

The Caddisfly Family Phryganeidae (Trichoptera)

The goal of much of the scientific work in natural history museums is to explore and document the biological diversity of the planet. This book is an outstanding example of the museum tradition, offering the results of global research on the biosystematics of one of the families of case-making caddisflies, the Phryganeidae. Throughout his career as a museum curator, Glenn Wiggins has studied and written extensively on caddisflies of the aquatic insect order Trichoptera.

Information acquired from field work and museum collections, and from the biological literature is synthesized into a taxonomic monograph. The Phryganeidae are the largest of all the caddisflies, but existing literature has led to problems in species identification, especially in Asia; nine species names were found to be synonyms of others, an unusually high proportion of 10 per cent of the described species. Fifteen genera comprising seventy-four species are recognized here, including three that are new to science. Generic keys are provided for adults, larvae, and pupae; keys to species are given for adults. Morphological structures used in the keys are fully illustrated in 246 line drawings and half-tone plates. Distribution maps are provided for most of the North American species.

Hypotheses are inferred for the phylogeny of the genera, and for the species in each genus; the fossil history of the Phryganeidae is reviewed. From this base, the biogeography of the family is interpreted. Of evolutionary interest is an extraordinary relationship between larval case-making and pupation behaviour and the degradation of functional pupal mandibles. Contrasting colour patterns of the wings in some species of the Phryganeidae are interpreted for the first time in the Trichoptera as part of a protective warning system to deter predators. Variation in genitalic morphology far exceeding normal species limits is documented in two species, and the evolutionary implications are considered. Combined with fossil evidence that the Phryganeidae are the oldest of the case-making Trichoptera still extant, several of the atypical morphological and behavioural attributes discussed in this book can be interpreted as plesiomorphic, placing the Phryganeidae in a pivotal position for inferring phylogeny in the Trichoptera. A revised classification embodying much new information is proposed for the family Phryganeidae.

The taxonomy, biology, and evolution of no other family of caddisflies have been treated as extensively.

GLENN B. WIGGINS is Curator Emeritus at the Royal Ontario Museum, Toronto. He is the author of *Larvae of the North American Caddisfly Genera*, which is now in its second edition.

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The Caddisfly Family Phryganeidae (Trichoptera)

Glenn B. Wiggins

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This volume is dedicated to natural history museums for their work to explore and document the biological diversity of the planet.

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THE CADDISFLY FAMILY PHRYGANEIDAE (TRICHOPTERA)

Abstract

Caddisflies of the family Phryganeidae are mainly confined to the world's north temperate zone, where most occur at higher latitudes. The larvae construct distinctive portable cases in habitats ranging from cool streams through rivers, lakes, and marshes to acidic bogs, temporary pools, and brackish coastal waters. In this study of the biosystematics of the Phryganeidae, available information on the morphology and behaviour of larvae, pupae, and adults is assembled in a taxonomic monograph, and synthesized into an interpretation of the evolutionary history of the family. Fifteen genera comprising seventy-four species are recognized.

From phylogenetic analysis, the monotypic western North American genus *Yphria* (Yphriinae) is interpreted as the sole representative of the most primitive phryganeid lineage still extant, and the sister group to all the other genera (Phryganeinae). In the Phryganeinae, *Trichostegia* is inferred to be a basal genus; the other genera fall into two groups. In the first group, larvae construct spiral cases; in the primitive genera the anterior end of the pupal case is sealed with silken mesh, and pupae have fully sclerotized pupal mandibles. In the second group, larvae construct ring cases; most do not seal the end of the case with silken mesh prior to pupation, and pupae have lost the sclerotized mandibles. This phylogenetic relationship between the case-making and pupation behaviour of larvae and the loss of functional pupal mandibles is unique in the Trichoptera.

Hypotheses are proposed for the biogeography of the genera; and existing knowledge on the extinct species of the Phryganeidae is reviewed.

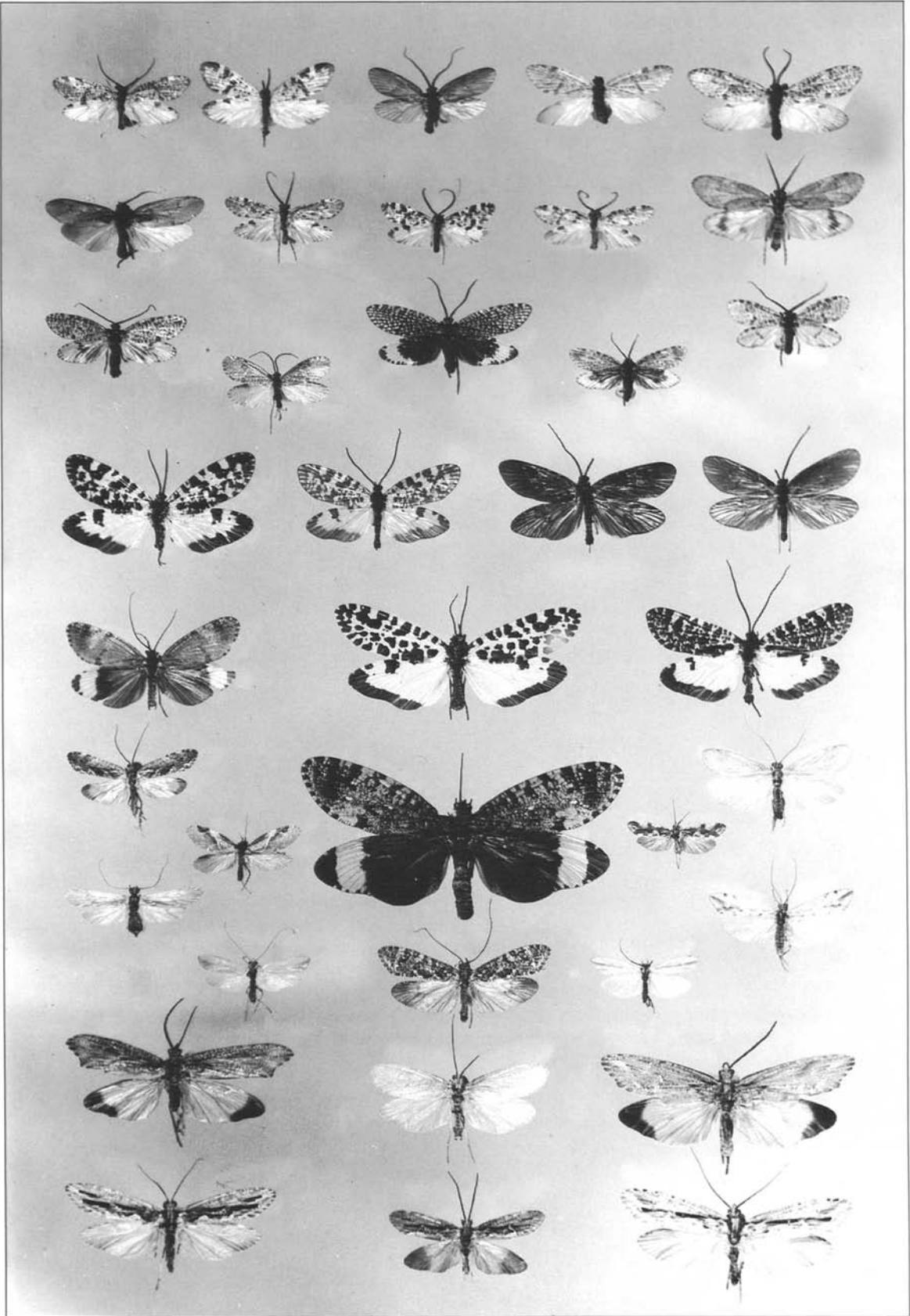
Generic keys are provided for adults, larvae, and pupae; keys to species are provided for adults. Geographic distribution is summarized for each species, and maps are provided for most of the North American species. Hypotheses of phylogeny are inferred for the species in each genus. A new interpretation is proposed

for phyletic relationships and classification of species in *Agrypnia*; and a phylogenetic basis is proposed in support of generic status for *Agrypnetes*.

Unprecedented variation in female genitalic morphology is documented in two species: in a series of *Hagenella apicalis* collected at one site in Hokkaido, and in *Agrypnia vestita* in North America. The female variants far exceed normal species limits in these genera, but the males are typical and constant in genitalic structure; the evolutionary implications are considered. Highly contrasting colour patterns of the wings in *Semblis*, *Oligostomis*, and *Eubasilissa* are interpreted as aposematic, and protective systems against predators are postulated.

Evidence is provided in support of proposals for nine new subjective synonyms, reducing the number of species recognized in the family by 10 per cent: *Agrypnia principalis* (Martynov) as a junior synonym of *A. colorata* Hagen; *Agrypnia umbrina* (Martynov) as a junior synonym of *A. sordida* (McLachlan); *Agrypnia dextra* Ross as a junior synonym of *A. glacialis* Hagen; *Phryganea ochrida* Malicky as a junior synonym of *P. grandis* Linnaeus; *Hagenella dentata* (Martynov) as a junior synonym of *H. apicalis* (Matsumura); *Semblis chaffanjoni* (Navas) as a junior synonym of *S. atrata* (Gmelin); *Semblis chishimana* Kuwayama as a junior synonym of *Semblis melaleuca* (McLachlan); *Eubasilissa reginella* Nakahara as a junior synonym of *Eubasilissa regina* (McLachlan); and *Eubasilissa nepalensis* Kuyawama as a junior synonym of *Eubasilissa rahtkirani* Schmid. Three new species are described: *Agrypnia acristata* sp. nov. from Japan; *Agrypnia incurvata* sp. nov. from Japan and Korea; and *Eubasilissa signata* sp. nov. from Korea. Lectotypes are designated for *Agrypnia ulmeri* (Martynov) and *Phryganea nattereri* Brauer.

