea; however, they have also arisen independently in six other lineages (Caenoidea, *Ephemer*, Ephemerelloidea, Polymitarcidae, Potamanthidae, and Prosopistomatidae), apparently in conjunction with a loss of attachment structures in those areas (usually equatorial) where the micropyles occur. Within the Heptagenioidea, ancestral Siphonurinae probably provided the potential for the evolution of a tageniform micropyle in the higher Heptagenioidea.

We theorize that the egg of the ancestral Ephemeroptera was round, lacked attachment structures of any kind, and possessed a funnellform micropyle without a sperm guide. A simple non-fibrous adhesive layer and a supra-chorionic sperm guide were probably early acquisitions.

Two lines of evolution apparently diverged early in mayfly history (Plate 24: fig. 232). One resulted in the Caenoidea (now with linear micropyles) plus the Prosopistomatoidea (now with tageniform micropyles), and the other gave rise to the remaining superfamilies (with funnellform micropyles originally and still existing in at least one primitive extant family in each superfamily except the Ephemerelloidea).

At the divergence of the heptagenioid and leptophlebioid ancestors, both lines appear to have maintained a suprachorionic funnel-shaped sperm guide. Early Ephemeroidea, as evidenced by the Behningiidae, retained the supra-chorionic funnel-shaped sperm guide but the Leptophlebioidea evolved a chorionic one. Subsequently the Ephemeroidea evolved linear and tageniform micropyles. The linear micropyles in the Ephemeroidea must have evolved independently of those in the Caenoidea. In the Heptagenioidea the funnellform micropyle evolved into the tageniform type after the origin of the Oniscogastrinae and Ameletopsinae.

Chorionic sculpturing

Evolution of chorionic sculpturing

In some of the more primitive groups (e.g. *Siphonurus*-complex, *Ametropus*, Behningiidae, Potamanthidae) the chorion is smooth or relatively unsculptured. In most families, however, chorionic sculpturing is too diverse to be of importance in studying familial relationships, although occasionally it is useful for generic level phylogenetic considerations. Sculpturing clearly arose independently in each superfamily and most likely independently in nearly every family and subfamily. There is sufficient evidence that certain extant genera have evolved from ancestors having a smooth chorion.

INTRAFAMILIAL PHYLOGENETIC RELATIONSHIPS

Siphonuridae

Plate 23: fig. 231 depicts the hypothesized phylogenetic history of the Siphonuridae as derived from a study of the eggs. The Siphonuridae appear to

be a stem-family of ancient origin, and the relationships of the various subfamilies are not easy to establish. Edmunds (1972) places the subfamilies in three lineages: (1) Oniscigastrinae; (2) Siphonurinae, from which Rallidentinae, Ameletopsinae and Acanthametropodinae are derived, and (3) Isonychiinae, from which the Coloburiscinae are derived. As is evident from Plate 23: fig. 231, the data from eggs suggest that the Ameletopsinae are more distantly related to the Siphonurinae than was suggested by Edmunds (1972). In most other details the data from eggs suggest a subfamilial classification compatible with that suggested by data from nymphs and adults. Eggs of the Oniscigastrinae appear to be the most plesiomorphic of all taxa studied and suggest that the lineage is a very primitive one. The chorion is relatively unsculptured, the only known means of attachment is a non-fibrous adhesive layer, and the micropyle of *Oniscigaster* is essentially of the funnellform type. The micropyle of *Tasmanophlebia* seems to represent a transitional stage between a funnellform type and a tagenofrom one (eggs of *Siphonella* were not examined).

Egg structures suggest that the Ameletopsinae also evolved very early from the basic stock since they likewise have a funnellform micropyle that has diverged very little from the proposed original type. The presence of a plesiomorphic micropyle in both the Ameletopsinae and the Oniscigastrinae, however, only infers that both lines originated from forms having the basic plesiomorphic funnellform micropyle. Eggs of Ameletopsinae are more apomorphic than Oniscigastrinae in details of the chorion and attachment structures. *Chiloporter* is probably the most primitive member of the Ameletopsinae since the strands of the reticulation are not raised ridges as in the other genera, but consist simply of flat chorion between a convex mesh. The remaining three genera (*Ameletopsis*, *Chaquihua*, and *Mirawara*) show evidence that they evolved from a common ancestor but there are no indications from egg structure of the sequence of splitting of the three genera. On other evidences, it appears that the New Zealand genus *Ameletopsis* was separated from the lineage before the split of the Chilean genus *Chaquihua* and the Australian *Mirawara*. The eggs of *Mirawara* evolved to the most apomorphic state in this subfamily, since they possess knob-terminated coiled threads.

The third branch of the ancestral siphonurid stock apparently gave rise to the Siphonurinae. Egg data suggests that subsequent to the split, the Siphonurinae evolved a uniform layer of fiber-coils and a tagenofrom micropyle with a suprachorionic sperm guide. Such features characterize eggs of extant members of the *Siphonurus*-complex (Siphonurinae), and those eggs appear to be representative of the type of egg possessed by the ancestral siphonurines. The *Siphonurus*-complex egg type also appears to be the ancestral form for the rest of the Heptagenioidea.

Within the Siphonurinae, the *Metamonius*-complex must have evolved from the ancestral *Siphonurus*-complex. Eggs of both groups have fiber-coils for attachment structures, but in the *Metamonius*-complex each fiber-coil is contained in, or protected by, a mesh of a large-mesh reticulation. The micropyle in the *Metamonius*-complex is a typical apomorphic, entirely chorionic tagenofrom type; the micropylar canal is acutely angled with the chorion and is perpendicular, or nearly so, to the long axis of the egg (typical condition). Eggs of the *Ameletus*-complex have the apomorphic characters of knob-terminated coiled threads, a reduction in number of KCTs, and the

formation of open-ended conical projections from the chorionic ridges which surround and possibly protect the remaining KCTs. Other apomorphic features in the *Ameletus*-complex are the concentration of larger KCTs at the poles, and a micropylar canal which is acutely angled with the chorion but is parallel or nearly so to the long axis of the egg (*Ameletus* only). Some *Ameletus* eggs show a degeneration of the chorionic ridges either in height (Plate 3: fig. 29) or completeness (Plate 3: fig. 28), such a degeneration being a secondary characteristic. Because this feature is found with the apomorphic condition of a micropylar canal parallel to the long axis of the egg, the presence of a well-developed large-mesh reticulation is considered intermediate in the evolutionary development of this generic complex.

Eggs of *Analetris* are very specialized and give no clues about the origin of the Acanthametropodinae. Although the micropyle (Plate 3: fig. 35) is somewhat similar in shape and position to that of *Coloburiscoides* (Plate 4: fig. 47), the Acanthametropodinae almost certainly did not evolve from a coloburiscine ancestor. The evidence from nymphal structures shows these two subfamilies to be rather remote from one another within the family. However, the similarity of the micropyles in these two subfamilies indicates that it is entirely possible that the unique micropyle of *Analetris* evolved from a tageniform type with a suprachorionic sperm guide. If so, this would not preclude the hypothesis that the Acanthametropodinae had common ancestry with the Siphonurinae, as suggested by Edmunds (1972). The eggs in no way indicate a close relationship between *Analetris* and *Ametropus* (Ametropodidae) although Edmunds (1972) and Riek (1973) suggested that *Ametropus* may have originated from an acanthametropodine siphonurid.

Undoubtedly, the monotypic Isonychiinae had common ancestry with the Siphonurinae. The *Siphonurus*-complex, the *Metamonius*-complex and *Isonychia* are the only siphonurid genera in which the egg is completely covered by a uniform layer of coiled fibrous attachment structures, but the eggs of *Isonychia* possess an additional presumably plesiomorphic character in that they are spherical rather than ovoid. Although the attachment structures are knob-terminated coiled threads in *Isonychia*, in some species the KCTs are distributed in a uniform layer covering the entire egg. This similarity in distribution of KCTs in some species of *Isonychia* to the distribution of fiber-coils in the Siphonurinae suggests that the development of KCTs from fiber-coils was preliminary to the localization of attachment structures at the poles. It also suggests that the Isonychiinae evolved from ancestral Siphonurinae and subsequent to the split, developed the apomorphic micropyle and attachment structures characteristic of the subfamily. Data from the eggs are in agreement with the origin of the subfamily as suggested by Edmunds (1972).

The egg data for the Coloburiscinae are equivocal concerning the origin of the subfamily. The eggs of the Coloburiscinae seem superficially plesiomorphic to those of Rallidentinae, but not obviously derived from any known egg type. Edmunds (1972) believes the Coloburiscinae to be derived from the Isonychiinae on the basis of larval feeding structures and the larval tracheal system (Landa, 1964). The lack in the Coloburiscinae of a chorionic sperm guide as well-developed as that in the Isonychiinae indicates that the coloburiscine lineage must have separated from the Isonychiinae stock while the eggs were in a relatively plesiomorphic state (i.e. relatively smooth chorion,

knob-terminated coiled threads distributed over the entire chorion, not concentrated at the poles and a suprachorionic sperm guide). Edmunds (1972) suggests that the New Zealand genus *Coloburiscus* split from the ancestral stock before the separation of the Australian *Coloburiscoides* and the Chilean *Murphyella*.

Egg data suggest that ancestral *Coloburiscus* may have given rise to the *Coloburiscoides* line while eggs were still in a relatively plesiomorphic state. After that split, subsequent evolution of *Coloburiscus* eggs resulted in concentrating the KCTs at the poles, whereas *Coloburiscoides* eggs lost some coiled threads and developed tubercle clusters around the remaining laterally distributed ones. This *Coloburiscoides* stock could have next given rise to the ancestral *Murphyella*, and then each subsequently evolved different structures which happened to be similar to certain features of the egg of *Rallidens* (clusters of large tubercles in *Murphyella*; polar KCTs in a reticulation in *Coloburiscoides*). If Edmunds is correct, then the concentration of KCTs at the poles is a convergent apomorphic development on eggs of *Coloburiscus* and *Coloburiscoides*. This convergence is not difficult to accept because of the selective advantage of such polar concentrations (see comparative evaluation of data).

From eggs alone it is difficult to determine the evolutionary relationships of *Rallidens* (Rallidentinae). Edmunds (1972) suggests that *Rallidens* evolved from a pre-*Metamonius* ancestor. *Rallidens* eggs have a large-mesh reticulation at each pole, and what appears to be scattered remnants of a large-mesh reticulation on the lateral surfaces; knob-terminated coiled threads occur in the lateral mesh, and in some of the polar mesh. Eggs of the *Metamonius*-complex have a large-mesh reticulation covering the entire egg, and a fiber-coil occurs in each mesh. *Rallidens*, therefore, could have evolved from a common ancestor with the *Metamonius*-complex, and trend in evolution (as in the *Ameletus*-complex) being toward a concentration of knob-terminated coiled threads at the poles and a reduction of the reticulation except at the polar areas and around any laterally distributed KCTs. Subsequent to the separation of the two phyletic lines the micropyle, chorionic sculpturing, and development and distribution of coiled attachment threads, evolved to a highly apomorphic state in the Rallidentinae. Such a conclusion is in agreement with data on nymphal morphology.

Metretopodidae

The few differences between the eggs of *Siphloplecton* and *Metretopus* suggest that *Metretopus* was derived from ancestral *Siphloplecton*. The chorionic ridges on eggs of *Metretopus* (Plate 11: fig. 121) may have resulted from a fusion of adjacent tubercles (Plate 11: fig. 119) on the egg of a *Siphloplecton*-like ancestor, and the sperm guide on *Metretopus* eggs is more definitely chorionic than the sperm guide on *Siphloplecton* eggs.

Heptageniidae

Most heptageniid eggs are so similar at generic level as to be of little value in an attempt to understand the phylogenetic relationships of the genera. Many

species of *Heptagenia* possess eggs with a smooth chorion, a uniform layer of closely-spaced knob-terminated coiled threads and an entirely chorionic tageniform micropyle; the latter feature is common to all heptageniid eggs except in the genus *Stenonema*. The smooth chorion, uniform layer of coiled fibrous attachment structures and tageniform micropyle (irrespective of the position of the sperm guide) are features also common to the *Siphonurus*-complex (Siphonuridae) and the Oligoneuriidae. This indicates a common ancestry of the Heptageniidae with one of these taxa or the Isonychiinae, and also indicates that the plesiomorphic egg type for the Heptageniidae is one with a smooth chorion and a uniform layer of closely-spaced coiled attachment structures.

The eggs of *Cinygmula*, *Ecdyonurus*, *Ororotsia* and some *Rhithrogena* are similar to those of the remaining *Heptagenia* in that chorionic tubercles are present and knob-terminated coiled threads are either randomly scattered over the entire surface of the chorion, or scattered laterally and concentrated at one or both poles. These eggs are the commonest types found in the Heptageniidae, and they could be categorized as "typical heptageniid eggs". Such data indicates that the above five genera are of relatively recent common or nearly common ancestry. Several species of *Rhithrogena*, and one each of *Afronurus*, *Cinygmina* and *Ecdyonurus* possess eggs that show apomorphic features (in tubercle or KCT size and arrangement) not found elsewhere in the groups listed above; such features, however, do not restrict these genera from having had common ancestry with the above named genera.

Of undeterminable origin are *Cinygma*, *Epeorus* s.l., and *Stenonema* except for the *interpunctatum* species-group. The first two genera lack attachment structures entirely, and the *Stenonema* species possess a non-fibrous adhesive layer; some species possess smooth chorions while others have tuberculate ones. The egg stage provides no clues as to the phylogenetic relationships of these taxa.

Eggs of *Arthroplea bipunctata* are costate and without fibrous attachment structures. Although they are entirely unlike any other known heptageniid egg, those of *A. congener* are quite similar to many Heptageniidae eggs except terminal knobs are lacking on the coiled threads. The lack of terminal knobs in *A. congener* suggests that the *Arthroplea* lineage evolved from the ancestral Heptageniidae prior to the development of terminal knobs in that family. *A. bipunctata* must have lost its attachment structures subsequent to that division of the ancestral *Arthroplea* population which eventually resulted in the extant two species of the genus. *Arthroplea* eggs are laid in slow moving vegetated water where there is probably little or no selection pressure for elaborate attachment structures.

Pseudiron eggs indicate that the genus should be considered a member of the Heptageniidae where it was placed by Edmunds & Traver (1954), rather than a member of the Ametropodidae as suggested by Needham *et al.* (1935), Demoulin (1958) and Burks (1953). The characteristic features of the eggs are knob-terminated coiled threads rather densely concentrated laterally but also localized at one or both poles, and an entirely chorionic tageniform micropyle. Both features are found elsewhere in the superfamily, but the *Metamonius*-complex of Siphonurinae, Isonychiinae (both are Siphonuridae) and the Heptageniidae are the only Heptagenioidea with a sperm guide that is actually

similar to that of *Pseudiron* (i.e. a well-developed, strongly bordered, oval, chorionic sperm guide). Coiled fibers instead of threads, and the presence of a large-mesh reticulation preclude the conclusion that the *Metamoni*-complex is closely related to Pseudironinae. A dense layer of coiled attachment threads is considered plesiomorphic for the Heptageniidae, but is found also in the Isonychiinae. Thus, both the well-developed chorionic sperm guide and the rather dense layer of KCTs covering the entire egg, or nearly so, indicate that *Pseudiron* probably evolved within the Heptageniidae. Although the possibility that they originated independently from the Isonychiinae is not totally excluded by egg data, other data from the nymphal stages definitely suggest that *Pseudiron* evolved relatively early within the Heptageniidae. Egg data suggests the time of origin as subsequent to the origin of the Arthropleinae (which lack terminal knobs on the attachment threads), but nymphal data (Edmunds, 1972) suggests that the Pseudironinae originated earlier than the Arthropleinae.

Oligoneuriidae

Although distinct characters could not be found to separate the genera studied, certain character gradients were observed. The terminal fiber-clusters of *Chromarcys*, *Oligoneuria* and *Elassoneuria* only slightly resemble terminal knobs (Plate 6: fig. 74) but in *Homooneuria*, *Oligoneuriella*, and *Lachlania* there is sufficient subapical fusion of fibers, so that the apical portion is readily distinguishable as a plesiomorphic terminal knob (Plate 7: figs 77, 78). In addition, the fiber-coils in some genera are more distinct as a unit than in other genera.

The similarity of the *Chromarcys* eggs to those of the other oligoneuriid genera indicates a very close genetic relationship of *Chromarcys* to the other Oligoneuriidae. Furthermore, *Chromarcys* eggs do not indicate that the genus is any more closely related to the extant Isonychiinae than is the remainder of the Oligoneuriidae.

Ephemeridae

The hypothesized phylogenetic relationships of the ephemerid genera are diagrammed in Plate 22: fig. 230.

The linear micropyle and copious adhesive layer on eggs of Ichthybotinae place the group in the Ephemeridae; however, the phylogenetic position of the group cannot be ascertained from a study of the eggs alone.

The variety of chorionic sculpturing found within this family suggests that it evolved from an ancestor whose eggs had a smooth chorion, and also that chorionic sculpturing did not evolve until each subfamily lineage was established.

A great diversity of chorionic sculpturing and sperm guide shapes have evolved on eggs of *Ephemer*; however, large-mesh reticulations and chorionic sperm guides are rare in the genus. For these reasons, *Ephemer* appears to be the most primitive ephemerid group.

The anagenetic sequence indicated by conditions of the micropyle and chorionic sculpturing in *Eatonigenia*, *Eatonica*, *Pseudeatonica* and *Hexagenia*

s.s. strongly suggests that *Litobranchna* must have become isolated relatively early from ancestral Ephemerinae and prior to the development of the more apomorphic sperm guides characteristic of the rest of the subfamily. *Litobranchna* eggs lack chorionic ridges and a channelized connection of the suprachorionic sperm guide to the chorion. *Eatonigenia* eggs lack chorionic ridges, but possess a shallow channel in the base of the suprachorionic sperm guide; this channel does not extend to any corresponding chorionic sperm guide. Below the suprachorionic part of the sperm guide on *Eatonica* and *Pseudeatonica* eggs an incompletely developed groove exists in the ridges of the reticulation; the groove is connected to the elongate suprachorionic portion of the sperm guide by a narrow channel (Plate 15: fig. 174; Plate 17: fig. 192; Plate 22: fig. 230). In *Hexagenia* s.s. the chorionic groove is completely developed and the suprachorionic portion is broadly based on the chorion, thus lacking the narrow channel (Plate 16: fig. 182; Plate 22: fig. 230).

Polymitarcidae

The many striking differences between the eggs of each subfamily in the Polymitarcidae indicate that genetically the three subfamilies are not closely related. Each lineage has existed for a relatively long time or else the rate of evolution in the egg stage has been rapid in all three groups.

Plate 21: fig. 229 illustrates the hypothesized phylogenetic relationships of the subfamilies and genera of the Polymitarcidae. Campsurinae, with its funnellform micropyle, and *Tortopus*, with its dense fibrous adhesive layer appear to be the most primitive subfamily and genus, respectively. Some *Campsurus* eggs possess a fibrous adhesive layer similar to that on *Tortopus* eggs, but many *Campsurus* have evolved the more apomorphic condition of polar caps.

Povilla is probably an anciently derived form since the chorion is unsculptured and the attachment structures essentially consist of an enveloping mass of attachment threads. *Asthenopodes* and *Asthenopus* have concentrated attachment threads at both poles, and undoubtedly represent a lineage that evolved from a *Povilla*-like ancestor. The polar caps in the Asthenopodinae must have evolved independently of those in the Campsurinae. In the Campsurinae, the C-shaped egg common to both *Campsurus* and *Tortopus* undoubtedly evolved prior to the origin of polar caps which are common only to some *Campsurus*.

Ephoron has little in common with the other subfamilies. If the Asthenopodinae have a tageniform micropyle as is suspected, then *Ephoron* may have had common ancestry with that subfamily very early in its history. Certainly the C-shaped egg of Campsurinae precludes any relatively recent common ancestry between that subfamily and *Ephoron*.

Tricorythidae

Obviously, little can be said about generic phylogeny in the Tricorythidae since eggs of only three of the 11 genera were studied. Of the three genera, the eggs of *Leptohyphes* are probably the most plesiomorphic since their overlapping plates are not as well-developed as those on eggs of *Tricorythodes*

or *Leptohyphodes*. Eggs of *Leptohyphodes* then are probably the most apomorphic of the three genera since their overlapping plates are extremely well-developed and elongate. The anagenetic sequence that can be surmised from this data is probably phylogenetically real.

Neoephemeridae

The egg of *Potamanthellus* must be considered more apomorphic than that of *Neoephemera* since the method of attachment has apparently evolved from a simple fibrous adhesive layer covering the entire egg (as in *Neoephemera*) to a Type III polar cap at each pole (*Potamanthellus*). Since eggs of the other neoephemerid genera are unknown, the exact ancestral relationships of *Potamanthellus* and *Neoephemera* cannot be determined. However, it is probable that *Neoephemeropsis* has an egg type similar to that of *Potamanthellus*. If so, then *Potamanthellus* and *Neoephemeropsis* represent the derived lineage of the Neoephemeridae.

INTERFAMILIAL PHYLOGENETIC RELATIONSHIPS

In this study an attempt was made to reconstruct the phylogeny of the Ephemeroptera from hypothesized evolutionary changes in egg structures alone. Upon comparison with nymphal and adult characters, if the proposed phylogeny seemed improbable, the data were re-examined for alternate hypothesized evolutionary pathways of either egg, nymphal or adult evolution. Convergent evolution was used to explain similarities in eggs only when the data from other sources strongly implied such an explanation.

In those cases where egg data seem to be in striking disharmony with phylogenies derived from other data the evidence is discussed in detail. In some situations the egg data led to the same theorized relationships as other studies which have led to recent changes in Ephemeroptera classification. In other situations the egg data suggest quite different relationships than those which are now regarded as the most probable interpretation from all data. In such cases the relative merits of the competing hypotheses are discussed.

There is always more difficulty involved in attempting to reconstruct phylogeny from a relatively low number of characters such as found on the eggs alone, than from stages with more characters such as nymphs and adults. The egg stage is probably not as useful as nymphal and adult stages for phylogenetic studies because the egg is seldom so long lived as the nymph and never as active as the nymph and adult. Nevertheless, morphological features found on eggs are of definite phylogenetic importance because survival of the egg is as necessary to survival of the species as is survival of the nymphs and adults.

As pointed out in the previous section, the evidence suggests that within the Ephemeroptera, chorionic sculpturing evolved independently in nearly every family and subfamily; therefore, it has little use as a tool for reconstructing a phylogeny indicating familial relationships. The micropyles and attachment structures supply the bulk of the data useful for phylogenetic studies of the order.

Total egg data suggest a classification which is similar to that proposed by

Edmunds and Traver (1954), Edmunds (1962, 1972) and Edmunds *et al.* (1963). The classification proposed from egg data suggests two major changes over most of these earlier classifications: the grouping of Ephemerellidae and Tricorythidae into a superfamily distinct from the Leptophlebioidea; and the elevation of Metretopodinae of those earlier classifications to the family level. Several authors (see Edmunds, 1972) also suggest the latter change.

The phylogeny suggested by egg data is inconsistent with the classification proposed by Demoulin (1958, 1961, 1968, 1969a, b, c) in a number of significant ways. The eggs of Neoephemeridae suggest that there is no close relationship of that family to the Ephemeroidea as suggested by Demoulin, and in fact strongly suggests that the Caenidae arose from *Potamanthellus*-like Neoephemeridae. There is no basis from egg structure for placing the siphonurid subfamilies Coloburiscinae and Isonychiinae in a separate family distinct from the Siphonuridae, and the eggs show no close relationship between *Rallidens* and *Isonychia*, despite an apparently superficial *apomorphic* relationships of *Rallidens* eggs to those of Coloburiscinae. Eggs of Baetiscidae show no affinities of structure with eggs of any genera in the families which Demoulin places in his Siphonuroidea, and the Leptophlebiidae do not have egg structure suggestive of close relationship with the Heptageniidae. In fact, the eggs of Heptageniidae seem to clearly indicate the close relationship of that family to other Heptagenioidea. The eggs of Prosopistomatidae and Caenidae show no structural similarities to the families in the Ephemerelloidea.

Within the evolution of the Siphonuridae is found the derivation of six other families of the Ephemeroptera: Ametropodidae, Baetidae, Siphlaenigmatidae, Metretopodidae, Heptageniidae, and Oligoneuriidae. Together with the Siphonuridae, these families comprise the superfamily Heptagenioidea.

The presence of attachment threads is the only known feature that Ametropodidae eggs have in common with those of the remaining Heptagenioidea. Except for laterally distributed, knob-terminated coiled threads in one species, the threads on Ametropodidae eggs are arranged in a polar cap (Plate 11: fig. 116) probably of Type III and unlike any known structure on other Heptagenioidea eggs. Although a heptagenioid relationship is not clearly demonstrated by the egg stage of Ametropodidae, the presence of attachment threads and laterally distributed coiled ones suggests that the family can be included in the Heptagenioidea as suggested from nymphal and adult evidence (Edmunds, 1962). Within the Heptagenioidea, egg structure suggests that the ametropodid egg was derived from an egg that had evolved the loose fiber-coils typical of eggs in the *Siphonurus*-complex. However, the nymphs of *Ametropus* possess some characters seemingly even more plesiomorphic than those of siphonurines.

Baetidae eggs have a mixture of features that indicate a relatively ancient origin of the family from the Siphonurinae stock. This diversity of egg morphology except in the type of micropyle (tageniform) indicates that the baetids must have evolved before chorionic sculpturing and fiber-coils had evolved in the Siphonurinae. The data support Demoulin's (1969) contention that the Baetidae arose independently of the Siphlaenigmatidae rather than Edmunds' (1972) view that the Baetidae and Siphlaenigmatidae share a common ancestor. This certainly suggests a re-examination of evidence of the cladistic position of the Baetidae.

In the nature of their coiled fibers, Siphlaenigmatidae eggs display a perfect intermediate condition in the development of knob-terminated coiled threads. In the Siphlaenigmatidae, as in the Oligoneuriidae, *Siphonurus*-complex, and *Metamonius*-complex, fiber-coils occur in a uniform layer encompassing the entire egg. However, unlike the fiber-coils of Oligoneuriidae and *Siphonurus*-complex, eggs of Siphlaenigmatidae lack all indications of a terminal fiber cluster or other terminal knob development. It is apparent, then, that the siphlaenigmatid ancestor arose from a Siphonurinae ancestor subsequent to the development of loosely coiled fibers, but prior to the development of terminal fiber clusters.

The structure of the egg generally only places the Metretopodidae in the Heptagenioidea; no obvious affinities with other heptagenioid families is demonstrated in the egg stage, nor is a relationship to the Ametropodidae necessarily precluded. Nymphal features, however, show most convincingly that the Metretopodidae should not be considered as having had common ancestry with *Ametropus*. Studies of the nymphal stage by Edmunds (1972), Landa (pers. comm.), and Riek (pers. comm.) demonstrate that the Metretopodidae evolved from a proto-*Siphonurus*-complex ancestor. There are no data in the egg stage which opposes this suggestion.

As discussed in the section on attachment structures the eggs of the Siphonurinae, Isonychiinae, Oligoneuriidae, and Heptageniidae show a probable sequence of steps in the evolution of knob-terminated coiled threads. The evolution of oval chorionic sperm guides from oval suprachorionic ones is apparently correlated with the evolution of knob-terminated coiled threads. Such well documented sequences are strong evidence for a close relationship of these taxa (Plate 23: fig. 231). The plesiomorphic fiber-coils and suprachorionic sperm guide occur in the *Siphonurus*-complex and the Oligoneuriidae; the apomorphic knob-terminated coiled threads and chorionic sperm guide have developed independently in the Isonychiinae, Heptageniidae, *Ameletus*-complex (Siphonurinae), and several other siphonurid subfamilies. The Heptageniidae and Isonychiinae originated from the same ancestral stock as is evidenced by the fact that the eggs of many *Heptagenia* species resemble those of *Isonychia* in chorionic smoothness and KCT distribution (Plate 9: fig. 98; Plate 4: fig. 40).

Nymphal evidence definitely implies that the Oligoneuriidae ancestor was *Isonychia*-like. However, eggs of most oligoneuriid genera possess fiber-coils and a suprachorionic sperm guide that are as plesiomorphic as those of the *Siphonurus*-complex. This means that the *Isonychia* ancestor must have maintained a *Siphonurus*-like egg up through the time when the pre-Isonychiines gave rise to the Heptageniidae and proto-*Isonychia* gave rise to the Oligoneuriidae. The Heptageniidae and Isonychiinae must have independently developed apomorphic knob-terminated coiled threads from the fiber-coils, and a chorionic tageniform micropyle on their eggs; this is easily acceptable because the two characters are inter-dependent and KCTs have obvious selective advantages. The Oligoneuriidae and the *Siphonurus*-complex have retained the relatively ancestral condition in the egg stage.

The Leptophlebiidae must have evolved very early from the ancestral Ephemeroptera because the leptophlebiids have retained a funnellform micropyle with the micropylar canal perpendicular to the chorion. The Lepto-

phlebiidae have evolved some of the most diverse chorionic sculpturings and attachment structures. However, this evolution must have taken place subsequent to the origin of the lineage since adhesive layers and smooth chorions are also found on eggs in extant leptophlebiid genera.

The phylogenetic origin of the Ephemerelloidea as suggested by the eggs, is entirely unlike that proposed by Edmunds (1962). The eggs do indicate, however, that the Ephemerellidae gave rise to the Tricorythidae. Although Edmunds (1962) suggested that the Ephemerelloidea may have evolved from a pre-Leptophlebiidae ancestor, the eggs of Ephemerelloidea are similar only to those of the Potamanthidae. The polar caps, lateral KCTs, and tageniform micropyles are too similar in the Potamanthidae and Ephemerellidae to allow easy acceptance of the hypothesis of independent origin of this combination of characters and thus independent origin of the two lineages. Furthermore, the eggs of the Potamanthidae are unlike those of any Ephemeroidea and differ from the Ephemerellidae (except subgenus *Eurylophella*) only by the possession of two Type I polar caps rather than one. This would tend to suggest that the Ephemerellidae arose either from pre- or proto-Potamanthidae. Evidences from other life stages do not preclude this possibility, but additional evidence for support for such a conclusion is not yet obvious either. Clearly, further studies of the eggs of the Potamanthidae and Ephemerellidae, and of the origin of the Ephemerellidae, are necessary.

Utilizing the egg stage alone, it is difficult to estimate the familial relationships of the Ephemeroidea except for the Behningiidae. On Behningiidae eggs chorionic sculpturing is virtually absent, the only attachment structure is a copious adhesive layer, and the micropyle is a funnellform type with a suprachorionic sperm guide. These data strongly suggest that the Behningiidae evolved very early from the Ephemeroidea ancestor, but do not preclude the hypothesis that it evolved from the ancestor common to the Ephemeroidea and the Leptophlebiidae. The latter suggestion tends to be negated by studies of nymphal structures which suggests that the Ephemeroidea arose from proto-Leptophlebiidae (Edmunds & Traver, 1959; Landa, pers. comm.).

Although several workable hypotheses can be proposed for the phylogeny of the remaining Ephemeroidea, they become unlikely when adult and nymphal structures are considered. One of the major obstacles to understanding the phylogeny of this group is the highly apomorphic eggs of the Potamanthidae (see above). Only nymphal and adult evidence (Edmunds, 1962; Edmunds *et al.*, 1963) suggests that the Potamanthidae is of relatively ancient ephemeroid lineage. Potamanthidae eggs are definitely derived and certainly not of an ancestral type to any known existing types in the Ephemeroidea. *Euthyplocia* (Euthyplociidae) eggs possess two small Type I polar caps much like the two found in the Potamanthidae. This is the only feature that associates Potamanthidae eggs with those of other Ephemeroidea, and if accepted it would suggest a common ancestor for Euthyplociidae and Potamanthidae that had eggs with polar caps. This would further suggest that all other Ephemeroidea lost the polar caps.

The most likely explanation is that the potamanthid-euthyplociid lineage must have evolved from the ancestral ephemeroid stock when eggs were still in the plesiomorphic "adhesive layer and funnellform micropyle" condition.

Evidence from other stages suggests that the ancestor to the Ephemeridae was a pre-potamanthid. If so, then the eggs maintained the adhesive layer as an attachment structure and evolved the linear micropyle in the Ephemeridae, but developed a tageniform micropyle and Type I polar cap in the Potamanthidae after the split of those two lineages. Prior to that split ancestral Euthyplociidae became isolated and subsequently gave rise to the Polymitarciidae. Evidence from other stages suggests that the ancestors of the Polymitarciidae were proto-euthyplociids, and some genera in both Euthyplociidae and Polymitarciidae still retain the plesiomorphic adhesive layer and a funnelliform micropyle on their eggs.

McCafferty (1972) established the family Pentageniidae, considering it to have evolved from the Ephemeridae and to have given rise to the Palingeniidae. That hypothesis is not precluded by egg data since the chorion was probably smooth at the time of origin of the Pentageniidae. The phylogenetic history of the Pentageniidae cannot be ascertained by a study of the egg data alone. The obvious adhesive layer and the suprachorionic, perhaps modified elongate sperm guide do indicate, however, that the Pentageniidae are more closely related to the Ephemeridae (esp. *Ephemer*) than to any other family of the Ephemeroidea (Palingeniidae not studied).

Undoubtedly the neophemerid lineage evolved very early from the ancestral stock, and later gave rise to the Caenidae. This is suggested by the fact that eggs of *Neoephemer* *purpurea* are covered by a dense fibrous adhesive layer, and the more apomorphic egg of *Potamanthellus* (Neoephemeridae) bears two Type III polar caps (Plate 19: fig. 216) which are nearly identical to those of the Caenidae. Although the caps on *Potamanthellus* eggs are highly apomorphic features, they seem plesiomorphic to the caenid type since they are not as tightly coiled about the poles as those on Caenidae eggs (Plate 20: fig. 220). Other evidence from nymphal and adult Caenoidea has led to the hypothesis that primitive Caenoidea were in most features similar to *Neoephemer*, and that the proto-*Potamanthellus-Neoephemeropsis* group was derived from this and gave rise to the Caenidae. The independent evidence from eggs supports this hypothesis and clearly shows that the Type III polar caps of the Caenidae originated earlier in the Neoephemeridae. The evidence from the eggs is the most convincing evidence obtained to date showing the relationship of the Caenidae to the Neoephemeridae.

Little satisfactory Prosopistomatoidea material was available, and it provided no data useful for our phylogenetic studies.

SYSTEMATICS

List of species studied

HEPTAGENIOIDEA

SIPHONURIDAE

Ameletopsinae

Ameletopsis perscitus (Eaton)*Chaquihua penai* Demoulin*C.* sp.*Chiloporter penai* Demoulin*Mirawara megaloprepria* Riek

Oniscigastrinae

Oniscigaster distans Eaton*Tasmanophlebia* spp.

Siphonurinae

Ameletoides lacus-albinae Tillyard*Ameletus montanus* Imanishi*A. sparsatus* McDunnough*A.* sp.

HEPTAGENIOIDEA—Cont.

SIPHONURIDAE—Cont.

Siphonurinae—Cont.

- Metamonius* sp.
Metreletus goetghebueri (Lestage)
Nesameletus sp.
Parameletus columbiae McDunnough
P. sp.
Siphlonisca aerodromia Needham
Siphlonurus alternatus (Say)
S. mirus Eaton
S. quebecensis (Provancher)
S. rapidus McDunnough

Acanthametropodinae

- Analetris eximia* Edmunds

Rallidentinae

- Rallidens macfarlanei* Penniket

Isonychiinae

- Isonychia bicolor* (Walker)
I. harperi Traver
I. intermedia Eaton
I. japonica (Ulmer)
I. sadleri Traver
I. sicca manca Eaton ?
I. velma Needham
I. sp.

