Life Sciences Contribution
Royal Ontario Museum 81

The Ejaculatory Complex
in Water Mites
(Acari: Parasitengona):
Morphology and Potential
Value for Systematics

David Barr

DEPARTMENT COPY

LIFE SCIENCES CONTRIBUTIONS
ROYAL ONTARIO MUSEUM
NUMBER 81

DAVID BARR

The Ejaculatory Complex
in Water Mites
(Acari: Parasitengona):
Morphology and Potential
Value for Systematics

Publication date: 30 October, 1972

Suggested citation: Life Sci. Contr., R. Ont. Mus.

ROYAL ONTARIO MUSEUM
PUBLICATIONS IN LIFE SCIENCES

The Royal Ontario Museum publishes three series in the Life Sciences:

LIFE SCIENCES CONTRIBUTIONS, a numbered series of original scientific publications, including monographic works.

LIFE SCIENCES OCCASIONAL PAPERS, a numbered series of original scientific publications, primarily short and usually of taxonomic significance.

LIFE SCIENCES MISCELLANEOUS PUBLICATIONS, an unnumbered series of publications of varied subject matter and format.

All manuscripts considered for publication are subject to the scrutiny and editorial policies of the Life Sciences Editorial Board, and to review by persons outside the Museum staff who are authorities in the particular field involved.

LIFE SCIENCES EDITORIAL BOARD, 1971-1972

Chairman: P. C. SWANN

Director, Royal Ontario Museum

Editors: E. J. CROSSMAN

J. R. TAMSITT

DAVID BARR is Assistant Curator of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

PRICE: \$5.50

© The Royal Ontario Museum, 1972

100 Queen's Park, Toronto, Canada

PRINTED AT HANSON & EDGAR LIMITED, KINGSTON, ONTARIO

Contents

Abstract, 1

Résumé, 2

Introduction, 3

Objectives, 3

History of Water Mite Classification, 3

The Genus as Operational Unit, 5

The Ejaculatory Complex, 5

Problems in Mite Taxonomy, 6

Methods, 7

Functional Morphology of the Ejaculatory Complex in *Hydrodroma*, 8

Historical Introduction, 8

Male Reproductive System, 9

Chitinous Skeleton of the Ejaculatory Complex, 12

Musculature, 17

Functional Interpretation, 17

Discussion, 22

Survey of the Ejaculatory Complex in Water Mites, 23

Historical Introduction, 23

Male Genital System in Terrestrial Mites, 23

Comparative Studies in Water Mites, 23

Descriptions: Species Ordered Alphabetically, 24

Albia

Arrenurus

Atractides

Aturus

Axonopsis

Brachypoda

Eylais

Feltria

Forelia

Frontipoda

Geayia

Hydrachna

Hydrovolzia

Hydryphantes

Hygrobates

Koenikea

Kongsbergia

Lebertia

Limnesia

Limnochares

Midea

Mideopsis
Neumania
Oxus
Piona
Protzia
Pseudohydryphantes
Sperchon
Sperchonopsis
Testudacarus
Thyas
Tiphys
Torrenticola
Tyrrellia
Unionicola

Assessment and Analysis of Similarities, 64

Homology, 64

The Generalized Water Mite EC, 64

Similarity Groupings, 65

Discussion, 71

Basic Conclusions, 71

Importance For Classification, 72

Phylogenetic Significance, 72

Summary, 74

Glossary of Morphological Terms, 75

Acknowledgments, 78

Literature Cited, 79

Appendix A: Traditional Classification of Water Mites (adapted from Viets and Viets, 1960), 84

Appendix B: Johnston's Classification (1965) of Water Mites (adapted), 84

Appendix C: Data for Collections Examined, 85

The Ejaculatory Complex in Water Mites (Acari: Parasitengona): Morphology and Potential Value for Systematics

Abstract

The water mite ejaculatory complex was investigated to provide new systematic information. As a basis for comparison, a functional morphological study was first completed for the ejaculatory complex (EC) of *Hydrodroma* sp. (nr. *H. despiciens*). Cleared skeletal mounts, serial sections, and other preparations were used to elucidate structure. Finally EC structure was compared for 45 species of water mites classified in 36 genera and 24 families. The most useful technique involved preparation of cleared skeletal mounts and observation by interference contrast (Nomarski phase) microscopy.

The EC of *Hydrodroma* is shown to be an elaborate, muscled, chitinous syringe-mechanism for the ejection of a mass of spermatozoa as a spermatophore. Structure is described and a working terminology established. A detailed functional hypothesis (based on morphology and general behaviour) is developed, and indications of the value of the EC character complex for systematic work are noted. The basic EC structure for all species studies (except *Hydrovolzia* sp.) is homologous with that of *Hydrodroma*. General EC function also appears to be similar throughout, although differences in detailed mechanism are suggested by variations in skeletal structure. Using the EC as an indicator of relationship, several informal suprageneric groupings, coinciding only partially with conventional classifications, are delimited.

A primary conclusion is that evidence from the EC is consistent with a hypothesis of monophyly for the water mites.

Résumé

On a examiné le complexe éjaculatoire des mites aquatiques à la recherche de nouvelle information systématique. Comme fondement d'une étude comparative, d'abord une investigation de morphologie fonctionnelle a été complétée pour le complexe éjaculatoire (abrégé EC) de *Hydrodroma* sp. (près de *H. despiciens*). Des préparations squelettiques claires, sections sériales, et des autres préparations ont été utilisés pour élucider la structure. C'est suivi par une évaluation comparative de la structure de l'EC pour 45 espèces de mites aquatiques classifiées en 36 genres et 24 familles. La méthode la plus convenable utilise les préparations claires du squelette chitineux et l'observation par microscopie d'interférence contrastée (Nomarski phase).

L'EC de *Hydrodroma* se montre comme un mécanisme de seringue élaboré, musculeux, chitineux, pour l'éjaculation d'une masse de spermatozoa en une spermatophore. La structure est décrite et une terminologie faisable est établie. Une hypothèse fonctionnelle détaillée (fondée sur la morphologie et sur le comportement général) est développée, et des indications sont notées donnant la valeur de la complexe de caractères pour le travail systématique. La structure fondamentale de l'EC pour toutes les autres espèces de mites aquatiques étudiées (avec l'exception de *Hydrovolzia* sp.) est homologeuse à cela de *Hydrodroma*. La fonction générale, elle aussi apparaît d'être pareille pour toutes les espèces, bien que des variations en mécanisme détaillé soient suggérées par des variations en structure squelettique. En employant l'EC comme indicateur de relations, plusieurs catégories supra-génériques informales sont délimitées, et celles-ci ne sont que partiellement d'accord avec les classifications conventionnelles.

Une première conclusion est que l'évidence de l'EC conforme à une hypothèse de monophylie pour les mites aquatiques.

Introduction

Objectives

An objective classification of animals based on a broad biological characterization rather than the narrow basis of descriptive external morphology is essential if classification is to serve as an information storage system with high predictive value. The need for this sort of approach at the supra-generic level is strikingly apparent in water mites. Mitchell (1964b) termed the family groupings arbitrary and inconsistent and, in proposing a solution to this undesirable situation, discussed studies in functional morphology, chromosome structure, larval morphology, and larval behaviour. He concluded that the most stable higher classification would be derived from a synthesis of a series of similar, independent investigations of biological systems.

Mitchell (1957a, 1958a) also indicated that characters other than those of the external plates of the body wall may form the *only* reliable basis for suprageneric classification in mites. His view arises from the probable assumption that small-bodied forms such as mites, with an unspecialized mode of locomotion, have little functional need for exoskeletal sclerites and may have undergone extensive evolutionary radiation while remaining in the "soft-bodied" condition.

Several modern comparative studies (Bader, 1954, 1969; Sokolow, 1954; Mitchell, 1957a, 1962; and Späring, 1959) of biological systems in water mites are now available, but more are needed before a stable and practical family classification can be derived. The same data are required for more realistic and complete estimates of water mite phylogeny.

Thus, the primary aim of the present study was to make available for systematic purposes a body of comparative data on one functional system within the water mites and to integrate this new material as another information module in our available knowledge. At the same time it has been possible to increase our understanding of the reproductive biology of aquatic Parasitengona and to elucidate the structure of an organ that will prove useful at all levels of taxonomy, in particular, that of specific discrimination and identification.

History of Water Mite Classification

Thor (1903) summarized some of the classification schemes used for mites before 1900, in most of which the true water mites were grouped in the single family Hydrachnidae. This family was gradually divided into subfamilies by Piersig and Lohman (1901), Koenike (1909), and K. Viets (1916). Eventually, Hydrachnidae was much restricted, and numbers of new families were erected (see Thor, 1903; K. Viets, 1929, 1936; Lundblad, 1941b).

The most widely accepted classification is perhaps best exemplified in that employed by Viets and Viets (1960, see Appendix A). It consists (for central European species) of 31 families, 16 of which are monotypic. The families are grouped into 11 superfamilies, and are arranged in

natural (evolutionary) order, the most primitive families listed first and the most advanced (derivative) last. This classification is based almost entirely on the external exoskeletal morphology of adult mites, particularly structures of the palp, genital plates, coxae, and legs, and it has been constructed by many workers over the past 70 years largely on the basis of intuition and tradition. Thus it is difficult to find an explicit statement in the literature as to why, for instance, the *Tormenticolidae* are more similar structurally to the *Lebertiidae* than to the *Sperchonidae*.

Grandjean (1935) discovered that all mites could be separated into two groups by the presence or absence of actinochitin (optically active chitin) in the core of simple setae. This and other correlated characters were incorporated into recent classifications of the *Acari* by Evans *et al.* (1961) and by Johnston (1965). Most recent authors agree that the water mites are *Prostigmata* and should be placed in the group *Parasitengona* (variously described as a Cohort, Suborder, etc.) with the closely related terrestrial families *Johnstonianidae*, *Trombiculidae*, *Trombidiidae*, *Erythraeidae*, *Smaridiidae*, and *Calyptostomidae*, where the larvae differ markedly from the adults in morphology and habits (usually parasitic larvae and free-living adults).

Mitchell has devoted much thought to water mite classification and has repeatedly advanced the idea that the group may be polyphyletic (1954, 1957a, 1962; Imamura and Mitchell, 1967), different groups having somewhat different affinities within the *Parasitengona*. Indeed, a number of recent authors regard the water mites as basically an ecological assemblage, with the great diversity of structure and of functional systems a result of diverse origin. Adult external morphology is so heterogeneous as to suggest that, in the extreme case, each family could be regarded as an individual phyletic lineage, independent of all the others. But the work of Bader (1954) and Mitchell (1957a, 1962) suggests that a smaller number of broad phyletic lines would best explain the situation. Johnston (1965) was apparently influenced, in part, by Mitchell's findings in the preparation of his catalogue of mites (see Appendix B).

Johnston included all water mites in 10 superfamilies, each equal in rank with those of the terrestrial mites also in the *Parasitengona*. The last seven superfamilies are informally grouped as the *Hydrachnellae* (s. str.), resulting in four main groups within the water mites; viz, *Hydrovolzioidea*, *Eylaoidea*, *Hydryphantoidea*, and *Hydrachnellae* (s. str.). The implication is that the four main groups of water mites are no more closely related among themselves than they are to any of the superfamilies of terrestrial mites. Krantz (1970) used a similar classification.

Except for the above-mentioned studies, a conscious and objective investigation of the problem of grouping genera into families has not been attempted. The genera are so distinctive that they form the units by which most students learn to recognize different types of water mites, and the most workable keys are to genera only (Newell, 1959). Keys to the families and family diagnoses (Baker and Wharton, 1952: 259-319) are so complex, full of exceptions, and difficult to grasp intuitively that the validity and objectivity of most of the presently accepted family groupings is doubtful.

The Genus as Operational Unit

As indicated above, the genus appears to be the most stable supraspecific taxon in water mites and is the most readily defined unit of diversity and evolutionary radiation. Few genera, once erected, have required further modification, and although the taxonomic level of a generic grouping of species may be changed, it has seldom been necessary to thoroughly dissociate the members of such a grouping in spite of the description of thousands of new species from all parts of the world since 1900. The corollary is that there are few, if any, "dumping ground" genera composed of a heterogeneous assemblage of species. As a further corollary, within the water mites, interspecific variation within generic bounds is almost invariably smaller than interspecific variation across generic lines. Consequently, the present study was based upon a comparison of genera as represented by one or a few available species.

This is the so-called exemplar method of comparative biology (Sokal and Sneath, 1963: 161), and its justification is based upon the observation that when it is not possible (for reasons of time, labour, poor collections, etc.) to base observations on large samples of the units of a given taxon, reasonably dependable results can be obtained by using representative units. The success of this method depends upon the probability that a randomly chosen taxonomic unit will be typical for the taxon it represents, a probability that is much increased when the taxa are as homogeneous as water mite genera. The method has been tested several times with favourable results (Sokal and Sneath, 1963: 162; Moss, 1968).

The Ejaculatory Complex

Throughout all groups of the Arthropoda, wherever genitalia or intromittent organs of complex form are found, the comparative morphology of these structures has provided a rich source of data for use in species definition, classification, and phylogenetic speculation at all taxonomic levels. This is true in such widely different groups as Anostraca (Dexter, 1959), Astacidae (Hobbs, 1942a, 1942b), Diplopoda (Keeton, 1960), Araneida (Comstock, 1948: 106-121) and Acarina (Feider, 1959), as well as for almost every order of Insecta (Tuxen, 1956). But until the present, the use of this fund of information for the elucidation of systematic problems in the water mites has been limited. Although the aquatic Parasitengona have been intensively studied for at least 100 years and constitute perhaps one of the best understood subunits of the Acari, and although the generic classification has reached a mature and stable level, the simple descriptive morphology of the chitinous male organ, known as the *penisgeriist* or ejaculatory complex, has so far been neglected.

The ejaculatory complex has been referred to in different ways by various authors. Perhaps the term most commonly applied to it is Penis, but it is inappropriate to continue this usage as penis commonly refers to a flexible membranous or muscular intromittent organ in other invertebrate and vertebrate groups. Phallus is unsatisfactory also, for it implies merely

an intromittent organ, a through passage for sperm transfer. The ejaculatory complex of water mites, however, is not always used for intromission and usually serves other functions in addition to simple sperm transfer. Aedeagus can be applied only to the sclerotized distal section of the phallus in insects, often little more than a sclerotized tube. Authors writing in German have generally applied the term *penisgerüst* to the organ, literally “(supporting) framework of the penis.” This term is correct in a narrow sense if the walls of the sperm passage are considered to represent a membranous penis, but its use seems to deny the probable ontogenetic origin of the sclerites from the walls of the passage and completely neglects the functional character of the organ in spermatophore formation. Thus, in every way, the name ejaculatory complex as defined by Mitchell (1964a) in his study of the trombiculid, *Blankaartia acuscutellaris*, describes best the muscled, chitinous framework that participates in formation of a spermatophore as well as ejection and deposition of the spermatophore outside the body of the male. This term will often be abbreviated to EC in the present report.

Problems in Mite Taxonomy

Although the limits and diagnostic characters for most genera of water mites are well understood, the species-level taxonomy, especially of non-European forms, is unsatisfactory. Of the approximately 75 genera known from North America, only about 15 have been revised since 1950, and keys are available for only a few of these. The other $60\pm$ genera are known only from scattered and inadequate species descriptions and a few dated monographs by Wolcott (see references in Crowell, 1961). A major revisionary effort is needed before even the adults of most North American species can be determined with confidence (for example, see Paterson, 1970).

The unsatisfactory taxonomic situation has proven a difficulty in the present study, and the following conventions were followed in discussing the water mite species examined. Each species was represented by individuals from a monospecific population (judged on morphological criteria) from a single locality (collection data in Appendix C). Thus, the unit of study was not a species but a representative (and relatively uniform) subpopulation (or deme) of that species. This practice will tend to insure that characters of more than one closely related species will not be confused. Species names are applied to such populations only where the identification seems unequivocal, and in each such case I have cited the source upon which the determination was based. The designation near (nr.) indicates that there are good reasons to believe that the mites examined are members of this species, but that revisionary work and/or reference to types is required before a precise determination can be made.

Methods

Cleared skeletal preparations of the EC were studied by light microscopy, both bright-field and interference contrast (Nomarski phase). Most of the structural detail is illustrated in paired anterior and lateral views. All illustrations are semi-diagrammatic in that sclerites are delimited somewhat more clearly than they appear in the preparation, while small changes were sometimes necessary to clarify structure or position. Each drawing is oriented with the distal end of the ejaculatory complex pointing towards the bottom of the page. Thus the lateral view is of the left hand side. The scale accompanying each pair of figures represents a length of 50 μ , and a single scale serves for both illustrations of each species.

Specimens for gross dissection and serial sectioning were prepared by the cellulose nitrate infiltration procedure described by Mitchell (1964a). Serial sections were stained with Mallory's triple stain (Gray 1964: 111).

Each species population examined is represented by a small series of voucher specimens deposited in the collection of the Department of Entomology and Invertebrate Zoology of the Royal Ontario Museum, Toronto, Ontario.

Abbreviations used in the figures and descriptive portions of the text are listed below.

AMScl: anterior margin sclerite.	DisRm: distal ramus.
AntHn: anterior horn.	DisSc: distal sclerite.
AntKl: anterior keel.	DLBd: distolateral border.
AntRm: anterior ramus.	EC: ejaculatory complex.
Apcl: apical development.	LtrSf: lateral shelf.
ApRm: apical ramus.	LWScl: lateral wall sclerite.
ApSt: apical seta.	PosKl: posterior keel.
BsPl: basal plate.	PrxAm: proximal arm.
Cmb: chamber.	PrxCmb: proximal chamber.
CmbRm: chamber ramus.	PrxHn: proximal horn.
DisAm: distal arm.	PrxSc: proximal sclerite.
DisRd: distal rod.	PstRm: posterior ramus.

Functional Morphology of the Ejaculatory Complex in *Hydrodroma*

Historical Introduction

Early workers investigated the male reproductive system of water mites in some detail. Koenike (1888), von Schaub (1888), Michael (1895), Pollock (1898), Nordenskiöld (1899), Thon (1900), Thor (1903), Lundblad (1930), and Schmidt (1935) considered some aspects of the sclerotized *penisgerüst*, but none succeeded in producing a meaningful, three-dimensional explanation of the structure. Thus, no adequate functional hypothesis was developed. Because Schmidt, the most thorough of these investigators, worked primarily with *Hydrodroma* (= *Diplodontus*) *despiciens*, this species was chosen for intensive investigation.

Additional evidence on the EC may be available in Croneberg (1878) or in Musselius (1912; cited by Mitchell, 1955). Neither publication could be obtained for the present study.

Purely taxonomic studies have made little use of the ejaculatory complex (see Koenike, 1901, 1902; Lundblad, 1941a, 1943, 1956; K.O. Viets, 1965, 1968). Usually, only a semi-detailed drawing has been offered with one or two prominent features noted in the text. There is no standard structural terminology.

Mitchell's morphological publications on *Unionicola* and *Najadicola* (1955), *Thermacarus* and other thermophiles (1960), water mite mouthparts (1962), and *Limnochares* and *Eylais* (1964b) did not treat the EC, but demonstrated a variety of little-used techniques that proved valuable in the present study.

I sought basically to repeat Schmidt's work, with the addition of gross dissection and skeletal preparation techniques to more thoroughly explore the three-dimensional structure of the ejaculatory complex and to discover its functional significance. Schmidt's (1935) observations on the soft parts of the genital system were accurate and are, in part, repeated here by way of summary and orientation.

The species studied has long been known as *Hydrodroma despiciens* Müller. It is common, shows little variation over its broad range in North America, and appears to be the same as the European species of that name. The assumption that North American mite populations belong to European species on the basis of adult morphology alone is, however, unwise. Several of these associations have been proven incorrect in the past. A thorough comparison of North American and European populations of *H. despiciens* might also show specific differences.

The *Hydrodroma* collected from Lake Myosotis, Rensselaerville, N.Y., are uniform in the structure of the ejaculatory complex. This population also is similar to samples examined from other collections in northeastern North America.

Male Reproductive System

The testes, multilobed and filling much of the body cavity, surround the gut and push anteriorly, crowding the salivary glands. Each lobule empties via a sperm duct that unites with others in a branching system leading ultimately to a pair of long, wide, seminal vesicles lying midway (dorso-ventrally and anteroposteriorly, Fig. 1c) in the body. These seminal vesicles are anteroposteriorly elongate and lie one on either side of the midline, with the products of the testes entering dorsoposteriorly. Exiting antero-ventrally from each seminal vesicle is a narrow, tubular, muscular-walled *vas deferens* that travels anteroventrad in the direction of the genital opening. After a short distance (Figs. 1c, 5a) the *vasa deferentia* turn posteromedial and unite to form a wide, thin-walled, muscular tube, the *ductus ejaculatorius*. The *ductus* proceeds posterad for a short distance and narrows, bending ventrally at the same time and entering the ejaculatory complex.

The ejaculatory complex lies in the median plane and is usually positioned with its longitudinal axis in an oblique anteroventral to posterodorsal direction, the free distal end pointing toward the genital opening (Fig. 1a). For clarity and ease of usage, all subsequent terminology associated with this organ will be based on the assumption that it is oriented directly dorsoventrally, the distal end being ventral and the proximal end dorsal. Thus, the cephalic-facing and caudal-facing surfaces will be termed simply anterior and posterior, respectively. The organ lies at the distal end of the ejaculatory duct and just inside the genital opening in the body wall. Lightly sclerotized distal membranes join its apex to the margins of the genital opening so that the extreme distal tip is an external structure concealed in a phallocrypt (Fig. 1b). The structure is apparently maintained in place in the body cavity by a network of thin, cross-banded fibers inserted generally over its surface (particularly on membranous areas), and having their origin on the inside of the genital plates, on the distal membranes, on the endosternite, and on denser tracts of such fibers lying in the body cavity. Schmidt (1935) interpreted these fibers to be muscular, but Mallory's triple stain (Gray 1964:111) preparations would indicate that they are chitinous endocuticular fibrils of the same nature as those forming muscle tendons. The endosternite is a short, transverse tract of endocuticular material lying anterior to the ejaculatory complex and serving as the point of origin for a number of important body muscles.

The external genitalia of male *Hydrodroma* consist of two ovoid plates that are somewhat pointed anteriorly and posteriorly and lie on either side of the elongate genital opening. Each bears approximately 60 (± 10) genital acetabula and, on the concave medial border, a narrow tract of setae. Convincing evidence that the acetabula are sensory organs was advanced by Thor (1903) and by Schmidt (1935).

Fig. 1 *Hydrodroma* anatomy: a, three-dimensional diagram to indicate the position of the ejaculatory complex; b, diagrammatic cross-section illustrating the relationship of the EC to the ventral body wall; c, diagrammatic sagittal section of a male showing the relationship of the EC to the rest of the male reproductive system.

Fig. 2 EC skeleton of *Hydrodroma*: a, anterior view; b, lateral view; c, partial posterior view; d, perspective view.

Chitinous Skeleton of the Ejaculatory Complex

The ejaculatory complex is typically a two-layered, chitinous structure of the same basic cuticular composition as those of the exoskeleton. It is probably produced by evagination and subsequent sclerotization of the internal wall of the distal portion of the *ductus ejaculatorius*, which is embryologically an invagination of the ectoderm. This interpretation is supported by the observation that even the heavily sclerotized arms of the ejaculatory complex show a circular pattern of cuticular structure (Fig. 4a) as though originating as tubular evaginations of the ductus.

Because of the method of its formation, the analysis of EC structure in terms of well-defined sclerites is difficult. Heavily sclerotized and apparently distinct areas often grade imperceptibly into lightly sclerotized or membranous areas. The articulation between sclerites may not be a definite suture or joint but an imperfectly defined membranous area that is continuous with both sclerotized structures. Thus, for the purpose of this study, sclerites were delimited somewhat arbitrarily so that they could be referred to as structural landmarks. Points of muscle attachment are usually recognizable because the sclerites are roughened and pitted to increase the surface area for bonding in a manner similar to that observed for muscle insertion on vertebrate bones.

New terms have been defined throughout this study for structures of the EC skeleton. The names proposed are derived from English and are descriptive of position and general shape. All such terms appear in bold-face where they first occur in the text and are redefined in the glossary, p. 75. Abbreviations used in the figures are shown with first usage of the term, in the glossary, and in a complete list, p. 7.

No attempt was made to homologize parts of the ejaculatory complex of this species with the sclerites described by Feider (1959) for the Trombidioidea although there is undoubtedly an evolutionary relationship. Until the relation of Feider's sclerites to the soft parts is better known, functional and structural homologies will be difficult to interpret. Needed are more investigations of the type done by Mitchell (1964a) for the trombiculid, *Blankaartia*.