A revised classification embodying all of these changes is proposed for the family Phryganeidae.



- | | | | | |
|--|---|---|--|--|
| 1. <i>Oligotricha lapponica</i>
♂ Finland | 2. <i>Oligotricha lapponica</i>
♂ Manchuria | 3. <i>Oligotricha striata</i>
♂ Germany | 4. <i>Oligotricha fluvipes</i>
♀ Japan | 5. <i>Oligotricha spicata</i>
♀ Japan |
| 6. <i>Ptilostomis angustipennis</i>
♀ Ontario | 7. <i>Banksiola crotchi</i>
♂ Ontario | 8. <i>Banksiola dossuaria</i>
♀ Nova Scotia | 9. <i>Banksiola concatenata</i>
♂ Massachusetts | 10. <i>Ptilostomis ocellifera</i>
♂ Nova Scotia |
| 11. <i>Hagenella clathrata</i>
♀ Finland | | 13. <i>Oligostomis pardalis</i>
♀ Ontario | | 15. <i>Oligostomis reticulata</i>
♂ Finland |
| | 12. <i>Hagenella canadensis</i>
♂ Ontario | | 14. <i>Oligostomis ocelligera</i>
♀ Nova Scotia | |
| 16. <i>Semblis atrata</i>
♂ Manchuria | 17. <i>Semblis atrata</i>
♂ Manchuria | 18. <i>Semblis atrata</i>
♂ Manchuria | | 19. <i>Semblis atrata</i>
♂ Manchuria |
| 20. <i>Eubasilissa asiatica</i>
♂ Kashmir | | 21. <i>Semblis phalaenoides</i>
♀ Manchuria | | 22. <i>Semblis melaleuca</i>
♂ Japan |
| 23. <i>Agrypnia vestita</i>
♂ Ontario | | 25. <i>Eubasilissa regina</i>
♀ Japan | | 27. <i>Fabria inornata</i>
♂ Illinois |
| | 24. <i>Phryganopsyche latipennis</i>
♂ Japan
(Phryganopsycheidae) | | 26. <i>Trichostegia minor</i>
♀ the Netherlands | |
| 28. <i>Agrypnetes crassicornis</i>
♀ Finland | 29. <i>Agrypnia pagetana</i>
♂ Finland | 30. <i>Agrypnia macdunnoughi</i>
♂ Nova Scotia | 31. <i>Agrypnia glacialis</i>
♂ Manitoba | 32. <i>Agrypnia picta</i>
♀ Manchuria |
| 33. <i>Phryganea sinensis</i>
♂ Russia | | 34. <i>Phryganea rotundata</i>
♂ Russia | | 35. <i>Phryganea japonica</i>
♀ Japan |
| 36. <i>Phryganea cinerea</i>
♀ Nova Scotia | | 37. <i>Phryganea sayi</i>
♂ Maine | | 38. <i>Phryganea grandis</i>
♀ the Netherlands |

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GENERAL SECTION

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Introduction

Freshwater habitats throughout the world are populated by an enormous fauna of aquatic insects; the ecological interactions of these insects sustain the flux of energy and nutrients which underlies productivity in all aquatic communities. Caddisflies of the order Trichoptera are one of the most diverse groups of these aquatic insects. Nearly ten thousand species of caddisflies are now known, although the world fauna is very much larger and many species new to science are discovered every year. This mounting global diversity is organized in a classification of some forty families; and although the winged adult insects are similar in structure and behaviour, it is in the aquatic larval stages that richly varied patterns of behaviour and biology have evolved to enable caddisflies to exploit virtually every existing type of freshwater habitat.

Three broad groups of caddisfly families are recognized. Larvae in the portable-case-making families (suborder Integripalpia) construct tubular cases of leaves, wood, and rock fragments fastened together with silk. The case covers the larva as it forages for food. In the fixed-retreat-making families (suborder Annulipalpia), larvae use silk and detritus to construct stationary shelters from which they gather food materials transported by water currents. In a third group, the cocoon-making families (suborder Spicipalpia), larvae obtain food through various behaviour patterns; larvae in some families are free-living predators, but in other families they construct a pupal enclosure precociously and use it as a shelter from which they graze on algae and detrital particles. However, at pupation, larvae in all families of the Spicipalpia construct a silken cocoon that is distinguished in being not only closed but also in having the extraordinary property of osmotic semi-permeability (Wiggins and Wichard, 1989).

The Trichoptera are most closely related to Lepidoptera – the moths and butterflies. Diversification in the Lepidoptera has proceeded mainly through specialization on particular groups of host plants, and very

successfully, for more than one hundred thousand species of moths and butterflies are now known, constituting one of the largest groups of insects. Diversification in the sister order Trichoptera, however, has taken place entirely in aquatic habitats, and has been based not on plant chemistry but on construction behaviour where larvae used silk to exploit similar food resources in different ways. Caddisflies are distinctive among all the insects for the richly varied construction behaviour of their larvae.

This monographic study concerns the systematics of one of the portable-case-making families, the Phryganeidae. Among caddisflies, phryganeids are, for the most part, large and conspicuous insects, and the largest of all Trichoptera are members of this family. Perhaps because they are conspicuous, many species in the Phryganeidae have a long taxonomic history, revealing conflicting concepts for some species and also for generic classification. In this study of the world fauna of the Phryganeidae fifteen genera comprising seventy-four species are deemed valid. Nine species names are found to be synonyms of others, an unusually high figure constituting 10 per cent of the species recognized for the family.

Consequently, the first goal of a systematic monograph is met in the consolidation of the taxonomy of this family; the species in the Phryganeidae are defined and distinguished in the adult stage with diagnostic keys. Larvae and pupae are distinguished at the generic level. Although many species still cannot be identified in the larval stage, the available diagnostic information is summarized and a foundation is provided for further taxonomic study of phryganeid larvae. Hence this work provides a starting point for continued study of the ecology of phryganeid species.

The second goal of a systematic monograph is a global view of the evolutionary relationships of the group, which for the Phryganeidae proves to be particularly illuminating. Study of life histories has revealed a phy-

logenetic relationship between the case-making and pupation behaviour of larvae and the loss of functional pupal mandibles. This relationship is without parallel in the Trichoptera, and provides new insight into a unique evolutionary system.

Caddisflies of the family Phryganeidae are confined for the most part to higher latitudes of the world's north temperate zone. They occur in habitats ranging from cool streams and rivers through lakes and marshes to acidic bogs, temporary pools, and brackish coastal waters. Among Trichoptera, members of this family are noteworthy for several reasons. Fossil wings from the Early Cretaceous period, between 98 and 144 million years ago, indicate that the Phryganeidae are one of the oldest of the case-making families of Trichoptera still extant, preceding the origin of flowering plants. Departing from the normal cryptic tones of caddisflies, many are brightly coloured, both as adults and as larvae. Phryganeid larvae are unique in behaviour because they are not dedicated to retaining their cases as most case-making larvae are, but on slight provocation will abandon them readily – their unusual agility enabling the larvae to escape quickly without a case. The slow-moving eruciform larvae of other case-making families are reluctant to abandon their cases. The term *suberuciform* was introduced long ago to describe the distinctive form of phryganeid larvae.

When natural scientists of the eighteenth century began systematic documentation of the animals and plants of the world, all caddisflies were placed in the genus *Phryganea*. In the tenth edition of *Systema Naturae* by Carolus Linnaeus (1758), which was the starting point for the binominal system of nomenclature adopted for classifying animals and plants, fifteen species of caddisflies were named, all placed under the single genus *Phryganea* in the order Neuroptera, along with all dragonflies under the genus *Libellula*, and all mayflies under the genus *Ephemera*. In a footnote to *Phryganea* Linnaeus observed:

Phryganeae Larvae latent sub aqua intra tubos cylindricos, mobiles, a se confectos; volatiles factae choreas vespertinas in aëre instituunt.

(The larvae of *Phryganea* lie hidden under water within portable cylindrical tubes made by the larvae themselves; when they become able to fly, in the evening they dance rings in the air.)

This observation on the larvae and their cases appears

to have guided Linnaeus's choice of the name *Phryganea*, derived from the diminutive form *phryganion* of the Greek noun *phryganon*, meaning 'firewood' or 'dry sticks' (Brown, 1956). Most of the caddisflies assigned by Linnaeus to *Phryganea* were in fact portable-case-makers. Three of these original Linnaean species were the first true phryganeids: *Phryganea grandis* L. which became the type species of the genus; *P. phalaenoides* L., now in *Semblis*; and *P. striata* L., now in *Oligotricha*. A fourth species, *Phryganea reticulata* L. now in *Oligostomis*, was added by Linnaeus in 1761. Subsequently the Trichoptera were recognized as a separate order by Kirby in 1813, and the family Phryganeidae by Leach in 1815, with *Phryganea* L. as type genus. From these beginnings, knowledge of the family was advanced, first in Europe, then in North America and Asia. Most of the early students of Trichoptera contributed to the taxonomic elaboration of the Phryganeidae – Francis Walker, Herman Hagen, Robert McLachlan, Nathan Banks, Georg Ulmer, and others. But understanding of the phyletic relationships was hampered by a generic classification based on the European fauna, and particularly by a broad and loose application of the generic names *Phryganea* for grey, narrow-winged species and *Neuronina* for more colourful, broad-winged species.