Coloburiscinae

- Coloburiscoides* sp.
Coloburiscus humeralis (Walker)
Murphyella needhami Lestage

SIPHLAENIGMATIDAE

- Siphlaenigma janae* Penniket

BAETIDAE

- Baetis bicaudatus* Dodds ?
Baetis sp.
Baetodes sp.
Centroptilum bifurcatum
 McDunnough ?
C. selanderorum Edmunds
Cloeon sp.
Pseudocloeon sp.

METRETOPODIDAE

- Metretopus borealis* Eaton
Siphloplecton basale (Walker)

OLIGONEURIIDAE

Chromarcyinae

- Chromarcys* sp.

Oligoneuriinae

- Elassoneuria insulicola* Demoulin

- E. trimeniiana* (McLachlan)
Homoeoneuria dolani Edmunds,
 Berner & Traver

H. sp.

- Lachlania dencyanna* Koss

- L. powelli* Edmunds

L. spp.

- Oligoneuria anomala* Pictet

- Oligoneuriella rhenana* (Imhoff)

HEPTAGENIIDAE

Heptageniinae

- Afronurus peringueyi* (Esben-
 Petersen)

- Cinygma integrum* Eaton

- Cinygmina* ? sp.

- Cinygmula mimus* (Eaton)

- C. par* (Eaton)

- C. ramaleyi* (Dodds)

- C. reticulata* McDunnough

- C. subaequalis* (Banks)

- C. tarda* (McDunnough)

- C. uniformis* McDunnough

- Ecdyonurus insignis* (Eaton)

- E. yoshidae* Takahashi

E. ally

- Epeorus (Epeorus) aesculus* (Imanishi)

- E. (Iron) dulciana* (McDunnough)

- E. (Iron)* spp.

- E. (Ironopsis) grandis* (McDunnough)

- E. (I.) permagnus* (Traver)

- Heptagenia aphrodite* McDunnough

- H. criddlei* McDunnough

- H. elegantula* (Eaton)

- H. kihada* Matsumura

- H. petersi* Allen

- H. rosea* Traver

- H. solitaria* McDunnough

H. spp.

- Ororotsia* sp.

- Rhithrogena hageni* Eaton

- R. impersonata* (McDunnough)

- R. japonica* Ueno

- R. morrisoni* (Banks)

- R. robusta* Dodds

- R. sanguinea* Ide

R. sp.

- Stenonema* spp.

- Thalerosphyrus* sp., nr. *sumatranus*

Ulmer

- Arthropleinae
Arthroplea bipunctata (McDunnough)
A. congener Bengtsson
- Pseudironinae
Pseudiron meridionalis Traver
P. spp.
- AMETROPODIDAE
Ametropus albrighti Traver
A. neavei McDunnough
- LEPTOPHLEBIOIDEA
- LEPTOPHLEBIIDAE
Atalomicria sp.
Atalophlebia spp.
Choroterpes sp.
Habrophlebia (Habrophlebia) fusca
 (Curtis)
H. (H.) vibrans Needham ?
H. (Habroleptoides) modesta
 (Hagen)
Habrophlebiodes americana (Banks)
H. annulata Traver
H. brunneipennis (Berner)
Jappa kutera Harker
Miroculus sp.
Paraleptophlebia adoptiva
 McDunnough
P. debilis (Walker)
P. mollis (Eaton)
Thraulodes brunneus Koss
T. speciosus Traver
T. sp.
 "Thraulus" sp. (caribbeanus-type)
Traverella albertana (McDunnough)
T. sp.
Ulmeritus s.l. ? sp.
Zephlebia sp.
- EPHEMERELLOIDEA
- EPHEMERELLIDAE
Ephemerella spp.
- TRICORYTHIDAE
- Leptohiphinae
Leptohiphes apache Allen
L. setosus Allen
Leptohiphodes sp.
Tricorythodes atratus (McDunnough)
T. explicatus (Eaton)
T. fallax Traver
T. stygiatus McDunnough
- EPHEMEROIDEA
- BEHNINGIIDAE
Behningia lestagei Motas &
 Bogoescu
Dolania americana Edmunds and
 Traver
- POTAMANTHIDAE
Potamanthodes formosus (Eaton)
Potamanthus myops (Walsh)
P. neglectus Traver
Rhoenanthopsis sp.
Rhoenanthus spp.
- EUTHYPLOCIIDAE
Campylocia sp.
Euthyplocia hecuba (Hagen)
- EPHEMERIDAE
- Ephemerinae
Ephemera (Ephemera) danica
 Muller
E. (E.) guttulata Pictet
E. (E.) japonica McLachlan
E. (E.) simulans Walker
E. (E.) supposita Eaton
E. (E.) vulgata Linnaeus
E. (E.) sp. near wuchowensis Hsu
E. (E.) spp.
- Hexagenia*-complex
Eatonica crassi McCafferty
E. schoutedeni (Navas)
Eatonigenia chaperi (Navas)
Hexagenia bilineata (Say)
H. limbata venusta Eaton
H. munda elegans Traver
H. m. munda Eaton
H. rigida McDunnough
Litobrantha recurvata (Morgan)
Pseudeatonica albivitta (Walker)
- Ichthybotinae
Ichthybotus bicolor Tillyard ?
- Pentageniidae
Pentagenia vittigera (Walsh)
P. sp.
- POLYMITARCIDAE
- Polymitarcinae
Ephoron album (Say)
E. leukon Williamson
- Campsurinae
Campsurus decoloratus (Hagen)
C. evanidus Needham & Murphy

EPHEMEROIDEA— <i>Cont.</i>	<i>B. sp.</i>
POLYMITARCIDAE— <i>Cont.</i>	<i>Caenis anceps</i> Traver
Campsurinae	<i>C. diminuta</i> Walker ?
<i>C. major</i> Needham & Murphy ?	<i>C. forcipata</i> McDunnough
<i>C. spp.</i>	<i>C. jocosa</i> McDunnough
<i>Tortopus spp.</i>	<i>C. simulans</i> McDunnough
Asthenopodinae	<i>C. tardata</i> McDunnough
<i>Asthenopodes sp.</i>	<i>Tasmanocoenis sp.</i>
<i>Asthenopus sp.</i>	
<i>Povilla adusta</i> Navas	
CAENOIDEA	PROSOPISTOMATOIDEA
NEOEPHEMERIDAE	BAETISCIDAE
<i>Neophemera (Oreianthus) purpurea</i>	<i>Baetisca bajkovi</i> Neave
(Traver)	<i>B. escambiensis</i> Berner
<i>Potamanthellus sp.</i>	<i>B. laurentina</i> McDunnough
CAENIDAE	<i>B. rogersi</i> Berner
<i>Brachycercus lacustris</i> (Needham)	PROSOPISTOMATIDAE
	<i>Prosopistoma africanum</i> Gillies

SUPERFAMILY HEPTAGENIOIDEA

FAMILY SIPHLONURIDAE

Siphonurid eggs cannot be characterized at the family level. This is to be expected since the family is characterized primarily by the retainment in the adult stage of a cluster of plesiomorphic characters that conveniently distinguish the group, although most of the extant genera may contain representative survivors from near the base of all of the more recent familial lineages.

Type V polar caps and a large-mesh reticulation occur in some genera, and coiled attachment structures are present on all eggs studied except those of the Oniscigastrinae and three of the four genera of the Ameletopsinae (*Ameletopsis*, *Chaquihua* and *Chiloporter*). The micropyle is funnellform or partly so in the Ameletopsinae and Oniscigastrinae, highly modified and perhaps a funnellform type in Rallidentinae and Acanthametropodinae, and tageniform in the remaining subfamilies.

Previous descriptions. *Ameletopsis*: Phillips (1930). *Ameletus*: Bengtsson (1913), Morgan (1913), Brodsky (1930), Smith (1935), Demoulin (1952). *Coloburiscus*: Phillips (1930), Wisely (1961). *Isonychia*: Morgan (1913), Clemens (1917), Smith (1935). *Metreletus*: Demoulin (1952). *Nesameletus*: Phillips (1930). *Oniscigaster*: Phillips (1930). *Parameletus*: Bengtsson (1913). *Siphlonisca*: Smith (1935). *Siphlonurus*: Bengtsson (1913), Morgan (1913), Percival & Whitehead (1928), Smith (1935), Degrange (1956, 1960), Koss (1968).

Key to subfamilies and genera

1. Fiber-coils or knob-terminated coiled threads present either laterally (Plate 2: fig. 21; Plate 3: fig. 28), at poles (Plate 3: fig. 34; Plate 4: figs 41, 48), or both 6
- Coiled attachment structures absent 2

2. Large-mesh reticulation present (Plate 1: figs 1-3, 7)
 - Ameletopsinae, in part, 3
 - Large-mesh reticulation absent (Plate 2: figs 18, 20)
 - *Oniscigastrinae*
3. Strands of reticulation formed by single rows of closely spaced cylindrical formations (Plate 1: figs 1, 3) 4
 - Strands of reticulation solid, not subdivided as above (Plate 1: figs 7, 9) 5
4. Margins of mesh sinuous (Plate 1: fig. 1) . . . *Ameletopsis perscitus*
 - Margins of mesh straight or nearly so (Plate 1: fig. 3)
 - *Chaquihua penai*
5. Strands of reticulation are furrows (Plate 1: fig. 9)
 - *Chiloporter penai*
 - Strands of reticulation are ridges (Plate 1: fig. 7) . . *Chaquihua* sp.
6. Large-mesh reticulation of ridges present on entire egg (Plate 2: figs 22-24; Plate 3: figs 28, 29), or if absent, coiled attachment structures are fiber-coils (Plate 2: fig. 21 and as in Plate 6: figs 72, 73) 7
 - Large-mesh reticulation of ridges absent or at least not covering the entire egg (Plate 3: fig. 36; Plate 4: fig. 44); coiled attachment structures are knob-terminated coiled threads (Plate 3: figs 35, 37; Plate 4: figs 45, 46; Plate 5: figs 50, 51) 10
7. Micropyle funnellform (Plate 1: figs 14, 16), micropylar canal perpendicular to the chorion; adhesive layer distributed as longitudinal rugula (Plate 1: fig. 14) Ameletopsinae, *Mirawara*
 - Micropyle tagenoform (Plate 2: fig. 23; Plate 3: fig. 32), micropylar canal acutely angled to chorion (Plate 3: fig. 32 and as in Plate 7: fig. 88); adhesive layer absent or at least never distributed as in Plate 1: fig. 14 Siphonurinae, 8
8. Large-mesh reticulation present (Plate 2: figs 22-24; Plate 3: figs 28, 29, 32), or if absent, coiled attachment structures not covering entire egg as in Plate 2: fig. 21 9
 - Large-mesh reticulation absent; coiled attachment structures covering entire egg (Plate 2: fig. 21) *Siphonurus*-complex
9. Each mesh of reticulation with a fiber-coil (Plate 2: figs 22, 25)
 - *Metamoni*us-complex
 - Fiber-coils absent; some mesh of reticulation contain a knob-terminated coiled thread, but threads do not occur in each mesh of the reticulation (Plate 3: figs 28-33) *Ameletus*-complex
10. Knob-terminated coiled threads covering nearly the entire egg (Plate 4: fig. 40), or densely concentrated at 1 or both poles (at 1 or 2 "areas" on spherical eggs) and scattered laterally (Plate 3: figs 34, 35; Plate 4: fig. 41); chorion smooth or with a reticulation formed by grooves (Plate 4: fig. 42) 11
 - Knob-terminated coiled threads not covering entire egg, but either randomly scattered on chorion, scattered laterally and densely concentrated at 1 or both poles in a polar reticulation of ridges (Plate 4: fig. 44), or lightly concentrated (3 or 4 threads) at both poles (Plate 4: fig. 48); chorion usually sculptured (Plate 4: figs 43, 44), but not with a reticulation formed by grooves 12

11. Knob-terminated coiled threads densely concentrated at one pole as a Type V polar cap (Plate 3: figs 34, 35); micropyle funnel-like projecting above the surface of the chorion and located in the midst of the polar coils (Plate 3: fig. 35); eggs ovoid
 Acanthametropodinae, *Analetris*
 Knob-terminated coiled threads nearly covering entire egg (Plate 4: fig. 40) or concentrated in 1 or 2 areas and scattered elsewhere; if polar concentrations of coiled threads occur, micropyle tageniform and not located in the midst of the "polar" coils (Plate 4: fig. 41); eggs usually spherical Isonychiinae, *Isonychia*
12. Micropyles located on surface of chorion, not in tubular chorionic projections; micropylar canals acutely angled to the chorion (Plate 4: figs 47, 49) Coloburiscinae, 13
 Micropyles located in walls of tubular chorionic projections; micropylar canals nearly perpendicular to chorion (Plate 4: figs 38, 39) Rallidentinae, *Rallidens*
13. Coiled threads at poles only (Plate 4: fig. 48; Plate 5: figs 50, 51); chorion granulate, granules with no obvious pattern of arrangement (Plate 4: fig. 49) *Coloburiscus*
 Coiled threads scattered laterally, but also may be concentrated at the poles (Plate 4: figs 43-45; Plate 5: fig. 52); chorion tuberculate, tubercles in circular or discal patterns of arrangement (Plate 4: fig. 43; Plate 5: fig. 52) 14
14. Large-mesh reticulation present at 1 pole; coiled threads scattered laterally and present in each mesh of polar reticulation (Plate 4: figs 43-47) *Coloburiscoides*
 Large-mesh reticulation absent; coiled threads evenly distributed about the eggs, with no polar concentrations (Plate 5: figs 52, 53)
 *Murphyella*

Subfamily Ameletopsinae

Ameletopsinae eggs are characterized by a complicated large-mesh reticulation (Plate 1: fig. 2) and a funnelform micropyle; coiled attachment structures are absent except in *Mirawara*. In all but *Mirawara* the mesh is either broadly convex with margins only slightly upturned (Plate 1: fig. 10) or else centrally convex with margins distinctly upturned (Plate 1: fig. 5); in *Mirawara* the strands of the reticulation are divided ridges, but the mesh is concave (Plate 1: fig. 13). The strands of the reticulation are formed in two ways. In *Chiloporter* they are the spaces or flat chorion between the raised mesh; in the other ameletopsine genera the strands are solid or divided ridges. In *Ameletopsis* and *Chaquihua* the ridges are separated from the upturned mesh margins by narrow grooves (Plate 1: figs 1, 7).

Adhesive material is distributed only over the strands of the reticulation as in Plate 1: figs 4-5, 8, 10. The micropyle is funnelform, and the funnel-shaped sperm guide is situated in the adhesive material (Plate 1: figs 4, 8, 11, 14, 16); the micropylar canal is usually acutely angled with the chorion.

Ameletopsis perscitus (Eaton)
(Plate 1: fig. 1)

Chorion. With a large-mesh (7-10 μm long) reticulation, the strands being formed by single rows of short, closely-spaced cylindrical formations which are separated by grooves from the sinuous upturned margins of the mesh (Plate 1: fig. 1). The mesh is weakly rugulose and centrally convex (as in Plate 1: fig. 5).

Attachment structures. An adhesive layer distributed only on the strands of the reticulation (as in Plate 1: figs 4, 5).

Micropyle. (Plate 1: fig. 1.) Micropylar canal indistinct, 3-5 μm long.

Chaquihua penai Demoulin
(Plate 1: figs 2-6)

Like *Ameletopsis perscitus* except margins of mesh less sinuous (Plate 1: fig. 3); mesh (9-13 μm long) more definitely rugulose, but centrally only slightly convex (Plate 1: fig. 5); and micropylar canal (Plate 1: fig. 6) 10-15 μm long.

Chaquihua sp.
(Plate 1: figs 7, 8)

Like *Ameletopsis perscitus* except strands of reticulation are solid ridges (Plate 1: fig. 7); margins of mesh nearly straight, mesh (9-13 μm long) broadly but weakly convex, and micropylar canal (8-15 μm long) is distinct.

Chiloporter penai Demoulin
(Plate 1: figs 9-11)

Like *Ameletopsis perscitus* except margins of mesh almost straight and only slightly upturned, mesh (8-13 μm long) broadly convex, strands of reticulation are spaces or flat chorion between raised mesh and thus appear as furrows rather than ridges (Plate 1: fig. 9), and micropylar canal 10-11 μm long.

Mirawara megaloprepria Riek
(Plate 1: figs 12-16)

Chorion. With a large-mesh reticulation (6-10 μm long), the strands being formed by double rows of short, closely spaced cylindrical formations which are much more weakly developed than in the other genera of Ameletopsinae (Plate 1: fig. 13); the mesh is concave.

Attachment structures. The adhesive layer almost completely covers the entire egg—it is not narrowly restricted to the chorionic ridges as in other genera of Ameletopsinae. In surface view (Plate 1: fig. 14), the adhesive layer is distributed as longitudinal rugae; midway in depth (Plate 1: fig. 15) the adjacent bends are inseparable, thus more closely resembling the chorionic reticulation below. A tubercle occurs in the mesh thus formed. Knob-terminated coiled threads are concentrated at both poles and very sparsely scattered laterally.

Micropyle. Micropylar canal nearly perpendicular to the chorion, difficult to measure, and at least 7 μm long; 12 micropyles on one egg is not uncommon.

Subfamily Oniscigastrinae

Oniscigastrinae eggs are distinguished by their micropyle and lack of coiled threads and large-mesh reticulation. The only apparent method of attachment is an adhesive layer (in *Tasmanophlebia* only). The micropyle may represent a transitional stage between funnellform and tagenoform types (Plate 2: figs 17-20). In *Tasmanophlebia* the micropylar canal is located to one side of a funnel-shaped chorionic sperm guide, and the micropylar canal is acutely angled to the chorion (Plate 21: fig. 228). The micropyle somewhat resembles a funnel lying on its side. In *Oniscigaster* the micropyle also bears the same "elbowed" shape in cross-section (Plate 21: fig. 227) but a sperm guide is not clearly distinguishable from the micropylar canal.

Oniscigaster distans Eaton (Plate 2: fig. 17; Plate 21: fig. 227)

Chorion. Divided into an outer smooth layer and an inner granular layer, each 2-3 μm thick.

Attachment structures. None.

Micropyle. Funnelform; micropylar opening 3-4 μm diam, micropylar canal 8-15 μm long; sperm guide absent.

Tasmanophlebia sp. no. 1 (Plate 2: fig. 18; Plate 21: fig. 228)

Chorion. Outer layer sparsely and randomly sulcate (Plate 2: fig. 18); inner layer finely granulate; total chorion 4-5 μm thick.

Attachment structures. A very transparent adhesive layer 1-1.5 μm thick.

Micropyle. (Plate 2: fig. 18; Plate 21: fig. 228). Sperm guide 8-11 μm long, 5-9 μm wide, indistinct distally, and with an inner flange formed by the adhesive layer; micropylar canal 8-10 μm long.

Tasmanophlebia sp. no. 2 (Plate 2: figs 19, 20)

Chorion. Outer layer with many irregularly shaped depressions (pale areas on Plate 2: fig. 20); inner layer finely reticulated with a small-mesh reticulation, the strands being formed by grooves.

Attachment structures. Adhesive layer ≤ 1 μm in thickness.

Micropyle. (Plate 2: fig. 19.) Borders of sperm guide quite indistinct; micropylar canal 12-13 μm long.

Subfamily Siphonurinae

A tagenoform micropyle and the presence of coiled attachment structures are the only features common to the eggs of all members of this subfamily.

Since three distinct groups of nearly indistinguishable eggs occur in this subfamily, it is most convenient to discuss the eggs for generic complexes rather than for individual genera. Eggs of *Dipteromimus* and *Edmundsius* were not studied.

Siphonurus-complex: *Parameletus*, *Siphonisca*, *Siphonurus*

Chorion. Maculate.

Attachment structures. Fiber-coils in a uniform layer covering the entire egg (Plate 2: fig. 21, and similar to Plate 6: figs 72, 73); some coils with terminal fiber-clusters (as in Plate 6: fig. 74). Degrange (1960) described the influence of water on these structures.

Micropyle. A weakly developed tageniform type. Sperm guide supra-chorionic, being an ovoid break in the layer of fiber-coils; micropylar canal acutely angled with the chorion.

Remarks. Characters could not be found to distinguish the genera.

Metamonius-complex: *Ameletoides*, *Metamonius*, *Nesameletus*

Chorion. (Plate 2: figs 22-24, 26, 27.) With a small-mesh ($\leq 2 \mu\text{m}$ long) reticulation, the strands being formed by grooves; and a large-mesh (9-19 μm long) reticulation, the strands being formed by ridges. The small-mesh reticulation is present throughout the height of the ridges (Plate 2: fig. 22).

Attachment structures. Each mesh of the large-mesh reticulation contains a fiber-coil which apparently lacks a terminal knob-like arrangement.

Micropyle. Typical tageniform type (Plate 2: figs 23, 24).

Remarks. Eggs of *Metamonius* and *Ameletoides* are similar, but perhaps recognizable from those of *Nesameletus* by the formers' possession of a central tubercle in each mesh of the large-mesh reticulation and by the height of the fiber-coils in relation to the height of the chorionic ridges (Plate 2: figs 25-27). However, these may well be specific rather than generic differences.

Ameletus-complex: *Ameletus*, *Metreletus*

Chorion. With a large-mesh (10-15 μm long) reticulation of nearly circular to irregular-polygonal mesh (Plate 3: figs 28, 29, 32), the strands being formed by ridges which are usually tallest at the junctions. Some junctions are open-ended cones (Plate 3: figs 28, 31, 33) and in at least one species these junctions (cones) are isolated from the ridges (Plate 3: fig. 28). At one pole (Plate 3: figs 30, 31) or both poles (Bengtsson, 1913) the open-ended cones are larger and more concentrated than elsewhere on the egg. The mesh may be either punctate (Plate 3: fig. 29) or smooth.

Attachment structures. A knob-terminated coiled thread occurs within each of the open-ended cones described above (Plate 3: figs 28, 31, 33); larger coils occur within the larger cones. Demoulin (1952) did not indicate any coils on his drawings of the egg of *Metreletus hessei* (Fizaine), but quite likely they are present on eggs of that species.

Micropyle. Typical tageniform type (Plate 3: fig. 32), located near one pole. When only one pole has a concentration of larger cones and coiled threads, the micropyle is located at that pole. Sperm guide usually shallower than the mesh, but otherwise indistinguishable from it.

Remarks. Bengtsson's (1913) interpretation of *Ameletus alpinus* Bengtsson

eggs agrees with the above description. The smaller mesh indicated in his description correspond to the open-ended cones; he noticed the attachment thread contained within the cones, and he found a concentration of larger cones at both poles. Brodsky (1930) illustrated the egg of *A. alexandrae* Brodsky as being somewhat *Metamonius*-like. There are two features which may possibly serve to distinguish eggs of *Ameletus* from *Metreletus*, but a variety of species needs to be studied before these points of distinction are definite. The cones on *Metreletus* eggs are 5-9 μm high as opposed to 1.5-5.5 μm high on *Ameletus* eggs; the long axis of the micropyle is at a 45°-90° angle to the long axis of the egg in *Metreletus* (as in Plate 8: fig. 94); but at a 0°-45° angle to the long axis on *Ameletus* eggs (i.e. micropylar canal parallel or nearly so to the long axis of the egg). Nevertheless, eggs of the *Ameletus*-complex are relatively inseparable, those of *Metreletus* being on the plesiomorphic end of the morphological gradient and those of various *Ameletus* species being progressively more apomorphic.

Subfamily Acanthametropodinae

Only the eggs of the monotypic *Analetris* are known. The polar cap and the unusual micropyle located in its midst may serve, however, as subfamilial characteristics.

Analetris eximia Edmunds

(Plate 3: figs 34, 35)

Chorion. With a faint, small-mesh (3-8 μm long) reticulation, the strands being formed by grooves.

Attachment structures. Knob-terminated coiled threads scattered laterally and densely concentrated at one pole forming a Type V polar cap (Plate 3: figs 34, 35). The polar coils are larger than the laterals.

Micropyle. (Plate 3: fig. 35.) Unique in position and form; one per egg, located amidst the polar coils. The structure could definitely be called a "micropylar process" (as used by Southwood, 1956), since the micropylar canal extends well above the surface level of the chorion via a chorionic projection. The polar coils surround but do not cover the process; a sperm guide is essentially absent. Micropylar process approximately 15 μm high, 13-15 μm outside diam at mid-point.

Subfamily Rallidentinae

This subfamily contains a single known species, *Rallidens macfarlanei*, and the species description therefore applies also to the subfamily and the genus.

Rallidens macfarlanei Penniket

(Plate 3: figs 36-37; Plate 4: figs 38, 39)

Chorion. (Plate 3: figs 36, 37; Plate 4: figs 38, 39.) With a sparse scattering of large, apically expanded and dissected, tubular structures. A sinuous ridge surrounds the base of every one or two tubular structures, and a large-mesh reticulation occurs at each pole.

Attachment structures. A knob-terminated coiled thread occurs within each tubular structure and within some mesh of the polar reticulation (Plate 3: fig. 37; Plate 4: fig. 38).

Micropyle. (Plate 4: figs 38, 39.) Unusual in number and position, since one is located just below the apical expansion on nearly all of the tubular structures. The sperm guide is lacking; the micropylar canal extends from inside the egg upward through the tube wall, and projects out slightly from below the apical expansion.

Subfamily Isonychiinae

The features of the single genus *Isonychia* apply also to the subfamily.

Genus *Isonychia* Eaton (Plate 4: figs 40-42)

Isonychia eggs are either biconvex (according to Smith, 1935) or spherical, and thus no obvious poles exist. Knob-terminated coiled threads are either closely spaced in a uniform layer covering the entire egg (Plate 4: fig. 40), or else they are localized in one area and randomly scattered on the remaining surface (Plate 4: fig. 41). Smith (1935) found eggs of two species with KCTs localized in two areas, or "poles".

When the KCTs cover the entire egg, the chorion is smooth. When the KCTs are localized in one area and scattered elsewhere, the chorion is usually tuberculate; *I. japonica*, however, has a rugose chorion and a large-mesh reticulation formed by grooves.

The micropyle is a typical tageniform type (Plate 4: figs 40-42), and the sperm guide is always chorionic. On eggs with a uniform layer of KCTs, the sperm guide also consists of an ovoid break in the coil layer (Plate 4: fig. 40). However, on these eggs having coiled threads localized in one area and randomly scattered on the rest of the chorion, the micropyle is located among the scattered threads and the sperm guide is entirely chorionic (Plate 4: fig. 41). The micropylar canal is always distinctly angled with the sperm guide, usually at a 135° angle or less.

Subfamily Coloburiscinae

Coloburiscinae eggs characteristically possess knob-terminated coiled threads and poorly-developed tageniform micropyles; they lack a large-mesh reticulation (except at one pole in *Coloburiscoides*). The micropylar canal is acutely angled to the chorion, but the sperm guide is either lacking or is a very shallow, poorly-defined, oval chorionic depression.

Coloburiscoides sp. (Plate 4: figs 43-47)

Chorion. Rugulose and with many circular arrangements of tubercles (Plate 4: fig. 43). One pole possesses a large-mesh reticulation, the strands being formed by ridges (Plate 4: fig. 44).

Attachment structures. A knob-terminated coiled thread occurs within each circular arrangement of tubercles and within each mesh of the polar reticulation. The polar coils are much larger than the lateral ones, and their multifilamented structure is more obvious (Plate 4: figs 43-46).

Micropyle. Located near the polar reticulation (Plate 4: fig. 47); sperm guide lacking, or a shallow, poorly-defined, oval chorionic depression (20-24 μm long, 16-17 μm wide); micropylar canal 8-16 μm long.

Coloburiscus humeralis (Walker)
(Plate 4: figs 48, 49; Plate 5: 50, 51)

Chorion. Granulated.

Attachment structures. Three or four (usually three) long, loosely coiled, knob-terminated threads at each pole (Plate 4: fig. 48; Plate 5: figs 50, 51).

Micropyle. (Plate 4: fig. 49.) Located in mid-region of egg; sperm guide lacking; micropylar canal 15-20 μm long.

Murphyella needhami Lestage
(Plate 5: figs 52, 53)

Chorion. With many discal aggregations of tubercles (Plate 5: fig. 52); the central tubercles in each accumulation larger than the outer ones and subdivided apically. Chorion finely punctate in areas between tubercle aggregations.

Attachment structures. A knob-terminated coiled thread occurs in the midst of each tubercle aggregation (Plate 5: figs 52, 53); there are no polar concentrations of attachment structures.

Micropyle. Sperm guide oval to circular (10-20 μm long and wide), very shallow, and poorly-defined; micropylar canal 8-15 μm long.

FAMILY SIPHLAENIGMATIDAE

This family contains a single known species, *Siphlaenigma janae*, and the species description, therefore, applies also to the family and genus.

Siphlaenigma janae Penniket
(Plate 5: figs 54-58)

Chorion. Tuberculate (Plate 5: figs 56, 57), tubercles 1-1.5 μm in height and diameter.

Attachment structures. Fiber-coils in a uniform layer covering the entire egg (Plate 5: figs 56-58); the coils lack terminal knobs or terminal fiber-clusters. The chorionic tubercles occur under the coils as well as between adjacent ones.

Micropyle. (Plate 5: figs 54, 55). Tageniform, located within half the distance from one pole to the equator. Sperm guide suprachorionic, being an oval break in the coil layer. It was not possible to determine if there is also a slight chorionic counterpart to the sperm guide; tubercles, however, occur within it. Sperm guide 16-20 μm long, 12-14 μm wide; micropylar canal 23-35 μm long.

Remarks. The fiber-coil layer is almost identical to those of the *Siphonurus*-

complex and the Oligoneuriidae, the only difference being the lack of terminal fiber clusters in *Siphlaenigma*.

FAMILY BAETIDAE

The only feature possibly common to all known Baetidae eggs is the tageniform micropyle and its location approximately midway between the equator and one pole. Degrange (1960) described and illustrated eggs of some species (e.g. *Baetis niger* (L.), *B. pumilus* (Burmeister), and *B. subatreatinus* Grandi) which show no sperm guide. It is possible that these species have an oval suprachorionic sperm guide which was lost when Degrange studied the eggs in water. Not enough material has been studied in this family to discuss generic phylogeny or to attempt the formation of reliable keys to the genera.

Previous descriptions. *Baetis*: Morgan (1911), Bengtsson (1913), Lestage (1919), Percival & Whitehead (1928), Smith (1935), Degrange (1956, 1960). *Callibaetis*: Needham & Murphy (1924), Smith (1935). *Centroptilum*: Smith (1935), Bogoescu (1951), Degrange (1956, 1960). *Cloeon*: Bernhard (1907), Bengtsson (1913), Smith (1935), Harker (1950), Davidson (1956), Degrange (1956, 1960). *Neocloeon*: Smith (1935). *Pseudocloeon*: Smith (1935), Bogoescu (1951).

Baetis bicaudatus Dodds?

The eggs of this species were collected from the underside of a partially submerged board. They were distributed in regular rows, and several females were collected in the process of laying eggs.

Chorion. With a medium-mesh (4-8 μm long) reticulation of very irregular polygonal mesh, the strands being formed by small tubercles connected by fine ridges.

Attachment structures. An adhesive layer.

Micropyle. Unknown; one indistinct micropylar canal found, approximately 20 μm long. Most likely the sperm guide is formed in the adhesive layer; however, because these eggs were collected from a stream the sperm guide would not be expected to be apparent.

Baetis sp.

(Plate 5: fig. 59)

Chorion. With a medium-mesh (2-5 μm long) reticulation, the strands being formed by ridges.

Attachment structures. There appears to be a coiled thread in each mesh of the reticulation.

Micropyle. Sperm guide chorionic, 9-10 μm long, 7-10 μm wide; micropylar canal 18-20 μm long.

Baetodes sp.

(Plate 5: fig. 60; Plate 6: figs 61, 62)

Chorion and attachment structures. Eggs covered with a compact layer of knob-terminated coiled threads; tubercles very sparsely scattered in spaces between coiled threads.

Micropyle. Located very near one pole (Plate 6: fig. 62); sperm guide chorionic, 10-11 μm long, 6-6.5 μm wide; micropylar canal indistinct, at least 3 μm long.

Centroptilum bifurcatum McDunnough?
(Plate 6: figs 63-65)

Chorion. Densely maculate and longitudinally sulcate.

Attachment structures. An adhesive layer 1-2 μm thick.

Micropyle. Sperm guide poorly-defined, suprachorionic, 5-7 μm long, 2.5-4.5 μm wide; micropylar canal 11-15 μm long.

Centroptilum selanderorum Edmunds
(Plate 6: figs 66-68)

Chorion. Alternately costate and longitudinally punctate (Plate 6: figs 66, 67).

Attachment structures. An undifferentiated adhesive layer 1.5-2 μm thick.

Micropyle. Sperm guide less distinct distally than proximally, suprachorionic, 5-7 μm long, 3-4 μm wide; micropylar canal 8-10 μm long.

Remarks. Eggs of these 2 species of *Centroptilum* are quite unlike those described by Smith, Bogoescu, and Degrange, except in details of the micropyle as described by Degrange.

Cloeon triangulifer McDunnough

Chorion. With a fine mesh (1.5-5.6 μm long) reticulation formed by distinct ridges. The ridges are approximately 1 μm in width.

Attachment structures. Only a thin, non-fibrous adhesive layer which is mostly contained within the mesh of the reticulation.

Micropyle. Tagenoform. Sperm guide 5.6-9.7 μm long, 3.5-4.2 μm wide; micropylar canal too indistinct for measurement.

Cloeon sp.
(Plate 6: figs 69, 70)

Chorion and attachment structures. Many longitudinal rows of knob-terminated coiled threads, each thread surrounded by a raised, punctated, chorionic wall.

Micropyle. Unknown.

Pseudocloeon sp.
(Plate 6: fig. 71)

Chorion. Longitudinally tuberculate. The appearance of the egg is very much like Degrange's (1960) illustration of the egg of *Baetis subatreatinus* Grandi, and Bogoescu's (1951) illustration of the egg of *Pseudocloeon hyalopterum* Bogoescu. Both authors state, however, that the chorionic patterns are formed by punctures.

Attachment structures. A filamentous adhesive layer 1.5-2.5 μm thick.

Micropyle. Sperm guide chorionic, 3-6 μm long, 2-4 μm wide; micropylar canal 7-12 μm long.

FAMILY METRETOPODIDAE

The presence of knob-terminated coiled threads is the only feature common to eggs of *Ametropus* (Ametropodidae), *Metretopus* and *Siphloplecton*. The threads of *Ametropus*, however, are entirely unlike those common to the latter two genera. In *Ametropus*, threads are coiled about the pole to form a distinct polar cap, probably of Type III. In *Metretopus* and *Siphloplecton* a polar cap is absent, and KCTs occur as single units scattered over the entire chorion (and localized at the poles in *Siphloplecton*). Thus the attachment structures of *Metretopus* and *Siphloplecton* are quite Heptagenioidea-like, and quite unlike the attachment structures of *Ametropus*. For this reason, the former two genera are considered to be of monophyletic origin in a family (Metretopodidae) distinct from the family (Ametropodidae) of the latter genus. The egg data, however, are not conclusive evidence for a theory of diphyletic origin of these two groups, but such an opinion is supported by studies of the nymphal stages. Edmunds and Landa (unpublished data) have each independently come to this conclusion by studying the external and internal morphology of the nymphs.

Previous descriptions. *Metretopus*: Bengtsson (1913), Demoulin (1952). *Siphloplecton*: Smith (1935), Demoulin (1952), Koss (1968).

Metretopus borealis Eaton (Plate 11: figs 120, 121)

Chorion. With a medium-mesh (5-14 μm long) reticulation, the strands being formed by the spaces between paired ridges (Plate 11: figs 120, 121); chorion rugose within the mesh.