The main supporting framework of the EC (Figs. 2, 3) consists of two pairs of sclerites, the paired **proximal arm sclerites** and paired **distal arm sclerites**. The *ductus ejaculatorius* proper empties into an enlarged **proximal chamber** (PrxCmb), which is roughly cubical, with lateral, proximal, and posterior walls sclerotized. The anterior wall is largely membranous and is the point of entry of the *ductus*. The lateral walls approach each other distally, and the chamber is narrowed and open on the distal side. The lateral walls are strengthened along their anterior and distal edges by the more heavily sclerotized **anterior margin sclerite** (AMScI). The anteroproximal edge of the chamber is especially heavy and bears a pair of **proximal horns** (PrxHn). The anterior third of the proximal wall is also heavily sclerotized, and a **lateral wall sclerite** (LWScI) travels diagonally across each lateral wall providing additional rigidity. The thickened sclerites of the distolateral borders of the chamber run posteriorly and join with the proximal arm sclerites.

After entering the anterior side of the proximal chamber, the sperm passage proceeds distally to the exterior. Lying on either side of the sperm passage are the main supporting elements of the EC, the paired proximal and distal arm sclerites. Each proximal arm sclerite consists of four rami. The largest is the thick, curved **proximal arm** (PrxAm) that projects proximolaterad from the body of the EC, then curves mediad to partially encircle the proximal chamber. The tips and lateral margins of this arm are roughened and pitted to facilitate muscle insertion. A **distal ramus** (DisRm) proceeds distally along the posterior wall of the EC, the distal rami of either side lying close together on either side of the midline. A medial ramus projects toward the midline of the EC and appears to articulate with its fellow from the opposite side. This articulation is the sole point of direct contact between the two proximal arm sclerites. A short **chamber ramus** (CmbRm) has its origin at the point where the proximal arm contacts the lateral wall of the proximal chamber. It travels proximad for a short distance in the lateral wall and articulates with the distal end of the lateral wall sclerite.

The posterior wall of the proximal chamber is moderately sclerotized and grades distally into the lightly sclerotized areas surrounding the distal rami of the proximal arm sclerites in the posterior wall of the midsection of the EC. This latter wall is strengthened in addition by three pairs of submedian **distal sclerites** (DisSc) (Fig. 2c) that appear to articulate with the distal rami. The members of each pair are proximodistally elongate and lie side by side in the posterior wall of the distal half of the EC. The proximal pair are short and thin, the middle pair short and thick, whereas the apical pair are long and taper distally to attenuate apices. The apical distal sclerites extend beyond the apex of the EC, and the attenuate tips project into the phallocrypt. The proximal distal sclerites appear to articulate proximally with the point of articulation of the medial rami (within the body of the EC). The articulation with the distal rami occurs in the posterior wall at the point at which middle and apical sclerites are in contact.

A laterally compressed evagination from the posterior wall of the proximal chamber forms a thin **posterior keel** (PosKl). The lateral walls of this structure and the posterior walls of the chamber are thickened at the point of contact, and the chamber cavity projects a short way into the keel. The keel is expanded into a flattened kidney-shape, and its surface is pitted and sculptured to facilitate muscle attachment. The keel bears a **distal rod** (DisRd) projecting distally and curving anteriorly so that it eventually lies adjacent to the posterior wall of the distal end of the EC and terminates in the distal membranes. This rod is lightly sclerotized (almost membranous) in *Hydrodroma*.

Each of the paired distal arm sclerites bears three main rami. The **distal arm**, projecting laterally from the EC at an angle of approximately 50° to the longitudinal axis, is strong, cylindrical, and relatively straight to the tip, where there is a gradual curve proximad. The tip of each arm is flattened and bears medial horizontal flanges that are sculptured for muscle attachment. The **anterior ramus** (AntRm) projects distally and

Fig. 3 Photomicrographs of the EC skeleton of *Hydrodroma*, overall length $220\ \mu$: *a*, anterior view, optical section in plane of proximal and distal arms, interference contrast; *b*, lateral view, optical section in median plane interference contrast; *c*, anterior view, scanning electron micrograph; *d*, three-quarter view (disto-antero-lateral), scanning electron micrograph.

anteriorly, arching over the EC and fusing, on the midline, with the tip of the same ramus from the opposite side. On the distal border of this ramus, there is no clear line of demarcation between the heavily sclerotized ramus and the sheet of gradually less sclerotized membrane that leads

externally to the margins of the genital opening. The **posterior rami** (PosRm) of the distal arm sclerite lie along the lateral margins of the posterior wall of the midsection of the EC and each is fused with an elongate sclerite lying in the same plane but slightly mediad. These paired **posterolateral sclerites** are attenuate distally (not projecting beyond the distal arm sclerites) and heavier posteriorly where they broaden and expand considerably to fuse with the distal, lateral, and posterior walls of the **lateral chambers** (Cmb 1).

On either side, the distal arm is attached to the posterior wall of the EC (and to the posterior rami) by a thin, sclerotized **lateral shelf** (LtrSf). The shelf fills the triangular axillary area between the distal arm and the posterior ramus and proceeds proximad to fuse with the posterior wall of the lateral chamber. The proximal margin of this shelf is irregular but roughly concave.

The anterior wall of the EC distal to the proximal chamber is covered by two **anterior sclerotized surfaces** that slope from the midline on the anterior surface posterad to the lateral shelf on either side. Proximally these surfaces expand to form part of the distal and anterior walls of the lateral chambers. Distally they narrow and proceed under the arch formed by the anterior rami of the distal arm sclerites, at the same time tapering, becoming less heavily sclerotized, and eventually uniting with the membranes delimiting the phallocrypt. Where the anterior sclerotized surfaces meet along the midline, they fuse and are expanded anteriorly to form a high, broad, thin, strongly sclerotized **anterior keel** (AntKl). Each of the sclerotized surfaces is strengthened by a thickened area lying along the base of the keel and extending part way up its distal edge. The keel is strongly sculptured and pitted for muscle attachment.

The area from the base of the proximal end of the anterior keel to the anterodistal border of the proximal chamber is membranous and continuous with the membranes of the anterior wall of the proximal chamber. The membranes of this area are supported by one pair of rod-like **proximal sclerites** (PrxSc 1). These sclerites extend obliquely from the anterior side of the lateral chambers, proximomedial to the anterior end of the distolateral border of the proximal chamber.

The **sperm passage** (Figs. 1c, 5a) enters the proximal chamber through the anterior side, expands, and narrows as it leaves the chamber distally. The shape of this passage in the distal part of the EC is elaborate (Fig. 4) with extensions into the lateral chambers, but the general course is distad, exiting between the distal apices of the distal arm sclerites. Schmidt (1935) described a series of setae along the sperm canal that were not observed here.

The distal membranous cone leading to the margins of the genital opening and forming the walls of the phallocrypt is attached to the ejaculatory complex along the following line: along the distal edge of the anterior rami of the distal arm sclerite (as previously described), along the basal half of the distal arm, under the distal arm, proximally along the lateral shelf, and across the entire posterior side of the EC at the level of the lateral chambers.

Fig. 4 Diagrammatic transverse sections of the *Hydrodroma* EC skeleton: *a*, in the region of the proximal chamber; *b*, in the region of the distal arm sclerites; *c*, in the region of the lateral chambers.

Fig. 5 Musculature of the *Hydrodroma* EC: *a*, general view of terminal elements of male genital tract; *b*, diagram of the deep muscle groups (4-6); *c*, diagram of the superficial muscle groups (1-3).

Musculature

The musculature of the EC is bilaterally symmetrical, being composed of six pairs of muscle groups that completely ensheath the sclerotized elements (Fig. 5). The number of muscle fibers involved in each group, as in all muscles of this species, is small, not over 10 or 15 at the most, and only three in the phallic retractors.

The superficial or lateral muscle groups are massive in cross section (Fig. 5c). The **distal dilators** (designated muscle group number 1) run laterally from their origin on the anterior and distal halves of the anterior keel to an insertion on the medial surface of the distal arm on either side. The **lateral-longitudinal compressors** (group 2) are oriented distoproximally, originating on the posterior and ventral portions of the lateral surfaces of the anterior keel and on the anterior sclerotized surfaces. They insert on the anterior and medial surfaces of the proximal arm. The **proximolateral compressors** (group 3) are another laterally directed group, originating on the medial and posterior surfaces of the proximal arm and inserting on the lateral surfaces of the posterior keel.

The deep or medial muscle groups are illustrated in Fig. 5b. The **mediolongitudinal compressors** (group 4) run in a distoproximal direction from their origin on the apex, proximal edge, and proximal half of the lateral surfaces of the anterior keel to their insertion on the proximal horns. The **proximomedial compressors** (group 5) originate on the proximal horns and insert on the proximal and anterior edges and proximal part of the lateral surfaces of the posterior keel. The **phallic retractors** (group 6), included with the deeper groups for convenience, originate laterally on the endosternite and insert on the distal arm sclerites near the bases of the distal arms. All of these muscle groups are of small to medium diameter.

Functional Interpretation

The construction of a hypothesis for the function of the *Hydrodroma* ejaculatory complex is based upon three principal kinds of evidence: the reproductive habits of the species, the form and articulations of the skeletal components, and the size and disposition of the muscle groups (plus the similarity to known spermatophore-forming water mites).

Transfer of spermatophores is a common method of fertilization in the Arthropoda (Snodgrass, 1935: 573; Green, 1961: 69-70; Alexander, 1964; Davey, 1965) and especially in the Acari (Hughes, 1959: 176; Evans *et al.*, 1961: 23-26). Indeed, it is probably safe to generalize in stating that, for mites, even where internal insemination takes place, a spermatophore is still formed and transferred (i.e., the sperm never travel freely in a fluid medium). Water mites appear to be typical in this respect (Lundblad, 1929; Mitchell, 1958b; Böttger, 1962, 1965; Efford, 1966). Whether *Hydrodroma* practices internal insemination or some form of spermatophore deposition (both are known for various water mites) is not yet known, but this point would likely affect only the behavioural aspects of insemination and not the function of the EC. The motions of

spermatophore deposition and internal fertilization should be much the same, unless perhaps in the latter the EC is extended farther out from the body (or is more elongate in structure). Therefore I assume that the functions of the ejaculatory complex in *Hydrodroma* are to (i) form a spermatophore, (ii) transport the spermatophore outside the body wall, and (iii) deposit the spermatophore.

The skeletal components of the EC can be divided into three functional groups (Figs. 6, 7). The component sclerites of each group are either fused or bound by tough, inextensible, ligament-like hinges, but the groups are attached to each other by flexible membrane and have a limited degree of movement relative to each other. The groups are: (i) the distal arm sclerites, (ii) the anterior keel and anterior sclerotized surfaces, and (iii) the proximal arm sclerites and proximal chamber. Groups (i) and (ii) are joined to each other by short membranous areas that permit only limited movement. Group (iii), in contrast, is joined to the other two groups by a wide band of thin, flexible, chitinous membrane that forms a conspicuous outpocketing on either side at the level of the lateral chambers. The assumption that each group of sclerites functions as a unit is difficult to support by movement of prepared specimens, as Eisner (1957) reported for the ant proventriculus, but is supported by the mode of deformation and breakage when coverslip pressure is applied.

Muscle groups 1, 2, and 3 are massive, each composed of 10-15 fibres of large diameter, whereas groups 5 and 4 are smaller because they are composed of a similar number of smaller fibers. Group 6 is a long, thin muscle group composed of only three slender fibers. The relative diameter of these groups is probably related to the force applied by each during EC movements.

The presence of group 6, the phallic retractors, indicates that the entire ejaculatory complex is probably projected at least part way out of the genital opening. But there are no muscles attached to the organ that would be capable of protraction, and so a different mechanism must be sought. Water mites, in common with a variety of other arthropods (Manton, 1958; Parry and Brown, 1959; Snodgrass, 1965: 88) utilize the pressure of the hemocoelic fluid for extension of the limbs (Mitchell 1955, 1957b, 1960), and this same pressure is probably the motive force pushing the ejaculatory complex out through the genital opening. Thus, the probable initial events of spermatophore deposition include: (i) contraction of the dorsoventral body muscles increasing pressure on the hemocoelic fluid, (ii) protrusion of the ejaculatory complex to the extent permitted by the distal membranes, and (iii) passive opening of the genital plates because of the pressure of the EC as it is forced outwards (Mitchell, 1957b).

In this position, the sensory setae inserted on the apices of the distal arm sclerites in some species (but not *Hydrodroma*) can be applied to the substrate to gather tactile information on surface texture, and perhaps help guide the animal to a suitable site for spermatophore deposition. In specimens preserved in GAW (Koenike's fluid) (Mitchell and Cook, 1952) the EC often extends through the genital opening, occasionally lying en-

Fig. 6 Postulated action of the distal arm sclerites, transverse section: *a*, muscle group 1 relaxed; *b*, muscle group 1 contracted.

Fig. 7 Postulated action of the sclerite groups of the EC, lateral view: *a*, all muscle groups relaxed; *i*, *ii* and *iii* are major sclerite groups; *b*, contraction of muscle group 4 rotates proximal chamber counter-clockwise; *c*, contraction of muscle group 2 adducts *iii* up to *ii* and through *i*; contraction of muscle group 1 spreads distal arm sclerites of *i* (see Fig. 6) and widens sperm passage; *d*, simultaneous contraction of muscle groups 5 and 3 violently compresses proximal chamber and expels the contained mass of spermatozoa.

tirely outside the body. In extreme cases the proximal end is free and farthest from the body, whereas the distal end is held close to the genital opening. This type of protrusion of the EC is not natural but is an artificial situation caused by the extreme osmotic pressures developed during the process of GAW preservation. When the internal pressure increases sufficiently, the membranous walls of the phallocrypt are ruptured, and the EC is forced out. Because the proximal end is held in position only by the soft tissues of the ejaculatory duct, it is easily displaced. The distal end is more firmly attached by the tough distal membranes and is the only part of the EC to remain fixed to the specimen.

A sequence of movements by the ejaculatory complex that results in spermatophore deposition, once the male has located a suitable site, can be postulated. Consider the following sequence where the word "and" indicates simultaneous contraction and the symbol indicates a pause in activity: 4, 2, 1, 4, 5 and 3, 6. Then the response of the sclerotized skeletal elements could be as follows (Figs. 6, 7): the proximal chamber is tipped distally, thus aiding in closing the open side (4); sclerite group (iii) slides forward under group (ii) and through group (i) until the widest part of the proximal arm sclerites (at base of the proximal arm) meets the distal walls of the lateral chambers (2); the distal arms are pulled medially and anteriorly, articulating with each other anteromedially and greatly widening the posteromedial area through which the sperm passage travels (1); the anteroproximal side of the proximal chamber is pulled distally, further rotating this chamber in a counterclockwise direction (4) and bracing it against clockwise torque; the posterior wall of the proximal chamber is thrust violently anterodistally by the simultaneous contraction of muscle groups 5 and 3, decreasing the volume of the chamber and propelling its contents distally and down the sperm passage. Such a mechanism would effectively expel the semen components of the spermatophore. The sequence of events described, however, is only one of several plausible schemes that could be advanced.

Two structural peculiarities present in *Hydrodroma* and also widespread in the EC of other water mites show some relevance to the proposed mode of action. If the proximal chamber is deformed during spermatophore deposition, then the lateral wall sclerite (Fig. 2b) clearly functions to control the direction of deformation by maintaining the distance between the base of the proximal arm and the anteroproximal corner of the chamber nearly constant on either side. Thus, the primary compression must be along the anterior-posterior axis. The distal rod (Fig. 2b) appears to be a second structure well suited to maintaining the distance between parts of the EC skeleton. Because the rod is membranous in *Hydrodroma* and a few other genera, it probably determines the maximum rather than the minimum distance between its point of origin (posterior keel) and its point of insertion (posterior surface of EC at level of distal arm sclerites). The proximal component of the pull exerted by muscle groups 3 and 5 on the posterior keel is thus balanced by the pull of the distal rod in the distal direction during the simultaneous contraction of these two groups. This mechanism would leave effective only the anterior component of the

force exerted by groups 3 and 5 and so provides a further means of controlling the direction of distortion of the proximal chamber.

The role played by the accessory gland (Fig. 1b, 5a) in spermatophore formation and deposition is not known. The organ was accurately described by Schmidt (1935), and his notes are summarized here. The gland lies posterior to the EC at the level of the anterior keel and is bipartite, an elongate, ovoid arm projecting laterally on either side, with each arm emptying medially into a broad common duct. The common duct opens, not into the sperm passage, but into the phallocrypt posterior to the distal tip of the EC. The canals of the two arms are lined with endocuticle which is uniformly perforated. The glandular tissue consists of columnar cells surrounding each of the arms and presumably discharging secretions through the perforations into the canals. The point at which the gland product enters the genital system indicates that it probably is not used in those aspects of spermatophore formation (e.g., compacting the sperm mass) that occur within the ejaculatory complex. The secretion must instead play some role during extrusion of the spermatophore from the body, perhaps forming a waterproof coating or an attachment stalk (types 3 and 4 of Brunhuber, 1969). The tubular, sac-like structure of these glands would make them well suited to the production of a liquid, proteinaceous coating material of the type described by Davey (1965: 31-33) for the spermatophore of *Rhodnius*.

In none of the specimens sectioned (collected in September and October) were products of the testes present in any part of the EC. Although in most males the lobes and sperm ducts of the testes, the seminal vesicle, and the proximal sections of the *vasa deferentia* were filled with spermatozoa and the carrying fluid (Schmidt, 1935), this material did not extend into the EC. In a number of water mites of other species, however, from which cleared skeletal preparations of the ejaculatory complex were made, dense boli of presumably seminal material were sometimes seen.

The distal parts of the *vasa deferentia* and the entire *ductus ejaculatorius* are provided with a thin circular coat of small muscle fibers that probably constrict these passages enough to prevent passage of reproductive products forward beyond the seminal vesicle. Similarly, once the proximal chamber of the ejaculatory complex has been charged with semen, the subsequent contraction of the muscle coats would effectively prevent backward movement of spermatophore materials during the contractions of the ejaculatory complex muscles responsible for spermatophore deposition. Backflow may be further alleviated by the constriction of the *ductus ejaculatorius* caused when muscle group 4 on either side enlarges during contraction.

As stated earlier, the lateral membranes in the area of the lateral chambers (Cmb 1) join sclerite group (iii) to the other two groups. It is possible that upon being charged with semen, the EC expands by separation of sclerite groups (i) and (ii) from group (iii), with the distention of the lateral membrane. Consequently a larger portion of the sperm canal would be filled with semen, but the series of contractions postulated could still expell the entire mass.

In summary, the ejaculatory complex of *Hydrodroma* is a syringe-like organ for the reception, compacting, and expulsion of masses of spermatozoa. The proximal chamber is charged with the contents of the seminal vesicle, and then a series of muscular contractions forces the chamber distally and compresses it, rapidly decreasing its volume. Simultaneously, the distal end of the sperm passage is dilated, and the sperm mass is propelled from the genital tract.

Discussion

Knowledge of the structure of the ejaculatory complex of *Hydrodroma* sp. (nr. *H. despiciens*) provides a useful criterion for investigation. As with any character complex, this structure may prove to be a sensitive indicator both of intraspecific, population interactions and of interspecific, taxonomic boundaries. *H. despiciens* has been reported from five continents and numerous islands (K. Viets, 1956), and it would be surprising if this widely-applied name has not been used for a number of distinct species. For example, a specimen from Brazil, determined to be *H. despiciens*, was examined during the present study and found to have an ejaculatory complex differing in significant details from that of populations in New York and Ontario.

A study of the functional aspects of the EC complements morphological data by broadening the biological significance of the observations and by permitting the recognition of homologies in other genera. Thus data are made available for classification and for phylogenetic speculation. Unfortunately, although the mode of operation proposed here provides a groundwork for the study of function in other genera of water mites, the extensive variations of detailed form and three-dimensional relations of the component sclerites found in these animals (pp. 24 - 64) suggest that many of the details of this hypothesis may be applicable only to *Hydrodroma* and closely related genera.

A number of obvious lines of future research are suggested by the results of the present study. The deduction of ejaculatory complex function from morphological data should now be checked by a life history study for the species. Emphasis should be on observation of the method of insemination and the condition of the reproductive organs at various times of the year. The ontogeny of the ejaculatory complex in immature forms should also be studied. Perhaps methods can be developed to fix specimens in various stages of spermatophore deposition allowing direct observation of the gross activities of the ejaculatory complex. However, there seems to be little chance that a way can be found to test the hypothesis of the method of expelling the spermatophore by a syringe-like contraction. A further possibility is that certain aspects of the operation of the apparatus in *Hydrodroma* may be clarified by functional studies in other genera.

Survey of the Ejaculatory Complex in Water Mites

Historical Introduction

MALE GENITAL SYSTEMS IN TERRESTRIAL MITES

There has been considerable comparative and detailed morphological work on the male reproductive system of mites (summarized by Hughes, 1959). As noted for water mites (page 8), this research has been concentrated on the soft parts of the system to the neglect of the sclerotized terminal portions (termed the penis by Hughes, *op. cit.*). Internal sclerotized reproductive structures are absent in male Mesostigmata and Metastigmata, and although they are present in both the Oribatei and the Acaridiae, the distant taxonomic relationship of these groups to the water mites renders comparisons of little interest. From the standpoint of the comparative morphology of water mites, the most important consideration is the structure of the ejaculatory complex in related families of the Prostigmata, especially the Parasitengona.

Blauvelt (1945), Hughes (*op. cit.*: 176), Thomae (1925), Thor (1903), Henking (1882), Fredrickson (1961), Moss (1962), and Feider (1959) reported on the male reproductive system for various Prostigmata and Parasitengona, but in none do the skeletal elements resemble the analogous structure in water mites. Mitchell (1964a) studied thoroughly the enlarged terminal portion of the *ductus ejaculatorius* in the trombiculid, *Blankaartia acuscutellaris*. Although this organ, which Mitchell termed the ejaculatory complex, is similar in function to the comparable structure in water mites, little morphological evidence exists upon which to base a hypothesis of homology. There is no indication, for instance, of an ontogenetic relationship between the genital sclerites and the walls of the *ductus*, as there appears to be in *Hydrodroma*. Thus, the consensus of the literature is that no other group of mites possesses a chitinous ejaculatory complex skeleton of the water mite type.

COMPARATIVE STUDIES IN WATER MITES

Most recent publications pertaining to phylogeny within the water mites have been cited (Bader, 1954, 1969; Mitchell, 1957a, 1958a, 1962; Späring, 1959; Sokolow, 1954). Wooley (1961) reviewed the phylogeny of mites and briefly discussed problems within the aquatic taxa. The early speculation on the phylogeny of this group was based only on exoskeletal morphology, a practice that was questioned by Mitchell (1958a). Nordenskiöld (1899) and later authors (Wooley, 1961: 279) variously concluded that the group was mono-, di-, oligo-, or polyphyletic. Even then, however, most authorities agreed that water mites evolved from one or more terrestrial ancestors whose affinities would be with the Prostigmata, probably among the Parasitengona.

Bader (1954) studied the comparative morphology of the midgut and distinguished four main lines of evolution. His scheme represented a considerable simplification from hypotheses based on exoskeletal data, and

Mitchell has since shown that other functional and biological systems may be considered concordant with Bader's findings; life histories and larvae (1957a), mouthparts (1962). Recently (1969) Bader extended his interpretation of midgut structure somewhat and made several tentative conclusions of the first report more concrete. He recognized explicitly six distinct subgroups of genera, and suggested specific, separate origins for five. Späring, who published (1959) the only comparative study of water mite larvae to date, concluded from larval morphology that the water mites (with the exception of *Hydrovolzia*) constitute a monophyletic grouping. Mitchell (1958a) also appeared willing in one instance to postulate a long-surviving, hypothetical water mite ancestor that gave rise successively to a small number of major evolutionary lines.

Descriptions: Species Ordered Alphabetically

The EC skeleton of the first species for each genus is described fully. Sclerites of additional species in the same genus are briefly compared to the first, and major differences are noted.

***Albia* sp.**

(nr. *A. caerulea*) Fig. 8

Chitinous skeleton of medium size, lightly built; body moderately sclerotized with walls of midsection largely membranous; arms well developed and strongly sclerotized.

PROXIMAL CHAMBER consisting of two main sections, anterior wide, rectangular, shallow, posterior narrow, elongate, deep, its walls moderately well sclerotized; anterior margin sclerite wide, not heavily sclerotized; proximal horns borne on an elongate, sclerotized rod-like proximal ramus, short, blunt, expanded at tips; lateral wall sclerite narrow, strongly sclerotized, following a sinuate course along lateral wall of anterior section of chamber from its anteroproximal margin to base of chamber ramus.