A landmark study of the world fauna of the Phryganeidae by A.V. Martynov (1924a, b) demonstrated that genitalic morphology provided more reliable evidence of phyletic relationships than did the traditional characters of colour, venation, and shape of the wings. Martynov's concepts, with some modifications, were only gradually adopted by European and Asian workers, although more readily accepted in North America (e.g., Milne, 1934; Ross, 1944); but eventually Martynov's work became the foundation for a global classification of the Phryganeidae. Continued geographic exploration of the family yielded, among other advances, discovery by Schmid (1962, etc.) of an aggregation of *Eubasilissa* species in the Himalayan Mountains.

Analysis of the family Phryganeidae was also developing from another perspective – morphology of the immature stages. The foundation was laid in the classic studies by A.J. Silfvenius (1902–7, etc.) in Finland. In due course, knowledge of the larvae and pupae of the Phryganeidae led to recognition that the Asian genus *Phryganopsyche* (a new name for *Phryganopsis*, preoccupied in the Lepidoptera) was not congruent with the Phryganeidae where it had been assigned traditionally,

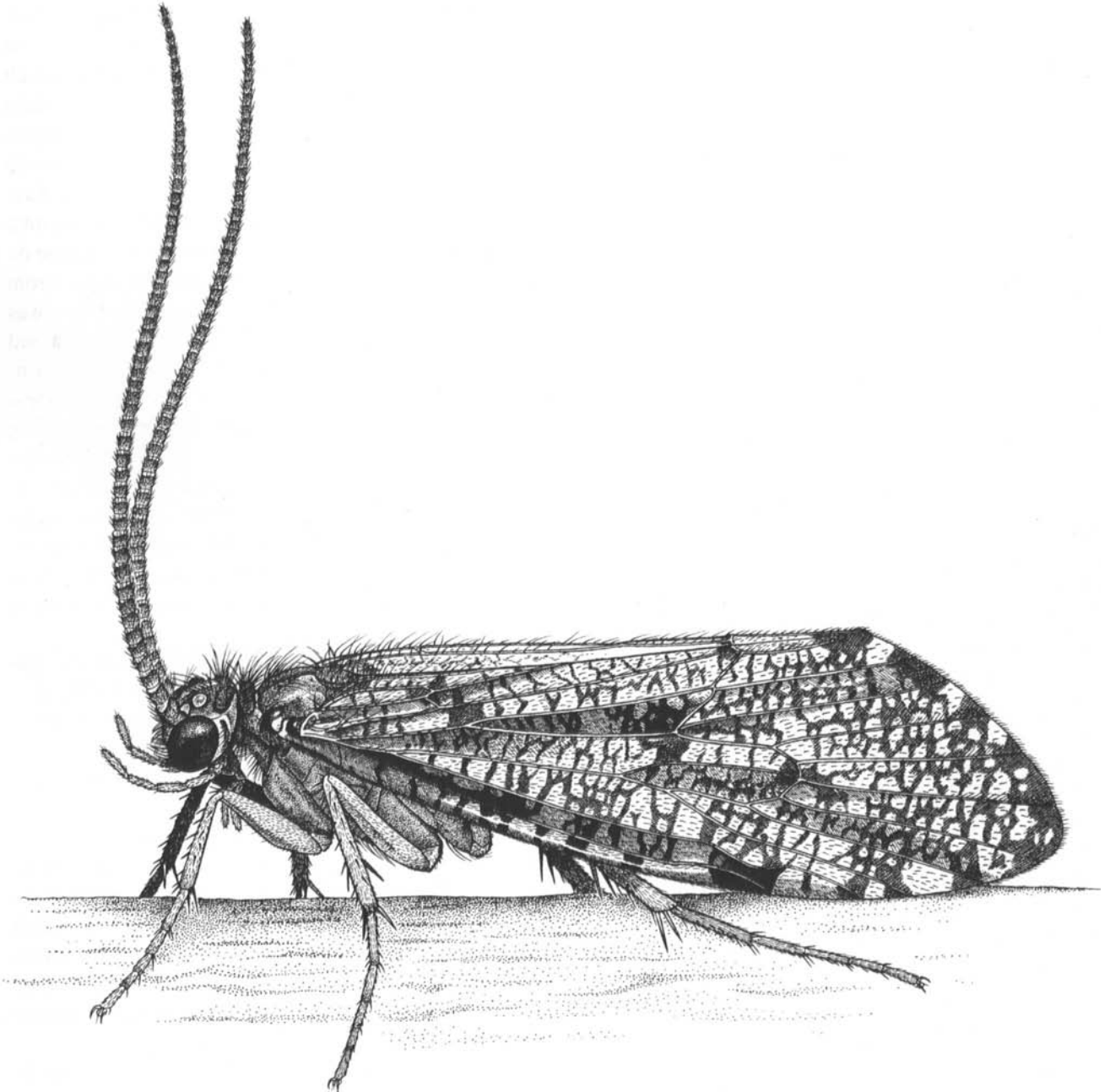


Fig. 1. *Banksiola crotchi* female (from *Synopsis and Classification of Living Organisms*, McGraw-Hill)

but was the sole representative of an independent and unusual new family Phryganopsychidae (Pl. I: 24) (Wiggins, 1959b). Study of life histories revealed a unique phylogenetic relationship between morphology of pupal mandibles and behaviour of larvae in case-making and pupation (Wiggins, 1960a, 1972; Ross, 1973). Discovery of the larval and pupal stages of the traditionally enigmatic species *Yphria californica* (Banks) showed that it represented a lineage of the Phryganeidae, and a new subfamily (Wiggins, 1962). Affinities of the puzzling North American genera *Fab-ria* and *Beothukus* were clarified after the immature stages were discovered (Wiggins, 1977; Wiggins and Larson, 1989). The immature stages and their behaviour in the Phryganeidae have proven especially useful in interpreting the phyletic relationships of the genera (see Phylogeny of the Genera, p. 20). Consequently, the

history of research on the Phryganeidae strongly supports the position that information on immature stages is essential in the systematics of Trichoptera (Wiggins, 1981).

Much has been learned about the family Phryganeidae, but the information has been patchy in content and often based on an outdated classification, widely scattered in the scientific literature, and largely retrievable only by specialists. A substantial body of behavioural and biological information has not been integrated previously into the systematic database. The objective of the present study is to provide in one volume a taxonomic synthesis of the Phryganeidae, and through phylogenetic analysis to find new insight about the evolutionary history of this distinctive family of the Trichoptera.

Materials and Methods

The principal taxonomic resource for this study is the collection built up in the Department of Entomology, Royal Ontario Museum. Many larvae were reared to the adult stage using the method outlined elsewhere (Wiggins, 1959a), and the larvae and pupae associated to species have been important sources of morphological and behavioural information. As opportunities became available, materials from the major collections in North America were examined, as were the following collections: Zoological Museum, St. Petersburg (Martynov Collection); Zoologisches Museum, Hamburg (Ulmer Collection); National Institute of Agro-Environmental Sciences, and Entomological Institute of Hokkaido University, Japan (Kuwayama Collection); Natural History Museum, London; Finnish Museum of Natural History, Helsinki; and Muséum National d'Histoire Naturelle, Paris.

Data from specimens examined are listed in the Appendix; institutional repositories for these materials are indicated by appropriate abbreviations, explained at the beginning of the Appendix. Sources for some other specimens, mainly from individuals, are cited solely with the records. Specimens without a source annotation are from the collection of the Department of Entomology, Royal Ontario Museum. Label data, for the most part, are transcribed in the original form. Where the number of males and females is not given, the symbols ♂♂ and ♀♀ indicate numerous specimens uncounted.

Distribution maps are provided for most of the North American species, and are assembled at the back of the

book. All peripheral records are plotted, but otherwise only selected localities are shown on the maps. Records from the literature are cited for North American species in the Appendix under Other Records, and for other species when distributional records are sparse. These records are used to supplement the distribution maps for North American species where the specimens examined do not document the distribution adequately. Solid squares on the maps indicate reports from the literature that a species occurs in a state, but lack specific data. Geographic ranges for European species are based primarily on the summary by Botoșăneanu and Malicky (1978); ranges for Asian species are derived from various regional studies. Repositories for type specimens are cited when known.

In a photograph of adults of a number of species situated at the front of the book, individuals are indicated by a notation, e.g., Plate I:10.

The taxonomic history of genera in the Phryganeidae is marked by extensive change; lists of synonymies for both genera and species have been selected to illustrate the evolution of these changes. All of the very early synonyms, long unused, are not necessarily included because they are fully documented in the *Trichoptero-um Catalogus* (Fischer, 1964, 1972).

Methods for developing the hypothesis of phylogeny for the genera are outlined under Evolution of the Phryganeidae (p. 25). Hypotheses of phylogeny are developed for species within a genus solely by inspection; cladograms are provided for genera with four or more subordinate taxa.

General Features of the Phryganeidae

This study of the biosystematics of the caddisfly family Phryganeidae is based on morphology, behaviour, and biology of adults, larvae, and pupae. These aspects of the Phryganeidae are considered in this section.