Attachment structures. Knob-terminated coiled threads scattered about the egg; each coil is surrounded by a chorionic "wall" (as in Plate 3: fig. 31).

Micropyle. Tagenoform, sperm guide irregularly oval (8-12 μm long, 6-8 μm wide), distinguished from the mesh of the reticulation by its lack of rugosity (Plate 11: fig. 121). Micropylar canal indistinct, 13-20 μm long; canal broadly joined to the sperm guide and tapered distally.

Remarks. Bengtsson's description of the eggs of this species is similar to the above.

Siphloplecton basale (Walker) (Plate 11: figs 117-119)

Chorion. Densely tuberculate; tubercules 3-7 μm long, 2-3 μm high and slightly dissected apically (Plate 11: figs 117-119).

Attachment structures. Knob-terminated coiled threads scattered laterally and concentrated in linear groupings at both poles; diameter of lateral coils approximately half that of linearly-arranged polar coils. A compact ring of tubercles surrounds each coil.

Micropyle. Sperm guide absent or merely a slight, very poorly defined, distally expanded chorionic depression (Plate 11: fig. 119). Perhaps this structure is similar to an early evolutionary stage leading to the development of a tagenoform micropyle. Micropylar canal 10-15 μm long, walls approximated distally.

Remarks. Smith (1935) stated that eggs of *S. signatum* Traver and *S. basale* are similar (his description agrees with the above), but they differ from those of *S. speciosum* Traver in that eggs of the latter have coils clumped at one pole rather than linearly arranged at both poles.

FAMILY OLIGONEURIIDAE

Eggs of the various genera of this family are remarkably similar and resemble those of the *Siphonurus*-complex (Siphonuridae). The chorion is usually smooth and polar caps are absent. The most striking feature is the dense, orderly layer of fiber-coils which covers the entire egg (Plate 6: fig. 72; Plate 7: fig. 76). The coils are denser and more orderly than illustrated by Degrange (1960) for *Oligoneuriella rhenana*. With some coils the fibers terminate collectively in a compact, centrally located cluster (Plate 6: fig. 74) which is often fused subapically and drawn out into a projecting formation (Plate 7: figs 77, 78). The remaining coils appear to terminate within themselves rather than in a distinct, centrally located unit. The terminal fiber clusters apparently represent a stage plesiomorphic to the development of terminal knobs, and therefore are probably homologous to them. These terminal fiber-clusters are the "mamelon hemispherique translucide" and the "formations caractéristiques" described by Degrange (1960) for *Siphonurus lacustris* Eaton and *Oligoneuriella rhenana*, respectively.

A criss-crossing of straight fibers in the spaces between the coils (Plate 6: figs 72, 73) appears to be fibers extending from one coil to another.

Degrange (1960) described, for *Oligoneuriella rhenana*, a thin layer external to the coils; the layer is coagulated by alcohol, it prevents the eggs from adhering to each other, and also prevents the uncoiling of the filaments. ("La surface externe de la couche adhesive semble recouverte d'une mince pellicule d'une substance coagulée par l'alcool qui empêche les oeufs d'adhérer entre eux et prévient le déroulement des filaments".) In our studies, the layer was found on eggs from nymphs, but on eggs from adults the layer was slight or absent.

The micropyle (Plate 7: fig. 75) is tagenoform, the sperm guide being an oval to circular break in the coil layer.

Although distinct characters could not be found to separate the genera studied, certain character gradients were observed. The terminal fiber-clusters of *Chromarcys*, *Oligoneuria* and *Elassoneuria* only slightly resemble terminal knobs (Plate 6: fig. 74) but in *Homoeoneuria*, *Oligoneuriella*, and *Lachlania* there is sufficient subapical fusion of fibers, so that the apical portion is readily distinguishable as a plesiomorphic terminal knob (Plate 7: figs 77, 78). In addition, the fiber-coils in some genera are more distinct as a unit than in other genera.

The egg of *Chromarcys* is entirely similar to those of the other oligoneuriid genera, and indicates a very close genetic relationship of *Chromarcys* to the Oligoneuriinae. Furthermore, *Chromarcys* eggs do not indicate that the genus is

any more closely related to the extant Isonychiinae than is the remainder of the Oligoneuriidae.

Previous descriptions. *Oligoneuria*: Needham & Murphy (1924). *Oligoneuriella*: Degrange (1960).

FAMILY HEPTAGENIIDAE

With the exception of the genus *Stenonema*, the only characters typical of the heptageniid genera studied are a tageniform, usually entirely chorionic micropyle and a lack of polar caps other than Type V. Within *Stenonema*, the *interpunctatum* species-group has a tageniform, chorionic micropyle and two Type IV polar caps; the other species-groups of *Stenonema* have linear micropyles with suprachorionic sperm guides, and no polar caps. The attachment structures are peglike in some *Rhithrogena*, knob-terminated coiled threads in most genera, and an adhesive layer in most *Stenonema* and perhaps in *Epeorus*. A Type V polar cap is common in the family, but not universal. When KCTs are concentrated at one or both poles, they are almost always of larger size at the poles than they are laterally (larger in diameter of coil and diameter of thread composing coil). Two or more micropyles are present on eggs of all species studied, and they are located in the mid-region of the eggs.

Very few heptageniid genera can be distinguished by the characteristics of their eggs; the presence of knob-terminated coiled threads and a tuberculate chorion are too widespread in the family to facilitate generic delimitations. Although separate descriptions are given for eggs of *Cinygmula*, *Ecdyonurus*, *Heptagenia*, *Ororotsia*, *Rhithrogena*, and *Thalerosphyrus*, we are unable to compose a key which will distinguish the eggs of these genera. In some cases, if the genus is determined by some other means, eggs can be keyed to species.

Previous descriptions. *Arthroplea*: Bengtsson (1913), Koss (1968). *Cinygma*: Smith (1935). *Cinygmula*: Smith (1935). *Ecdyonurus*: Palmen (1884), Bengtsson (1913), Gros (1923), Percival & Whitehead (1928), Takahashi (1929), Rawlinson (1939), Degrange (1956, 1960). *Epeorus* (*Epeorus*): Degrange (1956, 1960). *E. (Iron)*: Brodsky (1930), Smith (1935), Koss (1968). *E. (Ironodes)*: Smith (1935). *Heptagenia*: Palmen (1884), Bengtsson (1913), Morgan (1913), Smith (1935), Degrange (1956, 1960), Koss (1968). *Pseudiron*: Smith (1935). *Rhithrogena*: Brodsky (1930), Smith (1935), Degrange (1956, 1957, 1960), Koss (1968). *Stenonema*: Morgan (1913), Smith (1935), Koss (1968).

Key to genera

1. Micropyle tageniform, sperm guide chorionic with or without a suprachorionic counterpart (Plate 7: figs 79, 81, 88; Plate 10: fig. 113) 2
- Micropyle linear, sperm guide absent or an elongate break in an adhesive layer most *Stenonema*
2. Three or fewer large coiled threads forming a Type IV cap at each pole *Stenonema interpunctatum*-group
- Polar caps absent or formed by numerous KCTs (Type V polar cap) (Plate 8: figs 89, 94) 3

3. Coiled attachment threads present 4
 Coiled attachment threads absent 7
4. Attachment structures are knobless coiled threads
 *Arthroplea congener*
 Attachment structures are knob-terminated coiled threads . . . 5
5. Small KCTs (coil 6-15 μm diam) densely concentrated at each pole,
 much larger coils (30 μm or more diam) equatorially (Plate 8: figs
 91, 94) *Afronurus peringueyi*,
 *Cinygmima?* sp., *Ecdyonurus yoshidae*
 Coils not as above 6
6. Tubercles absent; coils concentrated at one or both poles and
 evenly distributed about remainder of egg (Plate 10: figs 114, 115),
 or situated in excavations in chorionic costae (Plate 10: figs
 110-112) *Pseudiron*
 Tubercles present; if tubercles absent and coils evenly distributed
 about entire egg, then coils never concentrated at poles
 . . . *Ecdyonurus*, *Heptagenia*, *Ororotsia* sp., *Thalerosphyrus*, some
 *Rhithrogena* and most *Cinygmula*
7. Chorion costate (Plate 10: fig. 109) . . . *Arthroplea bipunctata*
 Chorion not costate 8
8. Chorion tuberculate or with peglike structures (Plate 7: fig. 87;
 Plate 9: figs 100-106) 9
 Chorion smooth or finely punctate 11
9. Chorion tuberculate, tubercles $\leq 1 \mu\text{m}$ in height (Plate 7: fig. 84) 10
 Chorion beset with peglike structures 3.5 μm or more in height
 (Plate 10: fig. 106) some *Rhithrogena*
10. Micropylar canal at approximately a 135° - 150° angle to the sperm
 guide (Plate 7: fig. 88); sperm guide 23-27 μm long, 18-22 μm wide
 *Cinygmula uniformis*
 Micropylar canal not significantly angled to the sperm guide (as in
 Plate 8: fig. 93); sperm guide 16-20 μm long, 12-15 μm wide
 *Cinygma integrum*
11. Chorion with a faint large-mesh reticulation, the strands formed by
 grooves *Cinygmula subequalis*
 Chorion lacking a large-mesh reticulation, and usually smooth
 *Epeorus*, s.l.

Subfamily Heptageniinae

Afronurus peringueyi (Esben-Petersen)

(Plate 7: figs 79, 80)

Chorion. Smooth, but with a sparse covering of variously sized and shaped globules (1-5 μm long) (Plate 7: fig. 79). These are on, but apparently not attached to the chorion. Their function and origin are unknown; perhaps they constitute an adhesive material, if they are not an artifact of some kind. The globules were, however, only on the eggs, not elsewhere on the slides.

Attachment structures. (Plate 7: fig. 80 and as in Plate 8: figs 91, 94). Small KCTs (coils 10-15 μm in diam) densely concentrated at each pole. Much larger KCTs (coils 67-115 μm long) situated equatorially.

Micropyle. (Plate 7: fig. 79.) Sperm guide oval to round, 15-20 μm long, 13-18 μm wide, border well-defined by a thickened rim. Sperm guide also with a small basal hood; whether it originates from the chorion or an adhesive layer is uncertain. Micropylar canal 18-20 μm long, perpendicular to long axis of sperm guide.

Cinygma integrum Eaton
(Plate 7: fig. 81)

Chorion. Densely tuberculate, tubercles 0.5 μm high, mostly 0.5-1.0 μm long.

Attachment structures. Absent.

Micropyle. Sperm guide 16-20 μm long, 12-15 μm wide, border well-defined by a thickened rim. Micropylar canal 6-8 μm long.

Cinygmina? sp.
(Plate 8: figs 94, 95)

Chorion. Smooth.

Attachment structures. Small KCTs (coils 8-10 μm diam) very densely concentrated into two Type V polar caps (Plate 8: fig. 94); much larger KCTs (coils 40-60 μm diam or length) situated equatorially (Plate 8: figs 94, 95 and as in Plate 8: fig. 91). Polar and large lateral KCTs situated in bordered pits in the chorion (Plate 8: fig. 95); when displaced, coils leave a distinct impression in the pits. Also present are a few small lateral coils similar to the polar coils in diameter, but lacking the bordered pits.

Micropyle. Sperm guide circular, 15-16 μm diam, border very well-defined by a thickened rim. Short sperm guide hood present. Micropylar canal 18-22 μm long.

Remarks. The eggs of this genus are very similar to those of *Afronurus peringueyi* and *Ecdyonurus yoshidae*. The egg type seems much too unusual to have evolved three times independently.

Genus *Cinygmula* McDunnough
(Plate 7: figs 82-88)

Seven of the 11 North American species of *Cinygmula* were studied, and no features were found common to all seven species. On the eggs of these species, the chorion is usually tuberculate with tubercles 1 μm or less in height (Plate 7: fig. 84). However, *C. tarda* has tubercles 1.5-2 μm high (Plate 7: fig. 86), and *C. subequalis* has a punctate and reticulate rather than tuberculate chorion. Knob-terminated coiled threads are present in all but *C. subequalis* and *C. uniformis* (Plate 7: figs 83, 85); they are scattered about the entire chorion, but also may be concentrated at one pole (as in Plate 8: fig. 89). When there is a concentration of KCTs at one pole, the polar coils and their component threads are larger in diameter than those coils that are laterally distributed (polar coils 6-9 μm diam, lateral coils 3-5 μm diam). The sperm guide is oval, and its border may or may not be well-defined by a thickened rim (Plate 7: figs 82, 88). In

some species the micropylar canal is distinctly angled less than 180° to the sperm guide (Plate 7: fig. 88).

The descriptions of *C. mimus* and *C. subaequalis* presented herein do not agree with those of Smith (1935) who found KCTs evenly distributed about the entire egg.

Key to species

1. Knob-terminated coiled threads present 2
 Knob-terminated coiled threads absent 4
2. KCTs randomly scattered about entire chorion, and approximately of similar size (Plate 7: figs 82, 83) *par* and *ramaleyi*
 KCTs distributed about entire chorion, but more concentrated and of larger size at one pole 3
3. Tubercles 1.5-2 μm high (Plate 7: fig. 86); border of sperm guide well-defined by a thickened rim (as in Plate 7: fig. 82); micropylar canal 13-15 μm long *tarda*
 Tubercles 1 μm or less in height (Plate 7: fig. 84); sperm guide border poorly defined, lacking a thickened rim (as in Plate 7: fig. 88); micropylar canal 18-33 μm long *mimus* and *reticulata*
4. Chorion tuberculate (Plate 7: fig. 87); micropylar canal at approximately a 135° - 150° angle to the sperm guide (Plate 7: fig. 88), and 25-29 μm long *uniformis*
 Chorion punctate and reticulate; micropylar canal aligned with long axis of sperm guide (as in Plate 7: fig. 82), 8-10 μm long *subaequalis*

Cinygmula mimus (Eaton) and *C. reticulata* McDunnough
 (Plate 7: figs 84, 85)

Chorion. Tubercles 0.5-3.0 μm , mostly 1-2 μm , long; larger tubercles occur at the pole with a concentration of attachment structures.

Attachment structures. KCTs scattered laterally and concentrated at one pole.

Micropyle. Sperm guide 17-28 μm long, 13-19 μm wide; sperm guide border poorly defined, lacking a thickened rim. Micropylar canal 18-33 μm long, slightly curved, and at approximately a 135° - 150° angle to the sperm guide.

Cinygmula par (Eaton)
 (Plate 7: fig. 82)

Chorion. Tubercles 0.5-1.5 μm long.

Attachment structures. KCTs randomly scattered about entire chorion.

Micropyle. Sperm guide 17-19 μm long, 16-18 μm wide, border well-defined by a thickened rim; micropylar canal 25-30 μm long, rarely curved, and at approximately a 165° - 180° angle to the sperm guide.

Cinygmula ramaleyi (Dodds)
 (Plate 7: fig. 83)

Like *C. par* except sperm guide 19-22 μm long, 14-20 μm wide; and micropylar canal 21-26 μm long.

Cinygmula subaequalis (Banks)

Chorion. Finely punctate, and with a faint, irregular polygonal, large-mesh (12-25 μm long) reticulation, the strands being formed by shallow grooves.

Attachment structures. Absent

Micropyle. Sperm guide 14-19 μm long, 10-11 μm wide; sperm guide border well-defined, but lacking a thickened rim. Micropylar canal straight or nearly so, 8-10 μm long.

Cinygmula tarda (McDunnough)

(Plate 7: fig. 86)

Chorion. Tubercles 1.5-2.0 μm high, 1.0-1.5 μm long.

Attachment structures. KCTs scattered laterally and concentrated at one pole.

Micropyle. Sperm guide 10-16 μm long, 9-14 μm wide, border well-defined by a thickened rim; micropylar canal 13-15 μm long, usually curved, and at approximately a 150°-180° angle to the sperm guide.

Cinygmula uniformis McDunnough

(Plate 7: figs 87, 88)

Chorion. Tubercles mostly 1-2 μm long.

Attachment structures. Absent.

Micropyle. Sperm guide 23-27 μm long, 18-22 μm wide; sperm guide border poorly defined, lacking a thickened rim. Micropylar canal 25-29 μm long, usually curved, and at approximately a 135°-150° angle to the sperm guide.

Genus *Ecdyonurus* Eaton

(Plate 8: figs 89, 91)

The genus has no characteristic features, although for most species the coiled threads are concentrated at both poles and scattered laterally. Bengtsson (1913) stated that the coiled threads densely covered the entire egg of *E. joernensis* Bengtsson; this feature is known to occur elsewhere in the family only in the genus *Heptagenia*. The chorion is usually tuberculate, although Degrange (1960) did not report tubercles on eggs of *Ecdyonurus fluminum*. It is not possible to construct a key for identification to species of most known *Ecdyonurus* eggs.

Ecdyonurus insignis (Eaton)

(Plate 8: fig. 89)

Chorion. Tubercles 1-2 μm long, 1-1.5 μm high.

Attachment structures. KCTs scattered laterally and concentrated at one pole (Plate 8: fig. 89).

Micropyle. Sperm guide 14-16 μm long, 11-14 μm wide, border well-defined by a thickened rim; micropylar canal 14-16 μm long.

Ecdyonurus yoshidae Takahashi
(Plate 8: fig. 91)

Chorion. Smooth.

Attachment structures. Small KCTs (coils 6-11 μm diam) very densely concentrated into two polar caps (as in Plate 8: fig. 94); much larger KCTs (30-50 μm diam) situated equatorially (Plate 8: fig. 91 and as in Plate 8: fig. 94).

Micropyle. Sperm guide oval to round, 13-17 μm long, 13-15 μm wide, with a small basal hood and a thickened, well-defined rim. Micropylar canal 17-23 μm long, perpendicular to long axis of the sperm guide.

Remarks. Because this unusual egg is similar to those of *Afronurus peringueyi* and *Cinygmina?* sp., but unlike any other known *Ecdyonurus* eggs, the generic assignment of this species is questionable.

Ecdyonurus ally

Chorion. Tubercles 0.5-2 μm long, 1 μm high.

Attachment structures. KCTs scattered laterally and concentrated at both poles; lateral coils 2-3 μm in diam, polar coils 4-5 μm in diam.

Micropyle. Sperm guide 13-15 μm long, 9-11 μm wide, border well-defined by a thickened rim beset with tubercles; micropylar canal 7-13 μm long.

Genus *Epeorus* Eaton
(Plate 8: figs 92, 93)

Smith (1935) studied eggs of the subgenera *Iron* and *Ironodes*, Degrange (1960) discussed two species of *Epeorus* s.s., and Koss (1968) discussed *E. (Iron) suffusus* (McD.). All observed that eggs of *Epeorus* s.l. have unsculptured chorions and no attachment structures. Of the species discussed herein, a species of *Epeorus* s.s. has a tuberculate chorion, a species of *Iron* has a smooth chorion, and two species of *Ironopsis* have finely punctate chorions. Known *Epeorus* s.l. eggs lack attachment structures except in some species a non-fibrous adhesive layer seems apparent.

Epeorus (Epeorus) aesculus (Imanishi)
(Plate 8: fig. 92)

Chorion. Finely tuberculate, tubercles approximately 0.5 μm in height and diameter.

Attachment structures. None.

Micropyle. Sperm guide 10-14 μm long, 9-13 μm wide, border well-defined by a narrowly thickened rim; micropylar canal 10-15 μm long.

Epeorus (Iron) dulciana (McDunnough)

Chorion. Smooth.

Attachment structures. An adhesive layer, approximately 1 μm thick.

Micropyle. Sperm guide 14-16 μm long, 12-14 μm wide; micropylar canal 10-19 μm long.

Epeorus (Ironopsis) grandis (McDunnough)
(Plate 8: fig. 93)

Chorion. Finely punctate.

Attachment structures. An adhesive layer approximately 0.75 μm thick.

Micropyle. Sperm guide shallow, border poorly-defined and lacking a thickened rim; micropylar canal 10-19 μm long.

Epeorus (Ironopsis) permagnus (Traver)

Like *E. grandis* except the sperm guide border is well-defined by a narrowly thickened rim.

Genus *Heptagenia* Walsh
(Plate 8: figs 96, 97; Plate 9: figs 98, 99)

The characterization of *Heptagenia* eggs by Koss (1968) should be expanded. All known *Heptagenia* eggs are ovoid. Although usually densely tuberculate (Plate 8: fig. 96; Plate 9: fig. 99), the chorion varies, among the species, from sparsely to densely tuberculate. The length and height of the tubercles also varies among the species, and in several species, ring-like markings replace the tubercles on some areas of the eggs (as in Plate 8: fig. 90) (see also, Koss, 1968).

The only attachment structures known for *Heptagenia* eggs are knob-terminated coiled threads. They may be concentrated at one or both poles (Plate 8: fig. 97; Plate 9: fig. 99 and as in Plate 8: fig. 89) and/or randomly scattered about the chorion (as in Plate 8: fig. 90; Plate 9: fig. 105), or they may be concentrated in a dense mat nearly covering the entire egg (Plate 9: fig. 98). When polar concentrations occur, KCTs are also scattered laterally, but the lateral coils are smaller in diameter. Frequently the concentration of KCTs at one pole is denser and consists of larger coils than those located at the other pole (Plate 8: fig. 97).

The most plesiomorphic egg type in the genus is that with the attachment structures concentrated in a dense mat nearly covering the entire egg (Plate 9: fig. 98); this condition is very similar to some *Isonychia* eggs (Plate 4: fig. 40).

Ororotsia sp.

The available eggs did not react satisfactorily to the preparation techniques. The chorion appears to be granulate, very sparsely tuberculate, and with a very sparse covering of KCTs. The micropyle is typical of the family.

Genus *Rhithrogena* Eaton
(Plate 9: figs 100-106; Plate 10: fig. 107)

Knob-terminated coiled threads and randomly distributed tubercles characterize eggs of most species of *Rhithrogena*. However, eggs of at least two species possess a particular tubercle arrangement, and eggs of at least two other species lack the coiled threads and short tubercles. Instead, the latter two possess peglike structures which probably serve as attachment structures.

Key to species

1. Chorion beset with peglike structures 3.5-5 μm high (Plate 9: fig. 106) *impersonata* and *sanguinea*
Chorion tuberculate, tubercles 2 μm or less in height (Plate 9: figs 100-105; Plate 10: fig. 107) 2
2. Chorion with circular arrangements of tubercles (Plate 9: fig. 100; Plate 10: fig. 107) 3
Chorionic tubercles randomly scattered about the egg, not in any particular pattern of arrangement (Plate 9: figs 103-105) 4
3. All tubercles in circular arrangements; 1-3 μm KCTs form part of circular tubercle arrangements; chorion marked with a large-mesh reticulation (Plate 9: figs 100, 101) *hageni*
Not all tubercles in circular arrangements, many smaller ones forming a background to the circular patterns (Plate 10: fig. 107); KCTs few, located at one pole only; large-mesh reticulation absent *R. sp.*
4. KCTs scattered laterally and concentrated at one pole (Plate 9: fig. 103); sperm guide with ring of tubercles just inside border (Plate 9: fig. 104) *morrisoni*
KCTs scattered laterally and concentrated at both poles (Plate 9: fig. 105); sperm guide lacking a ring of tubercles inside border 5
5. KCTs concentrated more at one pole than the other; sperm guide border poorly defined, lacking a thickened rim *japonica*
KCTs equally concentrated at both poles; sperm guide border well-defined by a thickened rim (Plate 9: fig. 105) *robusta*

Rhithrogena hageni Eaton

(Plate 9: figs 100-102)

Chorion. Marked with a faint, large-mesh reticulation, each mesh containing a disorganized, circular arrangement of large tubercles (Plate 9: fig. 100); tubercles 2-5 μm long, 1-2 μm high.

Attachment structures. Laterally 1-3 KCTs form part of each circular arrangement of tubercles; at one pole, a single large KCT fills most of the area within each of the circular arrangements (Plate 9: fig. 101).

Micropyle. Sperm guide 13-16 μm long, 10-14 μm wide; sperm guide border well-defined by a thickened rim and a compact ring of tubercles external to the rim (Plate 9: fig. 102). Micropylar canal 13-19 μm long, at a 165°-180° angle to the sperm guide.

Rhithrogena impersonata (McDunnough)and *R. sanguinea* Ide

(Plate 9: fig. 106)

Chorion and attachment structures. (Plate 9: fig. 106.) The chorion is covered with short peglike structures (3.5-5 μm high) which probably serve for attachment as do those of some Leptophlebiidae (e.g. *Paraleptophlebia*, see Koss, 1968); KCTs are lacking.

Micropyle. Sperm guide 11-17 μm long, 8-10 μm wide, border well-defined by a thickened rim (Plate 9: fig. 106); micropylar canal 11-17 μm long.

Rhithrogena japonica Ueno

Chorion. Densely tuberculate, tubercles 1 μm in length and height.

Attachment structures. KCTs scattered laterally and concentrated at both poles, although at one pole the concentration is greater than at the other.

Micropyle. Sperm guide 9-11 μm long, 8-11 μm wide, border poorly defined; micropylar canal 17-20 μm long, at a 150°-180° angle to the sperm guide.

Rhithrogena morrisoni (Banks)

(Plate 9: figs 103, 104)

Chorion. Densely tuberculate, tubercles 1-1.5 μm long, 1-2 μm high.

Attachment structures. KCTs scattered laterally and concentrated at one pole; lateral coils 4-7 μm in diam, polar coils 8-10 μm in diam.

Micropyle. Sperm guide 13-16 μm long, 9-12 μm wide, with a ring of small tubercles just inside the fairly well-defined border. Micropylar canal 13-15 μm long, not significantly angled with the sperm guide.

Rhithrogena robusta Dodds

(Plate 9: fig. 105)

Chorion. Sparsely to densely tuberculate, tubercles 0.5-1.3 μm long, 1 μm high.

Attachment structures. KCTs scattered laterally and concentrated at both poles; lateral coils 3-5 μm in diam, polar coils 6-7 μm in diam.

Micropyle. Sperm guide 11-15 μm long, 8-11 μm wide, border well-defined by a thickened rim; micropylar canal 15-18 μm long, not significantly angled with the sperm guide.

Rhithrogena sp.

(Plate 10: fig. 107)

Chorion. Many circular arrangements of large tubercles evenly distributed about the chorion; randomly distributed smaller tubercles form a background.

Attachment structures. A few KCTs present, restricted to one pole.

Micropyle. Sperm guide 11-15 μm long, 9-12 μm wide; sperm guide border well-defined by a slightly thickened rim and a sparse ring of small tubercles external to the rim. Micropylar canal 12-18 μm long, not significantly angled with the sperm guide.

Genus *Stenonema* Traver

Koss (1968) characterized the eggs for the genus and described eggs of 11 species. Two types of eggs exist in the genus. Eggs of the *interpunctatum*-group have 1-3 large coiled threads at each pole and a tageniform micropyle typical of the family. Terminal knobs are not apparent on the coiled threads. The remaining species-groups have eggs with only an adhesive layer for an attachment structure and a linear micropyle which is unique within the family. The sperm guide is an elongate break in the adhesive layer (not a chorionic depression as described by Koss, 1968), and frequently it possesses a basal

hood which is formed by the adhesive layer. Most of the known *Stenonema* eggs possess chorionic tubercles, and in some species the tubercles have a definite reticular pattern of arrangement.

Thalerosphyrus sp., nr. *sumatranus* Ulmer
(Plate 8: fig. 90)

Chorion. Tubercles 1-2 μm long, 1-1.5 μm high. Ring-like markings, similar to those found on some *Heptagenia* eggs (see Koss, 1968), occur singly or in small groups (Plate 8: fig. 90).

Attachment structures. KCTs scattered laterally and concentrated at both poles, although larger and more numerous at one pole.

Micropyle. Sperm guide 14-17 μm long, 9-10 μm wide; sperm guide border well-defined, but rim not strongly thickened; micropylar canal 12-15 μm long.

Subfamily Arthropleinae
Genus *Arthroplea* Bengtsson

Eggs of the two described species of *Arthroplea* are quite different from each other. Typical of most heptageniid eggs, those of *A. congener* are tuberculate and possess coiled attachment threads; however, the threads lack terminal knobs. *A. bipunctata* eggs, on the other hand, lack coiled attachment threads and tubercles, and possess instead a thin adhesive layer and a costate chorion. Both species have tagenoform micropyles typical of the family.

Arthroplea bipunctata (McDunnough)
(Plate 10: fig. 109)

Chorion. Costate.

Attachment structures. An adhesive layer approximately 1 μm in depth between the chorionic costate, 2 μm in depth on them. The costate appearance of the egg is mostly due to the excess of adhesive material deposited on the low chorionic costae.

Micropyle. Sperm guide 9.5-11.5 μm long, 5.5-7.5 μm wide, border lacking a thickened rim; micropylar canal 7.5-9.5 μm long.

Arthroplea congener Bengtsson
(Plate 10: fig. 108)

Chorion. Densely tuberculate, tubercles 0.5-1.3 μm long, approx. 1 μm high.

Attachment structures. Knobless coiled threads evenly scattered over the entire chorion (Plate 10: fig. 108); coils 6-7 μm in diam.

Micropyle. Sperm guide 8-11 μm long, 5.5-9 μm wide, border well-defined by a narrowly thickened rim; micropylar canal 25-30 μm long.

Remarks. The small granulated anchor devices described by Bengtsson (1913) are actually the chorionic tubercles.

Subfamily Pseudironinae
Genus *Pseudiron* McDunnough

By their possession of knob-terminated coiled threads and tageniform micropyles *Pseudiron* eggs indicate a definite relationship of the genus to the Heptagenioidea. The eggs are also characterized by the presence of at least one Type V polar cap whose threads are much thicker than any other observed in the Ephemeroptera, and by the absence of chorionic tubercles, a feature common to most other Heptageniidae.

Key to species

1. Chorion costate, lateral KCTs situated in circular excavations within these costae (Plate 10: figs 110-112) *meridionalis*
Chorion not costate, lateral coiled threads uniformly scattered over the chorion (Plate 10: figs 113, 115) 2
2. KCTs concentrated at 1 pole (Plate 10: figs 114, 115) . *P. sp. no. 1*
KCTs concentrated at both poles *P. sp. no. 2*

Pseudiron meridionalis Traver
(Plate 10: figs 110-112)

Chorion. (Plate 10: figs 111, 112.) Costate; costae 30-40 μm wide, subdivided into many rectangular units which contain a discoidal, central excavation.

Attachment structures. Presumably a knob-terminated coiled thread occurs in each of the discoidal excavations in the costae. Coils of thread are not distinguishable (only preserved eggs were available), but terminal knobs are (Plate 10: fig. 110). Larger KCTs are concentrated at one pole (as in Plate 10: fig. 114). Adhesive layer lacking.

Micropyle. (Plate 10: fig. 111.) Sperm guide 16-18 μm long, 12-14 μm wide, and with an inner flange; sperm guide border well-defined by a thickened rim. Micropylar canal 8-10 μm long.

Pseudiron sp. no. 1
(Plate 10: figs 113-115)

Chorion. The egg is evenly covered with many ring-like structures 18-28 μm in outside diameter (Plate 10: figs 113, 115).

Attachment structures. Either a knob-terminated coiled thread occurs in the area enclosed by each chorionic ring, or else each ring itself is a coiled thread. As in *P. meridionalis*, only preserved material was available, and the lateral threads were not visible although the terminal knobs were. Obvious knob-terminated coiled threads are concentrated at one pole (Plate 10: fig. 114). A thin adhesive layer occurs on the lateral surfaces and it is quite wrinkled in the spaces between the chorionic rings.

Micropyle. (Plate 10: fig. 113.) Sperm guide oval to round, 14-19 μm long, 15-17 μm wide, and with an inner flange formed by the adhesive layer; sperm guide border well-defined by a narrowly thickened rim. The sperm guide

dimensions include the flange but not the rim. Micropylar canal short (5-9 μm long) and weak.

Pseudiron sp. no. 2

Like *Pseudiron* sp. no. 1 except large, knob-terminated coiled threads are concentrated at both poles.

FAMILY AMETROPODIDAE

The family consists of the single known genus *Ametropus*, and the features of its egg must serve as typical for the family.

Genus *Ametropus* Albarda
(Plate 11: fig. 116)

Chorion. Densely granulate, granules 1 μm or less in height.

Attachment structures. A single polar cap apparently composed of many long, compactly coiled threads (Type III), thus similar to caps found in the Caenidae; eggs laid in water were unavailable. *A. neavei* also has coiled threads scattered laterally, but none could be found on eggs of *A. albrighti*.

Micropyle. Unknown.

SUPERFAMILY LEPTOPHLEBIOIDEA

FAMILY LEPTOPHLEBIIDAE

Within the Ephemeroptera, Leptophlebiidae eggs have the greatest diversity in chorionic sculpturing and attachment structures. The chorion may be smooth, costate, tuberculate, punctate, reticulate etc. or even sculptured with a floristic pattern of ridges. Attachment structures at least consist of thin adhesive layers, knob-terminated coiled threads, sucker-like plates, and peglike structures; polar caps have not been observed. The arrangement of attachment structures varies, and includes a localization of peglike structures into a longitudinal band around the egg or in a discal clump (Plate 11: figs 122, 123), localization of KCTs in the mesh of a large-mesh reticulation or in the center of a circular arrangement of tubercles (Plate 11: fig. 128), and distribution of KCTs in a uniform layer covering the entire egg.

A funnellform micropyle and the lack of polar caps are the only features that are constant on all Leptophlebiidae eggs observed. The sperm guide is chorionic (Plate 11: fig. 125) or absent (Plate 11: fig. 126). In the latter case the micropylar canal is always perpendicular to the chorion at least throughout most of the chorion's depth (Plate 11: figs 125, 126), and thus the micropyle may still be considered as funnellform.

An adhesive layer is lacking in most species studied, but a thin layer was observed on some eggs (Plate 11: fig. 124); in such cases the adhesive material was absent over the micropyle.

The knob-terminated coiled threads in this family are not as apomorphic as those in the Heptageniidae or Ephemerellidae. In some genera the knob is

merely a gradual apical expansion of the thread (Plate 11: fig. 127), but in others a more distinct terminal knob does occur. In the latter case, however, the knobs are still not compact units like those in Plate 7: fig. 80 and Plate 11: fig. 130. Although the threads do not reveal the multifibered condition shown in Plate 5: figs 50 and 51, the terminal knobs often appear multifibered.

The consistent lack of polar caps and the presence of an entirely chorionic funnellform micropyle is considered important enough to merit the separation of this family from the Tricorythidae and Ephemerellidae at the superfamily level. This decision is more fully discussed under "Ephemerelloidea".

Previous descriptions. *Adenophlebiodes*: Crass (1947). *Aprionyx*: Crass (1947). *Atalonella*: Harker (1950). *Atalophlebia*: Harker (1950). *Atalophlebioides*: Phillips (1930), Harker (1950). *Choroterpes*: Morgan (1913), Smith (1935), Grandi (1941), Degrange (1960). *C. (Euthraulius)*: Gillies (1957). *Deleatidium*: Phillips (1930), Harker (1950). *Habrophlebia*: Pleskot (1953), Degrange (1956, 1960), Koss (1968). *Habrophlebiodes*: Morrison (1919), Smith (1935), Demoulin (1954), Koss (1968). *Leptophlebia*: Bengtsson (1913), Morgan (1913), Smith (1935), Degrange (1956, 1960), Koss (1968). *Paraleptophlebia*: Smith (1935), Degrange (1960), Koss (1968). *Thraulodes*: Traver & Edmunds (1967), Koss (1968). *Thraululus*: Degrange (1956, 1960), Peters, Gillies, Edmunds (1964).