POSTERIOR KEEL reduced, narrow anteroposteriorly, proximal end angular with margin irregular; distal rod wide proximally, heavily sclerotized throughout its length, strongly bonded with distal arm sclerites distally.

PROXIMAL ARMS shorter than distal arms, strongly sclerotized throughout, curved, projecting proximally beyond proximal horns, almost parallel to longitudinal axis of EC in lateral view; distal rami short, not extending beyond proximal end of anterior keel; chamber ramus narrow, proceeding anterad then angled proximad, tapering to a fine point, not articulating apically with any sclerites of proximal chamber; basal plate not developed.

MIDSECTION of EC with one pair of L-shaped proximal sclerites (PrxScl), shorter, less heavily sclerotized arm lying proximodistally, its proximal end continuous with membranous anterior wall of proximal chamber, longer, more heavily sclerotized arm projecting laterally, ending in a blunt, expanded tip that is free of the membranes attached to its base; no distal sclerites; large, membranous lateral chamber (Cmb 1) located in axillary position on either side proximal to distal arm, walls continuous with distal membranes.

ANTERIOR KEEL low, rounded, surface area reduced, moderately sclerotized, margins heavily sclerotized, projecting distally beneath distal arch; subtended by a broadened, moderately sclerotized, U-shaped plate lying in anterior wall of midsection of EC.

Fig. 8 *Albia sp.* (nr. *A. caerulea*): a, anterior view; b, lateral view.
 Fig. 9 *Arrenurus crenellatus*: a, anterior view; b, lateral view.
 Fig. 10 *Arrenurus intermedius*: a, anterior view; b, lateral view.
 Fig. 11 *Arrenurus lyriger*: a, anterior view; b, lateral view.

DISTAL ARMS long, narrow, strongly sclerotized, projecting proximolaterad at approximately 30° to longitudinal axis of EC, straight in midportion, curved at either end; lateral shelf absent; anterior rami forming anterior arch, massive, heavily sclerotized, not fused anteromedially, broad posteriorly, tapering slightly anteriorly, then flaring to form an anterior tip that is subtriangular in lateral view; posterior rami short, heavy, strongly sclerotized, each provided apically with a medial lobe; distal arm sclerites each with a long, distally tapering, sclerotized, horn-like **apical ramus** (ApRm) projecting distad, forming $1/3$ of total length of EC curved (concave anteriorly in lateral view, laterally in anterior view), generally convergent distally, slightly divergent at tips; no apical setae detected.

Arrenurus crenellatus

Fig. 9

Chitinous skeleton small, compact, only lightly sclerotized; distal and proximal arms reduced, few strong sclerites. Determined from Cook, 1954a, 1954b, 1955a.

PROXIMAL CHAMBER oblong in anterior view, deep anteroposteriorly, anterior side only $1/2$ length of posterior, posterior wall strongly convex so that open anterior side is rotated counter-clockwise through approximately 30° to face anterodistally; proximal and posterior sides moderately sclerotized, lateral and anteroproximal walls lightly sclerotized; anterior margin sclerite thickened, moderately sclerotized; no lateral wall sclerite; distolateral border indistinct; proximal horns absent.

POSTERIOR KEEL elongate in lateral view, tapering gradually into distal rod which is fused along entire length with posterior surface of EC.

PROXIMAL ARMS reduced, thin, short, not reaching proximally to apex of proximal chamber; distal ramus and short chamber ramus present; basal plate of two main sections, one rectangular section proximal to base of proximal arm and another triangular section distal to base of proximal arm and tapering distally, strengthened by an oblique, anteroproximal to posterodistal strut fused with base of proximal arm.

MIDSECTION of EC between proximal chamber and anterior keel largely membranous, supported by a set of proximal sclerites consisting of a pair of elongate, sinuate lateral rods (PrxSc 1) and a pair of short, anteriorly bifid, club-like, anterolateral rods (PrxSc 2); lateral rod of either side (PrxSc 1) incorporated as a strengthening strut in distal section of basal plate.

ANTERIOR KEEL of medium size, sclerotized, margin irregular; proximal margin strengthened by a narrow sclerotized rod that is bifurcate anteriorly and curved distally along base of keel; keel tapering rapidly distally, narrow end extending under anterior arch.

DISTAL ARMS greatly modified; rami of distal arm sclerites flattened, expanded and fused so that sclerites of either side form together a cone-shaped, sclerotized structure, blunt distally, open posteriorly, encircling distal end of EC; distal arms recognizable as sclerotized lateral and posterior margins of proximal end of cone; anterior rami as thickened anterior margin; posterior rami retain a degree of individuality, forming lateral margins of posterior gap in cone, projecting proximally beyond cone to level of proximal end of anterior keel, situated far apart, one on either side of broad posterior surface of EC; lateral shelf also forms part of lateral and posterior walls of cone; a pair of simple setae situated subdistally, one on either side of cone.

Arrenurus intermedius

Fig. 10

The EC of this species differs from *A. crenellatus* primarily in being proportionately narrower and more elongate. Anterior margin sclerite more heavily sclerotized; distal rod free from body of EC in midsection; basal plate reduced; only a single pair of proximal sclerites (PrxSc 1) associated with midsection; apical cone elongate; posterior rami not distinct. Determined from Cook, *op. cit.*

Arrenurus lyriger

Fig. 11

Differs from *A. crenellatus* in being larger and more heavily sclerotized, as well as proportionately more elongate. Anterior margin sclerite stronger; lateral wall of proximal chamber supported by a pyriform sclerite; distal rod free from body of EC in midsection; proximal arms short; basal plate small, triangular; proximal sclerites (PrxSc 1-3) of midsection differ in number, size and shape; distal arm sclerites heavily sclerotized; apical cone separated into two sections joined only across anterior arch, more inflated and higher. Determined from Cook, *op. cit.*

Arrenurus magnicaudatus

Fig. 12

The EC of this species is larger, more elongate and more heavily sclerotized than that of *A. crenellatus*. Anterior margin sclerite moderately sclerotized; proximal margin of posterior keel strongly concave; distal rod free from body of EC in midsection area; proximal arms longer; chamber ramus rudimentary; basal plate small, crescentic, lying entirely distal to base of proximal arm; one elongate, obliquely placed pair of proximal sclerites (PrxSc 1) in midsection; apical cone narrower; distal arms and posterior rami distinct. Determined from Cook, *op. cit.*

Arrenurus major

Fig. 13

This species has the largest EC of any member of the genus examined. It is proportionately more elongate and more heavily sclerotized than that of *A. crenellatus*. Anterior surface of proximal chamber more strongly rotated counter-clockwise; lateral walls strengthened by a small subtriangular sclerite; distal rod completely free from posterior surface of EC; proximal arms heavier; basal plate lying entirely distal to base of proximal arm; two pairs of spindle-shaped proximal sclerites (PrxSc 1, 2) in midsection; distal arms well sclerotized, projecting farther laterally so that base of apical cone flared broadly. Determined from Cook, *op. cit.*

Arrenurus planus

(not illus.)

The EC of this species is narrower than that of *A. crenellatus* and somewhat more heavily sclerotized. Anterior margin sclerite more prominent; proximal arms shorter and heavier; basal plate narrower and tongue-like; posterior keel reduced; distal rod free from posterior surface of EC; two pairs of oblique sclerites (PrxSc 1, 2) present in midsection; anterior keel low, linear; apical cone small and proportionately very short. Determined from Cook, *op. cit.*

Fig. 12 *Arrenurus magnicaudatus*: a, anterior view; b, lateral view.
 Fig. 13 *Arrenurus major*: a, anterior view; b, lateral view.
 Fig. 14 *Arrenurus semicircularis*: a, anterior view; b, lateral view.
 Fig. 15 *Arrenurus trifolius*: a, anterior view; b, lateral view.

Arrenurus semicircularis

Fig. 14

The EC of this species is about the same size as, but proportionately narrower and shallower than that of *A. crenellatus*. Anterior surface of proximal chamber less strongly rotated counter-clockwise; posterior keel much reduced; distal rod completely free from posterior surface of EC, proximal arms stronger basally; basal plate much reduced; only a single oblique proximal sclerite (PrxSc 1) in midsection, anteroproximal tip expanded and subtriangular; apical cone narrow and elongate. Determined from Cook, *op. cit.*

Arrenurus trifoliatus

Fig. 15

This species has the EC less sclerotized, with most sclerites reduced in size and complexity. Proximal chamber greatly expanded and produced proximally; anterior margin sclerite reduced; lateral walls of chamber supported by a large subtriangular sclerite; proximal arms short, heavy; distal rami prominent; basal plate absent; posterior keel and distal rod absent; no sclerites in midsection; anterior keel low, elongate; distal arm sclerites drastically reduced, represented only by two pairs of sclerites lying distally in lateral walls of EC, homologies uncertain; no apical setae observed. Determined from Wilson, 1961.

Arrenurus wardi

Fig. 16

The EC of this species is proportionately narrower and more elongate than that of *A. crenellatus* and is also more heavily sclerotized. Proximal chamber smaller; proximal arm heavier; basal plate reduced in size, extending proximally as a narrow, curved strap; posterior keel truncate posteriorly; distal rod entirely free from posterior surface of EC; a single pair of oblique proximal sclerites (PrxSc 1) present in lateral walls of midsection, distoposterior tip expanded, club-shaped; apical cone narrow and elongate. Determined from Cook, *op. cit.*

***Atractides* sp.**

Fig. 17

The EC of this species is of the general *Hydrodroma* type but is more massively built and more heavily sclerotized.

PROXIMAL CHAMBER square in anterior view, semicircular, with flat side facing anteriorly in lateral view; anterior margin sclerite strongly chitinized, wide proximally in lateral view, interrupted midway by an ovoid excavation, tapering distally to a blunt apex; no special strengthening sclerites in lateral walls; anteroproximal margin of chamber drawn out medially to form a proximal ramus, expanded at either end, wide in lateral view, narrow in anterior view; proximal horns absent.

POSTERIOR KEEL arises from convex posterior surface of chamber, proceeds posteroproximally as a narrow bar, then expands into a large oval plate, sculptured for muscle insertion; posterior keel gives rise to distal rod from posterodistal margin of its narrow basal portion; rod curved, free from EC until level of anterior keel, then closely applied to posterior surface, grading insensibly into distal membranes.

PROXIMAL ARMS massive, heavily sclerotized, strongly curved in anterior view, projecting proximally to tip of proximal ramus, apices expanded, sculptured, with margins finely divided for muscle attachment; distal rami strong; chamber ramus

Fig. 16 *Arrenurus wardi*: a, anterior view; b, lateral view.
 Fig. 17 *Atractides* sp.: a, anterior view; b, lateral view.
 Fig. 18 *Aturus* (s. str.) sp. (nr. *A. deceptor*): a, anterior view; b, lateral view.
 Fig. 19 *Axonopsis* (*Hexaxonopsis*) sp.: a, anterior view; b, lateral view.

short, strong, grading into lateral chamber wall; a small, triangular basal plate present in lateral chamber wall posterior to base of proximal arm.

MIDSECTION of EC largely membranous, supported primarily by a heavy, Y-shaped proximal sclerite (PrxSc 1) on either side; this sclerite with base (long arm) beginning posteriorly and running anteriorly, one short blunt inflated arm projecting proximad as far as distal margin of proximal chamber, another longer, thinner, apically expanded arm proceeding laterodistad to middle of anterior keel, these sclerites especially prominent in anterior view; one pair of laterally-placed, hook-shaped, distal sclerites (DisSc 1) aids in support of membranes of midsection just proximal to distal arms, rod-like, distoproximally oriented, distal fifth tapering, abruptly curved medially.

ANTERIOR KEEL strongly sclerotized; arising from a long base and proceeding anteriorly, first tapering, then expanding abruptly into a large, subtriangular plate that is sculptured for muscle attachment; base supported by a thickened, sclerotized band travelling distally beneath anterior arch.

DISTAL ARMS massive, strong, heavily sclerotized, each projecting in a broad arc laterally from body of EC, apices slightly expanded, sculptured, margins divided for muscle attachment; anterior rami robust, apices apparently attached but not fused medially; lateral shelf reduced to a small flange near base of distal arm; posterior rami greatly expanded in lateral view, thickened basally in anterior view, forming a partial support for lateral walls of distal portion of EC; no apical development of distal arm sclerite; strong chitinous ligaments leading distad from bases of distal arms appear to strengthen connections with distal membranes; apical setae not noted.

Aturus (s. str.) sp.

(nr. *A. deceptor*) Fig. 18

The EC of this species is of the general *Hydrodroma* type.

PROXIMAL CHAMBER elongate in anterior view, widest midway, tapering distally and proximally, greatly compressed anteroposteriorly, appearing narrow in lateral view; anterior margin sclerite a thickened, sclerotized band, narrow proximally, projecting beyond proximal wall, gradually broadening over strongly sinuate course distad, grading gradually into lateral walls distally; no strengthening sclerites in narrow, sclerotized, lateral walls; proximal horns absent.

POSTERIOR KEEL a slight broadening of base of distal rod, attached to posterior surface of proximal chamber proximal to base of proximal arms, rod tapered gradually, curving distad beneath EC, apex joining posterior surface of EC again at level of distal arm sclerites.

PROXIMAL ARMS broad basally, strongly curved, gradually tapering apically in anterior view, of subequal width and straight in lateral view; distal rami strong, prominent in anterior and lateral views; chamber rami absent; basal plate absent.

MIDSECTION of EC membranous; no proximal sclerites; a pair of small, sinuate, spindle-shaped distal sclerites (DisSc 1) lie either side of base of anterior keel, sclerites narrow, angulate in anterior view; a single, median, lightly sclerotized, semispherical chamber (Cmb 1) at base of anterior keel; three pairs of lateral, membranous chambers (Cmb 2-4) visible in anterior view, largest, axillary pair Cmb 4) semispherical, supported posteriorly by posterior rami of distal arm sclerites.

ANTERIOR KEEL high, subtriangular in lateral view, much inflated, with a broad base in anterior view, moderately sclerotized, continuous with membranous lateral surfaces of EC.

DISTAL ARMS slender, strong, well sclerotized, strongly curved, tapering apically; anterior rami long, slender, pointed, strongly sclerotized, apices apposed medially; posterior rami short, strong; each distal arm sclerite bears a flat, plate-like apical development, subrectangular in lateral view, each bearing subapically a short simple seta on lateral surface; lateral shelf forming part of posterior surface of distal-most lateral outpocketing (Cmb 4).

Axonopsis (Hexaxonopsis) sp.

Fig. 19

The EC of this species is of the general *Hydrodroma* type but is more compact and heavily sclerotized.

PROXIMAL CHAMBER elongate in anterior view ($1/2$ length of EC), broadest at bases of proximal arms, tapering rapidly distad, gradually proximad; chamber strongly compressed anteroposteriorly, long and narrow in lateral view; lateral walls narrow, heavily sclerotized; anterior margin sclerite a strong bar, V-shaped in anterior view, bent at an angle of approximately 45° in lateral view, projecting proximad beyond end of chamber, ending in a short, broad proximal ramus; proximal horns present, projecting laterally and posteriorly from lateral apices of proximal ramus.

POSTERIOR KEEL attached to distal part of sclerotized posterior surface of proximal chamber, elongate, anterior and posterior margins subparallel, tapering distad to form a distal rod, produced posterad into a curved projection with rounded apex; distal rod sinuate, attached to posterior surface of EC at level of distal arm sclerites.

PROXIMAL ARMS short (projecting proximad only $2/3$ length of proximal chamber), heavily sclerotized, strongly curved in anterior view, with a wide, flange-like lateral expansion from base, basal area broad in anterior view, tapering apically, apex somewhat expanded, sculptured, margin divided for muscle attachment; chamber ramus absent; distal ramus not prominent; basal plate large, pyriform, rounded distally, grading insensibly into sclerotized lateral walls of midsection, portion proximal to base of proximal arm tapering gradually, occupying most of lateral surface of proximal chamber.

MIDSECTION of EC short, sclerotized laterally, membranous anteriorly and anterolaterally; a lightly sclerotized, elongate, inflated sac (Cmb 1) arises on midline anteriorly, just proximal to base of anterior keel; membranes of anterolateral area doubly outpocketed (Cmb 2, 3) on either side; a compressed, sclerotized sac (Cmb 4) subtends base of anterior keel on either side in axillary position, subquadrate in anterior view.

ANTERIOR KEEL a right-angled triangle with hypotenuse facing anterodistally, moderately sclerotized.

DISTAL ARMS strong, heavily sclerotized, crescent-shaped, tapering apically in anterior view, almost straight in lateral view; anterior rami short with a thick base, almost square in anterior view; posterior rami short, heavy; a small, triangular lateral shelf joins base of distal arms to body of EC; apical setae absent.

Brachypoda (s. str.) sp.

(nr. *B. cornipes*) Fig. 20

The EC of *Brachypoda* is of the general *Hydrodroma* type but is more compact and heavily sclerotized. Furthermore, the midsection displays a complex structure.

PROXIMAL CHAMBER elongate, oval in anterior view, anteroposteriorly compressed, narrow in lateral view; proximal and posterior walls heavily sclerotized, lateral walls narrow, moderately sclerotized; anterior margin sclerite strong, heavily sclerotized, U-shaped (in anterior view), curved (concave face anteriorly) in lateral view, broadened and truncate proximally, ending in a small lobe on either side distally, projecting proximad and anterad beyond proximal wall of chamber as a quadrate proximal ramus; a proximal horn projects laterally on either side from proximal ramus.

POSTERIOR KEEL attached to posterior side of proximal chamber, roughly rhomboid, produced proximally into a short, triangular apex, tapering distally to base of distal rod which travels straight, approximately parallel to longitudinal axis of distal half of EC, tapering and grading imperceptibly into distal membranes.

PROXIMAL ARMS short, heavily sclerotized, curved, with laterodistal margins expanded into a thin plate laterally, tapering apically in anterior view, tips slightly expanded and sculptured; chamber ramus short and broad, articulating with distal end of anterior margin sclerite; basal plate somewhat pyriform, broad distally, grading insensibly into sclerotized lateral surfaces of EC, proximal part tapering, acute, fused anteriorly with anterior margin sclerite.

MIDSECTION of EC with lateral walls lightly sclerotized, forming 4 main inflated chambers (Cmb 1-4) on either side; Cmb 3 more heavily sclerotized than others, apparently incorporating lateral shelf into its structure; lateral walls strengthened by a curved, pyriform, proximal sclerite (PrxSc 1) located distal to distal tips of anterior margin sclerite on either side.

ANTERIOR KEEL of extremely complex structure, composed of a distal and a proximal section; proximal section in form of an irregular cone lying on midline, tapered end facing distally, broad end closed, facing proximally, composed of several overlapping, inflated, sclerotized sacs with thickened, sinuate proximal surfaces in lateral view; distal section composed of three structures arising from midline, distal-most laterally compressed, high, T-shaped in anterior view, middle structure lower, somewhat inflated, proximal structure still lower, inflated, wide in anterior view.

DISTAL ARMS long, strongly curved in anterior view, nearly straight in lateral view, heavily sclerotized, apices expanded; anterior rami long, slender, heavily sclerotized; lateral shelf forming part of Cmb 3; several ligaments arise from distal edges of anterior rami and base of distal arms and appear to strengthen attachment of distal membranes.

Eylais sp.

Fig. 21

The EC in *Eylais* is considerably different from the *Hydrodroma* type, although most structures can be easily homologized. The body is largely membranous with only isolated sclerotized structures.

PROXIMAL CHAMBER large ($\frac{2}{3}$ length of EC in anterior view, $\frac{1}{2}$ of lateral area), mostly membranous, somewhat variable in form; in anterior view main (anterior) section of chamber oval (longitudinal axis laterally directed), with a median proximal outpocketing; more posteriorly a pair of membranous outpocketings lie one on either side, each supported by a posterolateral extension of anterior margin sclerite; in lateral view chamber high, posterior surfaces lightly sclerotized; lateral walls largely membranous, supported by basal plate of proximal arm sclerites and a semicircular sclerite articulated with, but posterior to, basal plate; posterior margin of semicircular sclerite strengthened by a sclerotized rod proceeding proximally to margin of chamber and terminating in a blunt apex; in anterior view, anterior margin sclerite a long, curved (convex distally) rod with

Fig. 20 *Brachypoda (s. str.)* sp. (nr. *B. cornipes*): a, anterior view; b, lateral view.

Fig. 21 *Eylais* sp.: a, anterior view; b, lateral view.

Fig. 22 *Forelia (Madawaska) borealis*: a, anterior view; b, lateral view.

Fig. 23 *Frontipoda* sp.: a, anterior view; b, lateral view.

expanded, subtriangular lateral apices (may correspond to proximal horns), lateral apices then produced posterad and finally proximad, tips tapering, merging imperceptibly with membranous walls of chamber, sclerite thickened medially, giving rise to a proximally directed arm, straight, dilated apically; in lateral view, anterior margin sclerite strongly S-shaped, median area high, arms curving posteriorly and proximally.

POSTERIOR KEEL small, narrow, convex posteriorly; distal rod absent.

PROXIMAL ARMS long, slender, slightly curved in anterior view, sinuate in lateral view, apices greatly expanded and sculptured for muscle attachment; medial rami strong, straight, fused medially so that in anterior view proximal arm sclerites appear as a single broadly curved bar (concave proximally); chamber ramus directed distad, fused with a proximally directed ramus of distal arm sclerite; basal plate large, subrectangular, strengthened by several sclerotized struts from base of proximal arm, connected posteriorly by a strut to semicircular lateral wall sclerite of proximal chamber.

MIDSECTION of EC virtually eliminated by close juxtaposition of bases of proximal and distal arm sclerites; anterior side apparently open (opening of anterior side of proximal chamber), membranes surrounding it joined distomedially to base of anterior keel and laterally draped over bases of proximal arms to attach to lateral walls of proximal chamber.

ANTERIOR KEEL large, subtriangular with apex truncate, broadly rounded, distal margin supported by a thickened, broad, heavily sclerotized band that tapers distally to support anterior wall of sperm passage, rest of structure less heavily sclerotized; base of keel entirely fused with distal arm sclerites on either side.

DISTAL ARMS short, arising from base of anterior keel, proceeding laterad and anterad on either side of keel, slender, heavily sclerotized, apices expanded and sculptured; subtended by a complex basal sclerite that is attached posteriorly by a strongly curved strut to basal plate of proximal arm sclerite; basal sclerite of distal arms giving rise to struts that proceed distad strengthening lateral walls of sperm passage, also posterad to semicircular sclerite. No other rami conspicuous; apical setae absent. Area of sperm passage distal to distal arms roughly tubular with a series of pairs of weakly sclerotized strengthening rods in walls, most readily seen in anterior view.

***Feltria* sp.**

(not illus.)

This species possesses an EC too minute ($< 100 \mu$) for successful separation from the large genital plate, and so detailed drawings could not be made. From limited observations, the EC is clearly of the general *Hydrodroma* type. Proximal arms well developed, proximal chamber heavily sclerotized only in proximal wall, distal arms reduced in relative size.

Forelia (Madawaska) borealis

Fig. 22

This EC has the typical *Hydrodroma* facies, differing primarily in the apical development of the distal arm sclerites. Determined from Cook, 1955b.

PROXIMAL CHAMBER elongate, subrectangular in anterior view, proximal margin broadly rounded, high and curved in lateral view, posterior and proximal sides elongate, anterior surface rotated counter-clockwise through approximately 30° with respect to longitudinal axis of EC, facing anterodistally; proximal and posterior

walls lightly sclerotized, semicircular in lateral view, no strengthening sclerites; anterior margin sclerite a narrow, moderately sclerotized band, thickest and strongest along proximal margin; proximal horns project laterad from proximolateral corners of anterior margin, each thin, strongly sclerotized, each a short, curved (convex proximally) rod with a flange-like plate developed distolaterally.

POSTERIOR KEEL small, linear, attached basally to posterior surface of chamber midway along its length, projecting proximad a short way parallel to longitudinal axis of EC; no distal rod; membranes along posterior surface of EC proximal to bases of distal arms containing an elongate, sclerotized rod that may correspond to distal section of distal rod.

PROXIMAL ARMS shorter than proximal chamber, strong basally, well sclerotized; chamber ramus short and indistinct; distal ramus well developed; no basal plate.

MIDSECTION of EC bearing proximally a pair of sclerotized plates (PrxSc 1) forming in anterior view, a U-shaped structure (convex distally) delimiting distal boundary of membranes of anterior surface of proximal chamber; lateral surfaces of midsection lightly sclerotized, inflated to form two chambers on either side; proximal-most chamber (Cmb 1) of small diameter, incorporating no other sclerites; more distal chamber (Cmb 2) large, supported mainly by posterior ramus and lateral shelf of distal arm sclerite; in lateral view, just above Cmb 2 is a narrow, spindle-shaped sclerite (DisSc 1) in lateral wall.