Morphology of Adults

Members of the Phryganeidae share the typical moth-like form of all Trichoptera, but for the most part they are stout-bodied insects, often with the setal covering of the fore wings reduced to reveal a reticulate pattern in the membrane (e.g., Fig. 1).

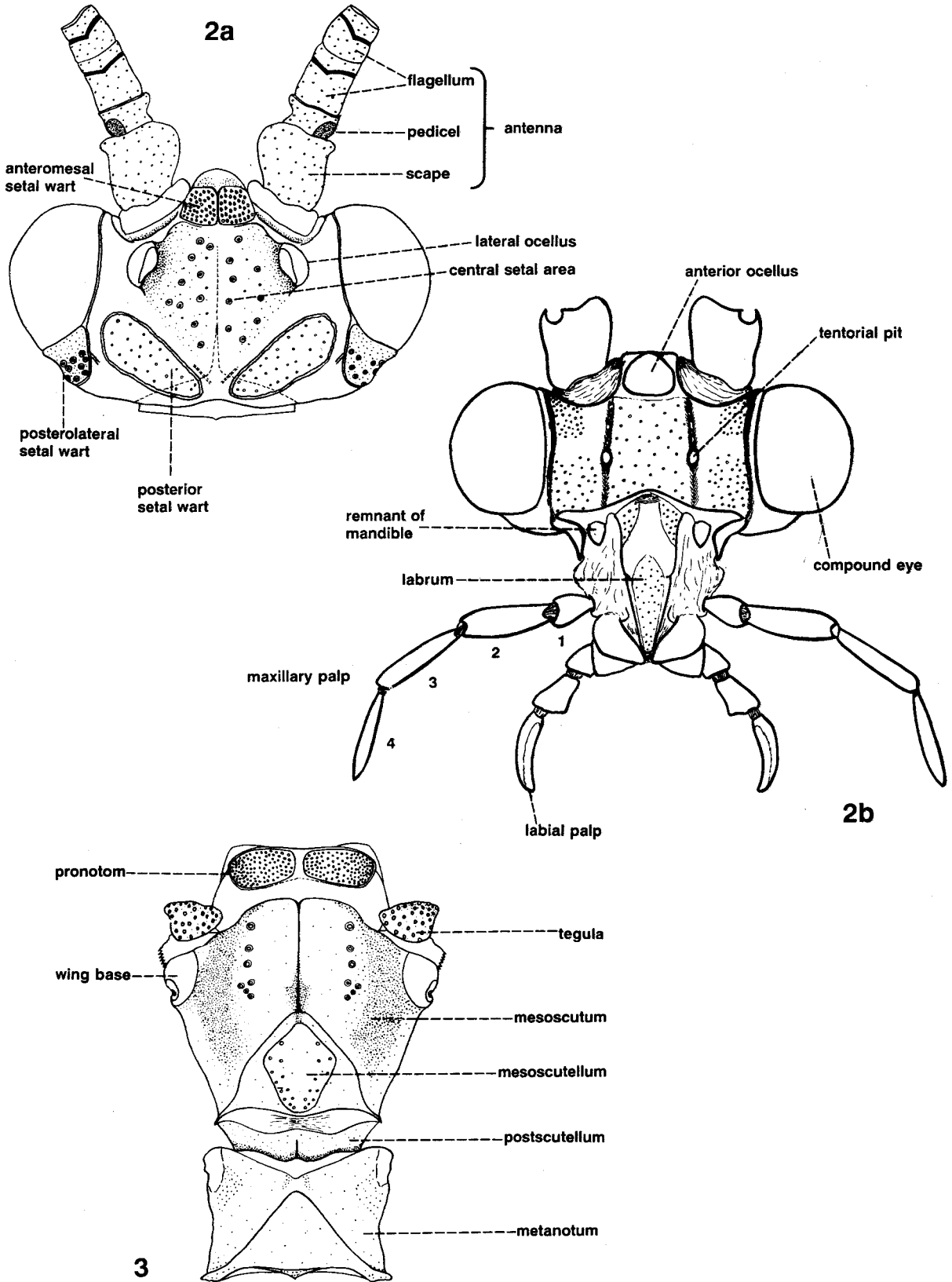
Head and appendages (Fig. 2). Three prominent ocelli are, in proportion to the size of the head, larger than the ocelli in other families. Setal warts on the dorsum of the head consist of anteromesal, posterior, and posterolateral pairs; a central setose area between the lateral ocelli in some species is reduced to a pair of smaller warts in others. The antennae are thick, about the same length as the fore wings, and the scape is short and bulbous; antennal segments are covered with a dense coating of setae, of one colour in some species but in most arranged in alternating light and dark rings. Most antennal segments bear a peripheral groove (Fig. 130).

In the subfamily Phryganeinae the maxillary palpi of the female usually have five segments and the male four; but females of *Agrypnetes crassicornis* are unique in having only four segments. In the Yphriinae both males and females have five. Labial palpi are three-segmented in both sexes, as in all Trichoptera. The labrum is longer than in most other families, usually equal to about twice its greatest width. A membranous lobe at each side of the labrum is the remnant of the mandibles, undeveloped in all adult Trichoptera. Morphology and function of the mouthparts have been studied by Crichton (1957, 1991).

Thorax and appendages (Fig. 3). The pronotum

bears one pair of large setal warts, as in most other families. On the mesoscutum there is a pair of irregular, somewhat wart-like, longitudinal lines of a few thick setae; the mesoscutellum bears a single median ovoid wart with marginal setae. The legs in most species have well-developed tibial spurs arranged in pairs, with one pair on the fore tibia, two pairs on the middle tibia, and two pairs on the hind tibia – expressed in taxonomic descriptions as a tibial spur count of 2, 4, 4. Stout spines are present on the tibiae and tarsi of most species; the traditional term notwithstanding, these are enlarged setae, as are the spurs. In species such as *Agrypnetes crassicornis* and *Agrypnia colorata*, spurs (e.g., Fig. 43) and spines are reduced in number; and in *A. crassicornis* the tarsi of the middle legs are flattened and fringed with setae (Fig. 30a).

The fore wings of phryganeid caddisflies show marked differences in colour and pattern (Plate I). On the membrane of most species there is a reticulate colour pattern, sometimes indistinct as in *Agrypnia pagetana* (Pl. I: 29), sometimes dark and prominent as in *Banksiola crotchi* (Fig. 1); the reticulations are obscured by a dense coating of fine setae in other species, giving the wing an entirely different colour pattern, as in *Phryganea cinerea* (Pl. I: 36). In some species the prominent reticulations of the membrane constitute the dominant colour pattern of the wing because the setae are sparse, as in *Banksiola* (Pl. I: 7, 8, 9) and *Semblis* (Pl. I: 16–19, 21, 22). In some of the species in which the reticulations of the membrane contribute the dominant colour pattern of the wing, there is a tendency for a golden-yellow colour to develop in the area between the brown reticulations, becoming a bril-



Figs. 2, 3. *Phryganea cinerea*. 2a, head of male, dorsal; 2b, head of male, frontal. 3, thorax, dorsal.

liant yellow in species such as *Oligostomis pardalis* (Pl. I: 13). In certain species of some of these same genera there is a colour variant in which the dark reticulations appear to have expanded and fused, obliterating most of the original reticulation, and resulting in a uniform dark brown fore wing. These dark variants occur in *Oligotricha lapponica*, *Oligostomis reticulata*, *Hagenella clathrata*, and *Semblis atrata*; the dark brown form in the last species shows variable light patches in some specimens (Pl. I: 16–19). In *Oligotricha striata* (Pl. I: 3), the uniform brown variant has completely replaced the reticulate morph. The shape of the fore wings also differs. In *Trichostegia* (Fig. 17) and *Agrypnia* (Fig. 44), and particularly in *Agrypnetes* (Fig. 30), the fore wings are narrow with a rather straight posterior edge. In other genera, such as *Hagenella* (Fig. 180) and *Oligostomis* (Fig. 166), the wings are broader and more rounded.

Wing venation in the Phryganeidae is illustrated by the female of *Fabria inornata* (Fig. 24), where the venation is complete for the Trichoptera, with all terminal veins separate in both wings – the only existing phryganeid species in which complete venation occurs. Reductions occur in the branches of M in the females of the other phryganeid species and in all males. In all species of the family the anal veins of the fore wing have a distinctive configuration: fused vein 1A + 2A + 3A is reduced to about one-third the length of the first anal cell and vein 3A is inflected. A significant feature of phryganeid venation is that few distinctions have been found that permit recognition of genera from the wings alone, and consequently venation is of questionable significance in placing fossil wings to genus in the Phryganeidae (see *Extinct Species*, p. 28).

Abdomen and appendages. Filamentous gill-like lobes arise from the pleural membrane of abdominal segments in adults of most species of the Phryganeidae. These are particularly prominent in *Phryganea*, but occur in other genera such as *Yphria* as short membranous stubs. The lobes are similar in texture and location to the tracheal gills of the pupa; they have been termed the hemo-branchial apparatus by Schmid (1980), who confirmed their occurrence in many families of case-making (Integrilpalpia) and retreat-making (Annulipalpia) Trichoptera. Tracheal gills in adults of Trichoptera and other ontogenetically amphibious orders are held to be remnants from the ancestry of pterygote insects, and now serve no function (Štys and Soldán, 1980).