SUPERFAMILY EPHEMERELLOIDEA

The eggs of the Ephemerellidae and Tricorythidae have features in common which make them distinctly different from those of any known leptophlebiid. The Ephemerellidae and Tricorythidae have tageniform micropyles and a Type I polar cap; the Type I polar cap is found elsewhere only in the Potamanthidae and Euthyplociidae (both of which possess two polar caps). These features are lacking in the Leptophlebiidae (which have funnellform micropyles and no polar caps), and there are no known features on the eggs that show a common relationship between the leptophlebiid and the ephemerellid-tricorythid mayflies. One possible exception would be the presence of fibrous attachment structures; however, attachment threads are known to occur in every family of mayflies except the Ephemeridae and Behningiidae (Palingeniidae not studied), so this could hardly be considered as indicative of close relationship of the three families involved. For these reasons, the Ephemerellidae and Tricorythidae are placed in a separate superfamily from the Leptophlebiidae.

Eggs of the two families can be readily distinguished. Overlapping chorionic plates characterize tricorythid eggs, whereas knob-terminated coiled threads and a small-mesh reticulation of ridges (all subgenera except *Eurylophella*), or a large-mesh reticulation of grooves (subgenus *Eurylophella*) characterize eggs of *Ephemerella* (the only genus of Ephemerellidae known in the egg stage). However, these differences may not hold true when more genera are sampled in both families. The eggs of only one subfamily of three are known in the Ephemerellidae, and of only one subfamily of five in the Tricorythidae. Demoulin (1958) placed the Caenidae and Prosopistomatidae in the superfamily Ephemerelloidea; however, egg data present no evidence in support of such a classification.

FAMILY EPHEMERELLIDAE

Only the genus *Ephemerella* s. l. is known in the egg stage, and therefore its features must presently serve as typical of the family.

Previous descriptions. *Ephemerella* s. l.: Morgan (1913), Percival & Whitehead (1928), Shepard (1929), Brodsky (1930), Smith (1935), Degrange (1956, 1960), Koss (1968).

Genus *Ephemerella* Walsh
(Plate 11: figs 129, 130)

A single Type I polar cap, knob-terminated coiled threads, ovoid form, and a tageniform, entirely chorionic micropyle characterize eggs of most *Ephemerella* except those of the subgenus *Eurylophella*. *E. maculata* (see Smith, 1935) and the subgenus *Eurylophella* are atypical, having a nearly rectangular form and lacking the coiled threads and polar cap typical of the remainder of the family. However, *Eurylophella* does have a micropyle typical of the family; that of *E. maculata* is unknown.

FAMILY TRICORYTHIDAE

The only tricorythid eggs studied were those of three genera of the Leptoxyphinae. Demoulin (1964) illustrated the egg of *Dicercomyzon* (*Dicercomyzinae*) as possessing a single polar cap. Most likely the cap is similar to those of the Leptoxyphinae. Little is known about tricorythid eggs except those of some Leptoxyphinae genera, and therefore the familial characterization must presently be the same as for that subfamily.

Subfamily Leptoxyphinae

Based on *Leptoxyphes*, *Leptoxyphodes* and *Tricorythodes*, the subfamily is characterized by its possession of a single Type I polar cap (Plate 12: figs 131, 133), a chorionic sculpturing of overlapping plates (Plate 12: figs 133, 137), and a tageniform micropyle (Plate 12: figs 132, 136). The overlapping plates appear to be hollow, and the chorion appears to be thinnest in the areas enclosed by their respective bases (Plate 12: figs 132, 134). These apparently thin areas correspond to the "small circular-mesh reticulation across the middle of each plate" described by Koss (1968) for *Tricorythodes* eggs. The significance of the chorionic plates is unknown, but perhaps they aid in respiration of the egg. The sperm guide lacks a well-defined border, and is chorionic.

Previous descriptions. *Dicercomyzon*: Demoulin (1964). *Tricorythodes*: Morgan (1913), Smith (1935), Koss (1968).

Key to genera

1. Chorionic plates elongate, those at the uncapped pole being $\frac{1}{2}$ - $4\frac{1}{2}$ times as long as the laterals (Plate 12: fig. 133) . *Leptoxyphodes*
Chorionic plates not very elongate, those at the uncapped pole

- subequal to the laterals (Plate 12: figs 131, 135, 137) 2
2. With one or more pairs of uncoiled attachment threads anchored between the lateral plates (Plate 12: fig. 135) . . . *Tricorythodes*
Attachment threads absent *Leptoxyphes*

Genus *Leptoxyphes* Eaton
(Plate 12: figs 131, 132)

Chorion. Overlapping plates short, those at the uncapped pole subequal to the laterals.

Attachment structures. A single polar cap.

Micropyle. Located anywhere from the equatorial region to the uncapped pole; one per egg. Sperm guide 14-16 μm long, 11-14 μm wide, a very poorly defined oval area which lacks a chorionic plate (Plate 12: fig. 132); micropylar canal 5-7 μm long.

Genus *Leptohyphodes* Ulmer
(Plate 12: figs 133, 134)

Chorion. Overlapping plates elongate, those at the uncapped pole being $\frac{1}{2}$ - $4\frac{1}{2}$ times as long as the laterals.

Attachment structures. A single polar cap.

Micropyle. Unknown.

Genus *Tricorythodes* Ulmer
(Plate 12: figs 135-137)

Chorion. Overlapping plates short, those at the uncapped pole subequal to the laterals (Plate 12: figs 135, 137). The "small circular-mesh reticulation across the middle of each plate" described by Koss (1968) is actually the area of thin chorion enclosed by the base of each plate (as in Plate 12: fig. 134).

Attachment structures. A single polar cap, and a few pairs of non-coiled lateral attachment threads which are attached between the plates and are not knob-terminated (Plate 12: fig. 135).

Micropyle. (Plate 12: fig. 136.) Situated near the uncapped pole; one per egg. Sperm guide 15-23 μm long, 13-17 μm wide; micropylar canal difficult to see, at least 9 μm long.

SUPERFAMILY EPHEMEROIDEA

FAMILY BEHNINGIIDAE

Behningiidae eggs are by far the largest known mayfly eggs, those of *Behningia* being as much as 1 mm long (measured free, not slide mounted). The eggs lack polar caps, have a weakly developed large-mesh reticulation, and have funnellform micropyles. The micropyles occur one each in and below large, circular accumulations of adhesive material found along the equatorial zone (Plate 12: figs 138, 139). The sperm guides are funnel-shaped excavations within these accumulations (Plate 12: figs 140, 141), and therefore are

suprachorionic. The micropylar canal consists of a distinct, double-walled, proximal part, and an indistinct, single-walled, distal part.

There are too little data in the egg stage for a discussion of the generic phylogeny of the Behningiidae.

Previous description. *Behningia*: Keffermuller (1959).

Key to species

Adhesive material accumulated at poles and along equatorial zone (Plate 12: fig. 138); walls of sperm guides steep; adhesive layer 1 μm or less in thickness except at polar and equatorial accumulations

..... *Behningia lestagei*

Adhesive material only accumulated along equatorial zone; walls of sperm guides of gradual slope (Plate 12: fig. 141); adhesive layer 2-5 μm thick except at equatorial accumulations *Dolania americana*

Behningia lestagei Motas & Bogoescu (Plate 12: figs 138, 139)

Size. 918-1020 μm long, 714-748 μm wide.

Chorion. Densely and finely punctate, 8-11 μm thick, and with a weakly developed large-mesh (10-28 μm long) reticulation.

Attachment structures. A very thin adhesive layer (approximately 0.75-1.0 μm thick) covering the egg except where thicker (18-35 μm thick), circular accumulations of adhesive material occur at the two poles and along the equatorial zone (Plate 12: fig. 138).

Micropyle. Located in and below equatorial adhesive layer accumulations only. Sperm guide 20-45 μm in diam, walls steep; micropylar canal 39-53 μm long proximally, at least 16 μm long distally.

Dolania americana Edmunds & Traver (Plate 12: figs 140, 141)

Size. 714-782 μm long, 544-578 μm wide.

Chorion. 8 to 12 μm thick, appearing smooth; some areas of the egg with parts of a faint large-mesh (18-29 μm long) reticulation. The inability to consistently find a continuous reticulation may be due to the copious adhesive layer.

Attachment structures. A dense, filamentous adhesive layer 2-5 μm thick; thicker, circular accumulations of adhesive material (10-14 μm thick) along the equatorial zone only.

Micropyle. Sperm guide 47-59 μm in diam, walls of gradual slope (Plate 12: figs 140, 141); micropylar canal 41-47 μm long proximally, at least 29 μm long distally.

FAMILY POTAMANTHIDAE

The eggs of *Potamanthodes*, *Potamanthus*, *Rhoenanthopsis*, and *Rhoenanthus* were observed, and all are remarkably similar; they possess

tuberculate chorions (Plate 13: fig. 143), two polar caps (Plate 13: fig. 142), approximately 6-12 laterally distributed, knob-terminated coiled threads (Plate 13: fig. 143), and an entirely chorionic tageniform micropyle (Plate 13: fig. 143). The descriptions of *Potamanthus* eggs by Degrange (1960) and Koss (1968) are adequately descriptive for the eggs of all the above named genera. The dark maculations (Plate 13: fig. 143) described by Koss (1968) are actually small tubercles which are less than $0.3 \mu\text{m}$ in height. On eggs of *Potamanthodes formosus* (Plate 13: figs 142, 143) and *Rhoenanthopsis* sp. the tubercles are slightly larger, approaching $1 \mu\text{m}$ in height; the tubercles of *Rhoenanthus* sp. are somewhat shorter.

Variations in tubercle heights are extremely subtle characters, and it is distinctly possible that these are merely specific differences. Therefore, we are of the impression that generic differences in the eggs cannot be found for the four genera listed above, as well as for the two genera not yet studied (*Neopotamanthodes* and *Potamanthindus*).

If some features are found to distinguish the genera, it is doubtful they will disprove the assertion that the eggs indicate a very close relationship among the four genera.

Previous descriptions. *Potamanthus*: Grenacher (1868), Palmen (1884), Ide (1935), Smith (1935), Degrange (1956, 1960), Koss (1968).

FAMILY EUTHYPLOCIIDAE

The only eggs available were those of one species each of *Campylocia* and *Euthyplocia*, and thus the features of two polar caps and a large-mesh reticulation formed by ridges may not be familial characters once the eggs of the remaining genera have been studied.

Previous descriptions. *Campylocia*: Needham & Murphy (1924). *Euthyplocia*: Roback (1966).

Key to genera

1. Each polar cap consists of many interwoven threads loosely coiled at each pole (Plate 13: figs 149, 150); micropyle funnellform, the sperm guide being a funnel-shaped chorionic depression devoid of sculpturing (Plate 13: fig. 151); adhesive layer absent *Campylocia*
Polar caps a solid-like mass of threads (Plate 13: figs 144-147); micropyle linear, with a suprachorionic sperm guide; adhesive layer present, distributed on strands of reticulation (Plate 13: fig. 148, and as in Plate 1: fig. 4) *Euthyplocia*

Campylocia sp. (Plate 13: figs 149-151)

Chorion. Sculptured with a large-mesh ($15-21 \mu\text{m}$ long) reticulation, the strands being formed by relatively well-developed ridges (Plate 13: fig. 151).

Attachment structures. Adhesive layer absent. Two Type III polar caps present (Plate 13: fig. 149), each composed of many interwoven threads loosely coiled about the respective poles; threads not knob-terminated, but

divided into a countless number of small fibers (Plate 13: fig. 150). Two completely uncoiled caps were measured at 3.031 mm and 2.968 mm respectively. Needham & Murphy (1924) stated that the caps of *C. anceps* (Eaton) (as *C. ampla* Needham & Murphy) each consist of a single filament. This is probably an error.

Micropyle. Funnelform (Plate 13: fig. 151). Sperm guide (75-90 μm in diam) a large, funnel-shaped chorionic depression devoid of sculpturing; micropylar canal (15-23 μm long) acutely angled to the chorion.

Remarks. Unlike most other eggs studied, the micropyle and the polar caps were usually the only parts of the *Campylocia* eggs to absorb the red stain in the CMC-S mounting medium.

Euthyplocia sp.

(Plate 13: figs 144-148)

Form. Eggs quite flattened, resulting in two distinct "sides"; each side is longitudinally concave on both sides of its midline (Plate 13: figs 145, 146).

Chorion. Sculptured with a large-mesh (6-15 μm long) reticulation, the strands being formed by low, weakly developed ridges (Plate 13: fig. 148).

Attachment structures. Two small polar caps which, in the preserved state, appear to be of Type I; eggs laid in water were not available. An adhesive layer is also present, and, as in the ameletopsine Siphonuridae, it is distributed primarily only over the chorionic ridges (Plate 13: fig. 148, and as in Plate 1: fig. 4).

Micropyle. Linear type. Sperm guide an elongate canal (28-35 μm long) penetrating the adhesive layer and acutely angled to the chorion; micropylar canal also acutely angled to the chorion, proximally 15-18 μm long, distally shriveled, distorted, and at least 10 μm long.

FAMILY EPHEMERIDAE

The non-*Ephemera* Ephemerinae are herein called the *Hexagenia*-complex because of the similarity of those genera to each other and their collective dissimilarity from the genus *Ephemera*.

The presence of an adhesive layer and a supra-chorionic or suprachorionic-chorionic type of sperm guide, and the absence of any other type of attachment structures are the only features common to the eggs of the Ephemeridae. Chorionic sculpturing is too diverse to be useful as a familial characteristic—in addition to smooth chorions, there are those with small and large-mesh reticulations, punctures, tubercles, granulations, and irregular ridges. The strands of the reticulation in *Eatonica crassi* are low, centrally divided chorionic ridges (Plate 15: figs 168, 169); in *Litobranca recurvata* they are shallow chorionic grooves (Plate 17: fig. 186). Such conditions undoubtedly indicate low secretive activity by the sides of the respective follicle cells.

The adhesive layer is copious in most Ephemeridae, and in *Eatonigenia*, *Eatonica*, *Hexagenia* and *Pseudeatonica* it frequently contains a large-mesh reticulation formed by splits (Plate 15: fig. 173). In some cases the splits are bordered by adhesive layer thickenings (Plate 15: fig. 175), and in all cases except *Eatonigenia* the adhesive layer reticulation corresponds to a chorionic

one; in *Eatonigenia* the chorion lacks a reticulation. Koss (1970) found that the adhesive layer on Ephemeroptera eggs must be laid down by the follicle cells. This adhesive layer reticulation could be an indication of secretive activity of the follicle cells, or it could reflect compaction of the eggs during storage in the lateral oviducts. The lack of a corresponding chorionic reticulation on *Eatonigenia* eggs opposes the latter view, but the incompleteness of the adhesive layer reticulation on many *Hexagenia* and *Pseudeatonica* eggs confirms it. If the adhesive layer reticulation is a result of compaction of eggs during storage, then the feature would be taxonomically useless. Since this is not yet known, the nature of the adhesive layer reticulation has been discussed for those genera and species where it occurs. Aside from the reticulation, the adhesive layer is undifferentiated and of uniform density in most ephemerid genera; it is granular in *Ephemera* (Degrange, 1960; Koss, 1968).

Although the micropyle is usually of the linear type, the sperm guides assume many shapes from circular to elongate, and thus linear micropyles are not entirely characteristic of the family. The sperm guide is most often suprachorionic (Plate 14: figs 155-157; Plate 16: figs 176-178), but it also occurs as a groove in a chorionic ridge in most species of the *Hexagenia*-complex (Plate 16: figs 179, 181; Plate 17: fig. 192). In *Eatonigenia*, *Eatonica* and *Pseudeatonica* the elongate suprachorionic part of the sperm guide possesses a narrow channel along its base. In *Eatonica* and *Pseudeatonica* this channel extends to the chorion and the correspondingly grooved chorionic ridge (Plate 15: fig. 174; Plate 17: fig. 194). In other genera, the suprachorionic sperm guide is usually broadly based on the chorion, and thus lacks a basal channel (Plate 14: fig. 157; Plate 16: fig. 182). The sperm guide may possess a proximal hood formed by the adhesive layer.

The thick adhesive layer on most Ephemeridae eggs requires the development of a sperm guide for sperm to reach the micropylar canal. Two species of *Ephemera* (*E. japonica* and *E. sp. no. 2*) have exceedingly thin adhesive layers. In these species the sperm guide is essentially absent, and an oval break occurs in the adhesive layer just above the micropylar opening. The absence of a sperm guide, however, is by far exceptional in the Ephemeridae.

The micropylar canal is usually the most conspicuous part of the micropyle, and frequently it partially projects out of the chorion (Plate 14: fig. 153; Plate 17: fig. 189). In optical cross-section the canal walls proximally are usually parallel, and frequently thickened (Plate 14: fig. 161; Plate 17: fig. 188) or double (Plate 18: fig. 195); distally they are usually not doubled or thickened, but they may approximate each other (Plate 14: fig. 161; Plate 17: fig. 188).

It is not entirely possible to characterize the ephemerid groups utilizing eggs alone. However, there are some typical conditions found in most species studied in the respective groups. Most *Ephemera* lack a large-mesh reticulation (sculpturing varies, usually it is a small-mesh reticulation) and they possess various types of suprachorionic sperm guides. Species in the *Hexagenia*-complex usually possess a large-mesh chorionic reticulation and an elongate suprachorionic-chorionic sperm guide. The chorion of Ichthyotinae is punctate rather than reticulate and the linear micropyle lacks a sperm guide.

Previous descriptions. *Ephemera*: Bengtsson (1913), Percival & Whitehead (1926), Mosely (1926, 1938), Smith (1935), Johannsen & Butt (1941), Ando & Kawana (1956), Degrange (1956, 1960), Britt (1962), Koss (1968).

Hexagenia: Needham (1908), Neave (1932), Smith (1935), Hunt (1953), Koss (1968). *Ichthyotus*: Phillips (1930).

Key to genera

1. Chorion with a large-mesh (9-38 μm long) reticulation (Plate 16: fig. 183) 7
 Chorion without a large-mesh reticulation 2
2. Chorion finely punctate (Plate 18: figs 201, 202) 3
 Chorion variously sculptured, but not punctate 4
3. Chorion 6-7 μm thick *Ichthyotus*
 Chorion less than 4 μm thick *Ephemera guttulata* Pictet
4. Chorion variously sculptured, usually with a small-mesh reticulation; hollow tubercles absent most *Ephemera*
 Chorion smooth or covered with small (1.5 μm or less in diam) hollow tubercles (Plate 17: figs 186, 187) 5
5. Sperm guide absent *Ephemera japonica*
 Sperm guide present 6
6. Sperm guide an elongate, proximally expanded depression in the adhesive layer (Plate 16: figs 176, 177) *Eatonigenia chaperi*
 Sperm guide short, with a nearly circular opening in the adhesive layer due to a proximal sperm guide hood (Plate 17: fig. 187) *Litobrancha*
7. Strands of chorionic reticulation are centrally divided ridges (Plate 15: fig. 168) or shallow grooves visible at $\times 1000$ only (Plate 17: fig. 186) 8
 Strands of chorionic reticulation are well-defined ridges and not divided centrally except at micropyle (Plate 15: fig. 172; Plate 16: fig. 181) 9
8. Sperm guide short, proximal sperm guide hood forming a nearly circular opening in the adhesive layer (Plate 17: fig. 187); chorion sparsely tuberculate, each tubercle situated on a funnel-like puncture in the chorion (Plate 17: figs 185-187); reticulation formed by shallow chorionic grooves (Plate 17: fig. 186) *Litobrancha*
 Sperm guide an elongate, proximally expanded depression in the adhesive layer (Plate 15: fig. 170 and as in Plate 16: fig. 176); chorion not tuberculate; reticulation formed by low, centrally divided, chorionic ridges (Plate 15: fig. 168) *Eatonica crassi*
9. Hollow chorionic tubercles present (Plate 15: fig. 172) *Eatonica schoutedeni*
 Hollow chorionic tubercles absent 10
10. Sperm guide groove in ridge of reticulation complete (Plate 16: fig. 181), or if incompletely developed (Plate 16: fig. 179), then a single tubercle present on adhesive layer within each area corresponding to a mesh of the reticulation *Hexagenia*
 Sperm guide groove in ridge of reticulation incompletely developed except proximally (Plate 17: fig. 192); adhesive layer tubercles absent *Pseudeatonica*

Subfamily Ephemerinae
Genus *Ephemer* Linnaeus

There are no features common to the genus except those common to the family. However, use of the combination of characters seen in the chorion, sperm guide and micropylar canal will serve to separate *Ephemer* eggs from those of other known Ephemeridae.

Although the commonest chorionic sculpturing in the genus is a small-mesh reticulation, there is a wide range of sculpturing patterns which include punctures, granulations and irregular ridges (Plate 14: figs 154, 162; Plate 15: fig. 165). At least one species has a smooth chorion. The adhesive layer is granular as noted by Degrange (1960) and Koss (1968).

The sperm guide is not "an elongate depression [in the chorion] devoid of sculpturing" as described by Koss (1968). Instead, it is suprachorionic, and only rarely does it bear a counterpart in the chorion (*E. guttulata* has a proximal depression in the chorion). The sperm guide is a complete break or void in the adhesive layer, and thus it extends completely to the chorion (Plate 14: fig. 157). The diversity of shapes includes elongate and narrow, elongate and distally expanded, and ovoid to nearly circular (Plate 14: figs 152, 155, 156, 159, 163, 164). If distally expanded, the expansion may be gradual (Plate 14: fig. 155) or sudden (Plate 14: figs 163, 164). A proximal sperm guide hood may be present.

The micropylar canal is as often definitely two-part as not. The walls may be thickened proximally, thinned and approximating distally, or they may be completely undifferentiated. The micropylar canal may or may not partially project out of the chorion (Plate 14: fig. 153).

Ephemer danica Muller
(Plate 14: fig. 152)

Details of the chorion and adhesive layer similar to that described by Degrange (1960) and Koss (1968, for *E. simulans* and *E. varia*).

Micropyle. Position and orientation like that described by Degrange (1960). However, Degrange describes for *E. danica* eggs a "tube" which projects out for 12 μm above the chorion and also internally for 22 μm) ["... d'un tube d'abord en saillie (12 μm) puis interne (22 μm)"]. The micropyle is not like this on the *E. danica* eggs available for this study. The micropyle (Plate 14: fig. 152) consists of a small, nearly circular sperm guide (5-8 μm long) and an elongate micropylar canal (at least 30 μm long). The canal is not of two parts; the walls are of uniform thickness, and they do not approximate inwardly or project above the chorion.

Ephemer japonica McLachlan

Chorion. Smooth.

Attachment structures. An exceptionally thin adhesive layer.

Micropyle. One per egg; sperm guide essentially absent, and oval break occurs in the adhesive layer just above the micropylar opening; micropylar canal elongate, 42-55 μm long.

Ephemera supposita Eaton
(Plate 14: figs 154-157)

Chorion. Sculptured with a small (2.0-5.5 μm long), irregular, circular-mesh reticulation (Plate 14: fig. 154).

Micropyle. Sperm guide elongate (65-73 μm long), usually with a gradual distal expansion (width varying from 4.5 μm at micropylar opening to 33 μm at widest area of expansion) (Plate 14: figs 155-157); micropylar canal 11-30 μm long, with undifferentiated parallel walls.

Ephemera vulgata Linnaeus
(Plate 14: fig. 159)

Degrange (1960) correctly stated that the chorion and adhesive layer are like that of *E. danica*. However, the micropyle of the two species differs. The sperm guide of *E. vulgata* (Plate 14: fig. 159) is elongate (18-25 μm long), not ovoid as in *E. danica*; and the micropylar canal has thick parallel wall proximally (17-22 μm long) and thinner, approximating wall distally (7-11 μm long).

Ephemera sp. no. 1
(Plate 14: fig. 158)

Chorion. Sculptured with a small-mesh (1-3 μm long) reticulation; the egg is longitudinally sulcate (Plate 14: fig. 158).

Attachment structures. Adhesive layer granular, mostly distributed in the sulci of the chorion (Plate 14: fig. 158); a thin coating of the adhesive material occurs on areas between the sulci.

Micropyle. Tagenoform; sperm guide (7-10 μm long, 6-11 μm wide) a nearly circular break in the adhesive layer (as in Plate 14: fig. 152); micropylar canal 16-30 μm long, thick-walled proximally, thin-walled distally.

Ephemera sp. no. 2
(Plate 14: figs 160, 161)

Chorion. The sculpturing may be interpreted as large punctures or a very small-mesh (0.75-1.2 μm long) reticulation (Plate 14: fig. 160).

Attachment structures. An exceedingly thin adhesive layer.

Micropyle. Sperm guide lacking, an oval break occurs in the adhesive layer just above the micropylar opening; micropylar canal 42-46 μm long, with wall slightly thickened proximally, slightly approximating distally (Plate 14: fig. 161).

Ephemera sp. no. 3
(Plate 14: fig. 162)

Chorion. Coarsely granulate with irregularly shaped granules (Plate 14: fig. 162).

Micropyle. A proximal sperm guide hood (3-8 μm long) forms an oval, distal

break (11-16 μm long, 6-8 μm wide) in the adhesive layer; micropylar canal 20-31 μm long, thick-walled proximally, and with thin, approximating walls distally.

Ephemera sp. no. 4

(Plate 14: fig. 164; Plate 15: fig. 165)

Chorion. Sculptured with an irregular, but not a reticular, pattern of ridges (1 μm wide) (Plate 15: fig. 165).

Micropyle. (Plate 14: fig. 164.) Sperm guide suprachorionic, elongate (37-50 μm long) with a sudden distal expansion (16-29 μm wide), and usually with a basal hood (3-4 μm long). Micropylar canal 24-28 μm long, with short (7-9 μm long), very thick, proximal walls (Plate 14: fig. 164), and longer (17-21 μm long), thin, distal wall.

Ephemera sp. no. 5

(Plate 15: fig. 166)

Chorion. With a small-mesh (2-4 μm long) reticulation formed by ridges.

Micropyle. Sperm guide ovoid, 5-6 μm long, 4-5 μm wide; micropylar canal with proximal part expanded (7-15 μm long, 4.5-6 μm wide), then suddenly narrowed at junction with double-walled distal part (13-20 μm long) (Plate 15: fig. 166).

Ephemera sp. no. 6

(Plate 15: fig. 167)

Chorion. Densely punctate, punctures 1-2 μm in diam; and with a faint large-mesh (20-27 μm long) reticulation the strands being formed by shallow chorionic grooves.

Micropyle. Sperm guide lacking; micropylar canal 25-29 μm long, with a "heart-shaped" proximal portion which projects above the chorion and through the adhesive layer.

Ephemera spp.

(Plate 14: fig. 163)

Chorion. With a small-mesh reticulation typical of most *Ephemera*, and characterized by *E. danica* and *E. simulans*; in some cases, mesh (1-5 μm long) more circular than irregular polygonal.

Micropyle. Depending on the species, the sperm guide may be either elongate and narrow, or elongate with a distal expansion. If distally expanded, the expansion may be gradual (as in Plate 14: fig. 155) or sudden (Plate 14: fig. 163). In most specimens examined from the listed localities, the micropylar canal is not as distinctly divided into two parts as described by Koss (1968) for the genus; the canal walls are only slightly thickened proximally, and slightly approximated distally (as in Plate 14: fig. 161). The walls do not project above the chorion.

Genus *Eatonica* Navas

A linear micropyle and a large-mesh chorionic reticulation formed by ridges are the only features common to both known species of *Eatonica*. These characters are insufficient to distinguish this genus from *Hexagenia* and *Pseudeatonica*. Eggs of the latter genera, however, lack the hollow chorionic tubercles found in *Eatonica schoutedeni* and the centrally divided ridges found in *Eatonica crassi*. In addition, the chorionic ridge portion of the sperm guide is a shallow and often incomplete groove, it is frequently connected to the adhesive layer portion of the sperm guide by a thin channel (Plate 15: figs 170, 174). These sperm guide features are also found on *Pseudeatonica* eggs, but not on those of *Hexagenia*.

Eatonica schoutedeni (Navas)

(Plate 15: figs 171-175)

Chorion. Large-mesh (16-28 μm long) reticulation formed by straight or slightly sinuous ridges 1-3.1 μm wide (Plate 15: fig. 172); many small hollow tubercles (2-3 μm outside diam at base) within the mesh and occasionally on or abutting the ridges (Plate 15: fig. 172). Chorion 5.5-7.8 μm thick including ridges; 3.9-6.6 μm thick excluding ridges.

Attachment structures. An adhesive layer varying from 2-31 μm in thickness; thicker regions at the poles, thinner regions (2-10 μm , usually 10 μm) located laterally. The adhesive layer possesses a large-mesh reticulation formed by splits in the adhesive material (Plate 15: figs 173, 175). A tangential view of the egg shows that these splits extend to the chorion and are bordered by thickenings in the basal two-thirds of the adhesive layer (Plate 15: fig. 175). They usually follow a slanted path, but their bases are always adjacent to or on ridges of the chorion.

Micropyle. Sperm guide an elongate depression in the adhesive layer, and usually a thin, shallow, often incompletely developed groove in a ridge of the reticulation. The suprachorionic portion is frequently shallow and ill-defined distally; and, for most of its length, there is a thin channel extending from its base to the chorion (Plate 15: fig. 174). This channel is especially apparent when the adhesive layer is thick; when thin, the shallow expansion contacts or nearly contacts the chorion and the channel is absent. The ill-defined nature of the suprachorionic portion of the sperm guide makes it impossible to find its terminus, and thus to measure its length; the apparent portion is 25-50 μm long, whereas the channel in the reticulation is as much as 65 μm long. It is also impossible to determine from the available material whether a sperm guide hood is present or absent. Micropylar canal with a double-walled proximal part (17-36 μm long) and a single-walled distal part (5.4-11 μm long). The canal projects above the surface of the chorion (Plate 15: fig. 171).

Eatonica crassi McCafferty

(Plate 15: figs 168-170)

Chorion. With a large-mesh reticulation formed by low, centrally divided chorionic ridges (Plate 15: figs 168-169). Chorion 3.9-5.4 μm thick, including

ridges; and coarsely tuberculate, tubercles not small and hollow like those in *E. schoutedeni*.

Attachment structures. Adhesive layer only 2-3 μm thick, lacking splits and reticulation (Plate 15: figs 169, 170).

Micropyle. (Plate 15: fig. 170.) Similar to *E. schoutedeni* except micropylar canal is longer (double-walled proximal part 34-39 μm long, single-walled distal part 3-13 μm long, on specimens from Sudan and Lake Victoria; proximal part 50-64 μm long, distal part 3-6 μm long on specimens from Nyasaland) and suprachorionic sperm guide distally ovoid, occasionally with a weakly developed proximal hood 5.5-11 μm long.

Genus *Eatonigenia* Ulmer

The single species then known was examined.

Eatonigenia chaperi (Navas) (Plate 16: figs 176, 177)

Chorion. Very finely granulate; reticulation absent. Chorion 2.0-2.7 μm thick.

Attachment structures. Adhesive layer 5-9 μm thick, showing on its surface a very weakly developed large-mesh (16-27 μm long) reticulation of straight strands (approx. 0.3 μm wide) formed by splits in the adhesive material (Plate 16: fig. 176). It was not possible to ascertain whether or not the splits extend to the chorion because they are not bordered by adhesive layer thickenings.

Micropyle. Sperm guide an elongate (45-57 μm long), shallow depression in the adhesive layer (Plate 16: figs 176, 177); it is not as deep as the sperm guide on *Pseudeatonica* eggs but it is more definite distally than those on *Eatonica* eggs. For most of its length, the sperm guide possesses a very shallow basal channel (Plate 16: fig. 177; Plate 22: fig. 230), but it does not extend to the chorion as in *Eatonica*. Sperm guide with a proximal hood (3-9 μm long), and with an oval expansion just distal to the hood. Micropylar canal 37-45 μm long, with double walls only.

Genus *Hexagenia* Walsh

The genus is characterized by the elongate suprachorionic-chorionic sperm guide and a large-mesh chorionic reticulation formed by well-defined ridges (Plate 16: figs 179-184). The sperm guide consists of an elongate, broadly-based void or depression in a thin adhesive layer (Plate 16: figs 178, 182), and a well-developed groove in a ridge of the reticulation (Plate 16: fig. 181). The suprachorionic part lacks a channel connecting it to the chorion, and a proximal expansion is the most readily visible portion of both the suprachorionic and chorionic portions.

Hexagenia eggs can be separated from those of *Pseudeatonica* only by the degree of development of the chorionic ridge portion of the sperm guide; the groove is deep and well-defined in *Hexagenia* (Plate 16: figs 179, 181), but shallow and often incomplete in *Pseudeatonica* (Plate 17: fig. 192). *Hexagenia* eggs lack the hollow chorionic tubercles found in *Eatonica schoutedeni*, and the centrally divided ridges found in *Eatonica crassi*.

Hexagenia bilineata (Say)
(Plate 16: figs 178-180)

Chorion. Large-mesh (15-34 μm long) reticulation formed by straight ridges 1.6-1.9 μm wide. Chorion 4.3-6.6 μm thick including ridges, 3.5-4.7 μm thick excluding ridges.

Attachment structures. Adhesive layer 2.3-3.9 μm thick, with a surface reticulation of splits which extend to the chorion. The reticulation, however, does not cover the entire surface of the egg, and the splits are not bordered by thickenings. On the surface of the adhesive layer, there is a single tubercle (2.5-3.7 μm in diam) within the area corresponding to each mesh of the chorionic reticulation (Plate 16: fig. 179). It is not always centrally located, and the presence of these tubercles is a feature common to *H. rigida* eggs also (Plate 16: fig. 184) (see Koss, 1968). Smith (1935) and Koss (1968) incorrectly ascribed these tubercles to the chorion.

Micropyle. Sperm guide an elongate (25-60 μm long), narrow depression in the adhesive layer (Plate 16: figs 178-180), and a slight groove in a ridge of the reticulation (Plate 16: fig. 179); sperm guide hood absent; micropylar canal 67-78 μm long. The weakness of the chorionic sperm guide groove in a ridge of the reticulation indicates that *H. bilineata* may be a primitive member of the genus.

Hexagenia limbata venusta Eaton

Chorion 5.4-6.2 μm thick including ridges, 4.6-5.4 μm thick excluding ridges. The adhesive layer (1.0-3.1 μm thick) possesses a surface reticulation of splits, but the reticulation does not encompass the entire egg. Sperm guide with a proximal hood 3.1-5.5 μm long.

Genus *Litobrancha* McCafferty

The genus contains a single known species.

Litobrancha recurvata (Morgan)
(Plate 17: figs 185-189)

Chorion. Chorion 4.0-6.2 μm thick. Inner layer very finely punctate; outer layer sparsely tuberculate, and with a faint, large-mesh (20-31 μm long) reticulation. The reticulation is formed by extremely shallow grooves in the chorion and is usually visible at $\times 1000$ only. The most obvious feature of the chorion is the sparse covering of small tubercles. Each tubercle is situated on a funnel-like puncture in the chorion; punctures 0.5-1.5 μm inside diam at surface of chorion.

Attachment structures. An adhesive layer (1.5-2.5 μm thick) which lacks all indications of a reticulation.

Micropyle. Sperm guide short, narrow and with a proximal sperm guide hood formed by the adhesive layer. Unhooded portion of sperm guide circular (Plate 17: fig. 187), 5.0-7.5 μm in diam; hood 1-7 μm long. Micropylar canal (Plate 17: figs 187, 188) with a thick double-walled proximal part (46-62 μm long)

which tapers suddenly at the junction with a thin single-walled distal part (3-7 μm long). The canal partially projects out of the chorion (Plate 17: fig. 189).

Genus *Pseudeatonica* Spieth

Since eggs of only one species were available, it is not possible to generically characterize the egg stage of *Pseudeatonica*. The large-mesh reticulation is probably typical of the genus.

Pseudeatonica albivitta (Walker)

(Plate 17: figs 190-194; Plate 18: figs 195-196)

Chorion. Large, irregular, polygonal mesh (9-38 μm long, usually 17-38 μm long) reticulation formed by well-developed ridges which are straight and narrow (1 μm wide) at the top, but wider (1.5-2.0 μm wide) and slightly sinuous at the base. Chorion 6-7 μm thick including ridges; 3.9-4.7 μm thick excluding ridges.