ANTERIOR KEEL not higher than anterior arch, anterior margin dissected, irregular, roughly rectangular, tapering distally, passing beneath anterior arch, merging with anterior wall of sperm passage.

DISTAL ARMS short, strong, heavily sclerotized, straight, projecting at an angle of 40° to longitudinal axis of EC in anterior view, strongly curved (convex posteriorly) in lateral view; continuous with high, triangular anterior ramus; area distal to these arms expanded (apical development), entire basal area of distal arm sclerite subtriangular in lateral view; posterior ramus strong, proximal portion strongly curved (convex laterally and posteriorly), supporting distal-most lateral chamber (Cmb 2); lateral shelf well developed.

***Frontipoda* sp.**

Fig. 23

Only one species of *Frontipoda* (*F. americana*) has been described from North America. However, genitalic dissections during the course of this study have revealed the presence of two different forms, so that a specific name will not be applied to the population described here.

The EC is more compact than that of *Hydrodroma* and most structures are reduced in relative size and degree of sclerotization.

PROXIMAL CHAMBER elongate in anterior view, subrectangular, narrower distally, wider and rounded proximally; in lateral view chamber high, subrectangular, a distinct angle between posterior and proximal surfaces; in lateral view, proximal and posterior walls only moderately sclerotized as are lateral walls; anterior margin sclerite a narrow sclerotized band, U-shaped in anterior view; distal ends of margin sclerite produced posteriorly to form well-defined, sclerotized, distolateral borders of chamber, these sclerites then curving distally to merge with lateral walls of midsection of EC; proximal horns absent.

POSTERIOR KEEL inflated, clearly an extension of cavity of proximal chamber, subtriangular, attached broadly to posterior side of chamber, curved and tapered distally to give rise to distal rod travelling straight distally to level of apex of EC where it grades gradually into distal membranes.

PROXIMAL ARMS short, stubby, wide in anterior view, expanded at apex, projecting at approximately 55° to longitudinal axis of EC; chamber ramus short, articulating with sclerotized distolateral border of chamber; an angular basal plate lies at base of proximal arms in lateral wall of EC, primarily distal to base of proximal arm, strengthened by two sclerotized struts from base of this arm.

MIDSECTION of EC lightly sclerotized, inflated to form a pair of large lateral chambers (Cmb 1); a series of parallel, distoproximally oriented, sclerotic ridges subtend anterior keel on either side; no other conspicuous sclerites.

ANTERIOR KEEL subtriangular, occupying approximately distal half of EC, supported and strengthened by a sclerotized anterodistal edge, proximal margin rounded, broad in anterior view.

DISTAL ARM sclerites much reduced, apparently represented by two small, spindle-shaped sclerites situated laterally on either side of distal end of EC, visible in anterior view.

Geayia sp.

Fig. 24

The EC of this species is easily referable to the *Hydrodroma* type, but the proportions of various areas are altered, and there is considerable apical development of the distal arm sclerites.

PROXIMAL CHAMBER oval in anterior view, widest at ends, narrower at mid-length, rounded distally and proximally; in lateral view subrectangular, rotated counter-clockwise through approximately 30° , anterior surface faces anterodistally; anterior margin sclerite a thickened, sclerotized band, oval in anterior view, in lateral view projecting proximad beyond end of proximal chamber, joined to chamber by an anteroproximal extension of proximal wall; lateral chamber walls supported and strengthened by a heavy, well-sclerotized, oblique, lateral wall sclerite, fused proximodistally with anterior margin sclerite, articulated posterodistally with base of proximal arm; proximal horns present, arising on either side from proximolateral corners of anterior margin sclerite, short, slender, straight in lateral view, curved in anterior view, slightly expanded at tips.

POSTERIOR KEEL attached broadly to posterior surface of proximal chamber midway along its length, expanding greatly to form a large, reniform plate, rounded proximally, tapering distally to give rise to a strongly curved, sclerotized, distal rod; distal rod sinuate, separate from body of EC through most of its length, proceeding anterad to lie immediately below EC at level of anterior keel.

PROXIMAL ARMS of medium length, broad, massive in anterior view, not proceeding proximad beyond proximal horns, strongly curved (convex posteriorly) in lateral view, apices little expanded, lateral margin expanded to form a thin, sculptured plate for muscle attachment; chamber ramus short, curved, closely associated with distal tip of lateral wall sclerite; distal ramus strong, proceeding distad to level of anterior keel.

MIDSECTION of EC with lateral walls lightly sclerotized, supported by heavily sclerotized rods and plates (PrxSc 1-3), anterior surface in this area membranous; structure of supporting sclerites most clearly seen in anterior view; most anteriorly lie a submedian pair of Y-shaped sclerites (PrxSc 1); lying below Y-shaped sclerite, a sinuate sclerite (PrxSc 2) proceeding distad irregularly from laterodistal corner of margin sclerite, ending in an enlarged, irregular, blunt apex; a pair of small submedian sclerites (PrxSc 3) lie slightly proximal to proximal margin of anterior keel; lateral walls of midsection inflated to form a median, elongate, rounded tube (Cmb 1) subtending anterior keel.

Fig. 24 *Geayia* sp.: a, anterior view; b, lateral view.

Fig. 25 *Hydrachna (Rhabdohydrachna)* sp.: a, anterior view; b, lateral view.

Fig. 26 *Hydrovolzia* sp.: a, anterior (?) view, distal end at top; b, lateral view, proximal end at top.

Fig. 27 *Hydryphantes* sp. (nr. *H. ruber*): a, anterior view; b, lateral view.

ANTERIOR KEEL large, well-sclerotized, subrectangular in lateral view, anterior surface rounded, irregular, strengthened by lightly sclerotized anterior and distal margins, part of proximal and posterior margins strengthened and supported by a strongly sclerotized, curved band that continues distad, tapering beneath anterior arch.

DISTAL ARMS short, strongly curved in anterior view, wide at base; in lateral view, almost straight; anterior ramus long, strong, heavily sclerotized, tips of two anterior rami not apposed medially but joined by a strong chitinous band or ligament; posterior rami strong, heavily sclerotized, projecting proximally to level of proximal margin of anterior keel; lateral shelf broad, produced proximally to form a quadrate, proximally truncate plate joining distal arm to posterior ramus, margins strengthened by sclerotized thickenings; base of distal arm sclerite gives rise to an apical development, moderately sclerotized, apparently lying along lateral wall of sperm passage, approximately tubular, provided with a subdistal, simple apical seta.

Hydrachna (Rhabdohydrachna) sp.

Fig. 25

The EC of this species is of the general *Hydrodroma* type modified by heavier sclerotization of the proximal chamber and midsection, and reduction in size and complexity of the distal arm sclerites.

PROXIMAL CHAMBER elongate, rectangular in anterior view, subquadrate in lateral view, walls heavily sclerotized, membranes of anterior surface thick and leathery; anterior margin sclerite not prominent, anterior section of distolateral border of chamber strongly sclerotized, continuous with proximal sclerite (PrxSc 1) of midsection; proximal horns absent.

POSTERIOR KEEL a broad curved plate attached at one end to posterior surface of proximal chamber, projecting posteriorly and distally; no distal rod present.

PROXIMAL ARMS massive, heavily sclerotized, strongly curved; chamber ramus short, grading into sclerotized lateral wall of proximal chamber, distal ramus strong, fused with sclerotized lateral and posterior walls of midsection; basal plate well developed, forming part of sclerotized lateral surface of EC.

MIDSECTION of EC sclerotized on all surfaces; strengthened by pair of proximal sclerites (PrxSc 1) that are narrow, sinuate anteriorly, broad, well sclerotized and V-shaped laterally, continuous proximally with distolateral border of proximal chamber; these sclerites support a pair of conical lateral chambers (Cmb 1).

ANTERIOR KEEL with a narrow, elongate, anterior projection and inflated basal section passing along anterior surface of EC.

DISTAL ARMS reduced, short, straight; anterior rami rudimentary, only lightly sclerotized, anterior arch low; other rami much reduced; no apical setae.

Hydrovolzia sp.

Fig. 26

Only a few alcohol-preserved specimens of this species were available for study, and no completely satisfactory skeletal preparations could be made. The EC is small and difficult to manipulate, and the alcohol preservation rendered the muscle tissue refractory to ordinary clearing agents. The sclerotized structures were not examined in detail, but Fig. 26 gives a general impression of the configuration. Except for an elongate pair of proximolateral sclerites, perhaps analogous to the

proximal arms, there appears to be no structural similarity to the *Hydrodroma* EC.

This genus may be more easily homologized with the Trombidioidea than with the water mites, once its structure is better understood.

***Hydryphantes* sp.**

(nr. *H. ruber*) Fig. 27

The EC of *Hydryphantes* resembles, in general, that of *Hydrodroma*, although the distal arm sclerites are reduced.

PROXIMAL CHAMBER subrectangular in anterior and lateral views, anterior surface wider than posterior section which tapers distally, posterior and proximal walls smoothly rounded, moderately sclerotized, as are lateral walls; no strengthening sclerite in lateral walls; anterior margin sclerite a thickened, sclerotized band, smoothly rounded proximally in anterior view, in lateral view proceeding distally parallel to longitudinal axis of EC, curving abruptly posterad at approximately 90°, forming strong, anterodistal shoulder of proximal chamber; distal tips of anterior margin sclerite project posterad and distolaterad forming strong distolateral borders of proximal chamber, greatly expanded apically; proximal horns absent, anterior margin sclerite of anterior surface produced proximally on midline into a small proximal ramus projecting anterodistad, narrow in lateral view, wider in anterior view, expanded proximally.

POSTERIOR KEEL a slight broadening of base of sinuate distal rod, attached to posterior surface of proximal chamber near its distal end.

PROXIMAL ARMS broad, strong, heavily sclerotized, strongly curved in anterior view, projecting proximad beyond tip of proximal ramus, slightly sinuate in lateral view; chamber ramus absent; distal ramus strong, curved, proceeding distally to midway along anterior keel; a subrectangular basal plate present, lying in lateral wall of proximal chamber, produced proximally to an acute, anteroproximal apex.

MIDSECTION of EC largely membranous proximally with two main pairs of sclerites (PrxSc 1, 2); anterior-most (PrxSc 1) L-shaped, one arm from each side joined anteriorly to form a raised, irregular, median projection; posterior-most sclerite (PrxSc 2) also roughly L-shaped, an inflated, sclerotized fold of lateral wall, anteriorly directed arm also fused with median projection, lateral surfaces sculptured for muscle attachment; a pair of lateral chambers (Cmb 1) supported by distolateral border sclerite of proximal chamber, another by proximal sclerites of midsection (Cmb 2); distal area of midsection a lightly sclerotized tube.

ANTERIOR KEEL elongate, roughly oval, anterior margin irregular, divided, proximal section of anterior margin elevated into a rounded projection strengthened by an anterior sclerotized thickening base of keel supported by a thickened, sclerotized band.

DISTAL ARMS short, spindle-shaped, almost straight in anterior view; anterior rami short, slender, strongly sclerotized, apices apposed on midline; posterior ramus strong, sinuate, spindle-shaped, proximal apices curving laterad to aid in support of Cmb 2; lateral shelf absent.

***Hygrobates* sp.**

Fig. 28

This species has an elaborate EC of the general *Hydrodroma* type.

PROXIMAL CHAMBER subrectangular in anterior view, anteroposteriorly compressed, narrow in lateral view, posterior side strongly sclerotized, proximal side

less so, lateral walls lightly sclerotized, anterior surface largely membranous; margins of anterior surface supported and strengthened by a narrow, thin, strongly sclerotized margin sclerite, broadly U-shaped in anterior view, produced proximally on median line to form a median proximal ramus which is straight, anteroproximally directed, expanded, bearing a pair of rudimentary proximal horns apically; margin sclerite of anterior surface dips posterad on either side into a broadly U-shaped excavation of lateral wall, membrane bridges this gap.

POSTERIOR KEEL elongate, bilobed; smaller proximal lobe rounded proximally, proximal margin lightly sculptured, keel attached to distal part of posterior surface of proximal chamber by a broad stalk; distal lobe large, tapering distally to a curved distal rod; distal rod free from posterior surface of EC, grading distally into distal membranes.

PROXIMAL ARMS project at almost 90° to body of EC basally, then bent proximad at almost 90° , straight, strong, wide, heavily sclerotized, expanded greatly at apices to form a thin, sculptured apical plate for muscle attachment; chamber ramus absent; distal ramus well developed; no basal plate.

MIDSECTION of EC moderately sclerotized laterally and posteriorly, primarily membranous anteriorly, strengthened and supported by two pairs of large, heavy sclerites; proximally, an anteroposteriorly directed rod (PrxSc 1) with a twisted, sculptured anterior arm on either side; distally, expanded anterior tips of paired L-shaped sclerites (DisSc 1) also project above anterior surface; both pairs of sclerites support folds of membranous anterior surface; a pair of posterolateral chambers (Cmb 1) formed by inflation of sclerotized lateral walls, an axillary pair of chambers (Cmb 2) strengthened by L-shaped sclerites (DisSc 1) and posterior rami of distal arm sclerites.

ANTERIOR KEEL narrow laterally and distoproximally, high, rounded apically, proximal margin angulate, distal margin sinuate, base subtended by a pair of sinuate, strongly sclerotized bars with proximal tips produced anteriorly and strongly hooked.

DISTAL ARMS long, strong, heavily sclerotized, almost straight in lateral view, in anterior view strongly curved, tapering regularly to apices, apices little expanded; anterior rami broad in anterior view; posterior ramus moderately strong, produced proximad to level of proximal margin of anterior keel; no apical development or apical setae.

Koenikea sp.

Fig. 29

The EC skeleton is of the general *Hydrodroma* type and is relatively simple in structure.

PROXIMAL CHAMBER circular in anterior view, subquadrate in lateral view; posterior and proximal walls moderately well sclerotized as are lateral walls; lateral and proximal margins of anterior surface supported and strengthened by a strong, heavily sclerotized, semicircular margin sclerite, thick and broad proximally, distal apices tapering, attenuate; proximally on midline, margin sclerite drawn out into a short, broad, almost square proximal ramus, directed anteroproximad in lateral view; an elongate, curved (convex proximally) proximal horn arises from each proximolateral corner of proximal ramus.

POSTERIOR KEEL narrow, elongate posteriorly, basal section narrower, stalk-like, expanding apically into a broader plate that is irregular proximally and tapers distally to form a narrow, strongly sclerotized, smoothly curved (convex posteriorly) distal rod; rod free from body of EC, merging abruptly with distal membranes below EC at level of distal arm sclerites.

Fig. 28 *Hygrobates* sp.: a, anterior view; b, lateral view.

Fig. 29 *Koenikea* sp.: a, anterior view; b, lateral view.

Fig. 30 *Kongsbergia* sp.: a, anterior view; b, lateral view.

Fig. 31 *Lebertia* sp.: a, anterior view; b, lateral view.

PROXIMAL ARMS strong, curved, heavily sclerotized, broad in anterior view; tips expanded, little sculptured; chamber ramus short, broad, heavy; distal ramus strong, well-developed, projecting distad to level of distal-most section of anterior keel; basal plate small.

MIDSECTION of EC with anterior and lateral surfaces moderately sclerotized, more membranous anteriorly; three pairs of lateral chambers form most prominent feature of area; proximal-most two chambers (Cmb 1, 2) merely semisclerotized outpocketings of wall; distal-most chamber (Cmb 3) with a moderately well-sclerotized, strongly curved (convex proximally) proximal wall, anterior and distolateral walls largely membranous.

ANTERIOR KEEL divided into two sections; proximal-most lying approximately midway along length of EC, short and narrow, basal stalk projecting anteroproximally, then expanding into a subcircular sculptured plate; distal-most section of keel wider, subrectangular, anterior margin convex but irregular, anterior area sculptured for muscle insertion; no prominent sclerotized supports for either section of anterior keel.

DISTAL ARMS strong, well-sclerotized, sinuate, tapering only gradually to curved, acute apices; anterior rami long, sinuate, in lateral view broad basally, rapidly tapering apically, apices apposed anteriorly on median line; posterior ramus short, broad, subtriangular in lateral view; lateral shelf absent; no apical setae present.

Kongsbergia sp.

Fig. 30

The EC of this species is similar to the basic *Hydrodroma* type.

PROXIMAL CHAMBER oval in anterior view, in lateral view anteroposteriorly flattened, narrow, subrectangular, anterior surface entirely membranous, posterior and proximal walls heavily sclerotized, lateral walls only moderately sclerotized; lateral and proximal margins strengthened and supported by a narrow, heavily sclerotized anterior margin sclerite, thicker proximally, tapering distally, projecting proximad as an over-hanging lip (rudimentary proximal ramus) beyond proximal end of chamber; no strengthening sclerites in lateral walls of chamber; proximal horns lacking.

POSTERIOR KEEL elongate, narrow, broadly attached to posterior surface of chamber, posterior and proximal margins irregular, tapering distally to form a strong, weakly curved (convex posteriorly), well-sclerotized distal rod; distal rod free from EC through most of its length, becoming closely associated with posterior surface distal to distal armsclerites.

PROXIMAL ARMS massive, strongly curved, heavily sclerotized, projecting proximad to apex of proximal chamber, basal areas broad, tapering rapidly to slightly expanded apices, sculptured for muscle insertion; chamber ramus absent; distal ramus strong, well developed.

MIDSECTION of EC elaborate in structure; primarily membranous anterior surface supported by three main sclerites; centre sclerite (PrxSc 1) distoproximally oriented, shaped as a tall letter "V" with truncate apex, arms of "V" concave laterally, forming anterolateral margins of anterior surface of proximal chamber; surrounded by this sclerite and more proximally placed, a tall, omega-shaped sclerite (PrxSc 2); distal-most of anterior sclerites (DisSc 1) forms a structure roughly reniform in anterior view, convex margin facing distally, two short, curved rami on either side; in lateral view anterior sclerites narrow, elevated, plate-like in form, anterior margins strengthened by sclerotized thickening; omega sclerite (PrxSc 2) elevated distally to a level equal to that of apices of anterior

arch; V-shaped sclerite (PrxSc 1) elevated proximally; reniform sclerite (DisSc 1) not distinctly visible in lateral view; in anterior view lateral surfaces of midsection of EC inflated into a pair of lateral chambers (Cmb 1) on either side, form irregular, walls lightly sclerotized.

ANTERIOR KEEL absent, its morphological position and function apparently assumed by anterior projections of proximal-most two anterior surface sclerites (PrxSc 1, 2).

DISTAL ARMS strong, heavily sclerotized, strongly curved in anterior view, broad basally, tapering gradually to lightly sculptured apices, margins divided for muscle insertion, almost straight in lateral view, expanded slightly; anterior ramus slender, especially in anterior view, tapering to an acute apex, curved proximally in lateral view; posterior rami situated in lateral wall apparently as a strengthening structure, elongate, inflated basally, narrower towards expanded, blunt apex; a broad subtriangular section of posterior ramus present in lateral wall; lateral shelf absent; apical setae lacking.

Lebertia sp.

Fig. 31

The EC of this species shows a typical *Hydrodroma* structure but is more compact, heavily sclerotized, and complex.

PROXIMAL CHAMBER oval in anterior view; in lateral view high, short disto-proximally, posterior and proximal walls moderately sclerotized, lateral walls lightly sclerotized; lateral walls strengthened by an oblique sclerite that articulates disto-posteriorly with base of proximal arm sclerite and is free anteroproximally; anterior surface largely membranous, lateral and proximal margins supported and strengthened by a thickened, broadly U-shaped margin sclerite, in anterior view of sub-equal width all way around, distal tips indistinct; in lateral view, distal arms of margin sclerite narrower proximally, broader distally, forming a distal shoulder, then directed posterad to form a broad, sclerotized distolateral border of proximal chamber, border sclerite fused with base of proximal arm, then sweeping distally along lateral wall of midsection of EC; proximal horns arise from proximal margin of anterior margin sclerite, bases fused, each large, broad, tapering to a blunt apex, curved (convex proximally), produced laterally so that apex almost apposed with proximal apex of proximal arm.

POSTERIOR KEEL elongate, narrow, roughly a curved oval, posterior and proximal margins sinuate, irregular, abruptly tapering distally to form a sinuate, strongly sclerotized distal rod that curves first posterad then abruptly anterad to follow general contour of posterior surface of EC, distal tip of rod closely associated with posterior surface of EC just distal to level of distal arm sclerite.

PROXIMAL ARMS short, weakly curved in anterior view, heavily sclerotized, widest basally, tapering to a blunt, rounded apex, sinuate, tapering in lateral view; chamber ramus indistinct; distal ramus strong, well developed, especially in lateral view; a subtriangular basal plate present, lying primarily distal to base of proximal arm.

MIDSECTION of EC lightly sclerotized, some small membranous areas anteriorly; main feature of this region in lateral view an oblique, lateral sclerite (DisSc 1) oriented from anteroproximal to posterodistal in lateral wall, a wide, heavily sclerotized band, sides subparallel, posterior side merging with lateral wall of EC, anterior side raised to form an elongate ridge, anteroproximally giving rise to a short, broad rod articulating with distal shoulder of anterior margin sclerite, posterodistally giving rise to a strong, laterally directed axillary arm that is expanded apically, sculptured for muscle attachment, and articulated with apex of

distal arm; anterolateral area of this section of EC greatly elevated, inflated, in anterior view an elongate pyriform anterior chamber (Cmb 1), rounded distally, tapering to an acute apex proximally.

ANTERIOR KEEL low, elongate, curved (convex anteriorly), truncate posteriorly, lying along median line of proximal half of anterior pyriform chamber (Cmb 1).

DISTAL ARMS strong, broad basally, heavily sclerotized, slightly curved (concave laterally) in anterior view, apices expanded, especially laterally, sculptured for muscle attachment; anterior ramus short, subtriangular, with rounded apex, apices of two sides apposed on midline; posterior ramus large, strongly curved (concave posteriorly), tapering proximally, apparently partially fused with distal ramus of proximal arm sclerite, proximal half free from body of EC; small, subtriangular lateral shelf joins distal arms to proximomedial rami and body of EC; apical setae not observed.

Limnesia (s. str.) sp.

Fig. 32

The EC of this species represents one of the most extensive elaborations of the basic *Hydrodroma* type observed in the present study.

PROXIMAL CHAMBER large, subrectangular in anterior view; posterior wall weakly curved; proximal wall high, so that anterior surface rotated counter-clockwise through approximately 50° with respect to longitudinal axis of EC; lateral wall strengthened by a narrow, curved sclerite, obliquely placed, anteroproximal end fused with anterior margin sclerite, posterodistal end articulating with chamber ramus of proximal arm sclerite; lateral and proximal margins of anterior surface supported and strengthened by a narrow, broadly rounded, anterior margin sclerite, tapering to apices distally, somewhat thickened proximally, giving rise to a short, blunt proximal horn at each proximolateral corner.

POSTERIOR KEEL large, elongate, broadly attached to posterior side of proximal chamber, produced proximally into an irregular subtriangular plate, tapering distally to form a narrow, strongly sclerotized, curved (convex posteriorly) distal rod; distal rod free from EC throughout most of its length, closely associated with posterior surface distally at level of distal arm sclerites.

PROXIMAL ARM broad basally, almost straight in anterior view, tapering apically, apex expanded, blunt, sculptured for muscle insertion; chamber ramus prominent, sinuate, directed anterodistally; distal ramus strong, heavily sclerotized, broad basally in anterior view.

MIDSECTION of EC; sclerites of anterior surface include a laterally-convex, narrow band (PrxSc 1) forming distal and distolateral margins of anterior surface of proximal chamber; distal to this sclerite lies a pair of submedian, bipartite sclerites (DisSc 1), in lateral view proximal portions of bipartite sclerites form an anterior subrectangular projection with truncate apex, arising proximal to base of anterior keel; final major sclerite an oblique strap in lateral wall (DisSc 2), giving rise distally to a strong, laterally directed axillary arm, evident in anterior view; lateral arm of DisSc 2 supports membranes forming an irregular axillary chamber (Cmb 1).

ANTERIOR KEEL subtriangular, high, margins irregular, apex rounded, curved proximally, proximal margin concave, surface sculptured for muscle attachment.

DISTAL ARMS broad, strong, heavily sclerotized, margins subparallel, tapering acutely only in apical section to a blunt apex; anterior ramus short, subtriangular, broad basally, rounded apically, almost square in anterior view, apices apposed but not connected on median line; lateral shelf replaced by an expanded axillary knob; each distal arm sclerite gives rise to a short, conical, lightly sclerotized apical development, bearing a short, strong apical seta.

Fig. 32 *Limnesia (s. str.)* sp.: a, anterior view; b, lateral view.