A pair of small glands open on the sternum of seg-

ment v in both males and females of many species. These glands are found in the Phryganeidae as well as several other families of all groups of Trichoptera (Schmid, 1980), and probably produce a pheromonal secretion.

In males of the Phryganeidae (e.g., Fig. 25) abdominal segment IX is a completely sclerotized ring; in lateral aspect segment IX is wider dorsolaterally in some species, but ventrolaterally in others. In certain species of *Agrypnia* the dorsum of segment IX is extended posteriorly as a ledge overhanging segment X (e.g., Fig. 53). In *Ptilostomis* the sternum of IX is produced as a deep ledge underlying the bases of the inferior appendages (Fig. 169a, c). The inferior appendages (claspers, gonopods, pedes genitales) are articulated ventrally with segment IX. In primitive caddisfly families and in several genera of the Phryganeidae, the inferior appendages are two-segmented, with the terminal segment freely articulated on the basal segment; the basal segment is variously shaped, but usually has an apical process which is often prominent.

Abdominal segment X (dorsal plate or penis cover) is, in its simplest form, a roof-like plate overhanging the anal opening and the phallus (e.g., Fig. 18). Preanal appendages (cerci) in most of the species appear as a setate knob or process on each side of segment X near the base (e.g., Fig. 18a). Other appendages of segment X are enlarged in several genera, where they are part of a complex development, as in *Beothukus* (Fig. 145), *Hagenella* (Fig. 185), *Phryganea* (Fig. 141), and *Ptilostomis* (Fig. 176). Although segment X is usually joined to the dorsum of IX by a membranous connection, there is a sclerotic fusion between the two in some species, such as *Fabria inornata* (Fig. 25) and *Agrypnia macdunnoughi* (Fig. 51).

The phallus consists typically of a simple sclerotized phallosome, usually with spines or sclerites arising on the invaginated membranous endotheca. In some genera, e.g., *Hagenella* (Fig. 185d) and *Eubasilissa* (Fig. 218d), the phallosome is short and thick; and in some species of *Banksiola* (Fig. 101c) a separate extensile appendage arises, tipped with a dense cluster of bristles. A terminal aedeagus and parameres typically do not occur in the Phryganeidae as they do in other families such as the Limnephilidae. However, in one genus, *Semblis*, a pair of slender, sclerotized processes arises near the base of the phallosome (Fig. 203a). These are similar to the parameres of other families in the Limnephiloidea, and their origin is obscure (see Phylogeny

of the Genera, character no. 17). Paired sclerotized lobes of different shapes often occur on the posteroventral edge of the phallosome, reaching their greatest development in *Beothukus complicatus* (Fig. 145d). The phallosome is frequently connected internally to the bases of the inferior appendages, as in *Yphria californica* (Fig. 10a).

In females (Fig. 26), the sternum of segment VIII is fused with IX to form the subgenital plate (ventral plate), a continuously sclerotized area extended posteriorly to terminate in vulval lobes (vulvar scale) of various shapes; a distinct boundary between the two is usually lacking. In most species the subgenital plate lies between free lateral lobes of sternum VIII. The dorsum of segment IX is fused with X in all phryganeid females. The posterior margin of segment X overhangs the anal opening, and in most species bears paired median and lateral lobes that are frequently diagnostic in form. On each side of the opening to the genital passage there is a dorsal sclerotized lobe; modifications in these lobes throughout the family provide useful taxonomic characters. In some species the lobes are small, as in *Oligostomis ocelligera* (Fig. 162); in others, such as *Trichostegia minor* (Fig. 19), they are much enlarged and form a hood overhanging the vulval lobes at the apex of the subgenital plate.

The genital passage or vagina leads to a concave genital chamber. In genera such as *Banksiola* (Fig. 114), *Semblis* (Fig. 194), *Neurocyta* (Fig. 207), and *Eubasilissa* (Fig. 230), a membranous invaginated blind pouch opens in the floor of the vagina, and is termed here the vaginal pouch; in *Eubasilissa* this pouch accommodates the endotheal sclerites of the phallus during copulation (Fig. 241). In females of *Oligotricha* (e.g., Fig. 86) and *Ptilostomis* (e.g., Fig. 170), a sclerotized crest or lobe extends ventrad from the vaginal floor. A simple vaginal ridge occurs in *Banksiola dossuaria* (Fig. 111) together with a vaginal pouch, indicating that the two structures are of independent origin. In *Ptilostomis semifasciata* (Fig. 175), the vaginal lobe has a small lumen, suggesting that it might provide a point of fixation for genital appendages of the male during copulation. Morphology of the internal reproductive system in females of *Phryganea cinerea* and *Yphria californica* has been studied by Unzicker (1968), and found to be essentially similar to other families of Trichoptera.

Genital morphology is treated here in general conformity with concepts underlying the terminology of most of the recent workers, e.g., Ross (1944, etc.),

Schmid (1980, etc.). However, in a comparative study of genitalic structure in families of Trichoptera, Nielsen (1957, 1980) interpreted segmental homologies somewhat differently. Thus, in *Agrypnia pagetana*, the exemplar species studied in the Phryganeidae, Nielsen (1980) concluded that the true venter of segment IX in females is lacking, but is represented by the fusion of VIII with the gonopods of VIII and IX, forming the 'ventral plate' (= subgenital plate); the 'vulvar scale' (= apical vulval lobe) comprises the fused external parts of the gonopods of VIII. These proposed homologies have not been tested on the Phryganeidae generally, or even throughout the genus *Agrypnia*.

The size of specimens is indicated by the length of the fore wing in millimetres; in the size ranges given, males are generally smaller than females.

Morphology of Larvae

Divisions between segments are deep and the segments are rounded in profile in Phryganeidae (Fig. 27), as in the free-living Rhyacophilidae. This differs from most other case-makers such as the Limnephilidae, in which the grooves between the abdominal segments are shallow and the segments rather flat and quadrate. The larval form of Phryganeidae is shared only with the Limnacentropodidae among case-making families (Wiggins, 1969); combined with the oval shape and anterior orientation of the head, these characteristics are subsumed in the term *suberuciform*.

The head of most phryganeid larvae (Fig. 27) is a characteristic bright yellowish or light reddish-brown colour with two dark brown or black dorsal bands extending from the coronal suture to the anterolateral margin of the head capsule at the antennae; in some species a dark median band is also present on the frontoclypeus. Dark lateral bands extend from a point close to the edge of the occipital foramen almost to the cluster of black stemmata (eye) on each side of the head. On the ventral surface of the head there are variable dark markings, diagnostic for some species but lacking in others. In almost all of the Phryganeidae the sclerotized pronotum is yellow or light reddish-brown with prominent black or dark brown markings (e.g., Fig. 196). The head and pronotum in *Hagenella* (Fig. 187) are atypically a uniform dark brown colour, as is the pronotum in *Trichostegia* (Fig. 20).

Since crypsis seems central in the evolution of case-making behaviour, and the sclerotized head and thorax of

most larval Trichoptera are neutral in colour, dark bands on a yellow background of the head and pronotum in the Phryganeidae are puzzling – especially since this is a classic combination for aposematic coloration. From experiments with fish predators on caddis larvae with a variety of head markings, Otto (1984) suggested that contrasting head patterns in caddis larvae such as phryganeids enhance crypsis under low light intensity, drawing an analogy with the role attributed to the markings of zebra at dusk. Hutchinson (1981) cited examples to show the importance of cryptic coloration in aquatic insects.

The head is oval in outline in dorsal aspect, and somewhat flattened in lateral view. In most of the related families, such as the Limnephilidae, the head is more circular and globose. The mandibles of most phryganeid larvae (Fig. 12d) lack the mesal brushes of setae that are present in many other closely related families, except in the genus *Trichostegia* where the setal brushes are present (Fig. 20d). The antennae are short in most genera, but longer in *Beothukus* (Fig. 148b). The maxillae (Fig. 136) have elongate palpi and slender maxillary lobes, quite different from the short palpi and suppressed maxillary lobes in other case-making families (e.g., Wiggins, 1996b, fig. v1).

A characteristic feature of the thorax in Phryganeidae is that in most genera the mesonotum and metanotum are membranous, except for small, ovoid *sa3* sclerites (Fig. 27). In *Oligostomis* and *Beothukus* (Fig. 148b), however, a pair of small *sa1* sclerites occurs on the mesonotum, and in *Semblis*, *Eubasilissa*, and *Neurocyta* these sclerites lie close together on the mid-dorsal line, suggesting a single, small median sclerite on the mesonotum (Fig. 196). In *Yphria* (Fig. 12) somewhat larger mesonotal *sa1* sclerites are also contiguous on the mid-line, and smaller *sa2* sclerites are present.

On the fore legs of most larvae there is a stout, prominent spur-like seta at the distal end of the tibia and another at the base of the tarsal claw (Fig. 62a). In two genera, *Semblis* and *Hagenella* (Fig. 187), these spurs are reduced to thin, bristle-like setae, appressed to the leg segments (Silfvenius, 1902: pl. 1A). A field of small, comb-like spines occurs on the ventral surface of the coxae in phryganeid larvae. These spines are small in most genera, and appear as tiny points (e.g., Fig. 171c). The spines are larger in *Agrypnia* (Fig. 62), *Agrypnetes* (Fig. 33b), and *Phryganea* (Figs. 134, 135), and the comb-like structure is apparent at magnifications of around 50x (see Phylogeny of the Genera, character no. 5). A small sclerite, the sternellum, lies between the

prothoracic coxae in all genera of the family (e.g., Fig. 60c) except *Phryganea*.