Attachment structures. An adhesive layer 7-12 μm thick. The reticulation seen on the surface of the adhesive layer is weak and incomplete. The splits extending to the chorion are thinner than in *Eatonica schoutedeni*, and they are bordered by weak thickenings.

Micropyle. Sperm guide an elongate (70-94 μm long) narrow depression in the adhesive layer (Plate 17: figs 190, 193, 194; Plate 18: fig. 196), and a slight, incompletely developed groove in a ridge of the reticulation (Plate 17: fig. 192). The suprachorionic portion closely follows the path of the grooved ridge below, and it possesses a proximal hood (3.9-11 μm long). The groove in the reticulation is not as well-developed as it is in *Hexagenia* except for the proximal 7-13 μm ; occasionally it is completely lacking. Suprachorionic part of sperm guide wider proximally and deeper than in *Eatonigenia* and *Eatonica*; it is either broadly based and lacking a channel connecting it to the chorion (Plate 18: fig. 196), or it possesses a very short one (Plate 17: fig. 194). Micropylar canal 30-54 μm long, with a long (20-47 μm long) double-walled proximal part, and a short (6-10 μm long) single-walled distal part (Plate 18: fig. 195).

Subfamily *Ichthybotinae*

Genus *Ichthybotus* Eaton

The subfamily and single genus are at least characterized by the punctate chorion. Phillips (1930, pl. 50) illustrated the egg of *I. hudsoni* (McLachlan) well enough to show the sculpturing and micropylar canal; he did not describe the egg.

Ichthybotus bicolor Tillyard?

(Plate 18: figs 201-203)

Chorion. The punctures seen in surface view (Plate 18: fig. 201) extend completely through the chorion, and bear a slight internal expansion (Plate 18: fig. 202); chorion 6-9 μm thick.

Attachment structures. An adhesive layer which is mostly concentrated at the poles of the eggs (Plate 18: figs 202, 203).

Micropyle. (Plate 18: fig. 201.) Sperm guide lacking; micropylar opening 7-10 μm in diameter. Micropylar canal elongate (59-84 μm long), walls slightly approximate distally. In the area of the micropylar canal, the punctures only extend from below the canal inward, i.e. they are always found below the canal, but not above it (Plate 18: fig. 202).

Remarks. In surface view and structure of the chorion, the egg of *Ichthybotus* is very similar to that described by Koss (1968) for *Ephemera guttulata* Pictet. However, the chorion of *E. guttulata* is only 2.5 μm thick, whereas it is 6-9 μm thick on *Ichthybotus* eggs.

FAMILY PENTAGENIIDAE

This family was recently erected for *Pentagenia* and tentatively for *Fontainica* (McCafferty, 1972). The features described below for the eggs of *P. vittigera* and *P. sp.* must presently be considered characteristic of the family, since other data are not available.

Previous description. *Pentagenia*: Smith (1935).

Genus *Pentagenia* Walsh
Pentagenia vittigera (Walsh)
(Plate 18: figs 197-200)

Chorion. With small (0.8-2.3 μm long) irregularly shaped punctures randomly scattered about the chorion. The smallness of the punctures, the amount of chorion between them, their irregular shapes, and random, uneven arrangement indicate that this may be a poorly developed form of the small-mesh reticulation common to most known *Ephemera*.

Attachment structures. An adhesive layer (Plate 18: figs 198, 200).

Micropyle. One per egg and tageniform, thus unique to the family. The sperm guide is elongate (55-94 μm long) but definitely ovoid (17-58 μm wide), and suprachorionic (Plate 18: fig. 197). The micropylar canal projects 10-16 μm above the chorion (not at a 90° angle) out of a shallow depression 14-22 μm in diameter (Plate 18: figs 198-199); the ovoid micropylar opening (3.9-6.0 μm long) is, therefore, positioned above the surface of the chorion (Plate 18: fig. 200). The non-projecting part of micropylar canal is 14 μm long. The homologue of this canal type is possibly seen in the pincer-like nature of the micropylar canal in *Ephemera* in which the walls of the canal project slightly above the chorion (Plate 17: fig. 153).

Pentagenia sp. Texas

Like *P. vittigera* except the chorion is smooth and the non-projecting part of the micropylar canal is long (16-33 μm long) and narrow (1-2 μm wide, outside dimensions).

FAMILY POLYMITARCIDAE

Eggs of the three subfamilies of Polymitarciidae have no characters in common except for the possession of attachment threads which lack terminal knobs. The threads are apically divided into countless fibers which spread in all directions, perhaps functioning as a terminal knob somewhat like that shown in Plate 13: fig. 150. Attachment threads are found in all subfamilies, but not in all genera. In at least one genus in each subfamily, the attachment threads are organized into polar caps; however, those of the Polymitarciinae are Type II and quite unlike the Type III caps of Campsurinae and Asthenopodinae. Also, strikingly different micropyles and chorionic sculpturing occur among the three subfamilies.

Previous descriptions. *Asthenopodes*: Traver (1956). *Campsurus*: Needham & Murphy (1924), Smith (1935), Roback (1966). *Ephoron*: Burmeister (1848), Leuckart (1855), Morgan (1913), Chopra (1927), Ide (1935), Smith (1935), Edmunds, Nielsen & Larsen (1956), Degrange (1956, 1960), Britt (1962), Koss (1968). *Povilla*: Hartland-Rowe (1958). *Tortopus*: Needham & Murphy (1924), Smith (1935), Koss (1968).

Key to subfamilies and genera

1. Polar cap (Type II) composed of many tubular-shaped accumulations of attachment threads (Plate 18: figs 204, 206)
 Polymitarciinae, *Ephoron*
 Polar cap(s) (Type III) composed of many threads loosely coiled about the pole(s) (Plate 19: figs 207, 211), or polar caps absent . 2
2. Eggs C-shaped, resembling a sphere with one side pushed in; chorion usually punctate (Plate 19: figs 207-210); polar caps, when present, at one pole only (Plate 19: fig. 207) Campsurinae
 Eggs ovoid, not C-shaped; chorion variously sculptured, but not punctate (Plate 19: figs 211-213); polar caps, when present, at both poles (Plate 19: fig. 211) Asthenopodinae, 3
3. Two polar caps present (Plate 19: fig. 211); chorion covered with many disc-like structures (Plate 19: figs 212, 213)
 *Asthenopodes* and *Asthenopus*
 Polar caps absent, eggs enveloped in a mass of loosely coiled threads (Plate 19: fig. 214); chorion maculate *Povilla*

Subfamily Campsurinae

Eggs of this subfamily are characterized by their unusual shape, the micropyle and usually the chorionic sculpturing. The eggs are more or less C-shaped, resembling a sphere that has had one side pushed in. The chorion is usually punctate, although the size of the punctures varies among the species; one unidentified species of *Campsurus* was observed to have a smooth chorion, and another to have a tuberculate one. There is one funnellform micropyle per egg, and it is located equatorially. The sperm guide is a shallow, often indistinct

chorionic depression with punctures slightly developed or absent. The micropylar opening is centrally located in this depression, and the micropylar canal is somewhat acutely angled to the chorion (Plate 19: fig. 209).

Genus *Campsurus* Eaton
(Plate 19: figs 207, 208)

Several different types of eggs occur in this genus, and the only features that they all have in common are those typical of the subfamily (i.e. a "C" shape, and funnelform micropyle).

One group of eggs (including *C. decoloratus*, as in Plate 19: fig. 207) possesses a single Type III polar cap composed of many threads loosely coiled about the pole. In this group, eggs have been found with either a finely punctate chorion or a smooth one. In one instance the polar threads were always disarranged, not coiled about the pole.

In a second group of eggs the polar cap is entirely absent, the only attachment structure being a copious adhesive layer (Plate 19: fig. 208). Most of these species have finely punctate chorions (punctures 1-3 μm in diam), but at least one species has a chorion with very large punctures (7.5-10 μm in diam).

In two other species the eggs are unique. One has a finely punctate chorion and an amorphous mass of fibers on the convex side of the egg. The other has a typical Type III polar cap and a tuberculate chorion. The tubercles are arranged into a large-mesh reticulation on some surfaces.

Genus *Tortopus* Needham & Murphy
(Plate 19: figs 209, 210)

Koss (1968) described eggs of two species of *Tortopus*. They are characterized by the absence of polar caps, and the presence of a well-developed filamentous adhesive layer (Plate 19: fig. 210), punctate chorion, and fairly distinct sperm guide (Plate 19: fig. 209).

Subfamily *Asthenopodinae*

Asthenopodes and *Asthenopus* are very similar and distinguished from *Povilla* by the lack of polar caps in the latter genus. The only feature common to all three genera is the presence of attachment threads. Only a single, broken micropyle was found, and thus the micropyle for this subfamily is not well known.

Asthenopodes sp.

Eggs of *Asthenopodes* sp. are very similar to those of *Asthenopus* sp. (see below), the only apparent distinction between them being the size of the polar caps. They average 135 μm or more in width on eggs of *Asthenopus* sp., but are about 100 μm or less in width on *Asthenopodes* sp. eggs. This distinction, however, is not based on very many specimens.

Asthenopus sp.
(Plate 19: figs 211-213)

Chorion. Densely covered with many discoid formations 25-35 μm in diameter which are usually subdivided 2-7 times; each subdivision contains a single peglike structure (Plate 19: figs 212-213). The discs sit on the chorion (Plate 19: fig. 212) and their function is unknown. Much smaller discs (4-12 μm in diam) occur in the spaces between the larger ones.

Attachment structures. Two Type III polar caps (Plate 19: fig. 211), each composed of many threads loosely coiled about the respective poles.

Micropyle. Unknown.

Povilla adusta Navas
(Plate 19: fig. 214)

Chorion. Maculate.

Attachment structures. Each egg is almost entirely enveloped in a mass of loosely coiled threads (Plate 19: fig. 214). A thin gelatinous-like adhesive layer is also present. Hartland-Rowe (1958 and pers. comm.) described the egg mass formed when the female lays the eggs in water. We have also examined egg masses laid in water and preserved later. The eggs are laid in two elongate gelatinous masses approximately 25-50 mm long; each egg mass bears a group of twisted fibers at each end. Although the eggs are enveloped in a fibrous mass, they can be separated from it and the attachment threads mentioned above can be discerned. The threads apparently aid in the formation and attachment of the egg mass rather than attachment of any individual egg.

Micropyle. Only a broken tageniform one was found, located in the equatorial region. The sperm guide is poorly defined, oval and seemingly situated in the thin adhesive layer; part of the micropylar canal appears to be raised above the chorion. Sperm guide approximately 16 μm long, 13 μm wide; micropylar canal 15 μm long.

Subfamily Polymitarcinae

A unique polar cap (Type II) separates this subfamily, and its single genus *Ephoron*, from the other subfamilies of Polymitarcidae. The single polar cap (Plate 18: figs 204, 206) is composed of several tubular-shaped accumulations of threads lacking terminal knobs. As many as five tageniform micropyles have been found at the capped end of the egg; the oval sperm guide is poorly-defined distally, and well-defined proximally. There is a proximal sperm guide hood formed by the chorion, and this, together with the proximal expansion of the micropylar canal, form the "demi-callote" referred to by Degrange (1960).

FAMILY PALINGENIIDAE

Eggs of Palingeniidae were not available for study, and the description of the egg of *Anagenesia minor* (Eaton) by Chopra (1927) is the only egg description known for the entire family. Chopra does not describe the chorionic sculpturing or micropyle, but indicates that the egg is discoidal and without any attachment structures.

SUPERFAMILY CAENOIDEA

A Type III polar cap is typical of most Caenoidea. One or two polar caps are present, and they are formed by many tightly spiraled, knob-terminated threads coiled about the pole(s). The knobs are usually small, only 2-3 times the diameter of the threads; however, the terminal knobs are 5-6 times the thread diameter in *Tasmanocoenis*. Upon contact with the water, the threads uncoil and unspiral to become entangled with submerged surfaces (Koss, 1968). *Neoephemera* eggs lack polar caps but instead possess a dense filamentous adhesive layer. The micropyle is usually a linear type but it may be a poorly developed tageniform type; the former seems plesiomorphic for the superfamily. Neoephemerid eggs are not known well enough to enable construction of keys to separate them familiarly or generically from the Caenidae.

FAMILY NEOEPHEMERIDAE

The chorion of *Potamanthellus* eggs may possibly be considered rugulose. If so, this is the only feature common to both *Potamanthellus* and *Neoephemera* (*Oreianthus*) eggs, since the chorion of the latter is definitely rugose.

Previous description. Neoephemera: Smith (1935).

Key to genera

1. With two polar caps; filamentous adhesive layer absent (Plate 19: fig. 216). *Potamanthellus* sp.
- Polar caps lacking; filamentous adhesive layer present (Plate 19: fig. 215). *Neoephemera* (*Oreianthus*) *purpurea*

Neoephemera (*Oreianthus*) *purpurea* (Traver)
(Plate 19: fig. 215)

Chorion. Rugose.

Attachment structures. A dense, filamentous adhesive layer covering the entire egg.

Micropyle. Unknown.

Potamanthellus sp.
(Plate 19: fig. 216)

Chorion. The chorion is so densely granulate with irregularly shaped granules that it may possibly be considered to be rugulose.

Attachment structures. Two Type III polar caps, each consisting of many knob-terminated threads coiled about the pole.

Micropyle. A very indistinct tageniform type. Sperm guide (approximately 20 μ m in diam) a poorly defined, shallow, circular depression in the chorion; micropylar canal with walls so weak that their length cannot be ascertained.

FAMILY CAENIDAE

Although eggs of only three of the six genera of Caenidae have been studied, it appears that the family can be characterized by the unique Type III polar cap(s), conspicuous micropylar canal, and the lack of a well-developed sperm guide. The micropyle is usually a linear type lacking a sperm guide, but a poorly developed oval sperm guide is frequently present on *Tasmanocoenis* eggs.

Previous descriptions. *Brachycercus*: Smith (1935). *Caenis*: Leuckart (1855), Ulmer (1913), Bengtsson (1913), Smith (1935), Grandi (1942), Harker (1950), Bruggen (1954), Degrange (1956, 1957, 1960), Koss (1968).

Key to genera

1. With one polar cap; chorion costate *Brachycercus*
With two polar caps, or if only one, chorion not costate 2
2. Usually two micropyles present; sperm guide occasionally absent, but usually a shallow, poorly-defined, oval chorionic depression; diameter of terminal knobs 5-6 times that of threads *Tasmanocoenis*
Usually one micropyle present; sperm guide lacking; diameter of terminal knobs 2-3 times that of threads *Caenis*

Genus *Brachycercus* Curtis
(Plate 20: figs 217-219)

Brachycercus eggs are characterized by a single polar cap and a costate chorion. Only one linear micropyle per egg has been found, and it is situated in or adjacent to a chorionic costa or traversing the space between two costae (Plate 20: fig. 218); a sperm guide is lacking.

Genus *Caenis* Stephens
(Plate 20: figs 220-221)

Numerous authors (see above) have described eggs of several species of *Caenis*, and there are no features unique to the genus. Most known species have two polar caps, but Degrange (1960) and Koss (1968) each report a species with a single polar cap. The sperm guide is lacking on all known *Caenis* eggs, and the description by Koss (1968) of its presence on *C. forcipata* and *C. jocosa* eggs is in error. What was previously described and illustrated as the sperm guide, is actually a distal portion of the micropylar canal. In Plate 20: fig. 221 the micropyle has been correctly labeled for a *C. jocosa* egg. Only *C. horaria* (L.) is known to have two micropyles per egg; all other known *Caenis* eggs have just one. No *Caenis* species are known to have chorionic costae as found in *Brachycercus*, and this feature will distinguish "one-capped" *Caenis* eggs from *Brachycercus* eggs.

Genus *Tasmanocoenis* Lestage
(Plate 20: fig. 222)

Tasmanocoenis eggs are very similar to those of many *Caenis* species, since two polar caps are present and the chorion is finely punctate. However, there are a few characters useful for separating eggs of *Tasmanocoenis* from *Caenis*. When present, the sperm guide is a very weakly-developed, shallow, unbordered, oval depression in the chorion. Two micropyles per egg is normal, and the terminal knob diameter is 5-6 times that of the attachment threads.

SUPERFAMILY PROSOPISTOMATOIDEA

FAMILY BAETISCIDAE

Genus *Baetisca* Walsh

Baetisca eggs apparently do not withstand preservation in alcohol well enough to be studied. They quickly shrivel beyond usefulness and apparently the best way to obtain eggs for study would be to dissect them from living adult females. This was not possible for this study. All that could be discerned on the available *Baetisca* eggs is that the chorion is smooth or finely granulate, and they possess a mass of fibers more or less resembling an undersized, unorganized Type III polar cap. As in the Caenidae the fibers are terminated by very small knobs.

Previous description. Smith (1935).

FAMILY PROSOPISTOMATIDAE

Genus *Prosopistoma* Latreille
Prosopistoma africanum Gillies
(Plate 20: figs 223-224)

Chorion. Densely tuberculate.

Attachment structures. An adhesive layer approximately 0.75 μm thick, and what appears to be a pair of irregularly coiled threads (Plate 20: fig. 223).

Micropyle. Tagenoform (Plate 20: fig. 224).

Remarks. These eggs are not at all similar to those of *P. pennigerus* described by Degrange (1960) except that they have tagenoform micropyles.

Previous descriptions. Vayssiere (1881), Gillies (1954), Degrange (1960).

ACKNOWLEDGEMENTS

During the course of this research, two graduate students in our lab, Steven L. Jensen and William P. McCafferty, were engaged in revisionary studies of the Heptageniidae and Ephemeridae, respectively. We are grateful to them for loaning us borrowed specimens under their care, and for contributing information about the families which they were studying.

The following individuals are thanked for supplying eggs of particular genera and species not available in the University of Utah collection: Richard K. Allen, Los Angeles State College; K. E. Gibbs, MacDonald College, Quebec; Charles D.

Grant, University of Ghana; Vladimir Landa, Institute of Entomology, Prague, Czechoslovakia; William L. Peters, Florida A. & M. University; and Jay R. Traver, University of Massachusetts.

REFERENCES

- ANDO, H. & KAWANA, T. 1956. Embryology of may-fly (*Ephemera strigata* Eaton) as studied by external observation. *Kontyu*, 24: 224-32.
- BEAMENT, J. W. L., 1946. The formation and structure of the chorion of the egg in an Hemipteran, *Rhodnius prolixus*. *Q. Jl microsc. Sci.*, 87: 393-439.
- BENGTSSON, S., 1913. Undersökningar öfver äggen hos Ephemeriderna. *Ent. Tidskr.*, 34: 271-320.
- BERNHARD, C., 1907. Über die vivipare Ephemeride *Chloeon dipterum*. *Biol. Zbl.*, 27: 467-79.
- BOGOESCU, C. D., 1951. Donă specii noi de Ephemeroptere in Republica Populară Română. *Comun. Acad. R. P. R.*, 1: 781-86.
- BRODSKY, K., 1930. Zur Kenntnis der mittelasiatischen Ephemeropteren I. (Imagines). *Zool. Jb. Abt. Syst.*, 59: 681-720.
- BRITT, N. W., 1962. Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. *Ohio biol. Surv. (N.S.)* 1(5): 1-70.
- BRUGGEN, A. C. VAN, 1954. *Caenis demoulini*, a new Ephemeroptera from Thailand. *Zoöl. Meded., Leiden*, 33: 11-5.
- BURKS, B. D., 1953. The mayflies, or Ephemeroptera, of Illinois. *Bull. Ill. St. nat. Hist. Surv.*, 26: 1-216.
- CHOPRA, B., 1927. The Indian Ephemeroptera. *Rec. Indian Mus.*, 29: 91-138.
- CLEMENS, W. A., 1917. An ecological study of the mayfly Chironetes. *Univ. Toronto Stud. Biol. Ser.*, 17: 1-43.
- COBLEN, R. H., 1968. *Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embryology and eclosion*, 475 pp. Centre for Agricultural Publishing and Documentation, Wageningen.
- CRASS, R. S., 1947. The mayflies (Ephemeroptera) of Natal and the Eastern Cape. *Ann. Natal Mus.*, 11: 37-110.
- DAVIDSON, A., 1956. A method of counting Ephemeroptera eggs. *Entomologist's mon. Mag.*, 92: 109.
- DEGRANGE, C., 1956. Sur les micropyles des oeufs des Éphéméroptères. *Bull. Soc. ent. Fr.*, 61: 146-8.
- DEGRANGE, C., 1957. Deux *Caenis* nouveaux pour la faune française: *C. robusta* Eaton et *C. rivulorum* Eaton (Ephem.). *Bull. Soc. ent. Fr.*, 62: 75-7.
- DEGRANGE, C., 1960. Recherches sur la reproduction des Éphéméroptères. *Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble*, 51: 7-193.
- DEGRANGE, C. & PERRIER, R., 1957. L'oeuf et la larve néonate de *Rhithrogena semitincta* (Pictet) (Éphéméroptère). *Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble*, 49: 9-16.
- DEMOULIN, G., 1952. Sur les affinités Siphonuridiennes du genre *Metreletus* Demoulin, 1951. (Insectes Éphéméroptères). *Bull. Inst. r. Sci. nat. Belg.*, 28(31): 1-11.
- DEMOULIN, G., 1958. Nouveau schema de classification des Archodonates et des Ephemeropteres. *Bull. Inst. r. Sci. nat. Belg.*, 34(27): 1-19.
- DEMOULIN, G., 1961. Encore les Behningiidae (Ephemeroptera). *Bull. Inst. r. Sci. nat. Belg.*, 37(41): 1-6.
- DEMOULIN, G., 1964. Ephemeroptera. *Parc National de l'Upemba-Mission G. F. De Witte*, 68(2): 13-27.
- DEMOULIN, G., 1968. A propos du genre *Stackelbergisca* Tschernova et des formes affines (Ephemeroptera, Siphonuridae). *Bull. Inst. r. Sci. nat. Belg.*, 44(1): 1-4.
- DEMOULIN, G., 1969a. Sur la position systematique et phylogenetique des Rallidentinae (Ephemeroptera). *Bull. Inst. r. Sci. nat. Belg.*, 45(15): 1-5.
- DEMOULIN, G., 1969b. Remarques critiques sur la position systematique des Baetiscidae et des Prosopistomatidae (Ephemeroptera). *Bull. Inst. r. Sci. nat. Belg.*, 45(17): 1-8.
- DEMOULIN, G., 1969c. Sur l'origine et les tendances evolutives des Baetidae et des Siphlaenigmatidae (Ephemeroptera). *Bull. Inst. r. Sci. nat. Belg.*, 45(18): 1-8.
- EDMUNDS, G. F., Jr. 1962. The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Syst. Zool.*, 11: 22-31.
- EDMUNDS, G. F., Jr., 1964 (1965). The classification of Ephemeroptera in relation to the evolutionary grade of nymphal and adult stages. *Proc. XII Int. Congr. Ent., Lond.*, p. 112.
- EDMUNDS, G. F., Jr., 1972. Biogeography and evolution of Ephemeroptera. *A. Rev. Ent.*, 17: 21-42.
- EDMUNDS, G. F., Jr. & ALLEN, R. K., 1966. The significance of nymphal stages in the study of Ephemeroptera. *Ann. ent. Soc. Am.*, 59: 300-3.
- EDMUNDS, G. F., Jr., ALLEN, R. K. & PETERS, W. L., 1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). *Univ. Utah biol. Ser.*, 13(1): 49 p.
- EDMUNDS, G. F., Jr., NIELSEN, L. T. & LARSEN, J. R., 1956. The life history of *Ephoron album* (Say). (Ephemeroptera: Polymitarcidae). *Wasmann J. Biol.*, 14: 145-53.

- EDMUNDS, G. F., Jr., & TRAVER, J. R., 1954. An outline of a reclassification of the Ephemeroptera. *Proc. ent. Soc. Wash.*, 56: 236-40.
- EDMUNDS, G. F., Jr., 1959. The classification of the Ephemeroptera I. Ephemeroidea: Behningiidae. *Ann. ent. Soc. Am.*, 52: 43-51.
- GILLIES, M. T., 1957. New records and species of *Euthraulus* Barnard (Ephemeroptera) from East Africa and the Oriental region. *Proc. R. ent. Soc. Lond. (B)*, 26: 43-8.
- GRANDI, M., 1941. Contributi allo studio degli Efemerotteri Italiana II. Reperti su *Choroterpes picteti* (Eaton). *Boll. Ist. Ent. Univ. Bologna*, 12: 179-205.
- GRANDI, M., 1942. Contributi allo studio degli Efemeroidi Italiani IV. *Caenis macrura* Stephens. *Boll. Ist. Ent. Univ. Bologna*, 13: 137-71.
- GRENACHER, H., 1868. Beitrag zur Kenntniss des Eis der Ephemeriden. *Z. wiss. Zool.*, 18(1): 95-8.
- GROS, A., 1923. Etudes sur les premiers stades des Ephémères du Jura français. *Annls Biol. lacustre*, 12: 49-74.
- HARKER, J. E., 1950. Australian Ephemeroptera. Part I. Taxonomy of New South Wales species and evaluation of taxonomic characters. *Proc. Linn. Soc. N.S.W.*, 75: 1-34.
- HARTLAND-ROWE, R. C. B., 1958. The biology of a tropical mayfly *Povilla adusta* Navas (Ephemeroptera, Polymitaecidae) with special reference to the lunar rhythm of emergence. *Revue Zool. Bot. afr.*, 58: 185-202.
- HINTON, H. E., 1963. The respiratory system of the eggshell of the blowfly *Calliphora erythrocephala* Meig., as seen with the electron microscope. *J. Insect. Physiol.*, 9: 121-9.
- HUNT, B. P., 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. *Bull. Mich. Inst. Fish. Res.*, 4: 1-151.
- IDE, F. P., 1935. Life history notes on *Ephoron*, *Potamanthus*, *Leptophlebia* and *Blasturus* with descriptions (Ephemeroptera). *Can. Ent.*, 67: 113-25.
- JOHANNSEN, O. A. & BUTT, F. H., 1941. *Embryology of insects and myriapods*, 462 p. New York: McGraw-Hill.
- KEFFERMÜLLER, M., 1959. Nowe dane dotyczący jeteł (Ephemeroptera) Z rodzaju *Ametropus* Alb. i *Behningia* Lest. (In Polish) (New data concerning Ephemeroptera within the genus *Ametropus* Alb. and *Behningia* Lest.) (English summary). *Poz. Towarz. Przy. Nauk. (Biol.)*, 19(5): 1-32.
- KOSS, R. W., 1968. Morphology and taxonomic use of Ephemeroptera eggs. *Ann. ent. Soc. Am.*, 61: 696-721.
- KOSS, R. W., 1970. Ephemeroptera eggs: sperm guide morphology and adhesive layer formation. *Trans. Am. microsc. Soc.*, 89: 295-9.
- LANDA, V., 1969. Comparative anatomy of mayfly larvae (Ephemeroptera). *Acta ent. bohemoslov.*, 66: 289-316.
- LESTAGE, J. A., 1919. Contribution a l'étude des larves des Ephémères Palearctiques. Série II. *Ann. Biol. Lacust.*, 9: 79-182.
- MCCAFFERTY, W. P., 1972. Pentageniidae: a new family of Ephemeroidea (Ephemeroptera). *J. Georgia ent. Soc.*, 7: 51-6.
- MORGAN, A. H., 1913. A contribution to the biology of mayflies. *Ann. ent. Soc. Am.*, 6: 371-441.
- MORRISON, E. R., 1919. The mayfly ovipositor, with notes on *Leptophlebia* and *Hagenulus*. *Can. Ent.*, 51: 139-46.
- MOSELY, M. E., 1926. *Insect life and the management of a trout fishery*. London.
- MOSELY, M. E., 1938. The spinner and its eggs. Observations of the habits of egg-laying spinners and the hatching of their eggs. *Salm. Trout Mag.*, 90: 18-23.
- NEAVE, F., 1932. A study of the mayflies (Hexagenia) of Lake Winnipeg. *Contr. Can. Biol.*, 7: 179-201.
- NEEDHAM, J. G. & MURPHY, H. E., 1924. Neotropical mayflies. *Bull. Lloyd Libr. (ent. ser. 4)*, 24: 1-79.
- NEEDHAM, J. G., TRAVER, J. R. & HSU, Y.-C., 1935. *The biology of mayflies*, xiv + 759 pp. Ithaca, N.Y.: Comstock.
- PERCIVAL, E. & WHITEHEAD, H., 1926. Observations on the biology of the mayfly *Ephemera danica* Muell. *Proc. Leeds phil. lit. Soc.*, 1: 136-48.
- PERCIVAL, E. & WHITEHEAD, H., 1928. Observations on the ova and oviposition of certain Ephemeroptera and Plecoptera. *Proc. Leeds phil. lit. Soc.*, 1: 271-88.
- PETERS, W. L., GILLIES, M. T. & EDMUNDS, G. F., Jr., 1964. Two new genera of mayflies from the Ethiopian and Oriental regions (Ephemeroptera: Leptophlebiidae). *Proc. R. ent. Soc. Lond. (B)*, 33: 117-24.
- PHILLIPS, J. S., 1930. A revision of New Zealand Ephemeroptera. *Trans. N.Z. Inst.*, 61: 271-390.
- PLESKOT, G., 1953. Zur ökologie der Leptophlebiiden (Ephemeroptera). *Öst. zool. Z.*, 4: 45-107.
- RAWLINSON, R., 1939. Studies on the life-history and breeding of *Ecdyonurus venosus* (Ephem.). *Proc. zool. Soc. Lond.*, 109: 377-450.
- ROBACK, S. S., 1966. The Catherwood Foundation Peruvian-Amazon Expedition. VI. Ephemeroptera nymphs. *Monogr. Acad. nat. Sci. Philad.*, No. 14: 129-99.
- SHEPARD, D., 1929. *Ephemerella hecuba* Eaton; description of various stages. (Ephemerida; Baetidae). *Can. Ent.*, 61(11): 260-4.

- SMITH, O. R., 1935. The eggs and egg-laying habits of North American mayflies. In J. G. Needham, J. R. Traver & Y.-C. Hsu, *The biology of mayflies*, pp. 67-89. Ithaca, N.Y.: Comstock.
- SOUTHWOOD, T. R. E., 1956. The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. *Trans. R. ent. Soc. Lond.*, 108: 163-221.
- SPIETH, H. T., 1947. Taxonomic studies on the Ephemeroptera IV. The genus *Stenonema*. *Ann. ent. Soc. Am.*, 40: 87-122.
- TAKAHASHI, Y., 1929. On a new mayfly with eggs. *Lansania*, 1(2): 30-2.
- THROCKMORTON, L. H., 1969. Concordance and discordance of taxonomic characters in *Drosophila* classification. *Syst. Zool.*, 17: 355-87.
- TRAVER, J. R., 1956. The genus *Asthenopodes* (Ephemeroptera). *Comun. zool. Mus. Hist. nat. Montev.*, 4: 1-10.
- TRAVER, J. R. & EDMUNDS, G. F., Jr., 1967. A revision of the genus *Thraulodes* (Ephemeroptera: Leptophlebiidae). *Misc. Publs ent. Soc. Am.*, 5: 349-95.
- ULMER, G., 1913. Ephemeriden aus Java, gesammelt von Edw. Jacobsen. *Not. Mus. Leyden*, 35: 102-20.
- VAYSSIERE, A., 1881. On the perfect state of *Prosopistoma punctifrons*. (Translated by W. S. Dallas). *Ann. Mag. nat. Hist.*, 8: 73-85.
- WISELY, B., 1961. Studies on Ephemeroptera I. *Coloburiscus humeralis* (Walker); early life history and nymph. *Trans. R. Soc. N.Z. (Zool.)*, 1: 249-57.

ABBREVIATIONS USED IN PLATES

al	adhesive layer	kctl	knob-terminated coiled thread layer
alr	adhesive layer reticulation	l	length
alt	adhesive layer tubercle	m	micropyle
am	adhesive material	mc	micropylar canal
amc	angle of micropylar canal to sperm guide	mo	micropylar opening
c	chorion	p	puncture
cc	chorionic costa	pa	peglike attachment structure
cl	coil layer	pc	polar cap
cm	chorionic mesh	pcs	polar coils
csg	chorionic sperm guide	pmc	proximal portion of micropylar canal
cw	chorionic wall	r	ridge (strand of chorionic reticulation)
d	diameter	scsg	suprachorionic-chorionic sperm guide
dmc	distal portion of micropylar canal	sg	sperm guide
f	furrow (strand of chorionic reticulation)	sgh	sperm guide hood
fc	fiber-coil attachment structure	ssg	suprachorionic sperm guide
fcl	fiber-coil layer	t	chorionic tubercle
fe	follicular epithelium	th	attachment thread
h	height	tk	terminal knob
if	inner flange of sperm guide	w	width
kct	knob-terminated coiled thread		

EXPLANATION OF PLATES

PLATE 1 (figs 1-16)

Fig. 1. *Ameletopsis perscitus*, chorion and micropylar opening (I. C., x933). Figs 2-6. *Chaquihua penai*: 2, egg (P. C., x373); 3, chorion and micropylar opening (I. C., x933); 4, adhesive layer and sperm guide (I. C., x933); 5, optical section of chorionic mesh and adhesive layer; tangential view (I. C., x933); 6, optical section of micropylar canal; tangential view (I. C., x933). Figs 7, 8. *Chaquihua* sp.: 7, chorion and micropylar opening (I. C., x933); 8, adhesive layer and sperm guide (I. C., x933). Figs 9-11. *Chilopter penai*: 9, chorion and micropylar opening (I. C., x933); 10, optical section of chorionic mesh and adhesive layer; tangential view (I. C., x843); 11, optical section of sperm guide and micropylar opening; tangential view (I. C., x843). Figs 12-16. *Mirawara megaloprepria*: 12, egg (P. C., x373); 13, chorion (I. C., x933); 14, outer surface of adhesive layer and sperm guide (I. C., x933); 15, adhesive layer and sperm guide midway in depth (I. C., x933); 16, optical section of micropyle; tangential view (I. C., x933).

PLATE 2 (figs 17-27)

Fig. 17. *Oniscigaster distans*? optical section of proximal portion of micropylar canal; tangential view (I. C., x 527). Fig. 18. *Tasmanophlebia* sp. no. 1, chorion, adhesive layer and sperm guide

(I. C., x843). Figs 19, 20. *Tasmanophlebia* sp. No. 2: 19, micropyle and inner layer of chorion (P. C., x933); 20, egg (P. C., x373). Fig. 21. *Siphonurus alternatus*, egg (P. C., x267). Fig. 22. *Nesameletus* sp., chorion, lower two mesh with fiber-coils in focus (I. C., x933). Figs 23, 24. *Metamonius* sp.: 23, chorion, fiber-coils and sperm guide (P. C., x933); 24, egg (P. C., x373). Fig. 25. *Ameletoides lacus-albinae*, optical section of three chorionic mesh and fiber-coils contained within; tangential view (I. C., x843). Fig. 26. *Nesameletus* sp., optical section of chorionic mesh and fiber-coil layer; tangential view (I. C., x843). Fig. 27. *Metamonius* sp., optical section of chorionic mesh, fiber-coils not in focus; tangential view (I. C., x933).