Fig. 33 *Limnochares* sp. (nr. *L. americana*): a, anterior view; b, lateral view.

Fig. 34 *Midea* sp.: a, anterior view; b, lateral view.

Fig. 35 *Mideopsis* sp.: a, anterior view; b, lateral view.

Limnochares sp.

(nr. *L. americana*) Fig. 33

The EC skeleton of *Limnochares* is little modified from a sclerotized tube and possesses fewer well-defined sclerites than that of *Hydrodroma*. In anterior view, two main sections are distinguished: a wide, subrectangular proximal section composed primarily of proximal chamber and proximal arm sclerites, and distally, a narrower tube, corresponding to distal portion of sperm passage, walls lightly sclerotized, some distal thickenings representing rudiments of distal arm sclerites but otherwise featureless.

PROXIMAL CHAMBER subrectangular in anterior and lateral views, chamber walls lightly sclerotized, anterior surface membranous, no prominent margin sclerite; lateral wall of proximal chamber strengthened by an array of sclerotized bands and narrow, sclerotic, surface ridges; in lateral view margins of proximal chamber constricted at various points suggesting division of chamber into cavities, some of which may function in semen retention or spermatophore formation; proximal horns absent.

POSTERIOR KEEL joined to body of EC in an unusual way; supported by a subtriangular sclerite in lateral wall of EC distal to proximal chamber, attached to these sclerites by a long, curved stalk, projecting as a subtriangular plate below posterior surface of chamber, margins irregular; no distal rod.

PROXIMAL ARMS short and curved in anterior view, not projecting proximad beyond apex of proximal chamber, basal area broad and fused with sclerotized lateral walls of chamber; a distinct basal plate not discernable; chamber ramus projects distally and anteriorly, joins with a rudiment of anterior arch of distal arm sclerites; medial rami present as short, thick, blunt, medial projections apposed on median line.

MIDSECTION of EC much reduced as anterior keel positioned immediately distal to proximal chamber; lateral surfaces without distinct sclerotized areas, strengthened by several sclerotic surface ridges.

ANTERIOR KEEL subtriangular, proximal margin sinuate, step-like, thickened by a sclerotized band, distal margin slopes concavely, proceeds distad to participate in formation of anterior wall of distal tube, apex blunt.

DISTAL ARM sclerites represented by sclerotizations situated on anterior surface of EC distal to anterior keel, (cf. basal sclerite of distal arms in *Eylais*), in lateral view appearing as a strongly arched sclerite, anterior margin supported by a thickened sclerotized band, continuous with chamber ramus of proximal arm sclerite, lateral surface strengthened by a sclerotic ridge curving posteriorly and proximally to fuse eventually with base of proximal arm sclerite; a more distal series of sclerotized folds partially surrounding distal tube not easily homologized with any structure in *Hydrodroma* EC.

From base of anterior keel and from base of proximal arm, run curved, strongly sclerotized rods that fuse distally and proceed forward as an anterior, internal rod, along length of sperm passage; on posterior side lie a pair of curved, spindle-shaped, rods, attenuate distally, broadened and truncate proximally, may be homologous with distal-most of distal sclerites of *Hydrodroma*.

Midea sp.

Fig. 34

The EC of *Midea* is greatly modified but is basically similar to that of *Hydrodroma*.

PROXIMAL CHAMBER in anterior view oval, slightly compressed, narrowed in

midlength, rounded anteriorly and posteriorly; in lateral view subrectangular, margins and corners smoothly rounded; lateral, proximal, and posterior walls of chamber lightly sclerotized; anterior surface primarily membranous; anterior margin sclerite strongly rounded, U-shaped, thicker along proximal margin, tapering distally on either side; on midline proximally a strong, proximal ramus produced, bifurcate at apex, each part of bifurcation short, subtriangular, blunt at apex, representing a rudimentary proximal horn.

POSTERIOR KEEL rudimentary, partially membranous, incorporating a small, irregular sclerite centrally; distal rod absent.

PROXIMAL ARM sclerites set more distally on EC than in *Hydrodroma*, base lying distal to distal side of proximal chamber; proximal arms strong, heavily sclerotized, strongly curved in anterior view, not reaching proximally to apex of proximal chamber; chamber ramus produced anteriorly and proximally, greatly expanded into a subtriangular sclerite strengthening lateral part of proximal and posterior walls of proximal chamber; distal rami strong, well sclerotized, proceeding forward slightly distal to distal arm sclerites; basal plate lying distal to base of proximal arm.

MIDSECTION of EC distal to proximal chamber primarily membranous; in lateral view, three small sclerites (PrxSc 1-3) support this area; PrxSc 1 irregular, forming a distal margin to anterior surface of proximal chamber; in anterior view membrane outpocketed into two median chambers (Cmb 1, 2); most proximal (Cmb 1) lying immediately distal to proximal chamber and supported in part by PrxSc 1 sclerites; distal-most chamber (Cmb 2) subtends base of anterior keel; two indistinct lateral chambers also evident in anterior view.

ANTERIOR KEEL rudimentary, partially membranous, in lateral view appearing as two distinct structures, each one a short, narrow plate projecting anteriorly from anterior surface of EC.

DISTAL ARM sclerites much modified; anterior ramus and base of sclerite appear fused and expanded to form a small, cone-shaped apical development, apices of cones sculptured and excavated for muscle insertion; distal arm projects laterad and proximad as a small, curved, smoothly tapering, rod-like sclerite; no trace of posterior rami; a small lateral shelf joins base of distal arm to cone section of sclerite; apical setae not present on this sclerite.

Mideopsis sp.

Fig. 35

The EC of this species is clearly of the *Hydrodroma* type, although the distal section is greatly modified.

PROXIMAL CHAMBER narrow, suboval in anterior view, long, narrow, antero-posteriorly compressed in lateral view; anterior surface primarily membranous, supported and strengthened by a strong, U-shaped margin sclerite, broad and heavy proximally, tapering distally, in lateral view margin sclerite strong, well sclerotized; in addition to following margin of anterior surface, margin sclerite has a posterior projection in lateral wall of proximal chamber almost to base of proximal arm sclerite, apex of this projection produced laterad, visible in anterior view; lateral, proximal, and posterior walls well sclerotized; anterop proximally a club-shaped lateral wall sclerite visible in lateral view, broad thickened end articulating with proximal end of anterior margin sclerite, more attenuate and paralleling posterior projection from margin sclerite, passing under it in wall of chamber and ending slightly distal to its apex; a proximal horn projects anterad from either proximolateral corner of anterior margin sclerite, each a short, stout, heavily sclerotized rod, apex expanded, sculptured for muscle insertion.

POSTERIOR KEEL attached to rounded, inflated apex of proximal chamber which is produced proximally, keel produced posteriorly from chamber as a narrow plate, tapering gradually distally, giving rise to a sinuate distal rod; distal rod free from body of EC throughout most of its length, closely associated with posterior surface only in area of distal arm sclerites.

PROXIMAL ARMS massive, strong, heavily sclerotized, short, straight in anterior view, projecting at an angle of approximately 35° to longitudinal axis of EC, apices greatly expanded, subtriangular, curved medially, not extending proximally beyond apex of proximal chamber; chamber ramus absent; distal ramus strong, well sclerotized; basal plate greatly developed, elongate in distoproximal direction, occupying posterior half of lateral wall of proximal chamber and part of proximal and posterior walls.

MIDSECTION of EC lightly sclerotized and elaborate, no well-defined sclerites strengthening walls, a number of sclerotized outpocketings and a number of surface sclerotic ridges serve to make area rigid and give it form.

ANTERIOR KEEL low, anterior margin sinuate, lateral surface heavily sculptured, supported basally by several surface sclerotic ridges, bifurcate proximally in anterior view.

DISTAL ARMS short, massive basally, tapering rapidly to an expanded apex, strongly curved, apices sculptured with divided margins for muscle attachment; anterior rami slender, tapering gradually to apex, rami of either side completely fused on midline so that anterior arch continuous; region distal to anterior arch and distal arm greatly expanded, in lateral view a high, broad, anterior section supported by a narrow, oval margin sclerite, area tapers posteriorly to form a subtriangular apical projection of distal arm sclerite, bearing subdistally a simple, curved seta; in anterior view apical projections narrowly subtriangular with a blunt apex, high anterior expanded portion supported also by anterior, sclerotized, J-shaped ridges on either side, small arm of "J" facing medially; area between "J" sclerites appears to be open as a large anterior fossa, with proximal margin bounded by anterior arch, distal margin bounded by a membrane folding over top of apical projections of distal arm sclerites; posterior rami not evident.

Neumania sp.

Fig. 36

This species is, in general, similar to *Hydrodroma* in the structure of the EC skeleton.

PROXIMAL CHAMBER circular to oval in anterior view, oval to subrectangular in lateral view, proximal and posterior walls moderately sclerotized, lateral walls lightly sclerotized; anterior surface primarily membranous, supported and strengthened laterally and proximally by a divided anterior margin sclerite; in anterior view each part of margin sclerite L-shaped, joined medially in proximal margin by a ligamentous band, not fused; distolateral borders of chamber not sclerotized; lateral walls strengthened by an oblique sclerite articulating anterop proximally with proximal edge of anterior margin sclerite, articulating distoposteriorly with base of proximal arm.

POSTERIOR KEEL attached to distal part of posterior surface of proximal chamber, broadly attached, subrectangular in shape, rounded proximally, tapering irregularly distally to a short, strong, sclerotized distal rod; distal rod free from body of EC throughout, merging gradually with distal membranes at level of anterior keel.

PROXIMAL ARMS long, slightly curved in anterior view, sturdy, heavily sclero-

Fig. 36 *Neumania* sp.: a, anterior view; b, lateral view.
 Fig. 37 *Neumania* sp. (nr. *N. distincta*): a, anterior view; b, lateral view.
 Fig. 38 *Oxus* sp. (nr. *O. connatus*): a, anterior view; b, lateral view.
 Fig. 39 *Oxus* sp. (nr. *O. intermedius*): a, anterior view; b, lateral view.

tized, broadest basally, tapering gradually to an expanded apex, approximately twice as long as proximal chamber in anterior view; chamber ramus absent; distal rami slender, strongly sclerotized, proceeding distad to level of anterior keel; basal plate small, subquadrate, lying in lateral wall of EC distal to base of proximal arm.

MIDSECTION of EC lightly sclerotized, complex in structure; in anterior view can be seen a proximal bilobed chamber (Cmb 1), a distal, axillary, rounded chamber (Cmb 2), and posterior and lateral to these two, an elongate, sac-like chamber (Cmb 3); in anterior view, a pair of short, heavy, laterally placed, dumb-bell-shaped sclerites (PrxSc 1), anterior expansion of each sculptured for muscle attachment.

ANTERIOR KEEL high, narrow, slightly curved (convex distally) oval, apex acute, lateral surfaces heavily sculptured for muscle attachment, base broad but not tapering distally beneath anterior arch.

DISTAL ARM strong, heavily sclerotized, wide basally, tapering regularly to an acute apex, curved in anterior view, apex only slightly expanded; anterior ramus high, broad basally, tapering to sharp, acute apex, apices of either side apposed on median line; distal arm joined to lateral wall of EC by a strongly sclerotized rod that is expanded medially into a subtriangular plate, broadly attached to lateral surface of lobe-shaped lateral chamber, probably representing a modified lateral shelf; no apical setae observed.

Neumania sp.

(nr. *N. distincta*) Fig. 37

The EC of this species differs from that of the previously described *Neumania sp.* in being somewhat larger and more heavily sclerotized. Stout, proximal ramus produced medially from anterior margin sclerite, bearing apically a pair of short, truncate, proximal horns; no lateral wall sclerite strengthening proximal chamber; posterior keel large and subtriangular; distal rod of normal length; midsection of EC elaborated into four pairs of lightly sclerotized lateral chambers (Cmb 1-4) and one short, twisted, spindle-shaped sclerite (PrxSc 1); all rami and projections of distal arm sclerite larger and stronger; a pair of short, stout, apical setae present.

Oxus sp.

(nr. *O. connatus*) Fig. 38

This species shows a great reduction of size and complexity of sclerotized EC structures as compared with *Hydrodroma*.

PROXIMAL CHAMBER narrowly oval, elongate in anterior view, in lateral view high, broad, subrhomboid proximal and posterior walls moderately sclerotized, lateral walls lightly sclerotized, anterior wall largely membranous; lateral and proximal margins of anterior surface supported by a narrow, U-shaped margin sclerite, distal tips proceeding posteriorly at distal edge of proximal chamber forming a shoulder and sclerotized distolateral border of chamber, fusing then with lateral sclerotized surfaces of EC and basal plate of proximal arm sclerite; lateral wall sclerite absent; no trace of proximal horns.

POSTERIOR KEEL rudimentary; a thin, narrow, lightly sclerotized distal rod appears to arise directly from posterior side of proximal chamber, proceeds forward curving slightly in a sinuate fashion not far from posterior surface of EC but not fused with it.

PROXIMAL ARM a short, hollow, subconical structure, roughly triangular in anterior view, in lateral view expanded anteroposteriorly, surface lightly sculptured for muscle insertion; chamber ramus not recognizable; distal rami proceed distad in an approximately lateral position parallel with lateral walls of EC to midway along length of distal arm sclerites; basal plate large, subtriangular, lying partially distal to proximal chamber in walls of midsection of EC, strengthened by three sclerotized struts, two proceeding from base of proximal arm, third lying in a central position on plate, proximal portion expanded into a thin, triangular plate in lateral walls of proximal chamber.

MIDSECTION of EC lightly sclerotized, relatively simple in structure; inflated in anterior view (Cmb 1), high in lateral view.

ANTERIOR KEEL narrow and elongate; obliquely placed in lateral view, lying along distal portion of anterior margin of midsection of EC; high at proximal end, sloping down distally to level of distal arm sclerites.

DISTAL ARM sclerites greatly expanded, fused and modified to form a lightly sclerotized, apical cone at distal end of EC; cone thin, membranous anteriorly, proximal margins moderately well sclerotized; no setae observed on this sclerite.

Oxus sp.

(nr. *O. intermedius*) Fig. 39

The EC of this species shows great modification of the *Hydrodroma* pattern and is altered as well from that previously described for *Oxus* sp. (nr. *O. connatus*). Proximal chamber greatly enlarged in lateral view but narrow in anterior view; anterior surface greatly elongated proximally, curving clockwise through 180°; distal tips of anterior margin sclerite produced posteriorly forming strong, subtriangular, distolateral border sclerites; two short, tapering, sclerotized ridges lie side-by-side in membranes of anterior surface at distal border of chamber, each giving rise to a short, subconical, blunt **anterior horn**; posterior keel and distal rod absent; proximal arm short, blunt, fused basally with distolateral border sclerite; basal plate produced posteriorly as a narrow, sinuate, strap-like sclerite further strengthening distolateral border of proximal chamber; midsection and distal region lightly sclerotized, inflated to form an irregular chamber (Cmb 1); distal arm sclerites reduced to sclerotized thickenings in walls of Cmb 1.

Piona pinguipalpis

Fig. 40

The EC of this species differs from that of *Hydrodroma* primarily in the remarkable development of the proximal chamber. Determined from Cook, 1960.

PROXIMAL CHAMBER greatly elongated, narrowly oval in anterior view, in lateral view subrectangular, long, low; unusual feature of proximal chamber is extension of posterior wall and of anterior surface into a curving, helical, proximal projection, an elongate, blunt, narrow, blind sac appended proximally to proximal chamber; lateral, posterior, and rest of proximal surfaces all more nearly normal, moderately sclerotized, lateral surfaces not strengthened by sclerites; anterior surface primarily membranous, elongate, forming anterior surface of proximal sac; anterior margin sclerite approximately normal in shape, in anterior view elongate, narrow, U-shaped, wide proximally, tapering distally on either side, proximal section of sclerite raised anteriorly, arched over anterior surface of chamber so that anterior surface proceeds beneath its proximal end, being attached to it by membranes and is then produced proximally into blind sac; proximal horns absent.

POSTERIOR KEEL hatchet-shaped, connected to posterior surface of proximal chamber by a thin, oblique stalk, broadening posteriorly into an obliquely placed, subrectangular plate, truncate proximally, tapering distally to give rise to a moderately well-sclerotized, evenly curved (convex posteriorly) distal rod; distal rod free from posterior surface of EC throughout most of its length, although closely applied to posterior surface.

PROXIMAL ARMS broad, strongly curved in anterior view, widest at shoulder, tapering basally and apically, proximal apex acute, blunt, lateral margins much expanded to form a thin, sculptured plate for muscle insertion; basal plate small, lying distal to base of proximal arm in lateral wall of midsection of EC; distal ramus strong, heavily sclerotized; chamber ramus absent.

MIDSECTION of EC in part lightly sclerotized, in part membranous; in lateral view most of area occupied by basal plate of proximal arm sclerite, by a T-sclerite (DisSc 1), linear in lateral view, and by an anterolateral chamber (Cmb 1), more fully visible in anterior view; in anterior view Cmb 1 lies above base of proximal arm, subtriangular, broad lateroproximally, tapering distomedially; a pair of short, curved sclerites (DisSc 2) subtend base of anterior keel on either side.

ANTERIOR KEEL subtriangular with a broad base and a tall, anteriorly produced apex that is slightly expanded and sculptured for muscle insertion.

DISTAL ARMS in anterior view narrow, well-sclerotized, strongly curved, basal and apical portions directed at approximately 90° to one another, tapering gradually to a truncate, slightly expanded apex; anterior rami high, broad basally, tapering rapidly to an acute apex, apices of either side apposed on median line; area distal to anterior ramus and distal arms expanded, produced into a thin, lightly sclerotized, subconical structure on either side; lateral shelf aids in formation of posterior side of this apical development, joins base of distal arm to lateral wall of EC; posterior rami short, blunt, subtriangular; no apical setae present.

Protzia sp.

Fig. 41

The EC of this species is unusual in that much of the lateral surface is covered by folds of membranous chitin. Otherwise, the general structure is similar to that of *Hydrodroma*.

PROXIMAL CHAMBER large, subrectangular in both anterior and lateral views, proximal, posterior, and lateral walls lightly sclerotized, anterior surface largely membranous, lateral margins of anterior surface not strengthened by sclerotized rods, proximal margin supported and strengthened by a margin sclerite, produced proximally on midline into a low, blunt, cone-shaped proximal ramus; lateral wall supported in part by an oblique sclerotized rod that is broader proximo-anteriorly at articulation with anterior margin sclerite, tapering distoposteriorly to a blunt apex at base of proximal arm; proximal horns absent.

POSTERIOR KEEL large, subquadrate, attached broadly to posterior surface of proximal chamber, margins irregular, produced anteriorly into a short, triangular section giving rise to a curved, partially membranous distal rod; distal rod short, merging at level of proximal margin of anterior keel with distal membranes attached to posterior surface of EC.

PROXIMAL ARMS strong, heavy, well sclerotized, tapering gradually to blunt apices; chamber ramus short, almost indistinguishable; distal ramus long, well sclerotized; basal plate subtriangular, lying in lateral wall of EC distal to base of proximal arm and distal in large part to proximal chamber.

MIDSECTION of EC lightly sclerotized; only prominent sclerites in this region a

Fig. 40 *Piona pinguipalpis*: a, anterior view; b, lateral view.
 Fig. 41 *Protzia* sp.: a, anterior view; b, lateral view.
 Fig. 42 *Pseudohydrhantes* sp.: a, anterior view; b, lateral view.
 Fig. 43 *Sperchon* sp.: a, anterior view; b, lateral view.

pair of long, narrow, sinuate rods (PrxSc 1) lying in submedian position on anterior surface next to base of anterior keel, proceeding proximad to edge of anterior surface of proximal chamber, in lateral view wide, sides subparallel, proximal apex expanded into a subtriangular plate; a well-sclerotized chamber (Cmb 1) present on either side in a subaxillary position.

ANTERIOR KEEL elongate, low, subrectangular, slightly curved in lateral view, lying obliquely, anterior margin facing anterodistally; anterior margin sinuate, excavated in distal portion to form a short, triangular projection at either end of excavation, well sclerotized, subtended by folds of membrane.

DISTAL ARMS short, almost straight in anterior view, sides subparallel, tapering rapidly to a blunt apex; anterior rami elongate, broad, heavy, well sclerotized, sinuate, tapering to an acute apex in lateral view, apices apposed on midline; area distal to anterior ramus and distal arms expanded, produced distally into a thin-walled, cone-shaped apical structure on either side, blunt apically, bearing a strong, straight, subapical, simple seta; posterior rami short, strong.

***Pseudohydryphantes* sp.**

Fig. 42

The EC of this species represents an elaboration of the basic *Hydrodroma* plan.

PROXIMAL CHAMBER oval to round in anterior view, subrectangular in lateral view, lateral, proximal, and posterior walls heavily sclerotized, anterior wall primarily membranous; anterior surface strengthened laterally and proximally by a broadly rounded, U-shaped margin sclerite, thicker proximally, produced on midline proximally into a short, rectangular, truncate proximal ramus appearing as a thin plate in lateral view; distal ends of anterior margin sclerite curved posteriorly forming a rounded shoulder, then swept posteriorly forming a sclerotized distolateral border of proximal chamber, and distally as a broad, crescent-shaped sclerite lying in lateral wall of midsection of EC; distal section of this sclerite closely associated with elongate base of proximal arm; no strengthening sclerites in lateral walls of proximal chamber; proximal horns absent.

POSTERIOR KEEL subtriangular, low, posterior apex rounded, base broadly attached to posterior surface of proximal chamber, distal margin gives rise to a gently curving, well-sclerotized distal rod; distal rod free from posterior surface of EC throughout its entire length, merging gradually with membranes at level of distal half of anterior keel.

PROXIMAL ARMS short, not strongly curved, broadest basally, tapering gradually to a slightly expanded, blunt apex, projecting proximally about as far as apex of proximal chamber; in lateral view proximal arms thin, sinuate, base placed far distad on lateral wall of EC; distal ramus long, sharply pointed, ending distal to anterior arch; chamber ramus directed proximally from base, curved, paralleling distal extension of anterior margin sclerite; basal plate little developed, small, triangular, lying in posterior area of lateral wall of midsection.

MIDSECTION of EC lightly sclerotized laterally, some membranous areas anteriorly; strong, narrow, sclerotized ridge (PrxSc 1) lies obliquely in lateral wall, articulating posteriorly and distally with posterior ramus of distal arm sclerite, then proceeding anteroproximad, ending at proximal end of basal margin of anterior keel; a second strong sclerite in lateral walls is a narrow, curved, elongate rod (DisSc 1) subtending base of anterior keel; in anterior view, sclerites and projections of lateral wall define and support lateral and posterior walls of two pairs of large lateral chambers (Cmb 1, 2), anterior walls of these chambers appear largely membranous; two spindle-shaped sclerites (PrxSc 2) lie submedially in anterior wall between distal margin of proximal chamber and proximal margin of anterior keel.

ANTERIOR KEEL subtriangular, high, rounded anteriorly and proximally, tapering distally to continue forward beneath anterior arch.

DISTAL ARMS short, curved in anterior and lateral views, broad basally, tapering to an acute, blunt apex; anterior rami short, blunt, subtriangular in anterior and lateral views; a well-developed lateral shelf present; area distal to anterior rami and distal arms expanded, produced to form a lightly sclerotized, cone-like structure; posterior ramus present, short, curved, tapering to an acute apex proximally; each apical cone bearing a short, stout, curved seta subapically.

Sperckon sp.

Fig. 43

The EC of this species is greatly modified from the *Hydrodroma* type. The body of the organ is composed of a long, inflated, lightly sclerotized sack consisting primarily of the proximal chamber and the inflated midregion. The typical sclerites are reduced and lie in the lateral walls of the structure.

PROXIMAL CHAMBER large, oval in anterior view, rounded in lateral view, posterior and lateral sides lightly sclerotized, anterior surface largely membranous; an oblique, lightly sclerotized band lies in anterior portion of lateral wall of proximal chamber; anterior margin sclerite U-shaped, thin in anterior view, broader and strap-like in lateral view, distal ends proceed posteriorly as a sclerotized, distolateral border of chamber, then distally as an oblique arm across lateral surface of midsection; small proximal horns, in anterior view, project laterally, apparently as continuations of sclerotized plate strengthening proximal surface of chamber.

POSTERIOR KEEL almost non-existent; distal rod produced directly from posterior surface of proximal chamber, curved slightly (convex posteriorly), following posterior surface of EC closely although not attached to it throughout most of its length, distally rod becomes completely fused with posterior surface at level of distal arm sclerites.

PROXIMAL ARM sclerites small, simple in anterior view; arms short, slightly curved, broad basally, tapering regularly to a blunt apex; only well-developed ramus is chamber ramus proceeding obliquely from base of proximal arm anteroproximad to fuse with distal end of anterior margin sclerite.