In all phryganeid larvae except *Trichostegia minor* (q.v.) the first abdominal segment bears a prominent lateral hump on each side and a single median dorsal hump (Fig. 12); in *T. minor* (Fig. 20) the lateral humps are prominent but the median dorsal hump is lacking.

Stout, single gills are present on the first eight abdominal segments and are variously arranged in different genera and species. Gills vary in arrangement to some extent within species, but usually the full complement is not acquired until the final (fifth) instar. The internal tracheal system in phryganeids differs from that of other case-making families in having an additional transverse branch in abdominal segments IV to VIII (Novák, 1952). A lateral abdominal fringe of slender bifid filaments is well developed in all Phryganeidae. The family is unique in having these filaments in all instars (Nielsen, 1942); in other families of the case-making Integripalpia filaments do not occur in the first instar. Phryganeid larvae lack chloride epithelia and forked lamellae, structures that do occur on the abdominal segments in other case-making families (e.g., Kerr and Wiggins, 1995). Osmoregulation in most case-making families is mediated through chloride epithelia, but in the Phryganeidae it is rectal papillae that are involved, a system regarded as relatively primitive among aquatic insects (Schmitz and Wichard, 1978). The larvae are similar to the Limnephilidae and other case-making families in having short anal prolegs.

Case-making Behaviour

Throughout the Phryganeidae, larval cases are constructed mainly of plant pieces fastened together with silk. These cases are of three types – spiral, ring, and irregular – depending on the arrangement of the plant pieces. Although larvae in certain species, such as *Agrypnia pagetana* and *Agrypnetes crassicornis*, sometimes use a single piece of hollow plant stem as a case, these same species also construct a larval case typical for the genus. Phryganeid larval cases are entirely open at the posterior end, in distinction from most other families where larvae reduce the size of the posterior opening with silk.

Spiral cases. Spiral cases (Figs. 132, 133) are constructed of pieces of plant material cut to shape and fastened side by side, with each new piece placed slightly ahead of the one preceding; the result is a continuous

spiral of five or six coils. If the coils of a spiral case are carefully separated along the line of junction, a continuous ribbon of plant pieces fastened side by side is the result. Spiral cases may be either dextral or sinistral, a variable feature within species. Spiral cases are straight, taper slightly from front to rear, and are somewhat more rigid than ring cases. Spiral cases are made by larvae in the genera *Agrypnetes*, *Agrypnia*, *Banksiola*, *Fabria*, *Oligotricha*, and *Phryganea*.

Ring cases. Ring cases (Fig. 172) are composed of complete rings joined end to end, with five or six in a series in the cases of fully grown larvae. Each ring is usually composed of broader leaf pieces from deciduous trees, cut to size. This type of case is slightly curved, tapers little from front to rear, and is somewhat less rigid than the spiral case. A ring case is made by larvae of *Beothukus*, *Eubasilissa*, *Hagenella*, *Neurocyta*, *Oligostomis*, *Ptilostomis*, and *Semblis*.

Irregular cases. Irregular cases (Figs. 13, 21) are constructed of pieces of plant, detrital, or mineral materials arranged irregularly over the surface of the tube. There is no regular arrangement as in the spiral and ring cases. Larvae in *Trichostegia* and *Yphria* construct irregular cases.

Abandoning cases. One aspect of case-related behaviour unique to the Phryganeidae is the readiness with which the case is abandoned. Larvae will defend their cases, usually successfully, against intrusion by a caseless larva (Otto, 1987a); but phryganeid larvae disturbed by some larger presence, such as the hand of a collector, frequently abandon the case entirely and crawl away rapidly to cover. In similar circumstances, larvae of other case-making families usually withdraw within the case. Under experimental conditions, fish (salmonids) consumed larvae that lacked cases before eating those with cases, indicating that the choice of retaining or abandoning the case is crucial in encounters with a large predator. Long cases provided more protection against predatory fish than short cases, but a longer case results in reduced mobility in dense vegetation (Otto, 1987a).

In abandoning their cases, phryganeid larvae have the option of leaving through either end; most larvae in other case-making families can escape only from the anterior opening because the diameter of the posterior opening is usually reduced with silk, presumably to restrict access by invertebrate predators. These eruciform larvae lack the agility of the suberuciform phryganeids, and thus case-making behaviour complements

larval morphology. The question arising here is whether phryganeid larvae evolved their unique suberuciform morphology and case-making behaviour from eruciform case-making ancestors, or whether phryganeid larvae retain the morphological and behavioural ground-plan of the antecedents of eruciform case-making families. Evidence tends to support the second of these possibilities because the Phryganeidae have other plesiomorphic attributes (see Family Relationships, p. 19).

Larvae of case-making Trichoptera make a substantial investment of proteinaceous silk in their cases (e.g., Otto, 1974), and without a case larvae are more vulnerable to predation (Otto, 1987a); the reluctance of larvae in most families to leave their cases is consistent with these factors. Only phryganeid larvae abandon that investment readily, but they compensate for this by a greater willingness to occupy empty cases (Merrill, 1969). One might predict that the amount of silk used in constructing a typical phryganeid case would be less in relation to the weight of the larva than in other families where the case is not abandoned. But the relatively small pieces of materials that are fastened together in constructing phryganeid cases would still seem to place a substantial demand on the production of silk. Moreover, the larva would be further exposed to predation while a new case was under construction. Larvae of *Agrypnia pagetana* are unusual among phryganeids in utilizing pieces of hollow stems of *Equisetum* or *Scirpus* as cases. Otto (1987b) found that a significantly smaller amount of silk was added to the interior of the stem case than to the spiral case; and that given a choice, larvae voluntarily abandoned typical spiral cases for pieces of hollow stem, perhaps because the greater rigidity of the stem case was a better deterrent to predation by fish than the typical spiral case. All of this leads to the question of why more species of the Phryganeidae do not use hollow plant stems as larval cases. Availability of hollow stems has to be a factor, and perhaps phryganeid larvae evolved in the absence of shoreline plants with hollow stems.

Case-making behaviour was analysed experimentally in *Oligotricha ruficrus* (= *striata*) by Diehm (1949). The role of setae in behavioural responses of *Phryganea* larvae was investigated by Sakhuja, Williams and Williams (1983).

Morphology of Pupae

The pupal stage in Trichoptera extends from larval-

pupal apolysis inside the pupal case until the fully formed pharate adult with folded wings leaves the pupal case, swims to the water surface, and emerges from the pupal skin. The pupal skin is a transparent membranous integument covering all parts of the body, but bearing several sclerotized structures that provide useful systematic information (e.g., Fig. 105).

The frons is uniformly rounded in most genera (e.g., Fig. 105), but is extended in *Hagenella* (Fig. 184) and *Eubasilissa* as a promontory; in at least one *Eubasilissa* species, the extended frons bears stout tubercles (Fig. 214). In *Agrypnetes* and *Phryganea grandis* the frons is raised in ridges (Bray, 1967: fig. 26).

Sclerotized pupal mandibles occur in almost all Trichoptera, and their apparent function is to cut an exit hole in the pupal case for the escape of the pharate adult. Sclerotized pupal mandibles also occur in several genera of the Phryganeidae (e.g., Fig. 4b), but in other genera the pupal mandibles have been reduced to membranous quadrate lobes (e.g., Fig. 5b). These are dectitious and adectitious pupae, respectively; the adectitious pupae in the Phryganeidae are some of the very few examples among Trichoptera (Hinton, 1971; Wiggins, 1960a).

The mesothoracic legs of the pupa are flattened and the edges densely lined with setae; these oar-like legs appear to be an asset for the pharate adult when it swims to the surface for eclosion.