PLATE 3 (figs 28-37)

Fig. 28. *Ameletus* sp., lateral region of egg (I. C., x373). Figs 29, 30. *A. sparsatus*: 29, lateral region of egg (I. C., x843); 30, polar concentration of knob-terminated coiled threads (I. C., x373). Fig. 31. *A. montanus*, optical section of polar open-ended chorionic cones and knob-terminated coiled threads contained within; tangential view (I. C., x583). Figs 32, 33. *Metreletus goetghebuerti*: 32, lateral and polar regions of egg (I. C., x373); 33, optical section of a lateral open-ended chorionic cone and the knob-terminated coiled thread contained within (I. C., x1167). Figs 34, 35. *Analetris eximia*: 34, general outline of egg, chorion not in focus (I. C., x147); 35, polar coils and micropyle (I. C., x933). Figs 36, 37. *Rallidens macfarlanei*: 36, egg (P. C., x187); 37, optical section of tubular structure and knob-terminated coiled thread contained within; tangential view (I. C., x933).

PLATE 4 (figs 38-49)

Figs. 38, 39. *Rallidens macfarlanei*: 38, optical section of tubular structure revealing part of the micropyle; surface view (I. C., x933); 39, same as Fig. 38, different tubular structure (I. C., x933). Fig. 40. *Isonychia bicolor*, egg (P. C., x187). Fig. 41. *I. intermedia*, two eggs, left egg showing layer of knob-terminated coiled threads partially covering egg, right egg showing opposite surface and two micropyles (P. C., x133). Fig. 42. *I. japonica*, chorion and sperm guide (I. C., x337). Fig. 43-47. *Coloburiscoides* sp.: 43, chorion, lateral surface of egg (P. C., x373); 44, polar reticulation and knob-terminated coiled threads (P. C., x373); 45, knob-terminated coiled thread on lateral surface of egg; tangential view (I. C., x583); 46, polar knob-terminated coiled thread (I. C., x583); 47, pole with two micropyles (P. C., x467). Figs 48, 49. *Coloburiscus humeralis*: 48, general outline of egg, chorion not in focus (P. C., x63); 49, chorion and micropyle (P. C., x933).

PLATE 5 (figs 50-60)

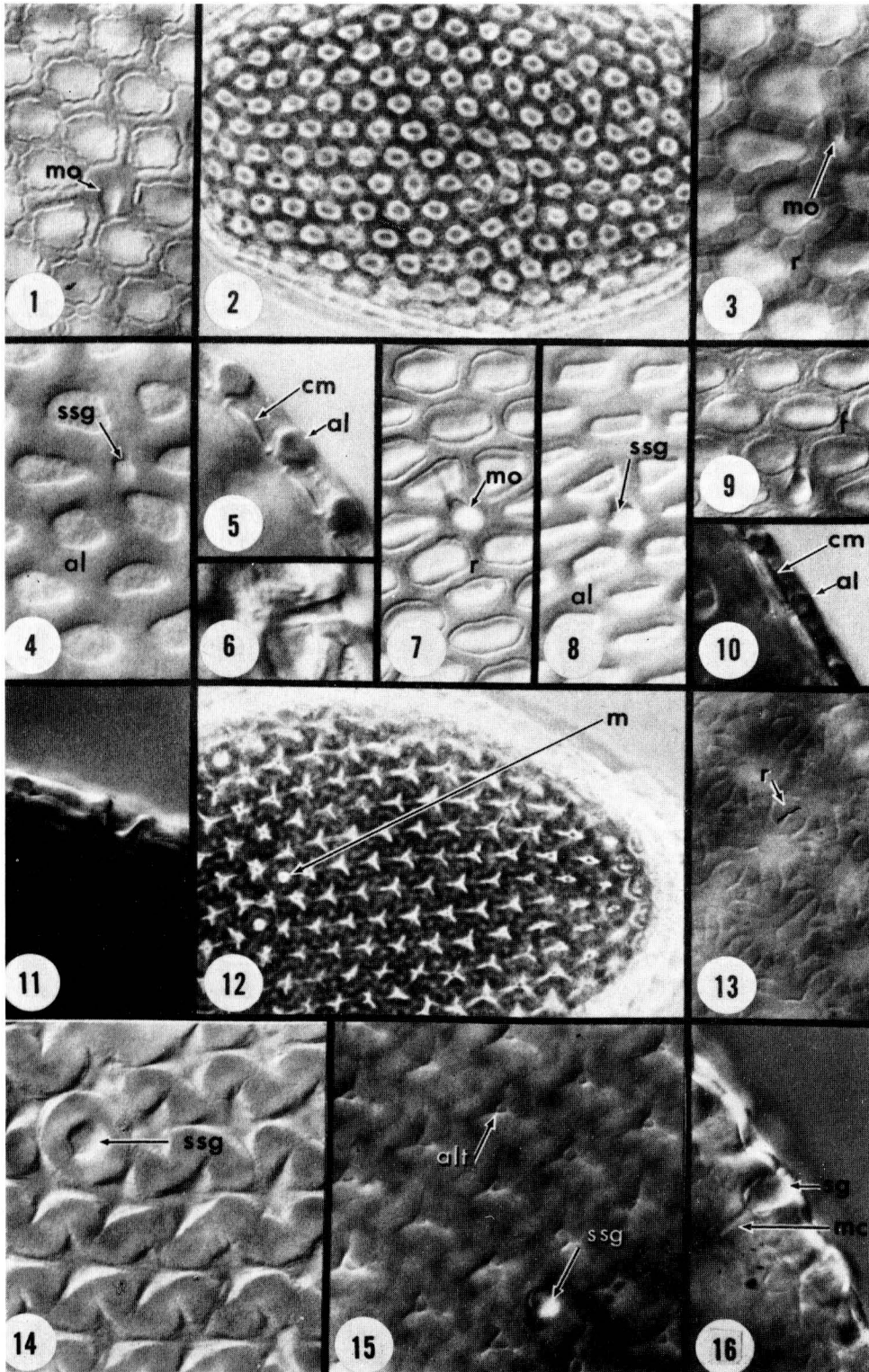
Figs 50, 51. *Coloburiscus humeralis*: 50, polar knob-terminated coiled thread (I. C., x933); 51, base of outstretched polar thread (I. C., x933). Figs 52, 53. *Murphyella needhami*: 52, knob-terminated coiled threads and surrounding tubercles, chorion and apex of large tubercles out of focus (I. C., x843); 53, same as Fig. 52, in optical section; tangential view (I. C., x933). Figs 54-58. *Siphlaenigma janae*: 54, micropyle (P. C., x843); 55, micropyle (P. C., x843); 56, fiber-coils and chorionic tubercles (P. C., x843); 57, same as Fig. 56 (I. C., x843); 58, egg (P. C., x337). Fig. 59. *Baetis* sp., egg, slight unnatural distortion (P. C., x373). Fig. 60. *Baetodes* sp., egg, the white "halo" is out-of-focus chorion (P. C., x467).

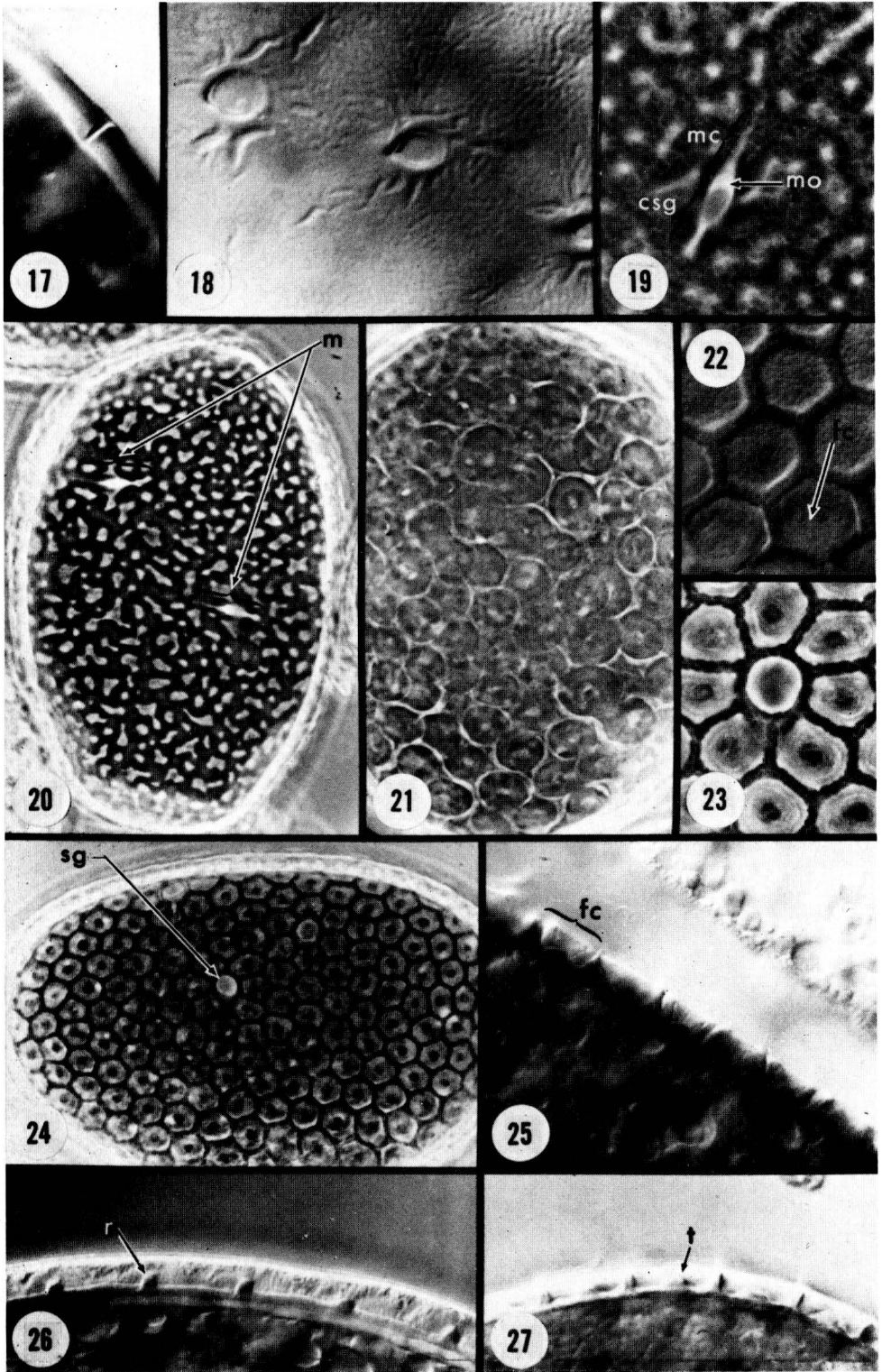
PLATE 6 (figs 61-74)

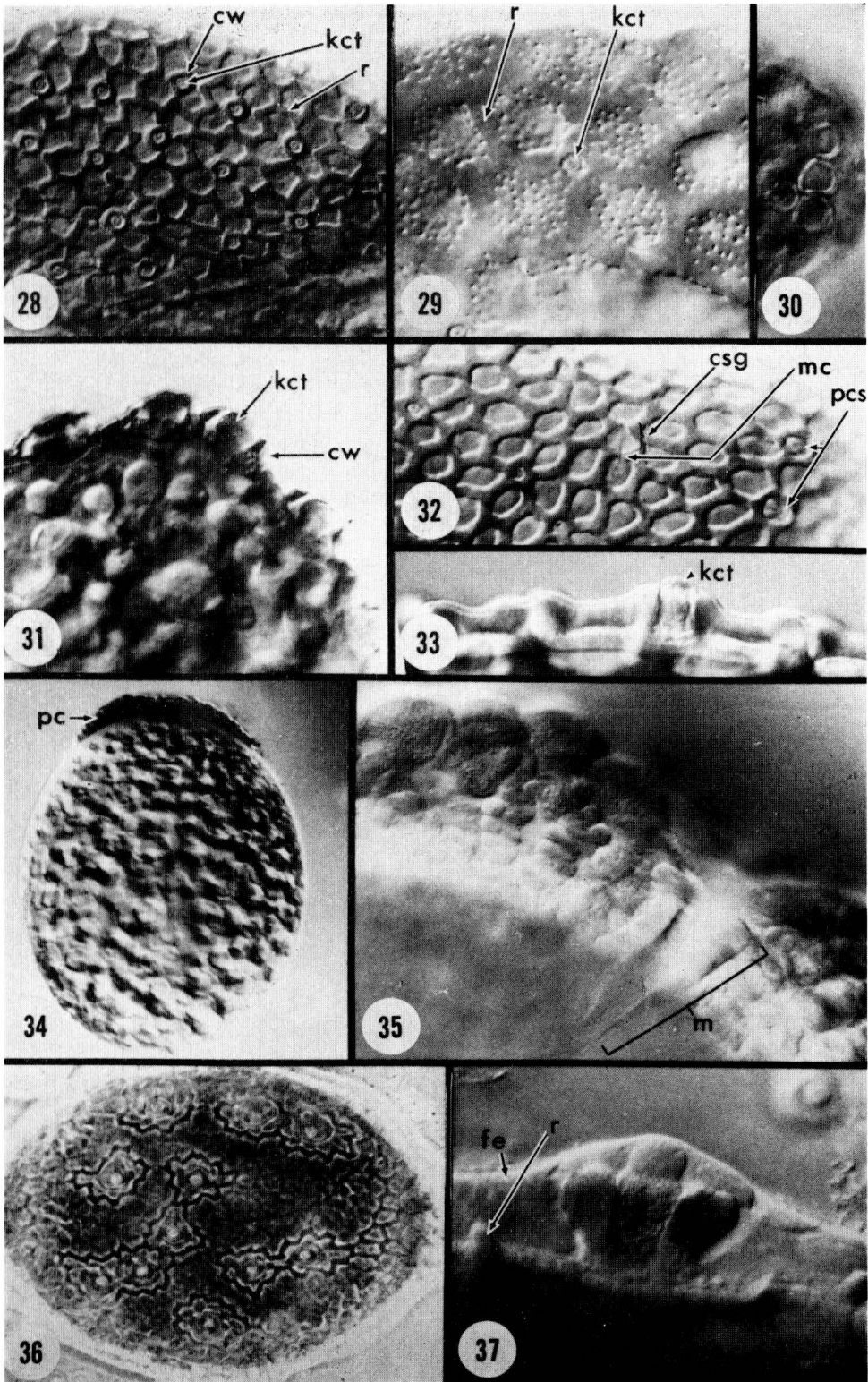
Figs 61, 62. *Baetodes* sp.: 61, tangential view showing knob-terminated coiled threads (I. C., x933); 62, sperm guide (P. C., x933). Figs 63-65. *Centroptilum bifurcatum*? 63, chorion (P. C., x933); 64, slightly more than 1/2 of egg (P. C., x373); 65, micropyle (P. C., x933). Figs 66-68. *Centroptilum selanderorum*: 66, chorion (P. C., x933); 67, egg (P. C., x233); 68, micropyle (P. C., x933). Figs 69, 70. *Cloeon* sp.: 69, optical section of attachment structures and surrounding chorionic wall; tangential view (P. C., x933); 70, egg (P. C., x373). Fig. 71. *Pseudocloeon* sp., micropyle at one pole of egg (P. C., x373). Figs 72-74. *Chromarcys* sp.: 72, fiber-coils (P. C., x373); 73, fiber-coils (I. C., x933); 74, terminal fiber-clusters (I. C., x373).

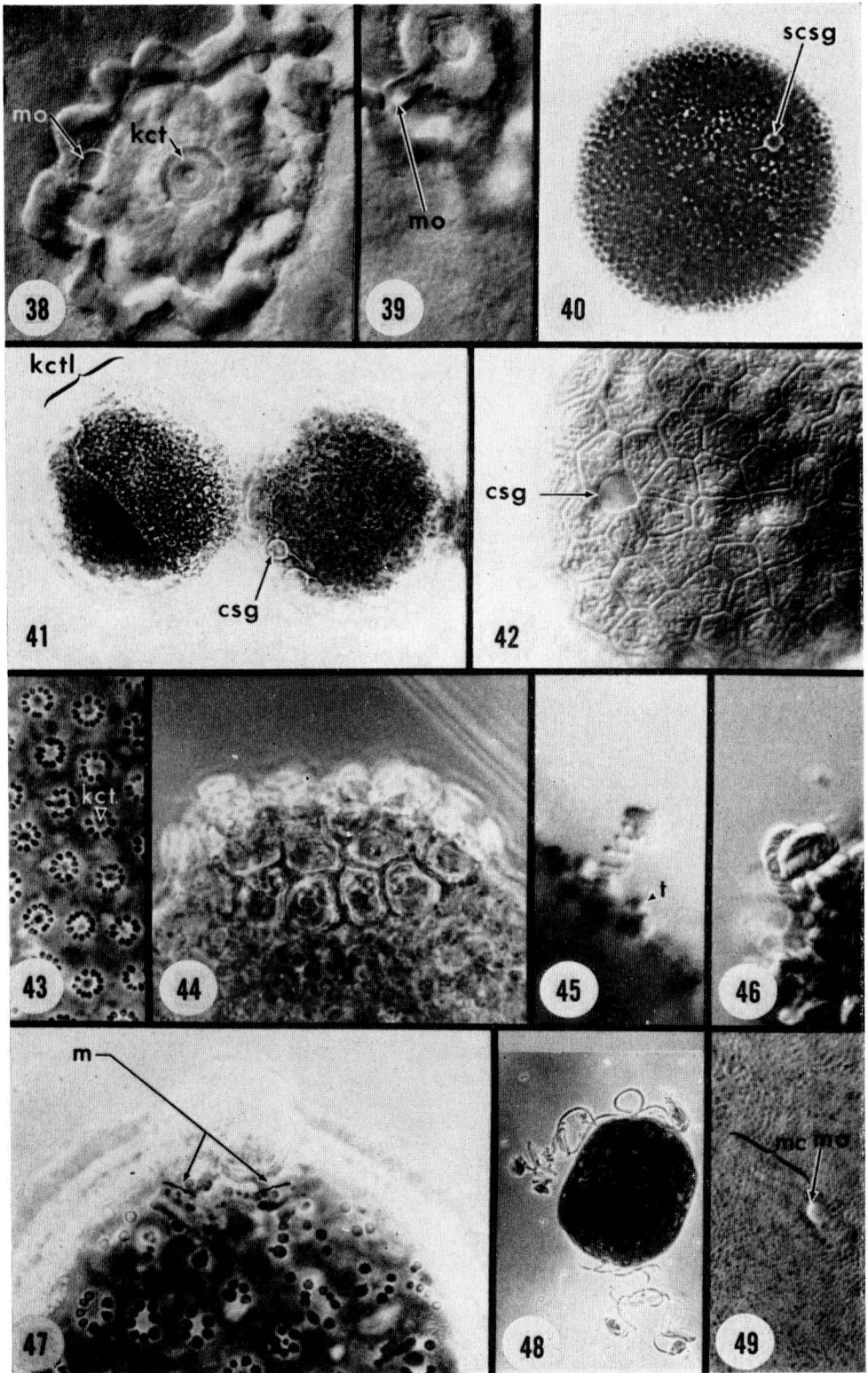
PLATE 7 (figs 75-88)

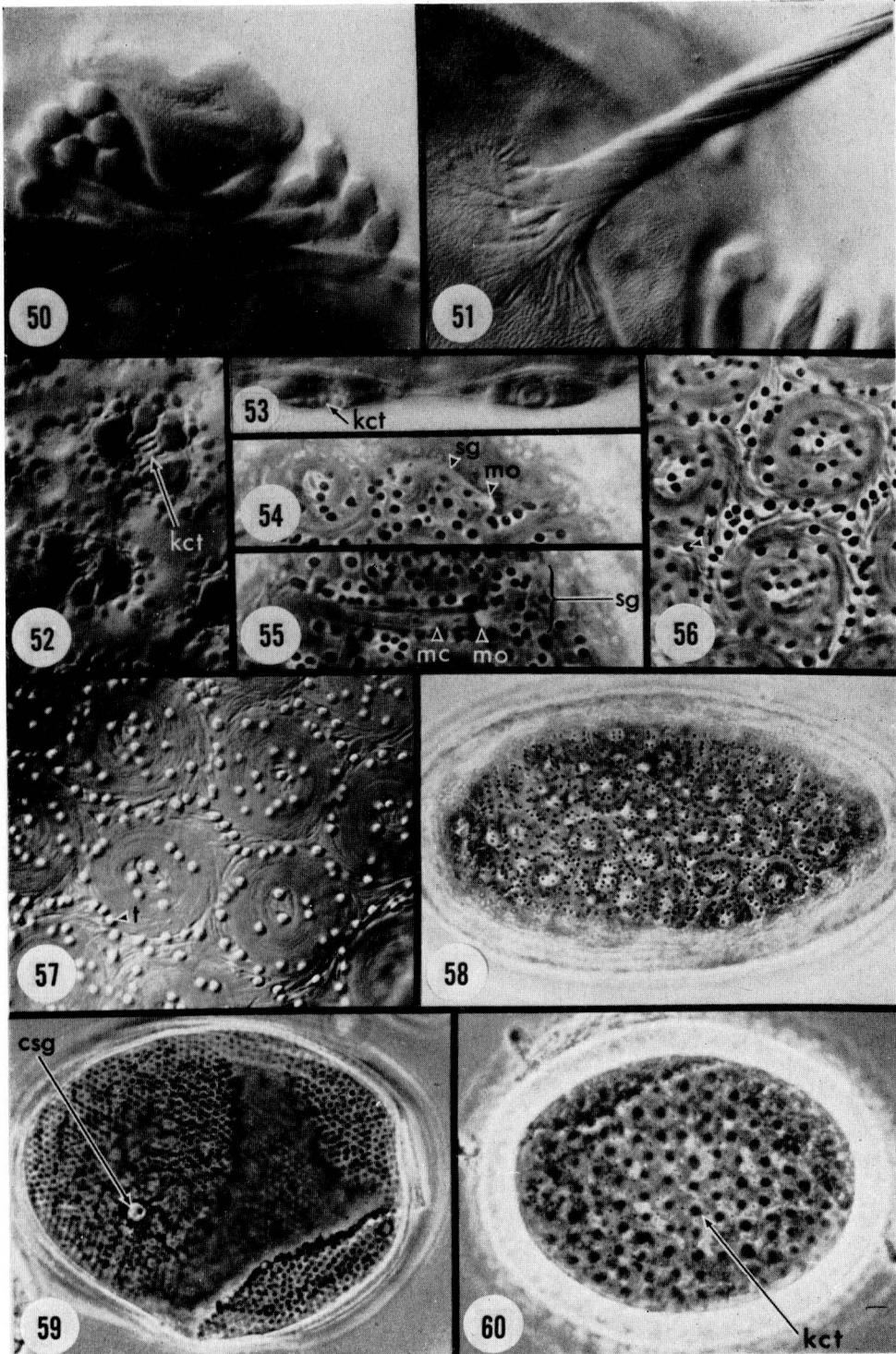
Fig. 75. *Elassoneuria insulicola*, micropyle (I. C., x933). Fig. 76. *Lachlania dencyanna*, egg (P. C., x147). Fig. 77. *Homoeoneuria dolani*, "terminal knob" (I. C., x933). Fig. 78. *Oligoneuriella rhenana*, terminal fiber-cluster (I. C., x933). Figs 79, 80. *Afronurus perengueyi*: 79, micropyle (P. C., x933); 80, knob-terminated coiled thread (P. C., x373). Fig. 81. *Cinygma integrum*, egg (P. C., x373). Fig. 82. *Cinygmula par*, chorion, attachment structures, and