MIDSECTION of EC large, approximately diamond-shaped in lateral view, anterior and lateral walls lightly sclerotized, anterior surface high, arched anteriorly, lateral walls expanded to form large axillary chamber (Cmb 1) on either side; a longitudinal median chamber (Cmb 2) subtends anterior keel; Cmb 1 strengthened by one oblique sclerite (DisSc 1) in distal half of lateral wall, tapering posterodistally, articulating with base of distal arm sclerites; a number of sclerotic ridges give additional support to lateral walls.

ANTERIOR KEEL low, elongate in lateral view, slightly curved (convex anteriorly), perched upon anterior surface of Cmb 2.

DISTAL ARM sclerites much reduced, distal arms short, slightly curved, tapering to a blunt apex; anterior rami directed distad, long, thin, curving almost to midline over anterior surface; posterior ramus indistinct, probably fused with DisSc 1; a semi-membranous, curved rod projects posteriorly, on either side, from posterior surface at level of distal arm (cf. posterior ramus in *Hydryphantes*); no apical development or apical setae.

Sperchonopsis sp.

Fig. 44

The chitinized EC skeleton of this species is similar to that of the *Sperchon* species just described. It differs primarily in being proportionally higher (anterior to posterior direction), more heavily sclerotized, and more elaborate. Proximal chamber larger, subquadrate in lateral view; proximal horns thin, lightly sclerotized, elongate; basal plate of proximal arm sclerite large, aiding in formation of a lateral over-hanging wall in midsection; lateral walls of axillary chambers (Cmb 1) well sclerotized; DisSc 1 broad, curved and strap-like; each distal arm sclerite giving rise to a cone-like apical development that curves posteriorly and bears subdistally a short, stout, apical seta; posterior ramus of distal arm sclerite evident.

Testudacarus sp.

Fig. 45

The EC of this species is a compact, moderately sclerotized structure, easily referable to the basic *Hydrodroma* type.

PROXIMAL CHAMBER large, subcircular in anterior view, subrectangular in lateral view; lateral, proximal and posterior walls moderately sclerotized; anterior portion of chamber more rounded, posterior portion narrower, more trough-like; anterior surface primarily membranous, supported and strengthened laterally and proximally by a margin sclerite; margin sclerite rounded, broadly V-shaped in anterior view, distal tips forming a shoulder at anterodistal corner of chamber, then proceeding obliquely posterodistad, finally curving distad across surface of lateral wall of midsection; margin sclerite produced proximally into a short, blunt, rounded proximal ramus, and laterally on either side to form a thin, tapering, lightly sclerotized proximal horn; lateral walls of proximal chamber strengthened and supported by a sinuate oblique sclerite.

POSTERIOR KEEL a short, low ridge, tapering distally and proximally, slightly curved (convex posteriorly), applied to posterior surface of proximal chamber near distal border of chamber; distal rod absent.

PROXIMAL ARMS short, strong, almost straight in anterior view, widest basally, tapering gradually to a slightly expanded, sculptured apex, reaching proximally only about half as far from their base as apex of proximal chamber; chamber ramus short, strong, fused with distal section of anterior margin sclerite where it travels across lateral surface of EC; distal rami curve posterad, then strongly anterad and distad; basal plate roughly triangular, lying wholly in lateral wall of EC distal to base of proximal arm, almost entirely covered by sclerotized flaps or chambers elaborated in lightly sclerotized wall.

MIDSECTION of EC moderately sclerotized, elaborated into a number of plates, chambers, and sclerotized structures, entire area large, subrectangular in anterior and lateral views; treating first structures of anterior surface, proximal-most anterior sclerite (PrxSc 1) horseshoe-shaped (concave distally), lying on midline just distal to anterior surface of proximal chamber, forming an anterior margin for this area; distal-most anterior surface sclerite (DisSc 1) in form of a long, narrow, U-shaped structure with sub-median ramus on either side elongate, narrow, tapering, sinuate, rami on either side joining on midline just proximal to base of anterior keel; both PrxSc 1 and DisSc 1 broad, plate-like in lateral view; lateral surface of midsection with a number of sclerotic surface ridges, folds, plates and some folded membranous areas posteriorly; most prominent feature, a subtriangular lateral chamber (Cmb 1) axillary to distal arms; walls of this chamber strengthened by a V-shaped (in anterior view) sclerite (DisSc 2), apex projecting laterally, arms fused basally with lateral walls of midsection.

Fig. 44 *Sperchonopsis* sp.: a, anterior view; b, lateral view.
 Fig. 45 *Testudacarus* sp.: a, anterior view; b, lateral view.
 Fig. 46 *Thyas barbiger*a: a, anterior view; b, lateral view.
 Fig. 47 *Tiphys* sp. (nr. *T. americana*): a, anterior view; b, lateral view.

ANTERIOR KEEL triangular in lateral view, broadly joined to anterior surface of area delimited by DisSc 1 and elevated on this structure, anterior margin almost straight, irregular, with a thin, finger-like proximal extension; proximal margin strongly concave.

DISTAL ARMS short, straight, tapering gradually to a blunt apex, apices sculptured slightly for muscle attachment; anterior ramus lacking entirely; posterior ramus forms part of lateral chamber (Cmb 1); area distal to base of distal arm expanded, produced to form an elongate, narrow, blunt, cone-like apical development, each cone bearing a short, curved, simple seta subapically.

Thyas barbiger

Fig. 46

The EC of this species is robust and heavily sclerotized but displays a tendency to reduction of the distal arm sclerites. Determined from Cook, 1959.

PROXIMAL CHAMBER subquadrate in anterior view, subrectangular in lateral view, lateral, proximal, and posterior walls lightly sclerotized; anterior surface primarily membranous; in lateral view, anterior margin sclerite forms a pronounced anterodistal shoulder to proximal chamber and distal tip of sclerite, then proceeds posterad and distad in a broad arc onto lateral surface of midsection of EC, in anterior view this broad crescentic sclerite narrow, entirely free from lateral surface of midsection; anterior portion of lateral chamber wall strengthened and supported by a curved, strongly sclerotized, oblique, rod-like wall sclerite; anterior margin sclerite produced proximally on midline into a short, subrectangular proximal ramus, truncate in anterior view.

POSTERIOR KEEL elongate, narrow, suboval, attached by a short, broad stalk to posterior surface of proximal chamber, proximal margin rounded, distal margin irregular, tapering to give rise to short, almost straight, distal rod; distal rod becomes indistinct just proximal to level of distal arm sclerites, fused at this point with portions of distal membranes.

PROXIMAL ARM massive, strongly curved, broadest basally, tapering gradually to slightly expanded apex, reaching proximad to about apex of proximal chamber; chamber ramus fused with sclerotized distolateral border of chamber and with lateral wall sclerite; distal ramus heavy, elongate, well sclerotized, strengthening posterior and lateral walls of midsection; basal plate small, broadly fused with distal section of anterior margin sclerite.

MIDSECTION of EC moderately well sclerotized; main feature of the region a subaxillary lateral chamber (Cmb 1) with sclerotized walls, subtending anterior keel; supported laterally by a strong, V-shaped sclerite (DisSc 1); a high, thin, membranous, median chamber (Cmb 2) lies proximally on anterior surface, extending part way over proximal chamber.

ANTERIOR KEEL elongate, slightly expanded distally, apex rounded.

DISTAL ARMS elongate, thin, well sclerotized, in anterior view almost straight, slightly curved near apices, broad basally, tapering apically; anterior rami short, massive, subtriangular in lateral view, subquadrate in anterior view, apices apposed medially; area distal to anterior ramus and distal arms expanded to form a short, blunt, cone-shaped apical development on either side bearing a simple apical seta subdistally; posterior rami short, but strong; a small, subtriangular, lateral shelf joins base of distal arm to lateral surface of EC.

***Tiphys* sp.**

(nr. *T. americana*) Fig. 47

This species possesses an EC of the generalized *Hydrodroma* type, with a pronounced elongation of the proximal chamber.

PROXIMAL CHAMBER long, narrowly oval in anterior view, subrectangular in lateral view; lateral and proximal surfaces lightly sclerotized, posterior surface more heavily sclerotized; anterior surface membranous, membrane thick and leathery in appearance; lateral and proximal margins of anterior surface supported by a long, narrow, U-shaped margin sclerite, arms subequal in width throughout their length, apices expanded, round, blunt; proximally, anterior margin sclerite gives rise to two long, stout proximal horns directed distolaterad, each with its base on midline, each possessing an expanded, sculptured apex for muscle attachment.

POSTERIOR KEEL an elongate, strap-like sclerite, produced and rounded proximally, broadly attached to posterior surface of proximal chamber, tapering distally to form a long narrow, well-sclerotized distal rod; distal rod only slightly curved, parallelling posterior surface of EC beyond distal arm sclerites, free from EC, merging with distal membranes at level of distal arms.

PROXIMAL ARMS short, broad basally, tapering to a narrow region subapically, apex expanded into an almost circular sculptured knob; chamber rami absent; distal rami strong, well sclerotized, proceeding forward to level of anterior keel; basal plate elongate, spindle-shaped in lateral view, lying two-thirds in lateral wall of proximal chamber, one-third in lateral wall of midsection of EC, strengthened by several strongly sclerotized struts from base of proximal arm.

MIDSECTION of EC lightly sclerotized, walls produced into four small, lobe-like chambers on either side and one small, sclerotized median chamber anteriorly, beneath over-hanging proximal section of anterior keel.

ANTERIOR KEEL an elongate subrectangular plate, obliquely placed; broader basal end fused distally with anterior surface of EC, keel then projects antero-proximally, over-hanging proximal portion of anterior surface; apex irregular, tip acuminate.

DISTAL ARMS slender, tapering from a broad base gradually to a narrow, blunt apex, only slightly curved in anterior and lateral views; anterior ramus a strong, short rod in lateral view, tapering to blunt apex, subtriangular in anterior view; apices and medial margins apposed on midline; lateral shelf apparently absent; apical setae absent.

***Torrenticola* sp.**

(designated species A) Fig. 48

The EC of this species is much modified from the *Hydrodroma* type. Both structural complexity and degree of sclerotization are reduced.

PROXIMAL CHAMBER elongate, oval in anterior view, subrectangular in lateral view; lateral, posterior, and proximal surfaces lightly sclerotized; anterior surface primarily membranous, supported laterally and proximally by a U-shaped margin sclerite; margin sclerite thin, of approximately uniform width, directed posterad at distal margin of anterior surface to form an anterodistal shoulder to proximal chamber, not proceeding far in lateral wall; upper surface of lateral wall of proximal chamber strengthened by an oblique, narrow, rod-like sclerite; proximal portion of anterior margin sclerite gives rise laterally on either side to a short, blunt proximal horn.

POSTERIOR KEEL small, subtriangular, attached to distal portion of posterior surface of proximal chamber, tapered apically to give rise to a slightly curved, moderately sclerotized distal rod, separated from body of EC throughout most of its length, fused with it again distally.

PROXIMAL ARMS short, blunt distally, apical and basal areas slightly expanded; chamber ramus and basal plate rudimentary; distal ramus proceeds posteriorly and distally in lateral wall of proximal chamber, fused at its distal tip with a sclerite (PrxSc 1) lying in posterolateral section of midpart of EC.

MIDSECTION of EC lightly sclerotized, simple; general configuration that of a tube, wider proximally, tapering slightly distal to level of distal arm sclerites; an approximately heart-shaped, membranous region delimited medially in proximal half of anterior surface; lightly sclerotized areas distal and lateral to this; strong rod-shaped sclerite (PrxSc 1) lies in posterior region of each lateral wall, with a small lateral arm projecting laterally on each side, one-third of distance from proximal end.

ANTERIOR KEEL elongate, low, anterior margin gently concave, distal margin convex, rounded, distal and anterior borders strengthened by a sclerotized thickening.

DISTAL ARMS thin, moderately well-sclerotized in anterior view, swept back, slightly concave laterally, apices narrow, simple; in lateral view arm subtriangular, wing-shaped, lateral and proximal margins strengthened by sclerotized thickenings; anterior ramus absent, only bases of distal arms apposed on midline; area of distal arm sclerites distal to base produced into an apical development forming a single, subconical structure; apical cone low, blunt, rounded distally; other rami of distal arm sclerites absent; apical setae absent.

Torrenticola sp.

(designated species B) Fig. 49

The EC of this species is greatly elongated and apparently modified for internal insemination. Proximal chamber small, oval, anteroposteriorly compressed, lightly sclerotized; proximal horns absent; distolateral border and anterodistal corner of chamber sclerotized; posterior keel elongate, linear; distal rod absent; distal ramus of proximal arm sclerite strong, heavily sclerotized; midsection short, lightly sclerotized; a broadly U-shaped anterior sclerite (PrxSc 1) in this section forms a distal margin to proximal chamber, gives rise on either side to a short, lateroposteriorly directed rod (PrxSc 2) strengthening lateral wall of lateral chamber (Cmb 1); anterior keel elongate, linear, membranous; distal arm sclerites strongly modified, consisting of a proximally directed distal arm extending to edge of proximal chamber and a greatly elongated, cylindrical apical development, blunt distally; each apical development bearing a long, simple, subdistal seta; posterior surface of EC also produced distad to form a shallow, lightly sclerotized trough partially supporting apical developments of distal arm sclerites.

Tyrrellia sp.

Fig. 50

The EC of this species is unusual and unlike any other that I studied. It is apparently strongly modified in response to some particular element of the mite's habits or habitat, for instance, the necessity of accomplishing insemination in a water-film environment. Structures can be compared only with difficulty with those of *Hydrodroma*, but the strong resemblance of the adult to the typical water mites justifies the following unsatisfactory attempt. The final elucidation of this organ awaits an intensive study of its functional morphology and of the behaviour and

Fig. 48 *Torrenticola* sp. A: a, anterior view; b, lateral view.
 Fig. 49 *Torrenticola* sp. B: a, anterior view; b, lateral view.
 Fig. 50 *Tyrrellia* sp.: a, anterior view; b, lateral view.
 Fig. 51 *Unionicola* sp.: a, anterior view; b, lateral view.

life history of the species. In the body of the adult male, the EC projects ventro-posterad into the phallocrypt so that the surface designated anterior in *Hydrodroma* faces ventrally. This is the surface illustrated in Fig. 50a. Sclerites are lettered (A-D) because of their uncertain homology.

Proximally, a capacious, lightly sclerotized (proximal ?) chamber surrounds the basal half of the organ. The paired sclerites (A) on the anterior surface may be homologous with the proximal arm sclerites of *Hydrodroma* or, in part, with the anterior margin sclerite. The conspicuous, broad, flat distal plates (D) bear a strong, anteriorly-directed spine at the mediodistal corner, and the lateral edges are toothed. These sclerites are probably homologous with some elements of the distal arm sclerites of *Hydrodroma*, but appear to serve a special function in *Tyrrellia*. The presence of a band of muscles joining a posterior projection (C) from these plates with a median posterior projection (B) suggests that the distal toothed plates (D) can be moved scissor-like, in the horizontal plane. This may be linked with an unusual method of spermatophore deposition. The triangular plate lying proximal and anterior to the EC and joined to it only by membrane is apparently the median anterior sclerite in the genital field of the ventral body wall. It appears to function as a point of anchorage for the EC.

Unionicola sp.

Fig. 51

The EC of this species is an elaboration of the basic *Hydrodroma* type. The organ is robust, complex, and heavily sclerotized.

PROXIMAL CHAMBER subquadrate in anterior view, subrectangular to oval in lateral view, lateral, posterior, and proximal surfaces moderately sclerotized, anterior surface primarily membranous; margins of anterior surface supported and strengthened only proximally by a wide, curved proximal sclerite, lateral arms of this sclerite absent; an oblique sclerite present in anterior portion of lateral wall, roughly L-shaped (convex posteriorly), short arm articulating anteroproximally with proximal section of anterior margin sclerite, tapering distal tip articulated and partially fused with base of proximal arm; anterior margin sclerite produced proximally on midline into a short, broad proximal ramus, subrectangular in anterior view, a short, stout rod in lateral view; from either proximal corner of proximal ramus is produced a stout, well-sclerotized, L-shaped, proximal horn, short limb of "L" fused with proximal arm, directed proximolaterally, long arm of "L" directed posteriorly, sinuate, tapering to a blunt apex.

POSTERIOR KEEL suboval, attached to distal portion of posterior wall by a short, narrow stalk, posterodistal corner of keel produced into a sinuate, strongly sclerotized distal rod; distal rod well separated from posterior surface of EC throughout its entire length, fusing with distal membranes and walls of sperm passage only distal to distal arm sclerites.

PROXIMAL ARMS long, stout, broad in anterior view, hardly tapering, expanded into a subtriangular apex, unusual in giving rise basally to a posteriorly directed **arm ramus**; arm ramus short, stout, tapering slightly, truncate apically, bearing a small apical projection possibly a tendon for muscle or membrane attachment; chamber ramus absent; distal rami short and stout.

MIDSECTION of EC lightly sclerotized; area characterized by a number of chambers or outpocketings both laterally and anteriorly, and by a pair of prominent T-shaped sclerites (PrxSc 1); in lateral view PrxSc 1 seen to have a complex structure consisting of a horizontal sclerite, broadly rounded distally, also rounded and narrower proximally, bearing two anteriorly directed, curved, thin rami; location of chambers follows: Cmb 1, in proximal section of lateral wall overlapping

anterodistal section of lateral surface of proximal chamber; Cmb 2 medially placed on anterior surface of midsection, subtending proximal end of base of anterior keel; Cmb 3, posteriorly in lateral wall directly below base of anterior keel; anterior surface also bears a small pair of sclerites (PrxSc 2) lying submedially, proximal to base of anterior keel in membranous area of anterior surface.

ANTERIOR KEEL high, crescent-shaped (convex distally), apex bluntly rounded.

DISTAL ARM sclerites massive, broadly expanded, heavily sculptured; distal arms short, almost straight, thin in lateral view, broad in anterior view because of medial, shelf-like expansions; anterior ramus elongate, narrow, tapering from a broad base to a small, blunt apex; lateral shelf greatly expanded, produced proximally near body of EC thus forming a broad connection between distal arm and lateral surface of midsection; this shelf also produced posteriorly as seen in lateral view, in concert with posterior ramus, forms a posterior wing-like projection beside lateral surface of EC, this extension then joined to lateral wall by a fold of membrane near base of proximal arm; lateral shelf divided so that distal arm also joined to lateral wall by a short, stout, well-sclerotized rod; entire sperm passage produced distal to these sclerites forming a lightly sclerotized tube, narrow in lateral view, somewhat oval in anterior view.

Assessment and Analysis of Similarities

HOMOLOGY

In the comparative morphological study of a given life history stage, embryological evidence is rarely available. Homology can, however, be justifiably inferred from similarity of form and of position in a well-defined functional system. The degree of confidence placed in conclusions based on this 'practical' homology is increased when (i) there is reasonable homogeneity of structure among the organisms studied, and (ii) both functional and anatomical relationships of structures are clearly understood. Conclusions are also strengthened by parallel but independent research on other functional systems for the same group of organisms. Such parallelism aids in exposing both misinterpretation and the confusing results of evolutionary convergence.

THE GENERALIZED WATER MITE EC

The chitinous skeletal elements of the EC are surprisingly similar throughout the water mites with only a few exceptions. The basic function in all genera is apparently to form and deposit the spermatophore, and the basic mode of action probably uniform. The first sclerotized section of the sperm passage is an enlarged proximal chamber that may be large, box-like and robust, or narrow and elongate, or inflated, membranous and sac-like. The lightly sclerotized anterior surface, usually supported by a U-shaped margin sclerite, is the point of entry for semen from the *ductus ejaculatorius*. The remainder of the mechanism consists of a narrow, often complex sperm passage to the exterior. The passage is surrounded by a series of sclerites giving purchase and leverage to several pairs of muscles that contract in concert to operate a syringe-like mechanism, compressing the proximal chamber and expelling its contents to the exterior.

The proximal edge of the anterior margin sclerite may be unmodified or may give rise to a proximal ramus or a pair of proximal horns. Fre-

quently a narrow, shelf-like posterior keel is attached to the posterior surface of the proximal chamber and is often produced distally into an elongate distal rod that may be free or variously fused to the body of the EC. The distal section of the proximal chamber is invariably supported on either side by a proximal arm sclerite giving rise to a laterally directed proximal arm. Other processes of this sclerite further strengthen the lateral walls of the chamber and midsection of the EC.

The midsection varies more than other areas of the EC in the species observed, often being elaborated into a number of different sclerites, projections, and chambers. A relatively constant feature of the region is a thin, sclerotized, longitudinal anterior keel. The keel varies in shape and degree of sclerotization but is consistent in its median position distally on the anterior surface of the midsection. The distal apex of the EC is provided with a pair of distal arm sclerites that may be greatly reduced but always persist in the form of some rudimentary sclerotization. When well developed, each bears a laterally directed distal arm and an anteromedially directed anterior ramus, the tips of the anterior rami apposed on the midline to form an anterior arch. Other processes of the distal arm sclerite strengthen the lateral and posterior walls of the midsection. In many species, these sclerites are expanded and developed apically and may bear a pair of simple, apical setae. Membranes are always inserted at some point on the distal half of the EC and attach it to the borders of the genital opening.

SIMILARITY GROUPINGS

With the data presented it is possible to assess the similarity of the chitinous skeleton of the EC from genus to genus and to present the results graphically as in Figures 52-55. *Feltia* is omitted from this analysis because of the lack of detailed morphological data. The figures illustrate similarity relationships only; the length of the line joining two taxa is inversely proportional to the degree of mutual similarity shown by the ejaculatory complexes of the taxa, with dotted lines indicating situations in which the precise relationship is based on only one or a few characters, and is tentative. There is no intent to illustrate phylogenetic relationships.

Group 1 of Fig. 52 is composed of the two genera, *Protzia* and *Hydrodroma*, showing a generalized structure of the EC skeleton. The two have in common relatively strong, well-developed distal and proximal arm sclerites, a pair of sclerotized lateral chambers, a well-developed distolateral border to the proximal chamber, lateral wall sclerites, and a weak, partially membranous distal rod. *Protzia* is similar to *Limnesia* in the form of distal arm sclerites, large, robust proximal chamber, and shape of distolateral border of proximal chamber. The latter relation indicates that the Group 1 genera show closest affinity with those of Group 3.

Group 2 is also composed of two genera, *Eylais* and *Limnochares*, that are characterized by a highly-modified EC. They are similar in the reduction of the distal arms, in the configuration of the proximal arm sclerites, with a great enlargement of the medial ramus, and in the un-

Fig. 52 Similarity relationships based on the morphology of the ejaculatory complex.

usual, arched structure formed on either side by the bases of the distal arm sclerites. Although the basic affinity of the Group 2 genera with other water mites is strong, the precise relationship is not clearly indicated by the structure of the EC. But the joining of proximal and distal arm sclerites by sclerotized struts, and the reduction of the distal arms may indicate some similarity to Group 3 (especially *Hydrachna*).

Group 3 consists of 11 genera and is a large and reasonably homogeneous group with a complex internal structure (Fig. 53). *Lebertia* occupies a central position in the similarity diagram. *Thyas* and *Hydryphantes* form a nucleus defined by the possession of a well-developed

Fig. 53 Similarity relationships among the genera of Group 3.

distolateral border of the proximal chamber with its extension into the lateral wall of the EC, sclerotized lateral chambers, and a slight reduction of the distal arms. The first and last of these features indicates similarity to *Lebertia*. *Sperchon* and *Sperchonopsis* are closely similar and share so many features that their species would perhaps be considered congeneric on the basis of EC characters alone. They are like *Lebertia* in having the midsection of the EC inflated and well sclerotized. Other similarities to *Lebertia* include the form of the proximal horns and the sclerite-complex formed by the anterior margin sclerite, distolateral border, and lateral wall sclerite of the proximal chamber. In addition, *Sperchon* and *Sperchonopsis*

have in common the sclerotized bands and chambers of the midsection, the swept-back configuration of the distal arms with low anterior rami, and the strongly elbowed proximal arms. *Testudacarus* is readily placed close to *Sperchon* by the virtually identical, sclerotized axillary chambers, the configuration of the distal arms, and the sclerotized distolateral borders. The EC in the two *Torrenticola* spp. examined was reduced and modified, and there is little reliable evidence to link the genus with *Testudacarus* on the basis of this structure. Nonetheless, the adult exoskeletal morphology of these genera is virtually identical so that, by association, *Torrenticola* is also shown to have a strong affinity with *Sperchon* and *Sperchonopsis*. The presence of one additional genus (*Testudacarus*) in the study can illuminate a previously obscure relationship.