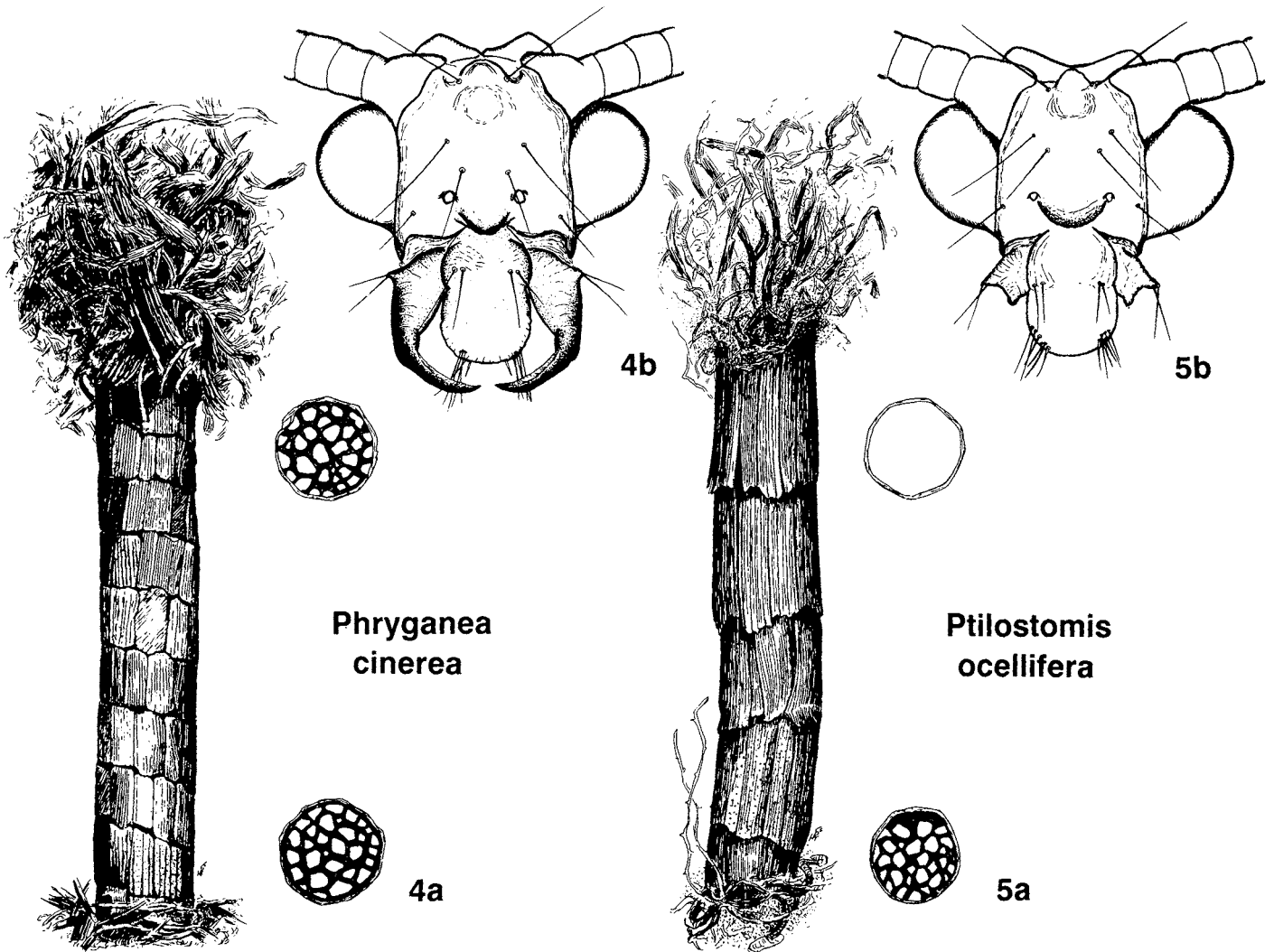
The first abdominal segment is produced posterodorsad as a short median lobe or process. In most genera this process is notched mesally, and terminates in two small points (Fig. 151b); in *Trichostegia* the process is bulbous and lacks a median notch (Fig. 23). In *Yphria* the median lobe is a unique transverse, roughened crest along the posterior edge of the segment. The sclerotized, hook-bearing plates of the abdominal segments (Fig. 105b) are similar in general form to other families of case-making Trichoptera, although stouter. As in the larvae, a dense lateral fringe of bifid hollow filaments arises on each side of the abdomen of phryganeid pupae (Fig. 151b). Gill filaments occur on pupae as on larvae. In pupae of some genera, e.g., *Banksiola*, spiral thickenings occur within the filaments (Kerr and Wiggins, 1995).

The pupal abdomen in most families of case-making caddisflies terminates with a pair of sclerotized anal processes. In most of the Phryganeidae these processes are short, more or less rounded apically, and concave dorsally (Fig. 105b); in *Trichostegia minor* each rounded process bears a small, thumb-like mesal point

(Fig. 23a), and in *Eubasilissa* (Fig. 215) the posterior margin of each anal process is deeply emarginate. In *Oligostomis* (Fig. 160) and *Semblis*, the anal processes are flattened dorsally with little concavity. In *Yphria californica* (subfamily Yphriinae) the lobes are short and triangular in dorsal aspect, but concave on the caudal surface (Fig. 15). Thus the short anal processes of pupae in Phryganeidae are quite different from the elongate rods of other case-making families such as Limnephilidae. It is widely believed that rod-like anal processes, often provided with long, stout setae, function to clear the openings of the posterior silken closure mesh to maintain circulation of water through the case for respiration during metamorphosis. The short, broad anal processes in the Phryganeidae seem unsuited to this function, but may be related to the fact that the silken closure meshes are more open than in other families, and perhaps less likely to be occluded by debris. Moreover, the broad concave anal processes in the Phryganeinae appear to be effective paddles that would maintain a larger volume of water flowing through the pupal case.

Pupation Behaviour

Correlated with the loss of pupal mandibles in some phryganeids is a change in behaviour through which these larvae ceased spinning a silken closure mesh across the anterior opening of the case (Fig. 5). Prior to pupation, larvae in these genera close the anterior end of the larval case with pieces of plant debris held in place with silk; the pharate adult, although lacking sclerotized pupal mandibles, is able to push through this loose closure at the time of eclosion (Wiggins, 1960a). These congruent changes in larval behaviour and pupal morphology occur in the genera *Banksiola*, *Beothukus*, *Hagenella*, *Oligostomis*, *Ptilostomis*, and *Semblis*; all species of these genera that are known as larvae and pupae are consistent in this correlation. Since this method of pupation and eclosion is evidently successful, the selective advantage of the anterior closure mesh becomes a question for other genera of the Phryganeidae, where sclerotized pupal mandibles and sealed pupal cases are the norm. If protection of the metamorphosing pupa from predators is the function of the anterior closure mesh, one must infer that the adectitious phryganeid pupae gain this protection in some other way – perhaps in the placement of the case for metamorphosis. Here it can be noted that pupal cases in all Phryganeidae are effectively concealed – certainly from



Figs. 4, 5. 4, *Phryganea cinerea*: a, pupal case showing silken mesh closing anterior and posterior ends; b, head of pupa showing fully sclerotized mandibles. 5, *Ptilostomis ocellifera*: a, pupal case showing lack of silken mesh at anterior end; b, head of pupa showing reduced membranous mandibles (from *The Canadian Entomologist*).

entomologists, because they are not often found.

It seems likely that in the evolution of these behavioural and morphological features, closure of the anterior end of the pupal case with silken mesh would have ceased before the sclerotized mandibles were lost, rather than the reverse. The genus *Agrypnia* appears to represent just such an intermediate stage because the pupal mandibles are fully sclerotized, and the anterior end of the pupal case lacks a silken closure mesh. Moreover, early literature wrongly attributed anterior closure membranes to pupal cases in several genera where evidently they do not exist (Wiggins, 1960a).

Puzzling arrangements occur in the Asian genus *Eubasilissa*, in which larvae spin a stout silken mesh sealing the anterior opening of the pupal case, even

though the pupae have lost the sclerotized pupal mandibles (Figs. 213, 214). Inference from other phryganeid genera implies that this arrangement would leave a pharate adult sealed within its own pupal case, but without the functional pupal mandibles required to escape for eclosion. This problem appears to have been resolved for the insects by an extended pupal frons (e.g., Fig. 214), which seems equal to the task of breaking through the silken closure mesh, although this has not yet been observed. Phylogenetic analysis (Fig. 6) indicates that the problem was created by an evolutionary reversal in behaviour; thus, from ancestors that had lost the behaviour for sealing the anterior opening of the pupal case, descendants appeared which did so. It seems likely that some enlargement of the pupal frons

must have preceded reimposition of the behaviour for spinning the silken closure mesh; and that reimposition suggests some selective advantage for closing the pupal case – perhaps added protection from predators during metamorphosis. Pleiotropy is an alternative explanation.

Also intriguing is that pupal mandibles are sclerotized in most genera where larvae construct spiral cases, but are membranous in most genera with ring cases. One exception is the genus *Banksiola*, in which larvae construct a spiral case that is not sealed at the anterior end for pupation, but pupal mandibles are lacking.

Pupation behaviour in the genus *Yphria*, the sole genus in the subfamily Yphriinae, is distinctive because larvae construct an entirely new and different case for pupation at the end of the final instar (cf. Figs. 13, 16; see *Y. californica*). In all other phryganeids and, to my knowledge, in all other case-making families except the Phryganopsychidae (Wiggins and Gall, 1993), pupation occurs in the larval case.

Flight Behaviour of Adults

Pupal development proceeds directly and without the intervention of diapause in all phryganeids in which life histories have been studied. A period of approximately three weeks is spent in the pupal case. Detailed observations on two species, *Agrypnia obsoleta* and *Phryganea bipunctata*, were compiled by Solem (1976) in Norway. Emergence and swarming for *A. obsoleta* occurred around midnight, but were scattered over a 24-hour period in *P. bipunctata*. Adults emerged from the pupal integument at the water surface within 25 to 30 seconds, and crawled or flew to the shoreline. Copulation followed within minutes of a female's emergence while the female was still in the lighter-coloured teneral condition; and coupling periods of 73 to 104 minutes were recorded for *A. obsoleta* (Solem, 1976). Observations on matings in *P. bipunctata* indicated that males were attracted by female pheromones.

Given the well-established common ancestry of the Trichoptera and Lepidoptera, it is not surprising that much of the activity of adult caddisflies is nocturnal. However, there are exceptions, and adults of autumn-emergent genera, such as *Frenesia* (Limnephilidae) and *Neophylax* (Uenoidae), are active during the sunny part of the day, perhaps because temperatures are too low for much activity at night. Mating swarms of Leptoceridae often occur during daylight hours. Variance is evi-

dent in the Phryganeidae, even within a single species; in contrast to the nocturnal activity of *Agrypnia obsoleta* observed in Norway, emergence and mating during daylight hours were reported for this species in England (Hickin, 1967). For three species in the Phryganeidae, *Semblis phalaenoides*, *Oligostomis pardalis*, and *O. ocelligera*, flight during the day is a distinctive and apparently obligatory behaviour; in an evolutionary context, these are the butterflies of the Trichoptera.