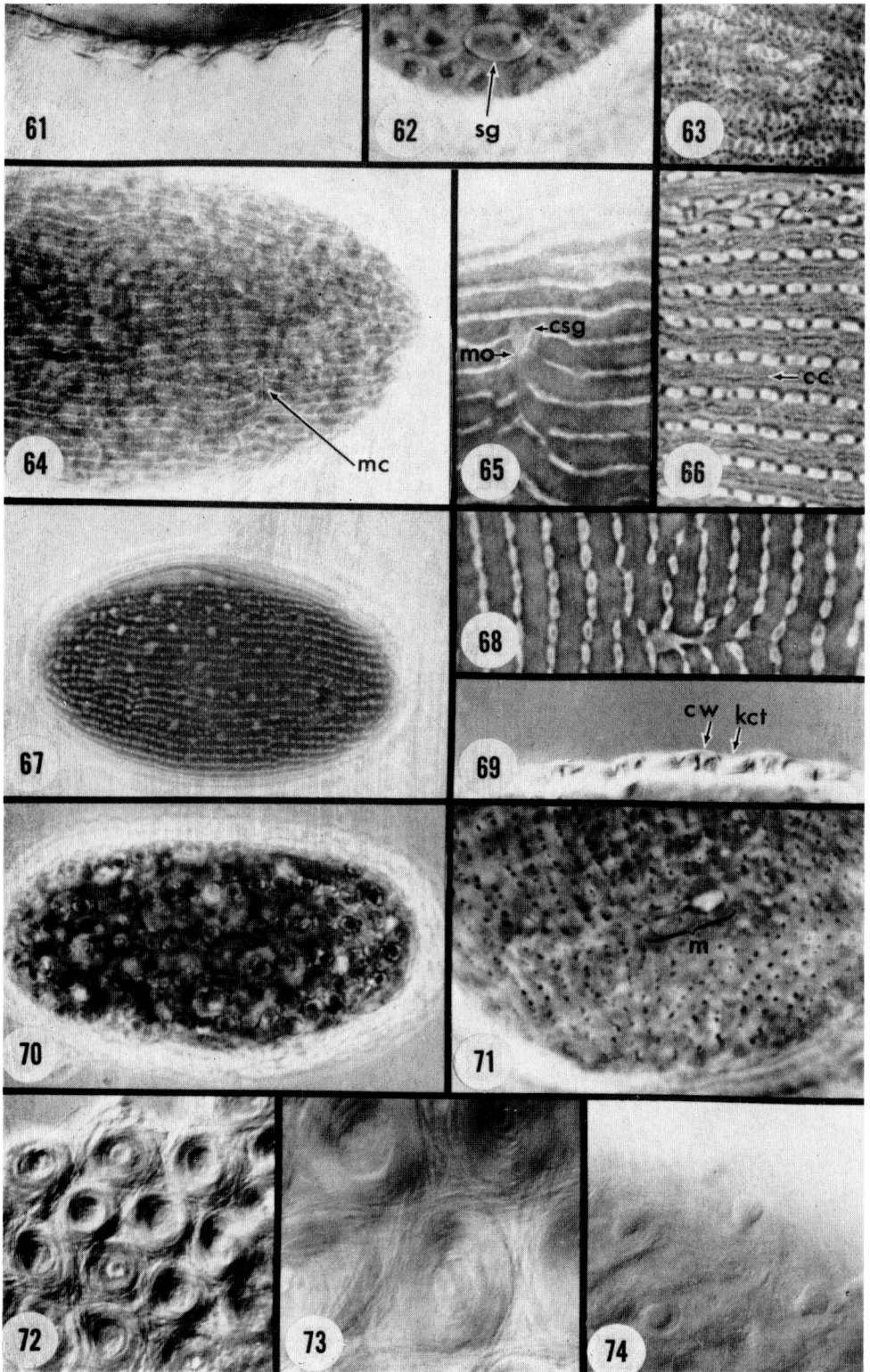


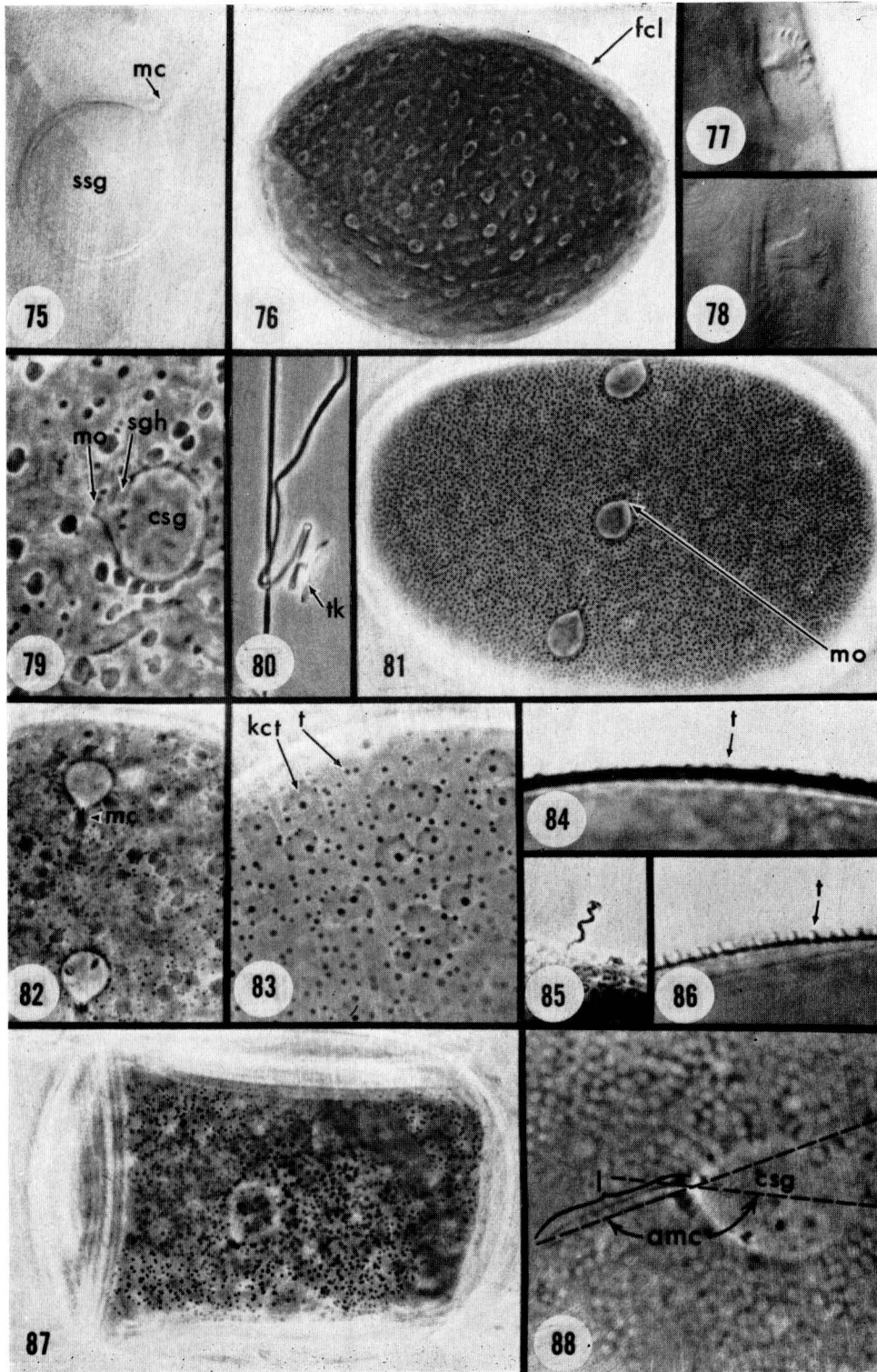


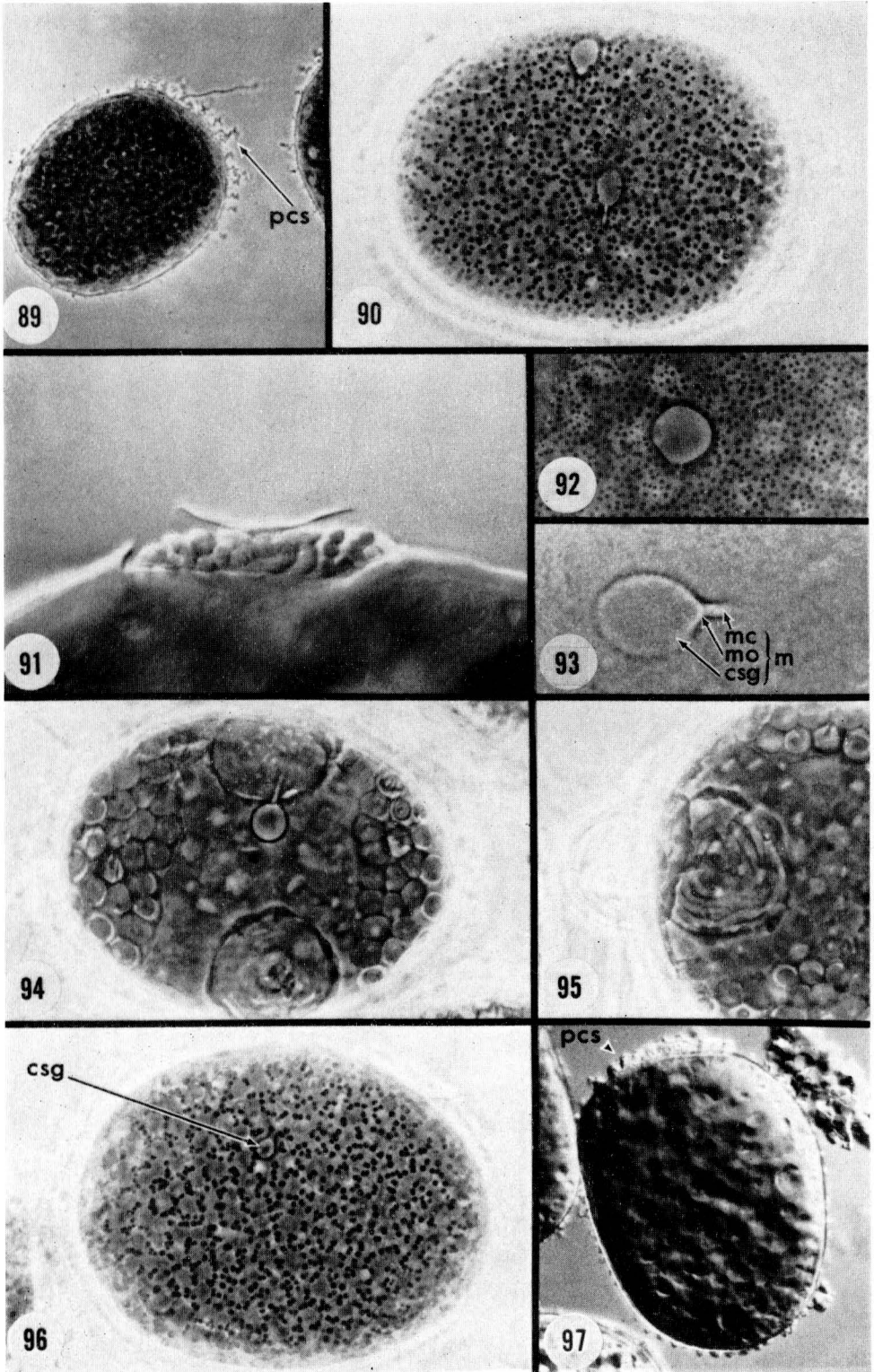


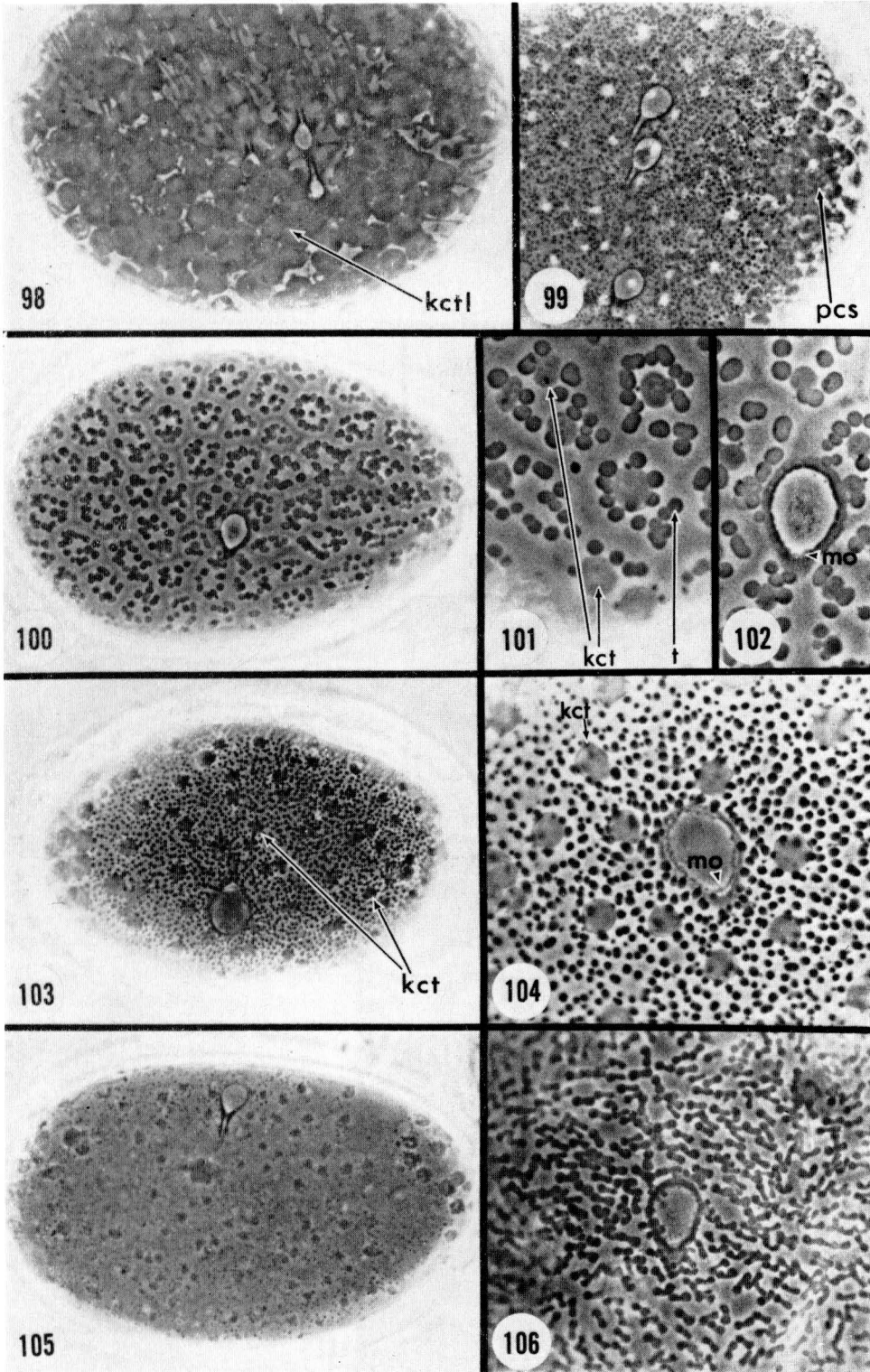


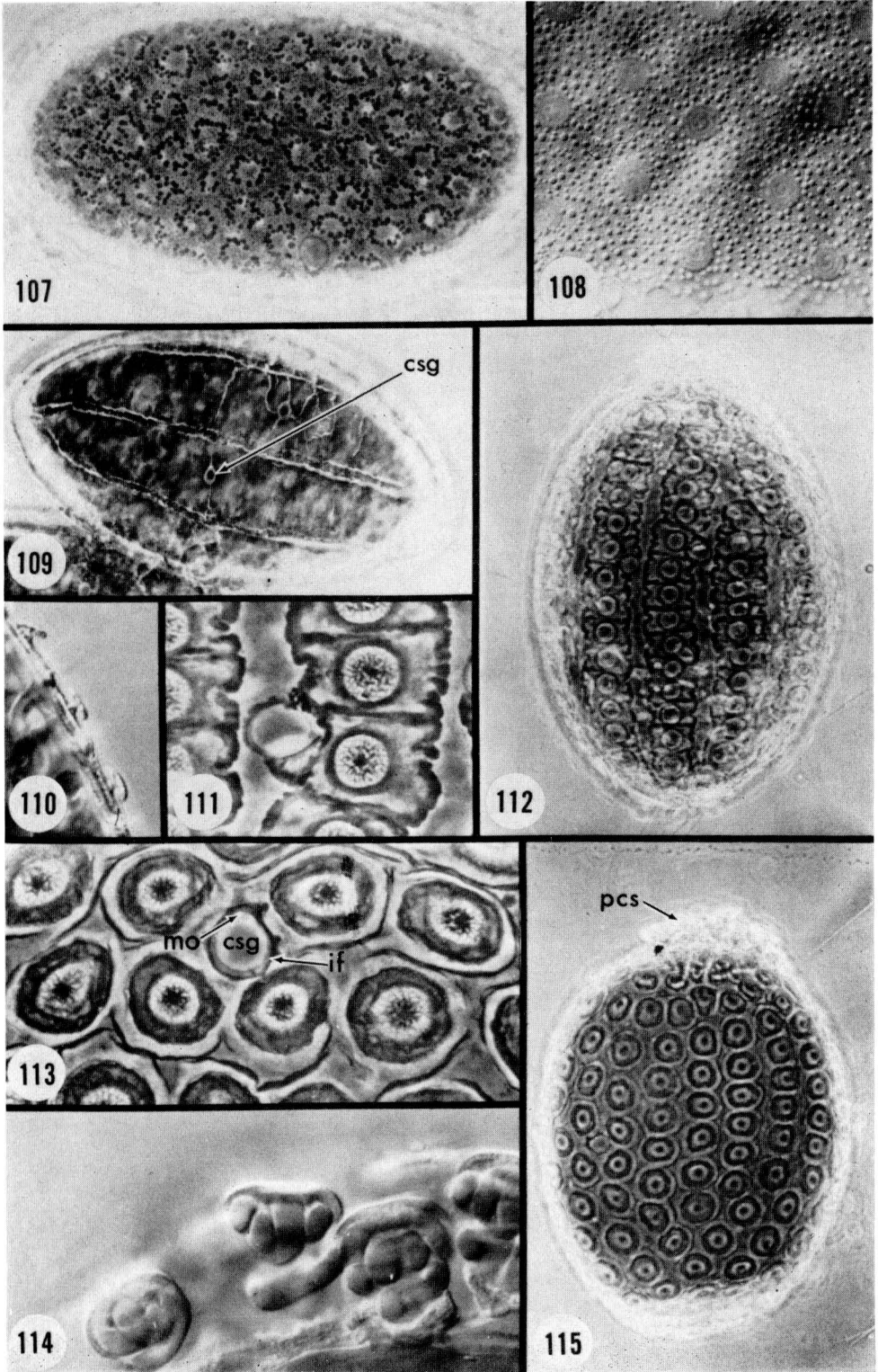


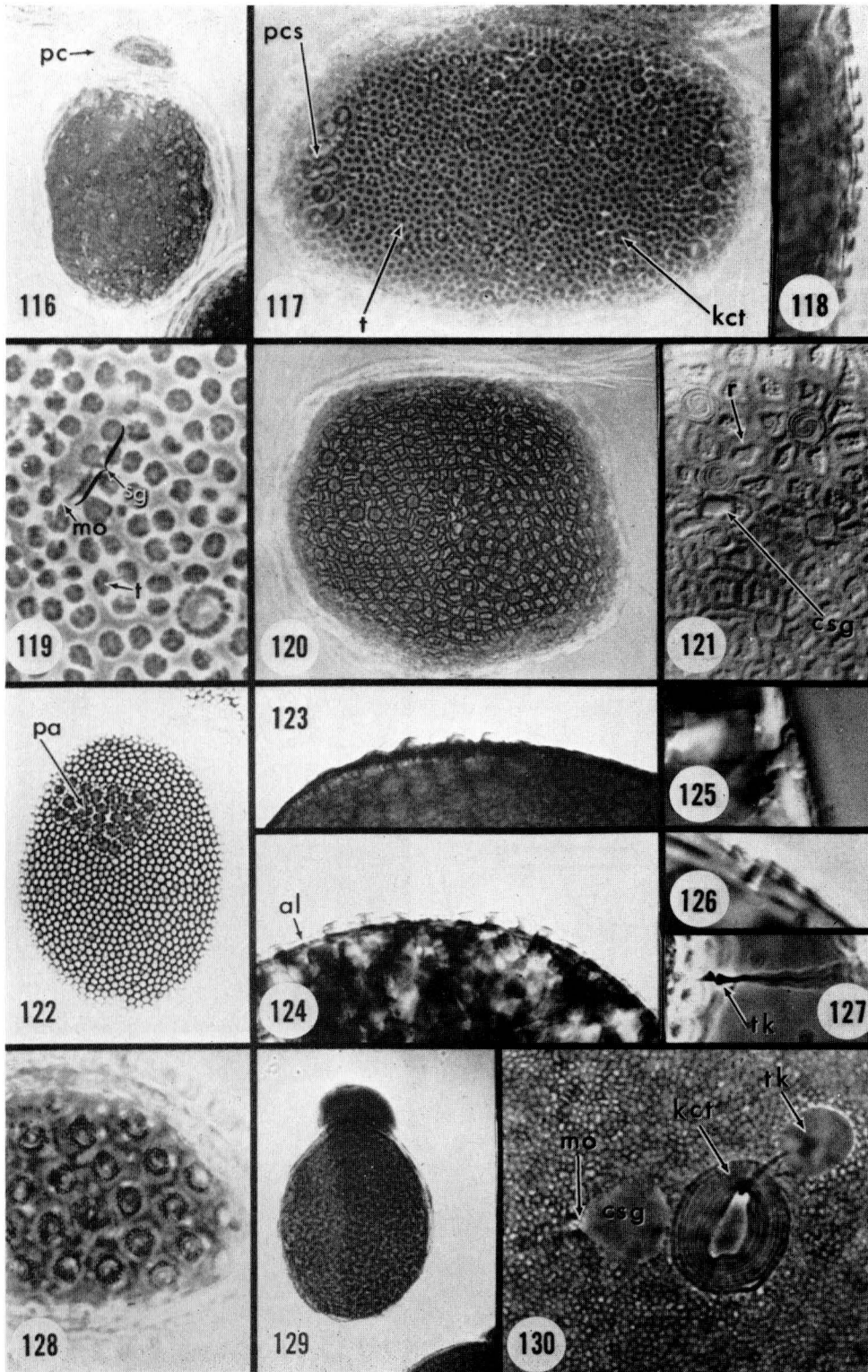


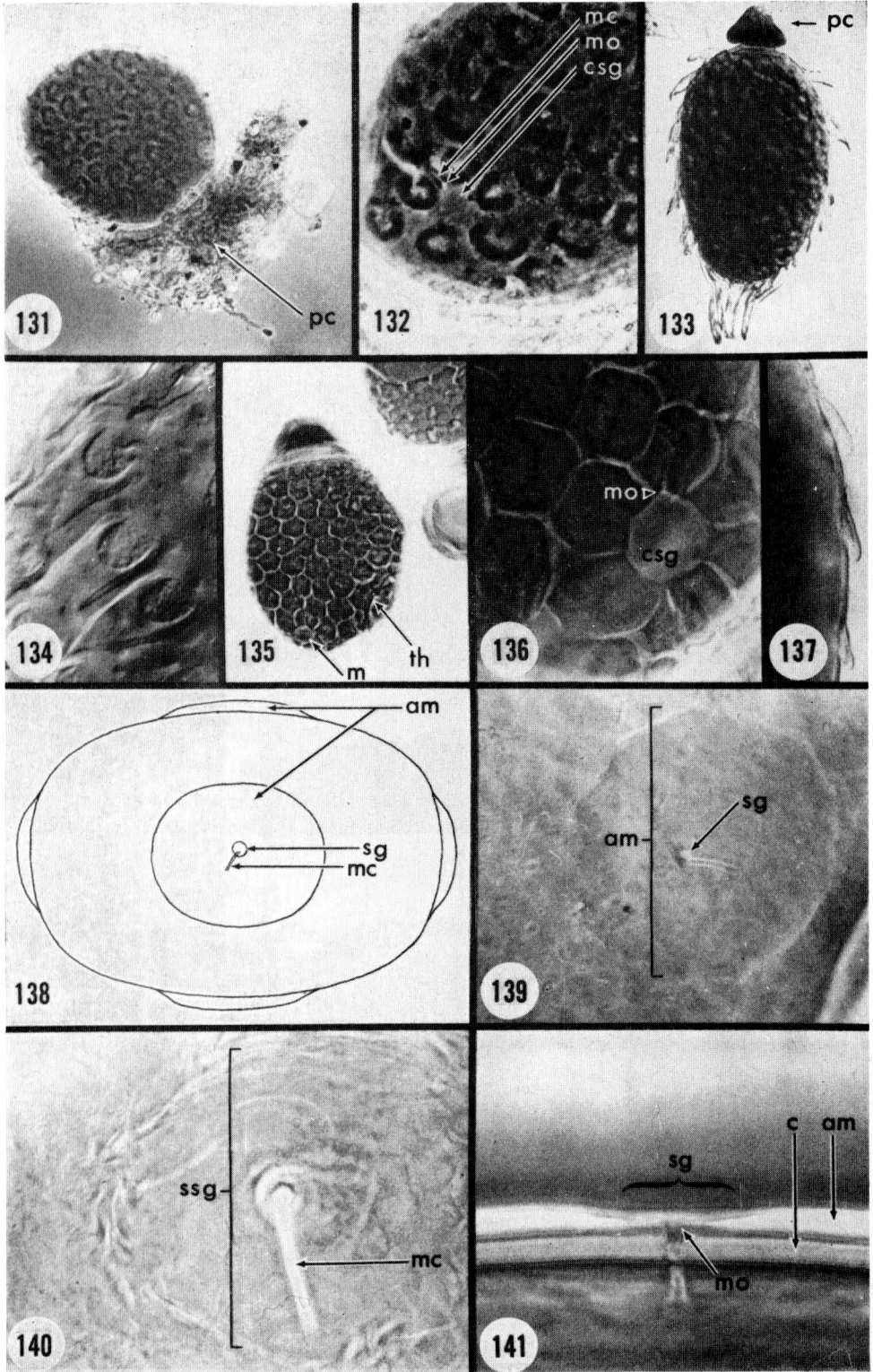


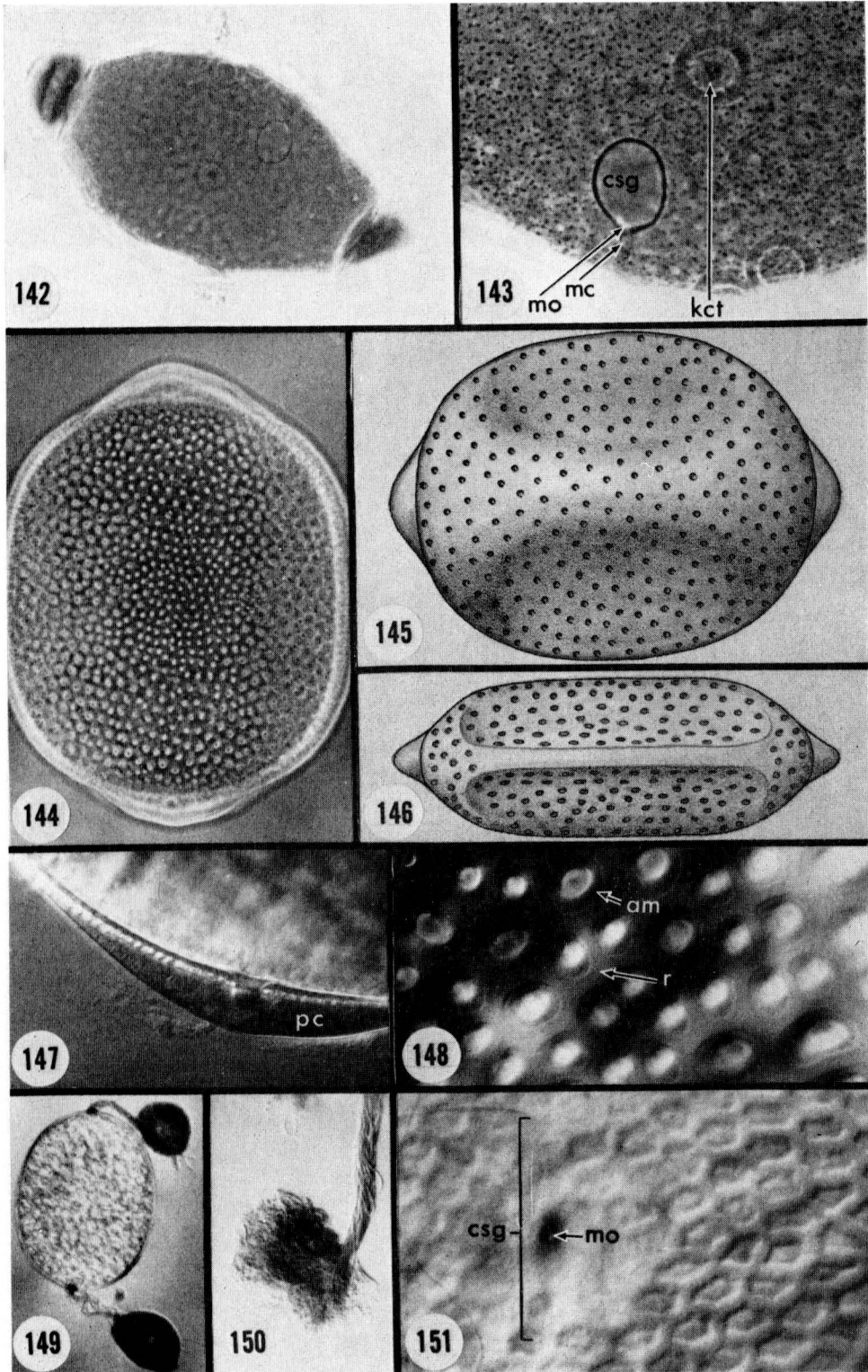


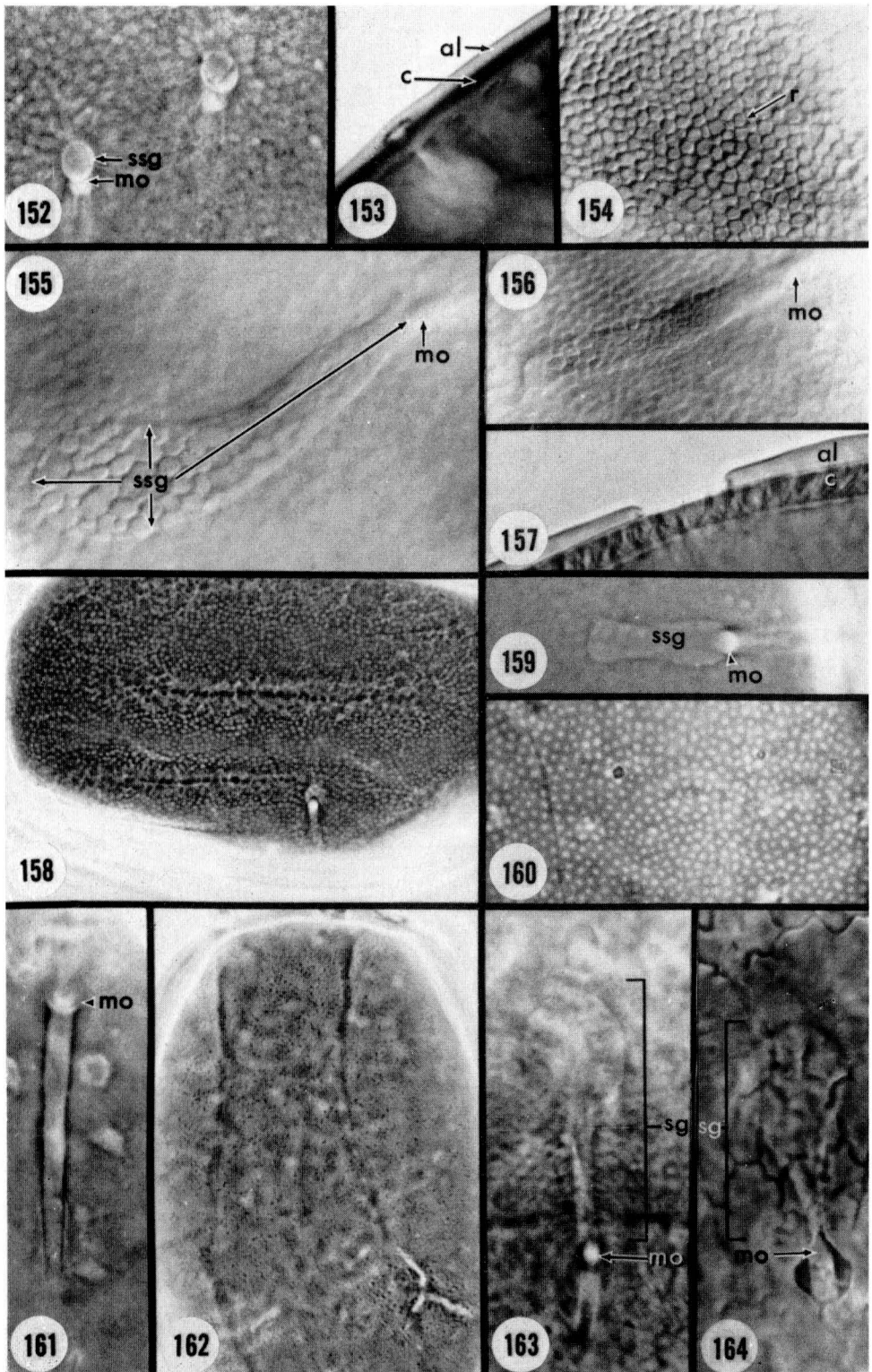


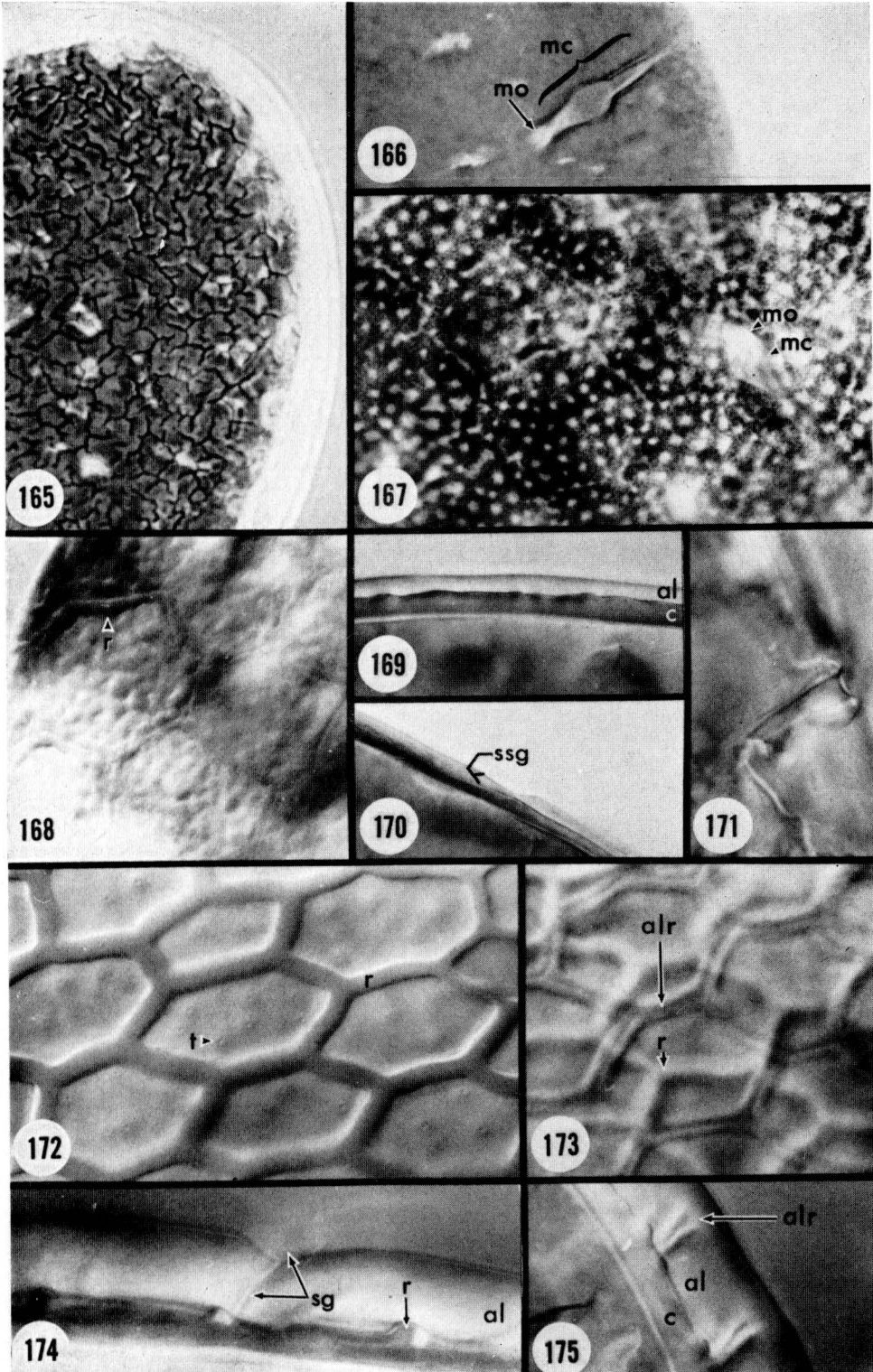


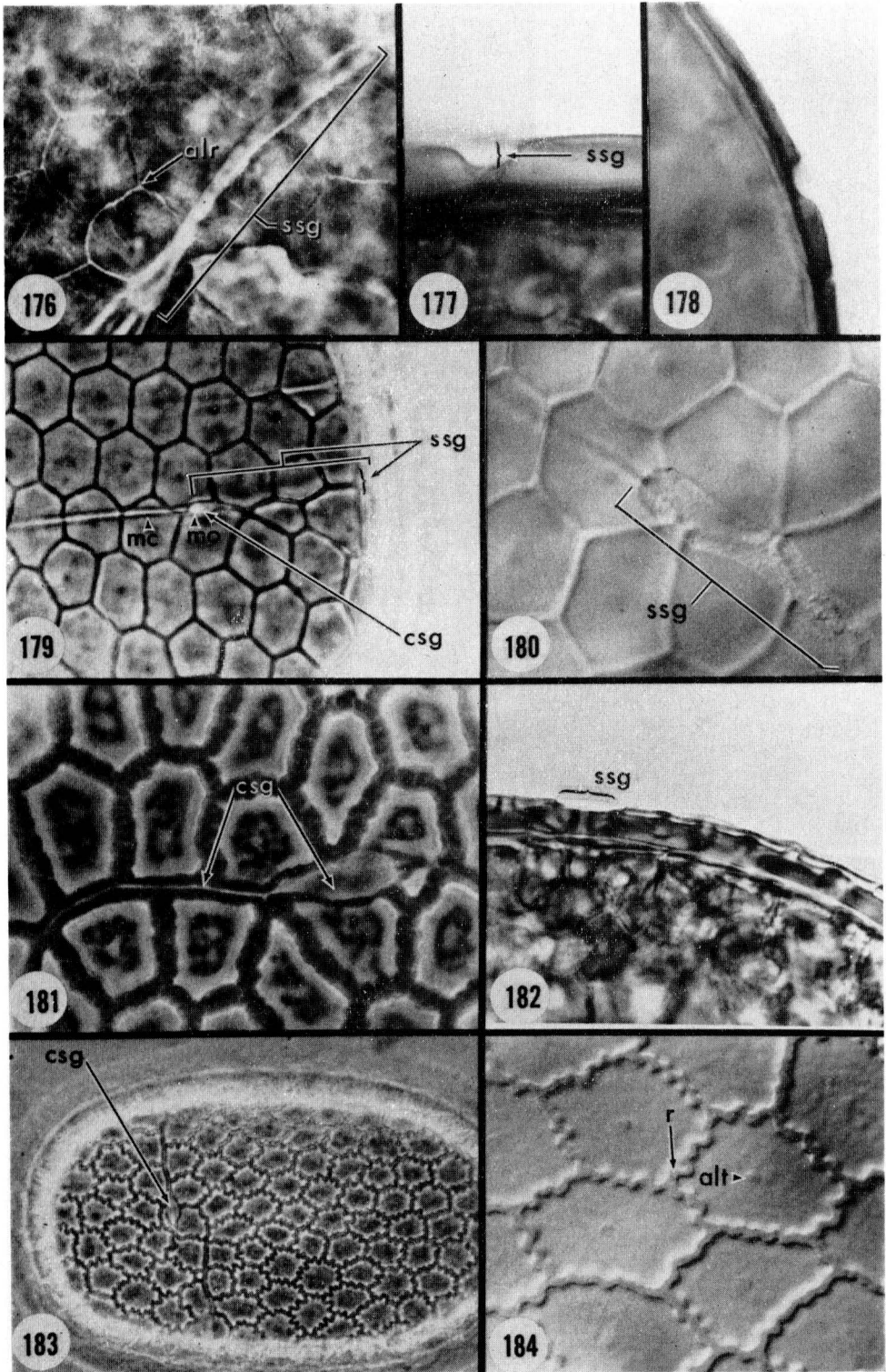


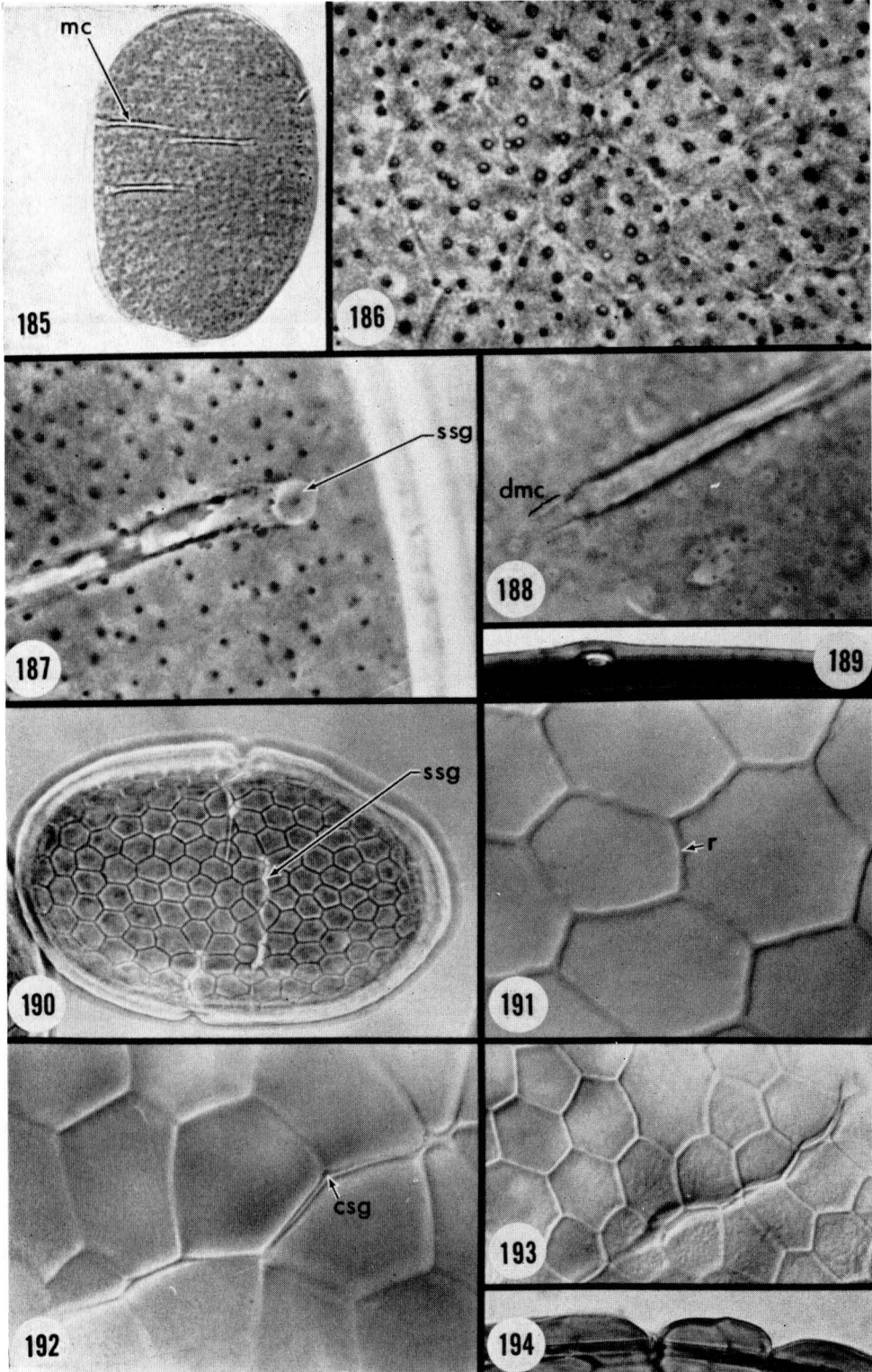


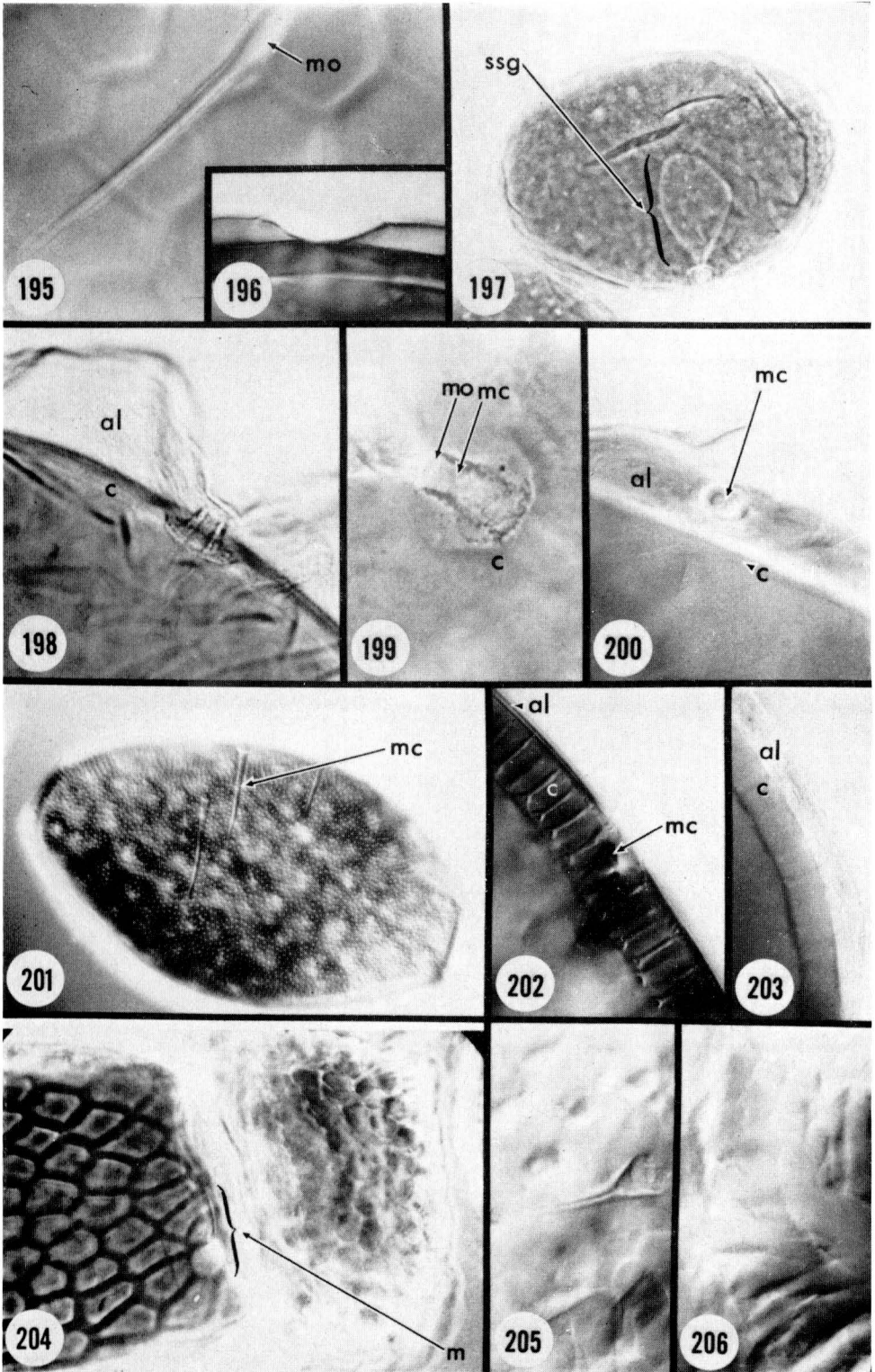


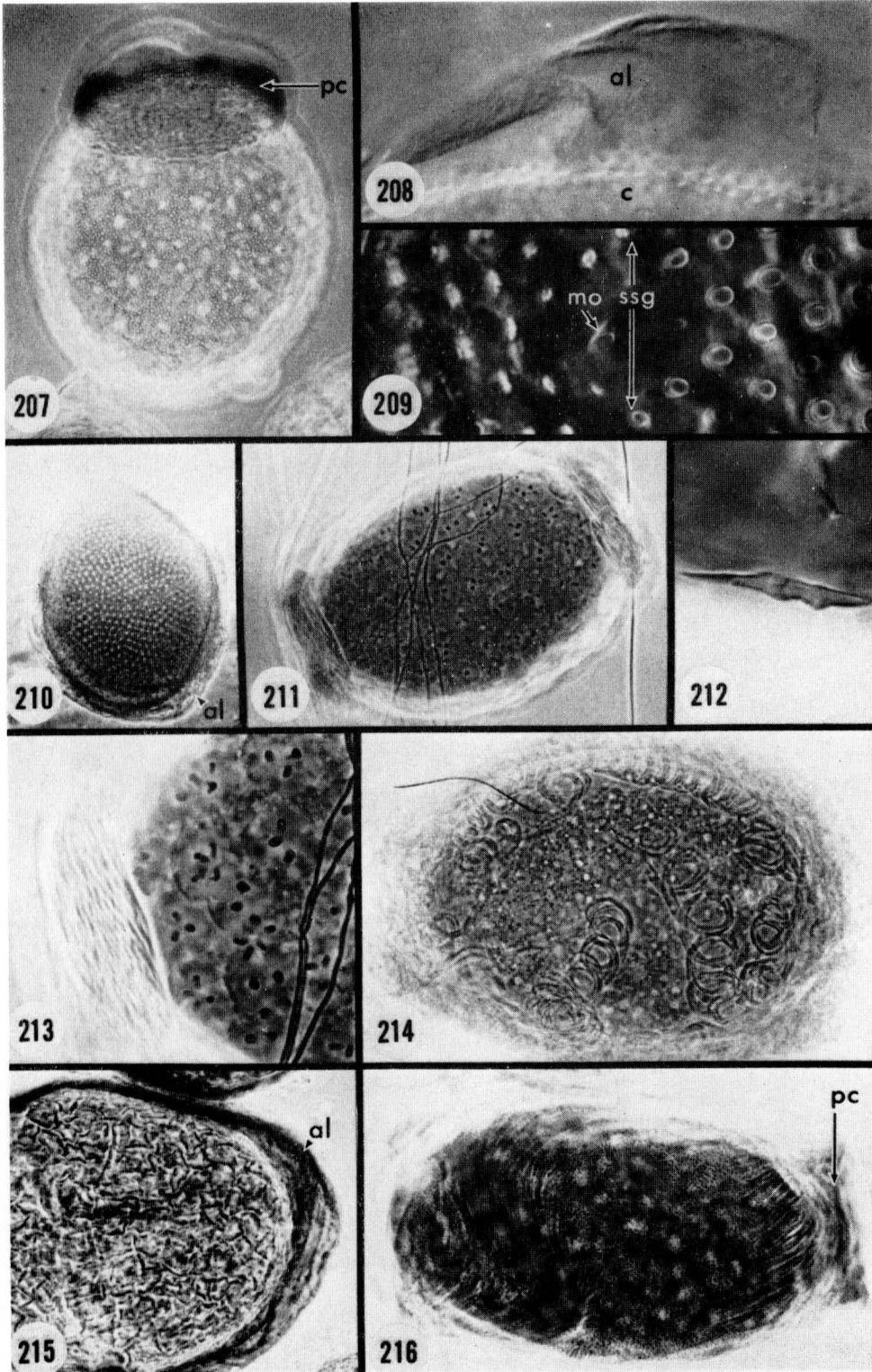




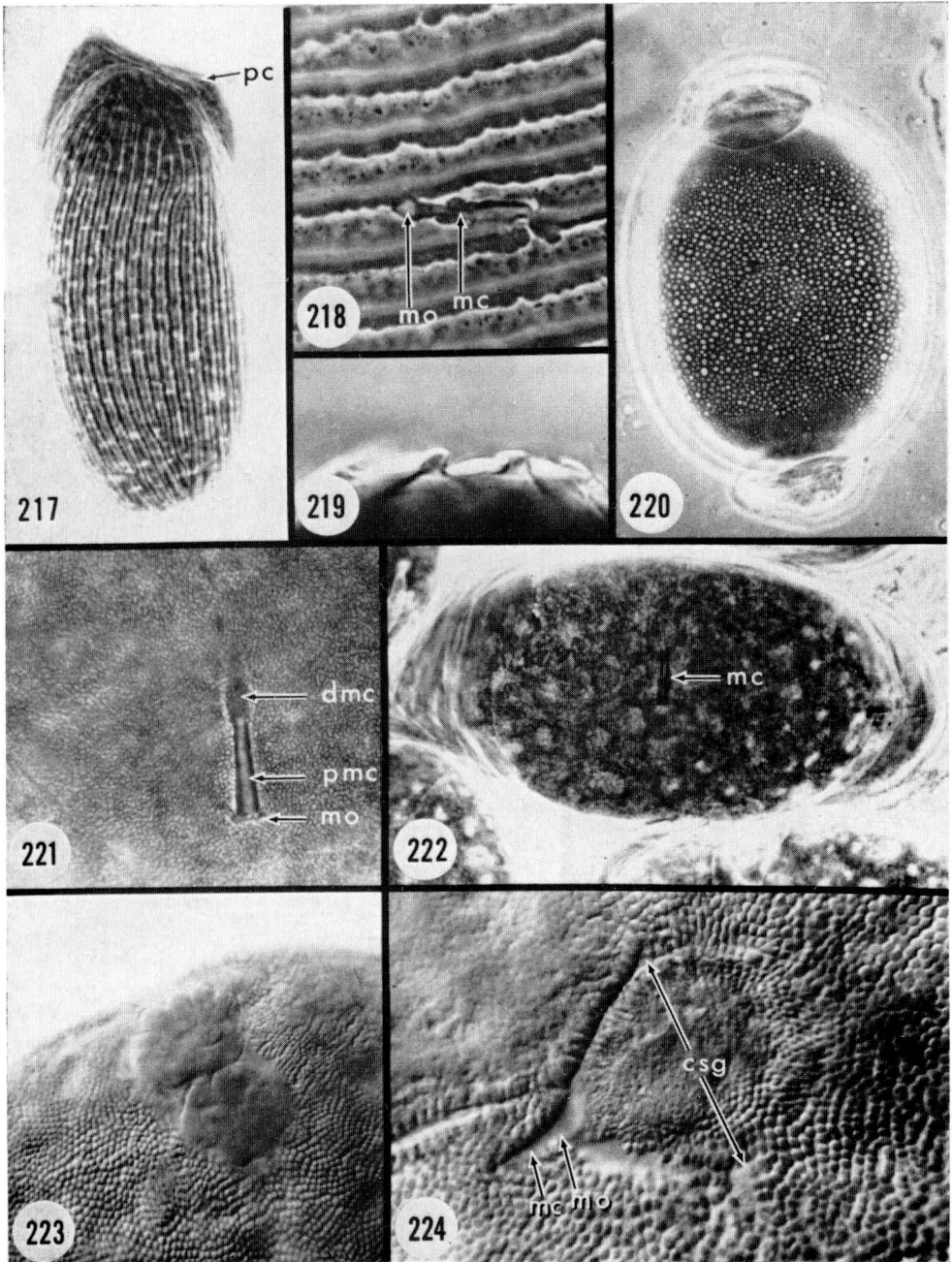


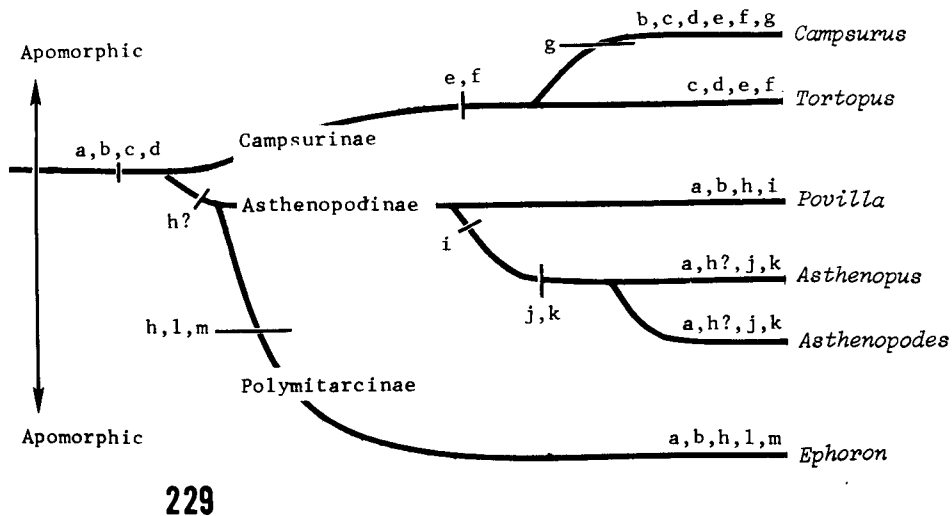
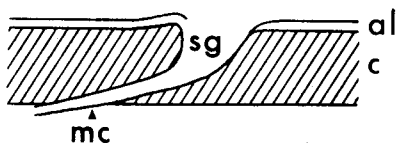
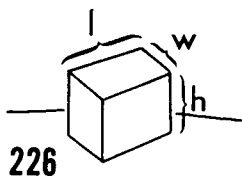
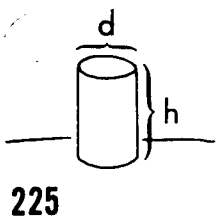


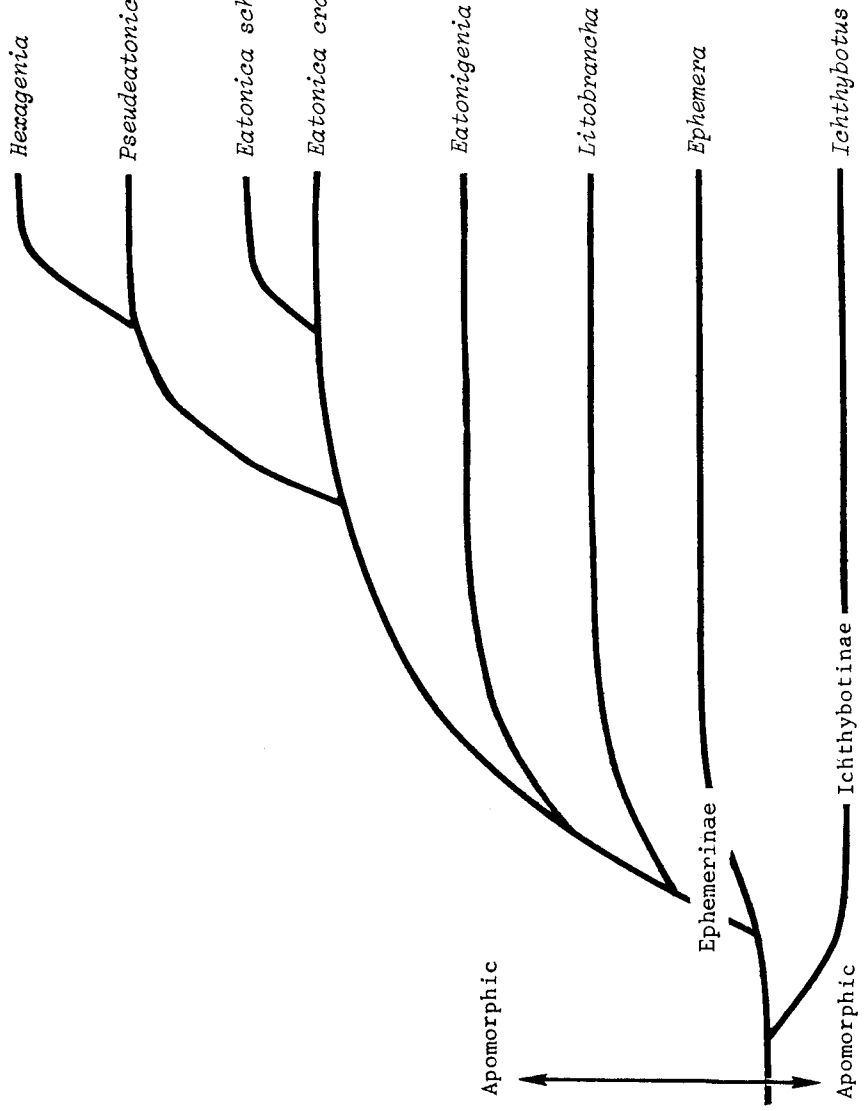
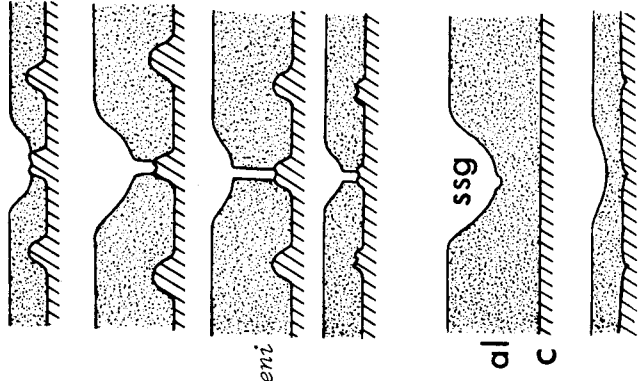


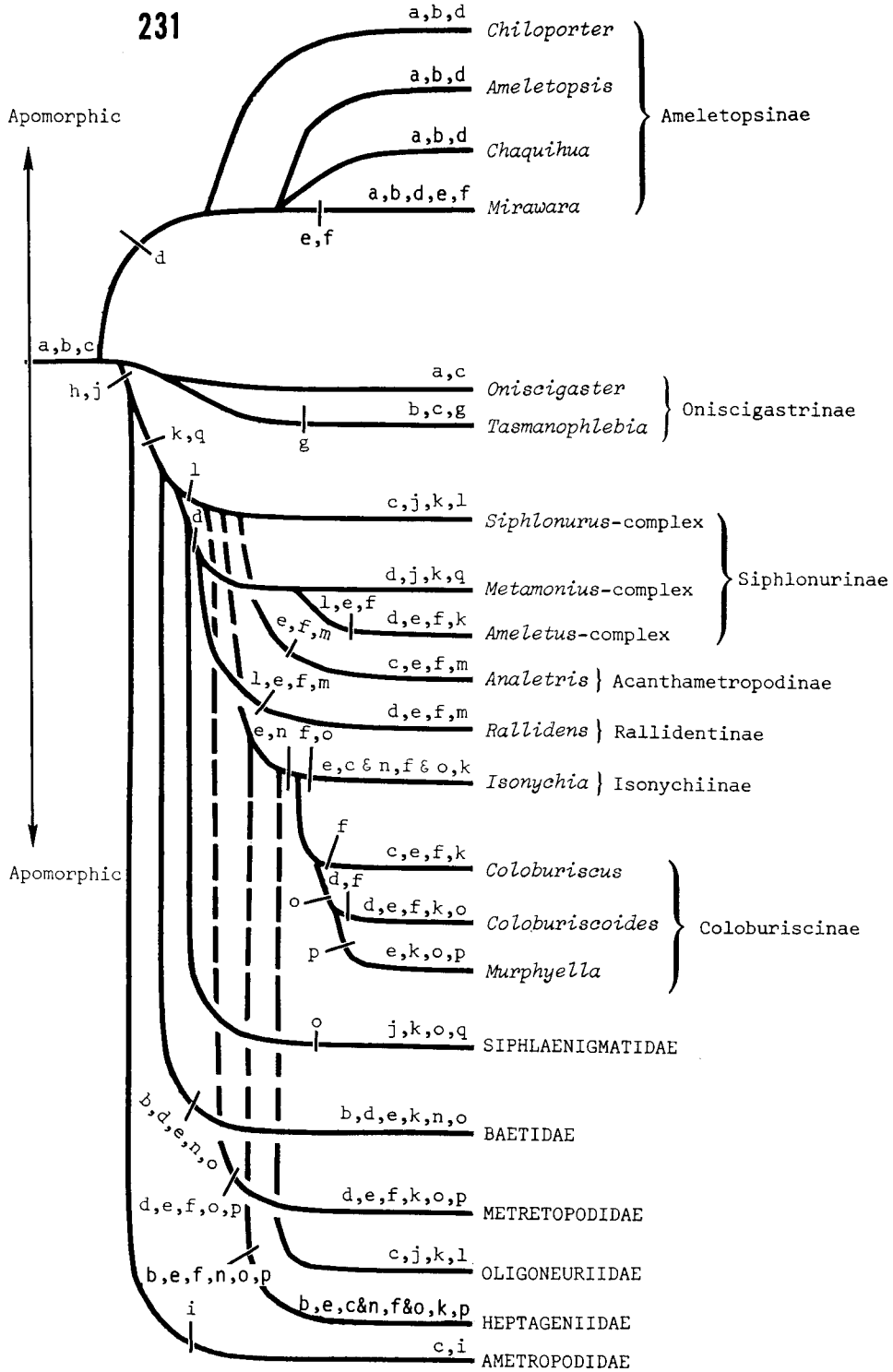


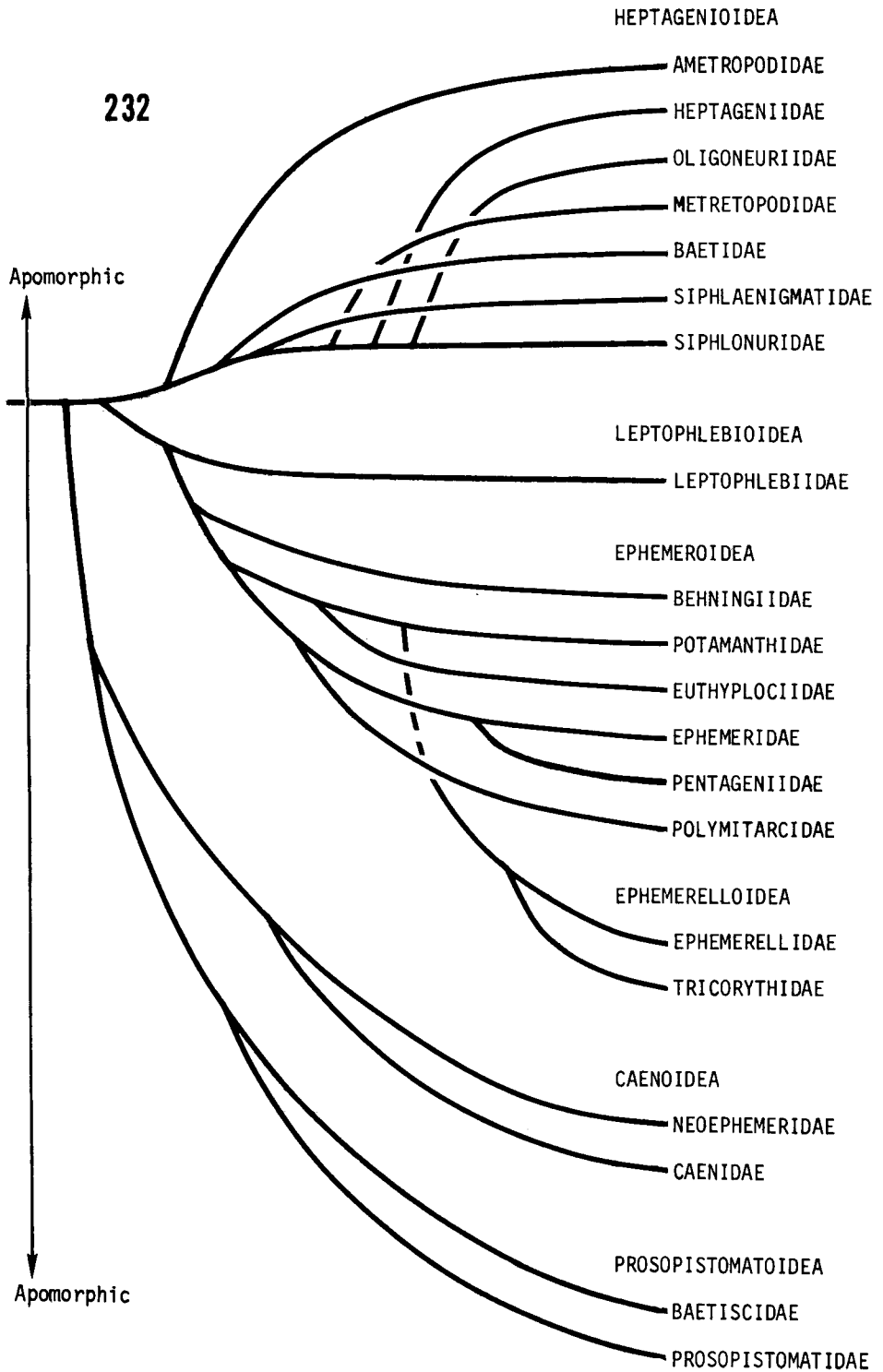
R. W. KOSS AND G. F. EDMUNDS











micropyles (P. C., x373). Fig. 83. *C. ramaleyi*, chorion and attachment structures (P. C., x933). Figs 84, 85. *C. reticulata*: 84, chorionic tubercles in tangential view (I. C., x933); 85, polar coil (P. C., x373). Fig. 86. *C. tarda*, chorionic tubercles in tangential view (I. C., x933). Figs 87, 88. *C. uniformis*: 87, egg, slight unnatural distortion (P. C., x933); 88, micropyle (P. C., x933).

PLATE 8 (figs 89-97)

Fig. 89. *Ecdyonurus insignis*, general outline of egg, chorion out of focus (P. C., x187). Fig. 90. *Thalerosphyrus* sp. (P. C., x373). Fig. 91. *E. yoshidae*, optical section of lateral, knob-terminated coiled thread; tangential view (I. C., x933). Fig. 92. *Epeorus (Epeorus) aesculus*, chorion and sperm guide (P. C., x933). Fig. 93. *E. (Ironopsis) grandis*, chorion and micropyle (P. C., x933). Figs 94, 95. *Cinygmmina?* sp.: 94, egg (P. C., x467); 95, displaced equatorial coiled thread, and chorionic impression of same (P. C., x373). Fig. 96. *Heptagenia aphrodite*, egg (P. C., x373). Fig. 97. *H. solitaria*, general outline of egg, chorion out of focus (I. C., x233).

PLATE 9 (figs 98-106)

Fig. 98. *Heptagenia* sp., egg (P. C., x373). Fig. 99. *H.* sp., near *elegantula*, approximately 2/3's of egg (P. C., x373). Figs 100-102. *Rhithrogena hageni*: 100, egg (P. C., x373); 101, pole of egg (P. C., x933); 102, micropyle (P. C., x933). Figs 103, 104. *R. morrisoni*: 103, egg (P. C., x373); 104, chorion, attachment structures, and sperm guide (P. C., x933). Fig. 105. *R. robusta*, egg (P. C., x373). Fig. 106. *R. impersonata*, peglike attachment structures and sperm guide (P. C., x667).

PLATE 10 (figs 107-115)

Fig. 107. *Rhithrogena* sp., egg (P. C., x373). Fig. 108. *Arthroplea congener*, chorion and coiled threads (I. C., x843). Fig. 109. *A. bipunctata*, egg (P. C., x240). Figs 110-112. *Pseudiron meridionalis*: 110, optical section of laterally distributed, knob-terminated coiled threads; tangential view (I. C., x583); 111, chorionic costae and sperm guide (P. C., x583); 112, egg (P. C., x192). Figs 113-115. *Pseudiron* sp. no. 1.: 113, chorion and sperm guide (P. C., x583); 114, polar coils (I. C., x933); 115, egg (P. C., x187).

PLATE 11 (figs 116-130)

Fig. 116. *Ametropus albrighti*, general outline of egg (P. C., x100). Figs 117-119. *Siphloplecton basale*: 117, egg (P. C., x233); 118, chorionic tubercles in tangential view (P. C., x583); 119, chorion and sperm guide (P. C., x933). Figs 120, 121. *Metretopus borealis*: 120, egg (P. C., x147); 121, chorion, attachment structures, and sperm guide (I. C., x373). Figs 122, 123. *Atalophlebia* sp. 122, egg (P. C., x211); 123, peglike attachment structures in tangential view (I. C., x422). Fig. 124. *Atalomicia* sp., peglike attachment structures in tangential view (I. C., x527). Fig. 125. *Habroleptoides modesta*, optical section of micropyle; tangential view (I. C., x1054). Fig. 126. "*Thraulius*" sp. (*carribeanus*-type), optical section of micropyle; tangential view (I. C., x933). Fig. 127. *Jappa* sp., two terminal knobs (I. C., x527). Fig. 128. *Miroculus* sp., slightly more than half of egg (P. C., x373). Fig. 129. *Ephemerella (Drunella) cornuta*, general outline of egg (P. C., x133). Fig. 130. *E. (Ephemerella) subvaria*, knob-terminated coiled thread and micropyle (P. C., x843).

PLATE 12 (figs 131-141)

Fig. 131, 132. *Leptohyphes apache*: 131, egg laid in water, removed to 70% ETOH 12 hours later (P. C., x187); 132, chorion and micropyle (P. C., x467). Figs 133, 134. *Leptohyphodes* sp.: 133, general outline of egg, chorion not in focus (I. C., x211); 134, chorionic plates (I. C., x583). Figs. 135-137. *Tricorythodes atratus*: 135, egg (P. C., x169); 136, chorion and micropyle (P. C., x667); 137, optical section of chorionic plates; tangential view (P. C., x667). Fig. 138, 139. *Behningia lestagei*: 138, general outline of egg (x60); 139, lateral accumulation of adhesive material (P. C., x147). Fig. 140, 141. *Dolania americana*: 140, micropyle (P. C., x373); 141, optical section of micropyle; tangential view (P. C., x187).

PLATE 13 (figs 142-151)

Figs 142, 143. *Potamanthodes formosus*: 142, general outline of egg, chorion not in focus (P. C., x233); 143, chorion, attachment structures, and micropyle (P. C., x467). Figs 144-148. *Euthyplocia* sp.: 144, egg with adhesive layer in focus (P. C., x147); 145, egg, broad surface

(drawing, x147); 146, egg, edge view (drawing, x147); 147, optical section of polar cap; tangential view (I. C., x337); 148, chorionic reticulation (I. C., x843). Figs 149-151. *Campylocia* sp.: 149, general outline of egg with polar coils displaced, chorion not in focus (P. C., x61); 150, terminal fiber-cluster (P. C., x187); 151, chorion and micropyle (I. C., x373).

PLATE 14 (figs 152-164)

Fig. 152. *Ephemera danica*, two micropyles (P. C., x933). Fig. 153. *E. simulans*, optical section of micropylar canal (I. C., x933). Figs 154-157. *E. supposita*: 154, chorion (I. C., x583); 155, sperm guide, chorion in focus only within sperm guide (I. C., x933); 156, same as Fig. 155, different sperm guide (I. C., x583); 157, optical section of sperm guide; tangential view (P. C., x933). Fig. 158. *Ephemera* sp. no. 1, egg (P. C., x187). Fig. 159. *E. vulgata*, micropyle (P. C., x933). Figs 160, 161. *Ephemera* sp. no. 2: 160, chorion (P. C., x843); 161, micropylar opening and micropylar canal (P. C., x933). Fig. 162. *Ephemera* sp. no. 3, slightly more than half of egg (P. C., x933). Fig. 163. *Ephemera* sp., micropyle (P. C., x843). Fig. 164. *Ephemera* sp. no. 4, micropyle (P. C., x933).

PLATE 15 (figs 165-175)