Frontipoda and *Oxus* possess a modified and reduced EC with a number of similar features: extreme reduction of the distal arm sclerites, similar shape of the basal plates, inflated chambers of the midsection, and similar, lightly sclerotized distolateral borders of the proximal chamber. The latter, together with the reduction of the distal arms and the possession of an inflated median chamber below the anterior keel, link the two genera to *Lebertia*. *Oxus* sp. (nr. *O. intermedius*) is more modified than the species near *O. connatus* and so supports the association with *Lebertia* to a lesser degree. *Pseudohydryphantes* is a definite, although peripheral member of Group 3. It possesses a distinct distolateral border, a sclerotized axillary chamber, and a proximal ramus and is most similar to *Thyas*. *Hydrachna* shows a general similarity to the rest of Group 3 and is placed there on the basis of over-all facies. Although it is not closely linked to any other genus, in the reduction of the distal arm sclerites and possession of a well-developed distolateral border it is most similar to *Thyas* or *Lebertia*.

Limnesia possesses a generalized EC skeleton and is distinct from any of the groups established here. It does, however, have a strong distal sclerite in a position axillary to the distal arms suggestive of that found in *Lebertia*. Also, the distal end of the distolateral border projects forward into the midsection of the EC in a manner reminiscent of the genera of Group 3. As suggested earlier, these features indicate that *Limnesia* may be intermediate between Group 1 and Group 3.

Group 4 represents seven genera (Fig. 54) forming a less closely-related unit than those of Group 3. *Unionicola* and *Neumania* are easily associated by the modification in each of the lateral shelf to form a supporting buttress and by the presence of a lateral wall sclerite. *Forelia* is similar to *Neumania*, especially in the formation of a buttress from part of the lateral shelf. And, through the form of its distal arm sclerites, its proximal horns, and free proximal lobe of the posterior keel, *Forelia* appears to be related to *Piona* and *Tiphys*, linking these to *Neumania* as well.

Atractides and *Hygrobates* comprise another well-defined nucleus within Group 4, sharing in common the shape of the anterior keel, the presence of a proximal ramus, and the lateral excavation of each arm of the anterior margin sclerite. In addition, *Atractides* is similar to *Unionicola* in the shape of the anterior keel and in the possession of a pair of laterally placed

Fig. 54 Similarity relationships among the genera of Group 4.

Y-sclerites. *Piona* and *Tiphys* are related by a similarity of overall facies, with an elongation of the proximal chamber, similar form of proximal and distal arms sclerites, and a narrow, oblique anterior keel. The lateral shelf and laterally placed Y-sclerite of *Piona* indicate a relationship to *Atractides*.

The four genera of Group 5 (Fig. 55) exhibit strong mutual affinities but their relationship to other mites is less clear. *Axonopsis* and *Brachypoda* are similar in general EC structure, each characterized by a compact, well-sclerotized skeleton of robust components. In particular, the strong, U-shaped anterior margin sclerite, the complex midsection, and the proximally-lobed posterior keel indicate the close phenetic relationship of these genera. *Aturus* presents a comparable facies and is strongly linked to *Axonopsis* and *Brachypoda* by the structure of the anterior margin sclerite. The *Kongsbergia* EC is less specialized, but the form of the anterior margin sclerite, the posterior keel, and the complex structure of the midsection tie it convincingly to the other Group 5 genera. Its more generalized structure points to an additional relationship with the genera of Group 4, and the complex basal area of the distal arm sclerite, together with the form of the anterior margin sclerite, suggest that of the Group 4

Fig. 55 Similarity relationships among the genera of Group 5.

genera in this study, it is most similar to *Unionicola*.

Koenikea does not fit easily into any of the groups formed thus far but seems to be intermediate between the genera of Groups 4 and 5. The shape of the distolateral border, the elongation of the anterior ramus, and the reduction of the posterior keel also occur in *Aturus*. On the other hand, the three pairs of lateral, midsection chambers and the medially-based proximal horns suggest a distant affinity with *Neumania*.

Four additional genera do not appear to fall within any one of the five main groups, but each can be tentatively related (Fig. 52) to one or another of them. *Mideopsis* shares a heavy sclerotization of the proximal chamber and the narrow shape of the posterior keel with *Axonopsis* in Group 5. *Geayia* in turn has the sclerotized proximal chamber and configuration of the strongly fused anterior margin and lateral wall sclerites in common with *Mideopsis*. The EC of *Albia* is similar to that of *Koenikea* in the medial placement of the proximal horns, form of the posterior keel, and elongate anterior ramus. Thus *Albia* also appears distantly related to Group 5. *Midea* can be linked to the same group via two features shared with *Kongsbergia*: a pair of elongate, curved, rod-like distal sclerites anteriorly in the midsection and a median, proximally-directed extension of the anterior margin sclerite (proximal ramus). Species of these genera are hard-bodied, actively-swimming mites, and associated modifications of the EC have possibly obscured relationships.

On the basis of overall homology of the EC skeleton, the genera of Groups 1, 2, and 3 have a strong basic affinity with those of Groups 4 and 5. The generalized, intermediate EC structure of *Limnesia* is at

present, however, our sole indicator of the probable details of intergroup relationships between these two larger divisions. Only the investigation of additional genera can provide the information needed to specify precise linkages.

The remaining three genera cannot on the basis of the morphology of the ejaculatory complex be successfully related to any of the previously considered groups of genera. It should eventually be possible to homologize the *Tyrrellia* EC with that of other water mites, especially since, as Dr. David R. Cook pointed out (*in lit.*), the closely related genus *Neotyrrellia* possesses a typical EC skeleton (Lundblad, 1941a: 176) of the *Hydrodroma* type. The position of *Tyrrellia* in the similarity diagram (Fig. 52), however, is at present uncertain. The modifications of the EC of *Arrenurus* also preclude a precise linkage with the genera studied, but its structure could be reached by progressive alteration of the fairly generalized EC characteristic either of Group 1 or of Group 4. *Hydrovolzia* possesses an EC apparently not homologous with that of typical water mites.

Discussion

BASIC CONCLUSIONS

Perhaps the most significant finding of the present study is the evidence that all of the genera commonly grouped by habitat as "water mites" are related as well by the possession of an elaborate, functional system, the ejaculatory complex. In addition, this organ is obviously homologous in all except two genera of the group. Substantiating evidence from genera not covered in this investigation is available in many published taxonomic illustrations that, although seldom detailed, reveal the basic EC skeletal structure to be virtually universal in "water mites". Equally important is the indication from published reports that similar structures do not occur in any related families of terrestrial mites. Thus, although many details of the inter-relationships of various water mite genera remain unclear, a distinctive, common character complex unites them all and separates them decisively from related terrestrial genera.

New efforts to locate the nearest relatives of water mites among the terrestrial taxa should take the ejaculatory complex into account along with all other available evidence. Feider's (1959) phylogenetic speculation was certainly premature, and based on the inadequate treatment in the literature of the water mite EC.

Several important factors in water mite systematics were discovered or confirmed. The genus in this group is indeed a homogeneous and stable taxonomic category, and the interspecific similarity of the EC within a single genus is great. Conversely, from observations on *Arrenurus*, *Oxus*, and *Torrenticola*, species similar in external exoskeletal morphology may regularly be expected to differ in significant details of the structure of the EC skeleton. Thus this organ can be used as a source of characters to provide increased resolution of species discrimination, especially in difficult taxa.

The EC may provide useful information for constructing suprageneric classifications, as many characters are common from genus to genus. One draw-back in the use of the organ at this classificatory level is that extensive modifications can obscure the affinities of a given EC type. For instance although the strong affinity of *Eylais*, *Limnochares*, and *Arrenurus* to each other and to other water mites is demonstrated, the EC gives little evidence of the precise nature of this relationship. Such problems are partially alleviated by the study of all available genera and of as many species within each genus as possible. Thus, it may be possible to discover situations transitional to each highly modified state.

IMPORTANCE FOR CLASSIFICATION

The generic coverage of the present study is not complete enough to form the basis for a thorough reclassification of the water mites. Indeed, it would be an unjustifiable and arbitrary procedure to base a classificatory system upon any such limited set of characters. Nevertheless, the results obtained raise important questions about the accepted classification and suggest changes that warrant further study.

The most obvious point raised is the strong cohesiveness of the genera comprising the water mites, suggesting that all families except the Hydrovolziidae be grouped in a single superfamily, equivalent to the Hydrovolzioidea and the terrestrial superfamilies of the Parasitengona. In addition, the number of families of water mites currently recognized could be decreased to offset the past over-emphasis on the diversity of adult forms.

Relationships within the genera of Group 3 (Fig. 53) differ considerably from those shown in Viets and Viets (1960, Appendix A). The Sperchonidae and Torrenticolidae cluster strongly, whereas the Oxidae, *Lebertia* and (to a lesser extent) *Hydrachna* are rather closer to the Thyasidae. The Group 4 genera (Fig. 54), however, cluster in much the same way as might be expected from the traditional classification. Only the absence of *Koenikea* from this group is surprising. The Axonopsae, Mideopsae, and Krendowskiaie exhibit a greater mutual affinity than is indicated by the current classification. But Group 5 and related genera demonstrate a configuration easily predicted from Appendix A.

PHYLOGENETIC SIGNIFICANCE

The discussion above has been concerned primarily with the related concepts of phenetic affinity and practical classification of similar organisms. Normally, such basic observations should lead to a clearer insight into the phylogenetic history of the taxa involved. Two main factors, however, prevent the immediate construction of satisfactory phylogenies for the water mites. The first is the lack of thorough cataloguing of the diversity of taxa to be found within the group and the primitive state of our knowledge of life histories, immature stages, behaviour, and physiology. An additional problem is the even greater lack of published data for those related terrestrial families from which the water mites almost certainly evolved. It is thus difficult to establish which are primitive and which are derived states, or to determine how many possible

ancestors exist within the Parasitengona.

Therefore the erection of a detailed phylogeny now is inadvisable, but data given here suggest an important guideline. In spite of the great diversity of adult exoskeletal morphology and of larval structure and behaviour, there are still good grounds for retaining the tentative hypothesis of a monophyletic origin for the freshwater Parasitengona (excepting *Hydrovolzia*).

No genus provides a convincing exception to the hypothesis of monophyly. The EC of *Tyrrellia* is as difficult to relate to the typical water mite structure as is that of *Hydrovolzia*. But *Hydrovolzia* is distinct in adult and larval morphology, whereas *Tyrrellia* is a typical water mite in every respect and is moreover closely related to the genus *Neotyrrellia*, with normal EC structure (Lundblad, 1941a: 176). Certain "lower" genera (e.g. *Eylais*, *Limnochares*) differ considerably in EC structure from other water mites. But so do such "higher" genera as *Oxus* and *Arrenurus*, and no intrinsic evidence exists to suggest whether these differences are primitive or derived. Evidence from other sources (Mitchell, 1957a) indicates that the group 3 genera, especially *Thyas*, may be closest to the terrestrial ancestor. Most important, the intergeneric differences are minor when compared to the great morphological discontinuity between the EC of water mites and that of related terrestrial Parasitengona.

Convergence is rejected at present as the explanation for uniformity of basic EC structure because there are no apparent factors (environmental or otherwise) to explain the widespread similarity observed in genera otherwise characterized by the most extreme diversity. Certainly requirements for sperm transfer in an aquatic habitat did not alone produce the effect, for *Hydrovolzia* and other aquatic and semi-aquatic Prostigmata have not developed in a similar manner. Parallel evolutionary development of the EC is a more plausible hypothesis but is usually based in turn on monophyly (Mayr, 1969: 82). For the moment, monophyly furnishes the most parsimonious explanation of the similarities observed in the EC of water mites.

Because of the restricted number of characters on which it is based, the evidence at hand cannot be considered as conclusive but has sufficient merit that the hypothesis of monophyly for all water mites (excluding *Hydrovolzia*) should be retained for further scrutiny.

Summary

1. A comparative study of the male reproductive system was undertaken to provide evidence pertinent to the classification of freshwater mites.
 - a. The water mite genus is the most convenient comparative unit for such a study.
 - b. The term ejaculatory complex (EC) is the most suitable of several for the terminal organ in the male genital tract.
 - c. Present deficiencies in the specific taxonomy of North American water mites dictate that the deme is often the only definable category below the genus.
2. The water mite EC has not previously been adequately explained either structurally or functionally.
3. The EC of *Hydrodroma* is a well-muscled, chitinous framework that functions as a syringe-like organ for the reception, compacting, and expulsion of masses of spermatozoa.
4. An analysis of EC structural similarities leads to the delimitation of several large groups of genera showing a high degree of internal affinity. These groups coincide only partially with conventional classifications.
5. The EC is shown to have potential value for classification and phylogenetic speculation at every taxonomic level.
6. No other group of mites possesses a chitinous EC skeleton of the type found in water mites.
7. The basic EC structure appears to be homologous in all water mite genera with the exception of *Hydrovolzia*.
8. Available evidence from the EC is consistent with a monophyletic origin for all water mite genera except *Hydrovolzia*.

Glossary of Morphological Terms

Terms are defined to correspond with the usage of the present report. Thus, even familiar terms are included where their application to mites may be unclear.

ANTERIOR: that surface of the EC usually facing in an anterodorsal direction when the organ is *in situ*; the surface through which the *ductus ejaculatorius* enters the EC.

ANTERIOR ARCH: the bridge-like structure formed by the apposed anterior rami (q. v.).

ANTERIOR HORN (AntHn): a short, subconical, sclerotized projection arising from each of a pair of sclerites lying in the anterior wall of the proximal chamber of *Oxus* sp. (nr. *O. intermedius*).

ANTERIOR KEEL (AntKl): a thin, plate-like structure usually borne medially on the anterior surface of the EC, often roughened for muscle attachment.

ANTERIOR MARGIN SCLERITE (AMScI): a sclerotized thickening in the lateral and proximal margins of the anterior surface of the proximal chamber.

ANTERIOR RAMUS (AntRm): an anteromedially directed rod arising from the base of the distal arm sclerite; apices of the anterior rami of either side usually apposed, often attached or fused on the midline.

ANTERIOR SCLEROTIZED SURFACE: anterolateral walls of midsection of *Hydrodroma* EC; subtending the anterior keel.

APICAL: pertaining to the free, unattached tip of any structure, especially the distal portion of the EC.

APICAL DEVELOPMENT (Apcl): any sclerotized elongation of the distal arm sclerites distal to the bases of distal arms and anterior rami.

APICAL RAMUS (ApRm): a distally directed rod arising from the base of the distal arms in *Albia*.

APICAL SETA (ApSt): a simple seta borne on the distal arm sclerite or on an apical development of the sclerite.

ARM RAMUS: a short, posteriorly directed rod arising from the base of the proximal arm; known only from *Unionicola*.

AXILLARY: positioned in or near the angle between the distal arm and the lateral surface of the midsection of the EC.

BASAL PLATE (BsPl): a sclerotized plate of varying dimensions, subtending the proximal arm and lying in the lateral walls of the proximal chamber and/or the midsection of the EC.

CARRIER FLUID: a secretory product of the testes noted by Schmidt (1935) and evident in sections of the testes and seminal vesicles of *Hydrodroma*; having a characteristic, globular histological appearance and presumably functioning as a transportation medium for the spermatozoa.

CHAMBER (Cmb): any widening of the sperm passage (q.v.); walls may be membranous or sclerotized.

CHAMBER RAMUS (CmbRm): a short, usually anteriorly directed rod or plate, arising from the base of the proximal arm and lying in the lateral wall of the proximal chamber.

- DISTAL:** pertaining to the free, unattached tip of any structure, the end farthest from any connection with a larger body; (**DISTAD:** in the distal direction).
- DISTAL ARM (DisAm):** a sclerotized rod (in the generalized condition) projecting laterally from the distal area of the EC, subtended by the distal arm sclerite; variously reduced and modified in different genera.
- DISTAL ARM SCLERITE:** one of a pair of sclerites situated on either side of the distal end of the EC; composed of three main rami and often produced distad into an apical development.
- DISTAL MEMBRANES:** a cone of lightly sclerotized membranes inserting around the EC, usually in its distal half, and attaching it to the borders of the genital opening in the body wall; these membranes thus form the walls of the phallocrypt (q.v.).
- DISTAL RAMUS (DisRm):** a distally directed rod arising from the proximal arm sclerite; usually lying lateroposteriorly in walls of midsection of EC.
- DISTAL ROD (DisRd):** a distally directed, sclerotized rod arising from the distal border of the proximal keel; lying along the median line.
- DISTAL SCLERITE (DisSc):** any sclerite lying distally in the midsection of the EC; usually laterally, but three posterior pairs are noted for *Hydrodroma*.
- DISTOLATERAL BORDER (DIBd):** referring to this edge of the proximal chamber, often strengthened by a sclerotized extension of the anterior margin sclerite.
- DUCTUS EJACULATORIUS:** the tube-like terminal portion of the male reproductive system; formed by fusion of the paired *vasa deferentia*.
- EJACULATORY COMPLEX (EC):** the well-muscled, chitinous framework of the walls of the distal portion of the *ductus ejaculatorius* (q.v.); functioning to form, exert, and deposit spermatophores (q.v.).
- ENDOSTERNITE:** a transverse bundle of endocuticular fibers lying just anterior to the EC in the body of *Hydrodroma*; serving as a point of origin for various body muscles.
- GENITAL ACETABULUM:** usually subcircular cuticular structures in the region of the external genitalia of almost all adult water mites; function probably sensory.
- GENITAL OPENING:** external opening in the body wall through which the genital products pass.
- GENITAL PLATE:** a sclerotized plate lying in the ventral body wall in close proximity to the genital opening.
- KEEL:** any flat, sclerotized, longitudinally oriented plate projecting from the median line of the EC.
- LATERAL:** a directional term having the same meaning for the EC as for the adult mite; (**LATERAD:** in a lateral direction).
- LATERAL SHELF (LtrSf):** a thin, sclerotized, subtriangular plate of varying size, joining the distal arm to the lateral wall of the midsection of the EC.
- LATERAL WALL SCLERITE (LWScl):** a rod-like, (usually) oblique sclerite situated in the lateral wall of the proximal chamber.
- MIDSECTION:** that area of the EC lying distal to the proximal chamber and proximal to the distal arm sclerites.
- PHALLIC RETRACTOR:** a small group of three muscle fibers having its origin on the lateral end of the endosternite and inserting near the base of the distal arm, apparently serving to withdraw the EC after spermatophore deposition.

- PHALLOCRYPT:** an invagination of the ventral body wall to form a protected (yet topologically external) cavity into which projects the distal tip of the EC.
- POSTERIOR:** that surface of the EC usually facing in a posteroventral position when the organ is *in situ*; the surface opposite that through which the *ductus ejaculatorius* enters the EC.
- POSTERIOR KEEL (PosKl):** a thin, plate-like structure, usually borne medially on the posterior surface of the proximal chamber, often roughened for muscle attachment.
- POSTERIOR RAMUS (PostRm):** a proximally directed, rod-like sclerite arising from the base of the distal arm sclerite, usually lying in the posterior and/or lateral walls of the midsection.
- POSTEROLATERAL SCLERITE:** a thickened, rod-like sclerotization lying laterally in the posterior surface of the distal third of the *Hydrodroma* EC.
- PROXIMAL:** pertaining to the basal, attached end of any structure, the end closest to any connection with a larger body; (**PROXIMAD:** in the proximal direction).
- PROXIMAL ARM (PrxAm):** an elongate, rod-like sclerite, projecting laterad from the body of the EC at approximately the level of the distal border of the proximal chamber; subtended by the proximal arm sclerite (q.v.).
- PROXIMAL ARM SCLERITE:** one of a pair of sclerites situated, one on either side of the body of the EC, proximally; composed of four main rami.
- PROXIMAL CHAMBER (PrxCmb):** a large median chamber in the proximal-most portion of the EC, constant in occurrence; constituting that part of the EC which receives semenaceous material directly from the *ductus ejaculatorius*.
- PROXIMAL HORN (PrxHn):** one of a pair of short, rod-like, sclerotized projections sometimes occurring on the anteroproximal border of the proximal chamber.
- PROXIMAL RAMUS:** a median, sclerotized, proximally directed projection of the anteroproximal border of the proximal chamber; often bearing the proximal horns (q.v.).
- PROXIMAL SCLERITE (PrxSc):** any sclerite lying proximally, in the anterior or lateral walls of the midsection.
- SEMINAL VESICLE:** one of a pair of anteroposteriorly elongate, thin-walled sacs collecting spermatozoa from the sperm ducts and acting as a reservoir; spermatozoa leave anteriorly via the *vasa deferentia*.
- SPERMATOPHORE:** a discrete unit of transfer containing a quantity of viable spermatozoa; of simple or complex structure; often complicated by the presence of a stalk or other hold-fast device; of wide occurrence in the Acari.
- SPERM PASSAGE:** the central cavity of the EC through which spermatozoa must pass.
- TESTIS:** the male water mite reproductive gland, producing spermatozoa and carrier fluid.
- VAS DEFERENS:** one of a pair of short, thin-walled tubes carrying semen anteriorly away from the seminal vesicles; the tubes fuse distally to form the median ejaculatory duct.

Acknowledgments

This report was adapted from a thesis submitted to the Faculty of the Graduate School of Cornell University, June 1969, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

I thank Dr. W. L. Brown, Jr. for his constructive criticism and advice during the course of the work and for a stimulating introduction to the principles of evolutionary theory. Dr. G. B. Wiggins gave early encouragement to my systematic interest in invertebrates and provided a basic instruction in systematic method. I am further indebted to Drs. Rodger Mitchell, David R. Cook, and Carmine A. Lanciani for advice and discussions on many aspects of water mite classification, evolution, and biology. Numerous colleagues have supplied useful reprints of their articles.

Support for the study came from two Fellowships and a Comstock Scholarship awarded by Cornell University, and from a two-year Special Scholarship granted by the National Research Council (Canada). A fund provided by the Allied Chemical Company supplied financial assistance for research and travel during the period 1965 - 1968.

Dr. Robert C. Dalgleish kindly made it possible to collect on the Edmund Niles Huyck Preserve, and the New York Finger Lakes State Parks Commission supplied the author with a permit to collect in several state parks. Part of the material was collected in Ontario by Mr. I. M. Smith for the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

Acknowledgment is made for use of the scanning electron microscope in the Royal Ontario Museum, established through a grant from the National Research Council to the Department of Zoology, University of Toronto, for the development of a programme in systematic and evolutionary zoology.

My wife, Carolyn, was of great assistance, both through her patience during the research and as an indefatigable collector of water mites. Miss Alix E. Hillmer typed several drafts of the manuscript and assisted with the task of proof-reading and editing. Mr. Anker Odum, Scientific Illustrator in the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, gave valuable advice in the preparation of figures and plates.

Literature Cited

ALEXANDER, R. D.

- 1964 The evolution of mating behaviour in arthropods. In Highnam, K.C. (ed.), Insect reproduction, Symp. R. Ent. Soc. Lond., no. 2, pp. 78-94.

BADER, C.

- 1954 Das Darmsystem der Hydracarinen. *Revue Suisse Zool.*, vol. 61, pp. 505-549.
1969 Contributions to the taxonomy of water mites. In Evans, G. Owen (ed.), Proc. 2nd Int. Congr. Acarology, 1967. Budapest, Akademiai Kiado. pp. 89-92.

BAKER, E. W. and G. W. WHARTON

- 1952 An introduction to acarology. New York, Macmillan. 465 p.

BLAUVELT, W. E.

- 1945 The internal morphology of the common red spider mite (*Tetranychus telarius* Linn.). Cornell Univ. Agric. Exp. Stn., Mem. 270. pp. 1-35.

BÖTTGER, K.

- 1962 Zur biologie und ethologie der einheimischen Wassermilben *Arrenurus* (*Megaluracarus*) *globator* (Müll.), 1776, *Piona nodata nodata* (Müll.), 1776 und *Eylais infundibulifera meridionalis* (Thon), 1899 (Hydrachnellae, Acari). *Zool. Jb., Abt. Syst., Okol. u. Geogr.*, vol. 89, pp. 501-584.
1965 Zur Ökologie und Fortpflanzungsbiologie von *Arrenurus valdiviensis* K. O. Viets, 1964 (Hydrachnellae, Acari). *Z. Morph. Okol. Tiere*, vol. 55, pp. 115-141.

BRUNHUBER, B. S.

- 1969 The mode of sperm transfer in the scolopendromorph centipede: *Cormocephalus anceps anceps* Porat. *Zool., J. Linn. Soc.*, vol. 48, no. 3, pp. 409-420.

COMSTOCK, J. H.

- 1948 The spider book. Rev. and edited by Willis J. Gertsch. Ithaca, New York, Comstock. 729 p.

COOK, D. R.

- 1954a Preliminary list of the arrenuri of Michigan. Part I. The subgenus *Arrenurus*. *Trans. Am. Microsc. Soc.*, vol. 73, pp. 39-58.
1954b Preliminary list of the arrenuri of Michigan. Part II. The subgenus *Megaluracarus*. *Trans. Am. Microsc. Soc.*, vol. 73, pp. 367-380.
1955a Preliminary list of the arrenuri of Michigan. Part III. The subgenera *Micruracarus* and *Truncaturus*. *Trans. Am. Microsc. Soc.*, vol. 74, pp. 60-67.
1955b Preliminary studies of the Hydracarina of Michigan: The subfamily Foreliinae Viets (Acarina: Pionidae). *Ann. Ent. Soc. Am.*, vol. 48, no. 4, pp. 299-307.
1959 Studies on the Thyasinae of North America (Acarina: Hydryphantidae). *Am. Midl. Nat.*, vol. 62, no. 2, pp. 402-428.
1960 Water mites of the genus *Piona* in the United States (Acarina: Pionidae). *Ann. Ent. Soc. Am.*, vol. 53, no. 1, pp. 35-60.

CRONEBERG, A. I.

- *1878 Über den Bau von *Eylais extendens* (O. F. Müller), nebst Bemerkungen über einige verwandte Formen. [in Russian]. *Obshchestvo ljubitelei estestvoznaniia Izvestia*. [Nachr. Ges. Freunde Naturw., Anthropol. Ethnogr. Moskau.], vol. 29, no. 2, pp. 1-40.

- CROWELL, R. M.
 1961 Catalogue of the distribution and ecological relationships of North American Hydracarina. *Can. Ent.*, vol. 93, no. 5, pp. 321-359.
- DAVEY, K. G.
 1965 Reproduction in the insects. Edinburgh and London, Oliver and Boyd. 96 p.
- DEXTER, R. W.
 1959 Anostraca. In Edmondson, W.T. (ed.), *Fresh-water biology*. 2d ed. New York, Wiley. pp. 558-571.
- EFFORD, I. E.
 1966 Observations on the life history of three stream-dwelling watermites. *Acarologia*, vol. 8, fasc. 1, pp. 86-93.
- EISNER, T.
 1957 A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bull. Mus. Comp. Zool. Harv.*, vol. 116, no. 8, pp. 440-490, pls. 1-25.
- EVANS, G. O., J. G. SHEALS and D. MACFARLANE
 1961 The terrestrial Acari of the British Isles. Vol. 1. London, British Museum (Natural History). 219 p.
- FEIDER, Z.
 1959 Etude des caractères sexuels chez les Trombidioidea. *Acarologia*, vol. 1, fasc. 1, pp. 56-85.
- FREDRICKSON, R. W.
 1961 The internal morphology of the Acarina with special reference to the Opilioacaridae. Doctoral thesis, Univ. Kansas, Lawrence. 540 p.
- GRANDJEAN, F.
 1935 Observations sur les acariens (1^{re} série). *Bull. Mus. Natn. Hist. Nat.*, 2^e série, vol. 7, no. 2, pp. 119-126.
- GRAY, P.
 1964 Handbook of basic microtechnique. New York, McGraw-Hill. 302 p.
- GREEN, J.
 1961 A biology of Crustacea. Chicago, Quadrangle Books. 180 p.
- HENKING, H.
 1882 Beiträge zur Anatomie, Entwicklungsgeschichte und Biologie von *Trombidium fuliginosum* Herm. *Z. wiss. Zool.*, vol. 37, no. 4, pp. 553-663.
- HOBBS, H. H., JR.
 1942a A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with description of a new genus and species. *Am. Midl. Nat.*, vol. 28, pp. 334-357.
 1942b On the first pleopod of the male cambari (Decapoda, Astacidae). *Proc. Fla. Acad. Sci.* (1940), vol. 5, pp. 55-61.
- HUGHES, T. E.
 1959 Mites or the Acari. London, Univ. London (Athlone) Press. 225 p.
- IMAMURA, T. and R. MITCHELL
 1967 The ecology and life cycle of the water mite, *Piersigia limophila* Protz. *Annotnes. Zool. Jap.*, vol. 40, pp. 37-44.

JOHNSTON, D. E.

- 1965 A catalogue of the determined species of Acari (excl. Ixodides) in the collections of the Institute of Acarology. Wooster, Ohio, Institute of Acarology Publ. No. 145, Ohio Agric. Exp. Stn., (Dept. of Zool. Ent. Publ. Ser. No. 29). 66 p.

KEETON, W. T.

- 1960 A taxonomic study of the milliped family Spirobolidae (Diplopoda: Spirobolida). Mem. Am. Ent. Soc., no. 17, pp. 1-146.

KOENIKE, F.

- 1888 Eine neue Hydrachnide aus schwach salzhaltigem Wasser. Abh. naturw. Ver. Bremen, vol. 10, pp. 273-293, pl. iii.
1901 Zur Kenntnis der Gattungen *Arrenurus* und *Eylais*. Zool. Anz., vol. 24, pp. 90-96.
1902 Acht neue *Lebertia*-Arten, eine *Arrenurus*-und eine neue *Atractides*-Art. Zool., Anz., vol. 25, pp. 610-616.
1909 Acarina, Milben. Die Süsswasserfauna Deutschlands, no. 12, pp. 13-184.

KRANTZ, G. W.

- 1970 A manual of acarology. Corvallis, O.S.U. Book Stores, Inc. 335 p.

LUNDBLAD, O.

- 1929 Über den Begattungsvorgang bei einigen *Arrhenurus*-Arten. Z. Morph. Ökol. Tiere, vol. 15, no. 4, pp. 705-722.
1930 Über die Anatomie von *Arrhenurus medio-rotundatus* und die Hautdrüsen der *Arrhenurus*-Arten. Z. Morph. Ökol. Tiere, vol. 17, no. 1-2, pp. 302-338.
1941a Die Hydracarinafauna Sudbrasiens und Paraguays. Erster Teil. K. Svenska Vetensk.-Akad. Handl., Stockholm, ser. 3, vol. 19, no. 7, pp. 1-183.
1941b Eine Übersicht des Hydrachnellensystems und der jetzt bekannten Verbreitung der Gattungen dieser Gruppe. Zool. Bidr. Upps. vol. 20, pp. 359-379.
1943 Die Hydracarinafauna Sudbrasiens und Paraguays. Vierter Teil. K. Svenska Vetensk.-Akad. Handl., Stockholm, ser. 3, vol. 20, no. 8, pp. 1-171.
1956 Zur Kenntnis süd- und mitteleuropäischer Hydrachellen. Arkiv För Zoologi. K. Svenska Vetensk.-Akad., ser. 2, vol. 10, no. 1, pp. 1-306.

MANTON, S. M.

- 1958 Hydrostatic pressure and leg extension in arthropods, with special reference to arachnids. Ann. Mag. Nat. Hist., ser. 13, vol. 1, pp. 161-182.

MAYR, E.

- 1969 Principles of systematic zoology. New York, McGraw-Hill. 428 p.

MICHAEL, A. D.

- 1895 A study of the internal anatomy of *Thyas petrophilus*, an unrecorded hydrachnid found in Cornwall. Proc. Zool. Soc. Lond., 1895, pp. 174-209.

MITCHELL, R. D.

- 1954 Check list of North American water-mites. Fieldiana: Zoology, vol. 35, no. 3, pp. 29-70.
1955 Anatomy, life history, and evolution of the mites parasitizing fresh-water mussels. Misc. Publs. Mus. Zool., Univ. Mich., no. 89, pp. 1-28.
1957a Major evolutionary lines in water mites. Syst. Zool., vol. 6, pp. 137-148.
1957b Locomotor adaptations of the family Hydrphantidae (Hydrachnellae, Acari). Abh. Naturw. Ver. Bremen, vol. 35, no. 1, pp. 75-100.

- 1958a The evolution of exoskeletons and mite phylogeny. Proc. Tenth Int. Congr. Entomology, 1956, vol. 1, pp. 863-865.
- 1958b Sperm transfer in the water-mite *Hydryphantes ruber* Geer. Am. Midl. Nat., vol. 60, no. 2, pp. 156-158.
- 1960 The evolution of thermophilous water mites. Evolution, vol. 14, pp. 361-377.
- 1962 The structure and evolution of water mite mouthparts. J. Morphol., vol. 110, pp. 41-59.
- 1964a The anatomy of an adult chigger mite *Blankaartia acuscutellaris* (Walch). J. Morph., vol. 114, pp. 373-391.
- 1964b An approach to the classification of water mites. C.R. 1^{er} Congrès Int. d'Acarologie, 1963. Acarologia, vol. 6, fasc. hors de sér., pp. 75-79.
- MITCHELL, R. D. and D. R. COOK
- 1952 The preservation and mounting of water-mites. Turtox News, vol. 30, no. 9, pp. 169-172.
- MOSS, W. W.
- 1962 Studies on the morphology of the trombidid mite *Allothrombium lerouxi* Moss (Acari). Acarologia, vol. 4, pp. 313-345.
- 1968 Experiments with various techniques of numerical taxonomy. Syst. Zool., vol. 17, pp. 31-47.
- MUSSELIUS, A. A.
- *1912 Beobachtungen über das Plankton des Sees Stav. und Beschreibung der Hydracarinen von Polen. [in Russian]. Varsava Raboty zool. Kab., pp. 27-131.
- NEWELL, I. M.
- 1959 Acari. In Edmondson, W. T. (ed.), Freshwater biology. 2d ed. New York, Wiley. pp. 1080-1116.
- NORDENSKIÖLD, N. E.
- 1899 Beiträge zur Kenntnis der Morphologie und Systematik der Hydrachniden. Finska vetenskaps-societeten, Helsingfors. [Acta Soc. Sci. Fenn. Helsingfors.], vol. 24, no. 5, pp. 1-75.
- PARRY, D. A. and R. H. J. BROWN
- 1959 The hydraulic mechanism of the spider leg. J. Exptl. Biol., vol. 36, no. 2, pp. 423-433.
- PATERSON, C. G.
- 1970 Water mites (Hydracarina) as predators of chironomid larvae (Insecta: Diptera). Can. J. Zool., vol. 48, no. 3, pp. 610-614.
- PIERSIG, R. and H. LOHMANN
- 1901 Hydrachnidae und Halacaridae. Das Tierreich, no. 13, pp. 1-336.
- POLLOCK, H. M.
- 1898 The anatomy of *Hydrachna inermis* Piersig. Diss., Leipzig. 52 p.
- SCHAUB, R. R. VON
- 1888 Über die Anatomie von *Hydrodroma* (C. L. Koch). Ein Beitrag zur Kenntnis der Hydrachniden. Sber. Akad. Wiss. Wien. math.-naturw. Klasse, vol. 97, part 1, pp. 98-151.
- SCHMIDT, U.
- 1935 Beiträge zur Anatomie und Histologie der Hydracarinen, besonders von *Diplodontus despiciens* O. F. Müller. Z. Morph. Okol. Tiere, vol. 30, pp. 99-176.

- SNODGRASS, R. E.
 1935 Principles of insect morphology. 1st ed. New York, McGraw-Hill. 667 p.
 1965 A textbook of arthropod anatomy. New York, Hafner. 363 p.
- SOKAL, R. R. and P. H. SNEATH
 1963 Principles of numerical taxonomy. San Francisco, W. H. Freeman. 359 p.
- SOKOLOV, I. I.
 1954 Die Chromosomenkomplexe der Milben und deren Bedeutung für Systematik und Phylogenie. [in Russian.] Arb. Leningrader naturforsch. Verein, vol. 77, no. 4, pp. 124-159.
- SPÄRING, I.
 1959 Die Larven der Hydrachnellae, ihre parasitische Entwicklung und ihre Systematik. Parasit. SchrReihe, no. 10, pp. 1-165.
- THOMAE, H.
 1925 Beiträge zur Anatomie der Halacariden. Zool. Jb. Abt. Anat. u. Ontog., vol. 47, pp. 155-190.
- THON, K.
 1900 Über die Copulations-Organen der Hydrachniden-Gattung *Arrhenurus* Dugès. Verh. dt. zool. Ges., 1900, pp. 108-129.
- THOR, S.
 1903 Recherches sur l'anatomie comparée des Acariens prostigmatiques. Annls. Sci. Natur., Paris. Zool., (ser. 8), vol. 19, no. 1, pp. 1-190.
- TUXEN, S. L. (ed.)
 1956 Taxonomist's glossary of genitalia in insects. Copenhagen, Ejnar Munksgaard. 284 p.
- VIETS, K.
 1916 Ergänzungen zur Hydracarinen-Fauna von Kamerun. (Neue Sammlungen). Arch. Hydrobiol., vol. 11, pp. 241-306 and 335-403.
 1929 Einige neue Hydracarinen-Gattungen aus Java und Bemerkungen zum System der Hydracarinen. Zool. Anz., vol. 80, no. 5-6 pp. 161-170.
 1936 Wassermilben oder Hydracarina (Hydrachnellae und Halacaridae). Die Tierwelt Dtl., vol. 31-32, pp. 1-574.
 1956 Die Milben des Süßwassers und des Meeres. Part 2-3. Jena, Fischer Verlag. 870 p.
- VIETS, K. and K. O. VIETS
 1960 Wassermilben, Hydracarina. Die Tierwelt Mitteleur., vol. 3, no. 4, pp. 1-44.
- VIETS, K. O.
 1965 Über neue und seltene Hydrachnellae (Acari) aus der Kap-Provinz (Südafrika). Zool. Anz., vol. 175, pp. 441-452.
 1968 Über neue und bekannte Wassermilben (Hydrachnellae, Acari) aus Chile. Beitr. Neotrop. Fauna, vol. 5, no. 3, pp. 209-228.
- WILSON, J. L.
 1961 Water mites of the genus *Arrenurus* of middle Tennessee (Acarina: Hydracarina). J. Tenn. Acad. Sci., vol. 36, pp. 171-242.
- WOOLLEY, T. A.
 1961 A review of the phylogeny of mites. A. Rev. Ent., vol. 6, pp. 263-284.

*References not seen by the author.

Appendix A: Traditional Classification of Water Mites

(adapted from Viets and Viets, 1960)

HYDRACHNELLAE

Hydrovolziae:	Hydrovolziidae:	<i>Hydrovolzia</i>
Hydrachnae:	Hydrachnidae:	<i>Hydrachna</i>
Limnocharae:	Limnocharidae:	<i>Limnochares</i>
	Eylaidae:	<i>Eylais</i>
	Protziidae:	<i>Protzia</i>
Hydryphantae:	Thyasidae:	<i>Thyas</i>
	Hydryphantidae:	<i>Hydryphantes</i>
	Hydrodromidae:	<i>Hydrodroma</i>
Lebertiae:	Pseudohydryphantidae:	<i>Pseudohydryphantes</i>
	Sperchonidae:	<i>Sperchon</i> , <i>Sperchonopsis</i>
	Lebertiidae:	<i>Lebertia</i>
	Oxidae:	<i>Frontipoda</i> , <i>Oxus</i>
	Torrenticolidae:	<i>Testudacarus*</i> , <i>Torrenticola</i>
Pionae:	Limnesiidae:	<i>Limnesia</i> , <i>Tyrrellia*</i>
	Hygrobatidae:	<i>Atractides</i> , <i>Hygrobates</i>
	Unionicolidae:	<i>Koenikea*</i> , <i>Neumania</i> , <i>Unionicola</i>
	Feltriidae:	<i>Feltria</i>
	Pionidae:	<i>Forelia</i> , <i>Piona</i> , <i>Tiphys</i>
Axonopsae:	Axonopsidae:	<i>Albia</i> , <i>Brachypoda</i> , <i>Axonopsis</i>
	Aturidae:	<i>Aturus</i> , <i>Kongsbergia</i>
Mideopsae:	Mideidae:	<i>Midea</i>
	Mideopsidae:	<i>Mideopsis</i>
Krendowskiae:	Krendowskiidae:	<i>Geayia*</i>
Arrenurae:	Arrenuridae:	<i>Arrenurus</i>

*These New World genera were not included by Viets and Viets (1960) and so have been inserted above on the basis of Mitchell's (1954) checklist.

Appendix B: Johnston's Classification (1965) of Water Mites (adapted)

ACARIFORMES — PARASITENGONA

Calyptostomoidea:	Calyptostomidae
Erythraeoidea:	Erythraeidae, Smarididae
Trombidoidea:	Trombiculidae, Trombidiidae (s. lat.)
Hydrovolzioidea:	<i>Hydrovolzia</i>
Eylaoidea:	<i>Eylais</i> , <i>Limnochares</i>
Hydryphantoidea:	<i>Hydrodroma</i> , <i>Hydryphantes</i> , <i>Protzia</i> , <i>Thyas</i>
HYDRACHNELLAE (s. str.)	
Hydrachnoidea:	<i>Hydrachna</i>
Lebertoidea:	<i>Frontipoda</i> , <i>Lebertia</i> , <i>Oxus</i> , <i>Pseudohydryphantes*</i> , <i>Sperchon</i> , <i>Sperchonopsis</i> , <i>Testudacarus</i> , <i>Torrenticola</i>
Hygrobatoidea:	<i>Atractides</i> , <i>Feltria</i> , <i>Forelia</i> , <i>Hygrobates</i> , <i>Koenikea</i> , <i>Limnesia</i> , <i>Neumania</i> , <i>Piona</i> , <i>Tiphys</i> , <i>Tyrrellia</i> , <i>Unionicola</i>
Aturoidea:	<i>Albia*</i> , <i>Aturus</i> , <i>Axonopsis</i> , <i>Brachypoda</i> , <i>Kongsbergia</i>
Mideopsoidea:	<i>Midea</i> , <i>Mideopsis</i>
Acalyptonotoidea:	<i>Geayia</i>
Arrenuroidea:	<i>Arrenurus</i>

*The position of these genera was not given by Johnston (1965). They have been inserted above on the basis of Mitchell's (1954) checklist.

Appendix C: Data For Specimens Examined

Collections are deposited in the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

Albia sp. (nr. *A. caerulea*) (p. 24)

ONT.: Baysville, Muskoka Dist.; Echo L., Sta. xv; 22 AUG 1965, I. M. Smith.

Arrenurus crenellatus (p. 26)

N.Y.: Rensselaerville, Albany Co.; Lake Myosotis, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

A. intermedius (p. 27)

As above.

A. lyriger (p. 27)

As above.

A. magnicaudatus (p. 27)

N.Y.: Dryden, Tompkins Co., Dryden Twp.; Dryden Lake; 21 JUNE 1966,
D.B.

A. major (p. 27)

N.Y.: Rensselaerville, Albany Co.; Lincoln Pond, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

A. planus (p. 27)

ONT.: Aberfoyle, Wellington Co.; pond 1; 16 MAY 1967, I. M. Smith.

A. semicircularis (p. 29)

N.Y.: Rensselaerville, Albany Co.; Lake Myosotis, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

A. trifolius (p. 29)

As above.

A. wardi (p. 29)

N.Y.: Rensselaerville, Albany Co.; Lincoln Pond, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

Atractides sp. (p. 29)

ONT.: Kendal, Durham Co.; cold, fast stream; 31 MAY 1966, I. M. Smith.

Aturus (*s. str.*) sp. (nr. *A. deceptor*) (p. 31)

N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Cayuga Inlet at Rt. 34; 26 AUG 1966,
D.B.

Axonopsis (*Hexaxonopsis*) sp. (p. 32)

N.Y.: Slaterville Springs, Tompkins Co., Caroline Twp.; Six Mile Creek, CU
wildflower preserve; 15 JULY 1966, D.B.

Brachypoda (*s. str.*) sp. (nr. *B. cornipes*) (p. 32)

N.Y.: Myers, Tompkins Co., Lansing Twp.; Cayuga Lake at Lansing Park;
5 JUNE 1967, D.B.

Eylais sp. (p. 33)

ONT.: Aberfoyle, Wellington Co.; temp. pond 1; 15 MAY 1966, I. M. Smith.

Feltria sp. (p. 35)

ONT.: Kendal, Durham Co.; moss, cold fast stream; 16 JUNE 1967, I. M. Smith.

Forelia (*Madawaska*) *borealis* (p. 35)

N.Y.: Rensselaerville, Albany Co.; Lincoln Pond, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

Frontipoda sp. (p. 36)

N.Y.: Rensselaerville, Albany Co.; Lake Myosotis, E. N. Huyck Preserve;
3 SEPT 1966, D.B.

Geayia sp. (p. 37)

ONT.: Chaffey's Locks, Leeds Co.; Lake Opinicon, Sta. v; 27 MAY 1965,
I. M. Smith.

Hydrachna (*Rhabdohydrachna*) sp. (p. 39)

ONT.: Kendal, Durham Co.; pond 1; 3 JUNE 1967, I. M. Smith.

- Hydrovolzia* sp. (p. 39)
ALTA.: Banff; spring fed stream, road to Sundance Canyon; 22 JUNE 1962, D.B.
- Hydryphantes* sp. (nr. *H. ruber*) (p. 40)
N.Y.: Waterburg, Tompkins Co., Ulysses Twp.; temp. pond s. of Indian Fort Road; 5 MAY 1966, D.B.
- Hygrobates* sp. (p. 40)
N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Cayuga Inlet at Rt. 34; 26 AUG 1966, D.B.
- Koenikea* sp. (p. 41)
N.Y.: Rensselaerville, Albany Co.; Lake Myosotis, E. N. Huyck Preserve; 3 SEPT 1966, D.B.
- Kongsbergia* sp. (p. 43)
ONT.: Caledon, Peel Co.; stream on Caledon sideroad no. 5; 12 SEPT 1966, I. M. Smith.
- Lebertia* sp. (p. 44)
N.Y.: Myers, Tompkins Co., Lansing Twp.; Cayuga Lake at Lansing Park; 20 AUG 1966, D.B.
- Limnesia* (s. str.) sp. (p. 45)
N.Y.: Dryden, Tompkins Co., Dryden Twp.; Dryden Lake; 16 APR 1966, D.B.
- Limnochares* sp. (nr. *L. americana*) (p. 47)
N.Y.: Dryden, Tompkins Co., Dryden Twp.; Dryden Lake; 24 AUG 1966, D.B.
- Midea* sp. (p. 47)
ONT.: Chaffey's Locks, Leeds Co.; Lake Opinicon, Sta. VII; 5 SEPT 1965, I. M. Smith.
- Mideopsis* sp. (p. 48)
As above.
- Neumania* sp. (p. 49)
N.Y.: Dryden, Tompkins Co., Dryden Twp.; Dryden Lake; 24 AUG 1966, D.B.
- Neumania* sp. (nr. *N. distincta*) (p. 51)
N.Y.: Rensselaerville, Albany Co.; Lake Myosotis, E. N. Huyck Preserve; 3 SEPT 1966, D.B.
- Oxus* sp. (nr. *O. connatus*) (p. 51)
As above.
- Oxus* sp. (nr. *O. intermedius*) (p. 52)
As above.
- Piona pinguipalpis* (p. 52)
N.Y.: Waterburg, Tompkins Co., Ulysses Twp.; temp. pond s. of Indian Fort Road; 5 MAY 1966, D.B.
- Protzia* sp. (p. 53)
ONT.: Kendal, Durham Co.; cold, fast stream; 31 MAY 1966, I. M. Smith.
- Pseudohydryphantes* sp. (p. 55)
ONT.: Baysville, Muskoka Dist.; Echo L., Sta. XV; 20 JULY 1966, I. M. Smith.
- Sperchon* sp. (p. 56)
N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Cayuga Inlet at Rt. 34; 25 JUNE 1966, D.B.
- Sperchonopsis* sp. (p. 57)
ONT.: Kendal, Durham Co.; cold, fast stream; 31 MAY 1966, I. M. Smith.
- Testudacarus* sp. (p. 57)
ONT.: Kendal, Durham Co.; cold, fast stream; 16 JUNE 1967, I. M. Smith.
- Thyas barbigera* (p. 59)
N.Y.: Waterburg, Tompkins Co., Ulysses Twp.; temp. pond s. of Indian Fort Road; 5 MAY 1966, D.B.
- Tiphys* sp. (nr. *T. americana*) (p. 60)
ONT.: Port Credit, Peel Co.; pond v; 21 MAY 1966, I. M. Smith.
- Torrenticola* sp. (designated species A) (p. 60)
N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Cayuga Inlet at Rt. 34; 26 AUG 1966, D.B.

Torrenticola sp. (designated species B) (p. 61)

N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Cayuga Inlet at Rt. 34; 5 AUG 1966, D.B.

Tyrrellia sp. (p. 61)

N.Y.: Ithaca, Tompkins Co., Ithaca Twp.; Buttermilk Ck. at 500 ft. elev.; 26 JULY 1966, D.B.

Unionicola sp. (p. 63)

N.Y.: Dryden, Tompkins Co., Dryden Twp.; Dryden Lake; 30 JULY 1966, D.B.