Fig. 165. *Ephemera* sp. no. 4, chorion (P. C., x933). Fig. 166. *Ephemera* sp. no. 5, micropyle (P. C., x933). Fig. 167. *Ephemera* sp. no. 6, chorion and micropyle (P. C., x933). Figs 168-170. *Eatonica crassi*: 168, chorion (I. C., x467); 169, optical section of adhesive layer and chorion; tangential view (I. C., x933); 170, optical section of sperm guide; tangential view (I. C., x583). Figs 171-175. *E. schoutedeni*: 171, micropylar opening and micropylar canal (I. C., x933); 172, chorion (I. C., x933); 173, adhesive layer reticulation; chorionic reticulation in background, out of focus (I. C., x933); 174, optical section of sperm guide; tangential view (I. C., x933); 175, optical section of adhesive layer and chorion (I. C., x933).

PLATE 16 (figs 176-184)

Figs 176,177. *Eatonigenia chaperi*: 176, adhesive layer reticulation and sperm guide (P. C., x933); 177, optical section of sperm guide; tangential view (I. C., x1167). Figs 178-180. *Hexagenia bilineata*: 178, optical section of suprachorionic portion of sperm guide; tangential view (I. C., x583); 179, chorion and micropyle (P. C., x467); 180, suprachorionic portion of sperm guide (I. C., x933). Figs 181, 182. *Hexagenia munda munda*: 181, chorion and chorionic portion of sperm guide (P. C., x033); 182, optical section of suprachorionic portion of sperm guide, proximal end; tangential view (P. C., x583). Figs 183, 184. *Hexagenia rigida*: 183, egg (P. C., x267); 184, adhesive layer tubercles and upper surface of chorionic ridges (I. C., x933).

PLATE 17 (figs 185-194)

Figs 185-189. *Litobrancha recurvata*: 185, egg (P. C., x169); 186, chorion (P. C., x933); 187, micropyle (P. C., x933); 188, micropylar canal (P. C., x933); 189, optical section of micropylar canal; tangential view (I. C., x933). Figs 190-194. *Pseudeatonica albivitta*: 190, egg (P. C., x187); 191, chorionic reticulation (I. C., x933); 192, chorionic portion of sperm guide (I. C., x933); 193, suprachorionic portion of sperm guide (I. C., x467); 194, optical section of suprachorionic portion of sperm guide; tangential view (I. C., x467).

PLATE 18 (figs 195-206)

Figs 195, 196. *Pseudeatonica albivitta*: 195, micropylar canal (I. C., x933); 196, optical section of suprachorionic portion of sperm guide (I. C., x933). Figs 197-200. *Pentagenia vittigera*: 197, egg (P. C., x233); 198, protruding portion of micropylar canal (I. C., x583); 199, same as Fig. 198 (P. C., x933); 200, optical section of protruding portion of micropylar canal (I. C., x933). Figs 201-203. *Icthybotus bicolor*?: 201, egg (I. C., x198); 202, optical section of chorion and adhesive layer on lateral surface of egg; tangential view (I. C., x933); 203, optical section of chorion and adhesive layer near pole of egg (I. C., x933). Figs 204-206. *Ephoron leukon*: 204, capped end of egg (P. C., x333); 205, micropylar canal (I. C., x583); 206, portion of polar cap (I. C., x583).

PLATE 19 (figs 207-216)

Fig. 207. *Campsurus* sp., egg (P. C., x147). Fig. 208. *C. major*?, chorion and adhesive layer (P. C., x933). Figs 209, 210. *Tortopus* sp.: 209, chorion and micropyle (P. C., x667); 210, egg

(P. C., x83). Figs 211-213. *Asthenopus* sp.: 211, egg (P. C., x187); 212, optical section of chorionic disc (I. C., x933); 213, a polar end of egg (P. C., x467). Fig. 214. *Povilla adusta*, egg (P. C., x147). Fig. 215. *Neoephemera (Oreianthus) purpurea*, slightly more than half of egg (P. C., x233). Fig. 216. *Potamanthellus* sp. egg (P. C., x373).

PLATE 20 (figs 217-224)

Figs 217-219. *Brachycercus lacustris*: 217, egg (P. C., x233); 218, chorion and micropyle (P. C., x933); 219, tangential view of uncapped pole of egg (I. C., x1167). Fig. 220. *Caenis simulans*, egg (P. C., x933). Fig. 221. *C. jocosa*, chorion and micropyle (P. C., x667). Fig. 222. *Tasmanocoenis*, egg (P. C., x373). Figs 223-224. *Prosopistoma africanum*: 223, chorion and attachment structures (I. C., x467); 224, chorion and micropyle (I. C., x933).

PLATE 21 (figs 225-229)

Figs 225, 226. Diagrammatic representation of projecting chorionic structures: 225, cylindrical structure; 226, rectangular structure. Fig. 227. *Oniscigaster distans*?, optical section of micropyle. Fig. 228. *Tasmanophlebia* sp. no. 1, optical section of micropyle. Fig. 229. Diagrammatic representation of the probable phylogenetic relationships of the subfamilies and genera of Polymitarciidae. Letters listed at the ends of the lines indicate those character states presently occurring in the respective taxa; letters accompanying hash marks within the diagram indicate attainment or change in character state, and estimated relative time of occurrence of such change in the respective lineage. Character states indicated by letters: a, ovoid-shaped egg; b, smooth chorion; c, filamentous adhesive layer; d, funnellform micropyle; e, C-shaped egg; f, punctate chorion; g, one polar cap (Type III) consisting of many long threads loosely coiled about one pole (not present in all species); h, tageniform micropyle; i, egg enveloped in a mass of long, loosely coiled threads; j, two polar caps (Type III), each consisting of many long threads loosely coiled about the respective poles; k, chorion densely covered with many discoid structures; l, one polar cap (Type II) consisting of many tubular-shaped structures; m, large-mesh chorionic reticulation formed by ridges.

PLATE 22 (fig. 230)

Fig. 230. Diagrammatic representation of the probable phylogenetic relationships of the subfamilies and genera of Ephemeridae, including optical sections of the sperm guides in the Hexagenia-complex.

PLATE 23 (fig. 231)

Fig. 231. Diagrammatic representation of the probable phylogenetic relationships within the Heptagenioidea, including the subfamilies and genera of the Siphonuridae. Letters listed at the ends of the lines indicate those character states presently occurring in the respective taxa; letters accompanying hash marks within the diagram indicate attainment or change in character state, and estimated relative time of occurrence of such change in the respective lineage. Character states indicated by letters: a, funnellform micropyle; b, undifferentiated adhesive layer; c, smooth or finely sculptured chorion (granulate, maculate, etc.); d, large-mesh reticulation on at least part of the chorion; e, knob-terminated coiled threads, knobs apomorphic; f, coiled threads localized at pole(s), scattered or absent laterally; g, funnellform-tangeniform intermediate micropyle; h, filamentous adhesive layer; i, polar cap (Type III) of many elongate threads tightly coiled about one pole; j, coils of loosely arranged fibers in a uniform layer covering entire egg; k, tangeniform micropyle; l, terminal fiber-clusters, or plesiomorphic terminal knobs; m, micropyle highly modified; n, coiled threads in a uniform layer covering entire egg; o, chorion tuberculate; p, coiled threads scattered over chorion, no polar concentrations; q, coil termini unorganized, no terminal fiber clusters or terminal knobs.

PLATE 24 (fig. 232)

Fig. 232. Diagrammatic representation of the probable phylogenetic relationships of the families of Ephemeroptera, Palingeniidae not included.