The Eurasian species, *Semblis phalaenoides*, has been recorded as flying high and wildly in large numbers at midday (McLachlan, 1874; Lackschewitz, 1922; Kuusela, 1991). The eastern North American species *Oligostomis pardalis* and *O. ocelligera* fly during the day. Lloyd (1921) recorded diurnal flight for *O. ocelligera* in New York, and it has also been observed for both *O. pardalis* and *O. ocelligera* in Maine and Nova Scotia, respectively (D.C. Ferguson, personal communication).

Perhaps related to their diurnal flight is the fact that adults in some species of *Oligostomis* and *Semblis* also possess some of the most brightly contrasting wing patterns in the Trichoptera. Since cryptic coloration and nocturnal or crepuscular flight are the norm for Trichoptera, the possibility of aposematic coloration arises for these brightly coloured day-flying species (Guilford, 1990). Selection of some sort must be operating because wing colour in *Oligostomis soochowica* (Fig. 163) resembles none of the other species in that genus, but is almost identical to the conspicuous brown spotted pattern in *Semblis* (e.g., Pl. I: 21). Species of *Semblis* (q.v.) are widespread in Asia, and the possibility exists for sympatry at some time with *O. soochowica*. Whether *O. soochowica* (q.v.) flies by day is not known, but it is a member of a genus in which other species do so.

Aposematic wing colours could be related to a distinct odour emitted by male and female phryganeids when disturbed (e.g., Kimmins, 1956). The source of this odour appears to be drops of viscous fluid emitted from the anal opening; it is possible that the odour could deter predators such as birds, or the fluid might provoke an avoidance reaction if tasted. Most phryganeid adults that I have encountered produce an odour, and it is distinctive in some genera. Adults of *Ptilostomis*, for example, emit an odour suggestive of burnt marshmallows; in *Phryganea* the odour is reminiscent of old cheese. Comparable odour has not been noted for *Oligostomis* or *Semblis*; I have handled few living adults of either genus. However, if the bright, contrast-

ing colour pattern of the wings is part of a warning system directed against predators of day-flying species, offensive secretions could be involved.

Adults in the Asian genus *Eubasilissa* also have brightly coloured wings, but are reported to be entirely nocturnal (Schmid, 1962). Strong odour has been recorded for *Eubasilissa regina* in Japan (T. Ito, personal communication). In all species of *Eubasilissa* a bright yellow band across a dark brown background on the hind wings (e.g., Pl. I: 25) is a highly unusual colour pattern for Trichoptera. Hind wings in almost all Trichoptera, and even in most Phryganeidae, lack prominent colour patterns. Perhaps relevant to the contrasting hind wings in all *Eubasilissa* species is the observation by Schmid (1962) that long, stout setae on the thorax and base of the fore wings of *E. avalokhita* are readily detached and stick into one's fingers when the insect is handled, causing an unpleasant feeling to the skin – clearly an example of urticating setae as a defence against predators. Urticating, detachable setae were not recorded for other Himalayan *Eubasilissa* collected by Schmid, and have not been found in other phryganeids. However, I have examined pinned adults of a number of other *Eubasilissa* species, and all of them have long, straight, sharp, setae on the dorsal warts of the head and thorax, and on the basal portions of the veins of the fore wings. These setae are similar in form to the ones in *E. avalokhita*, and are distinctive from the more slender, curved setae in these areas in other phryganeid genera such as *Neurocyta*, *Semblis*, and *Oligostomis*. Further observations on other species of *Eubasilissa* are required to ascertain whether the setae detach when the insect is seized by a predator. In light of all of these aspects, the conspicuous pattern on the hind wings could be part of a warning system in *Eubasilissa*. If so, the basis for a predator defence system of unique stout, sharp setae and an aposematic colour pattern appears to have been in place in the common ancestor of the *Eubasilissa* species now known. Moreover, if urticating, detachable setae are confined to one or a few species, is the evolution of these conditions to be interpreted as the basic model for protective mimicry (e.g., Rettenmeyer, 1970), or as apomorphic specialization?

Much of this is speculative and subject to further observation of the living insects; but the colour pattern is real enough, and is similar to patterns in Lepidoptera which are interpreted as aposematic. Relevant comparison could be made with underwing moths of the noctuid genus *Catocala*, where contrasting colours on

the hind wings are interpreted as a 'startle defence' against predators when the insect is at rest (Sargent, 1990). Startle display is a secondary defence, usually employed after a primary defensive mechanism such as crypsis has failed to deter the predator, and in *Eubasilissa* could be reinforced by the stout, sharp setae.

Finally, surprising behaviour occurs in the adults of some species of *Agrypnia* when adults run across the surface like a water strider. I have seen this behaviour in *A. straminea*, and similar observations have been recorded for *A. obsoleta* (Brindle, 1957). This behaviour is remarkable because, having passed successfully through the vulnerable period of eclosion from the pupal integument at the water surface, the insects again expose themselves to predation by fish; and this raises a question as to whether in these species the ability to fly is impaired. Similar behaviour was said to occur in *Agrypnetes crassicornis* because the adults are unable to fly (Bray, 1971).

Oviposition

Only a few observations have been made on egg-laying behaviour in the Phryganeidae. Females of *Phryganea grandis* and *bipunctata* were seen to crawl beneath the water surface on vegetation, enveloped in an air film, to deposit eggs (Hanna, 1961). Similar behaviour was recorded for *Yphria californica* (Erman, 1987).

Eggs in most species where they are known are embedded in a clear gelatinous matrix that expands as water is absorbed. In *Phryganea* one end of the elongate egg matrix is fastened to a support; the remainder is extruded around a submerged twig or similar support and the two ends fastened together as a circular wreath. Similar egg wreaths are known in *Agrypnetes* and several species of *Agrypnia* (Silfvenius, 1906; Ulmer, 1925; Balduf, 1939). In most other phryganeid genera, including some of the same species of *Agrypnia*, the egg matrix is deposited in a globular mass on a submerged substrate. Globular egg masses of *Ptilostomis* are sometimes found on damp leaves or logs in the basins of temporary pools in advanced stages of drying. How long the gelatinous matrix around the eggs retains its moisture, and when the eggs hatch, are unknown; but *Ptilostomis* larvae appear in the pool when surface water is restored the following spring (Wiggins, Mackay, and Smith, 1980).

Larvae of *Trichostegia minor* also develop successfully in temporary pools (Iversen, 1971), but the egg

matrix is unique among all other Phryganeidae in its firm, sculptured form (Fig. 22) (I.D. Wallace, personal communication). Differences in the physical nature of the matrix suggests analogy with the spumalin of the Limnephilidae, which disintegrates in a short time in species where eggs hatch in a few days but is firm and resists desiccation for several months in species inhabiting temporary pools (Wiggins, 1973).

Ecological Aspects

After hatching from the egg, first instar phryganeid larvae have some limited ability to swim before construction of the case begins; elevated into the water column by this means, the larvae can be dispersed by natural currents (Bray, 1971).

Feeding habits of few phryganeid larvae have been studied intensively. Gut analyses of late instars in several genera show that the larvae feed primarily on aquatic insects, crustaceans, and worms, although algae and vascular plant fragments were also eaten (Wiggins, 1977, 1996b). Larvae of *Phryganea grandis* fed mainly on higher plants such as *Potamogeton*, but also readily consumed insects; about 10 per cent of the food of *Oligostomis reticulata* was higher plants, and the balance was insects and other invertebrates (Smirnov, 1962). Larvae of *Agrypnia picta* were reported to be destructive of cultivated rice in the Ussuri region of Russia (Martynov, 1935). In a study of the life cycle of *Banksiola crotchii* in British Columbia, Winterbourn (1971) found that early instars fed mainly on filamentous algae, but the final instars were predaceous. This pattern of increasing predation may extend through life cycles in other genera; however, larvae of *Eubasilissa regina* were found to be predaceous in early as well as later instars (Ito, 1988).

Genera of the Phryganeidae can be grouped according to the habitats in which the larvae occur:

ponds and marshes:	<i>Agrypnia</i> , <i>Banksiola</i> , <i>Oligotricha</i> , <i>Phryganea</i>
lakes:	<i>Agrypnetes</i> , <i>Agrypnia</i> , <i>Banksiola</i> , <i>Fabria</i> , <i>Phryganea</i>
cool streams:	<i>Eubasilissa</i> , <i>Neurocyta</i> , <i>Oligostomis</i> , <i>Ptilostomis</i> , <i>Semblis</i> , <i>Yphria</i>

acidic bog pools:	<i>Beothukus</i> , <i>Hagenella</i> , <i>Oligostomis</i> , <i>Oligotricha</i>
brackish coastal waters:	<i>Agrypnetes</i>
temporary pools:	<i>Ptilostomis</i> , <i>Trichostegia</i>

Restriction of larvae of the primitive phryganeid *Yphria californica* to cool streams might imply that other primitive species in this family occur in stream habitats. However, according to the hypothesis of phylogeny proposed for phryganeid genera (Fig. 6), *Trichostegia* is a plesiomorphic genus with larvae in lentic sites, including temporary pools; and *Beothukus*, inferred to be the basal genus of the ring-case group, lives in acidic bog pools.

Finally, from this study of the Phryganeidae, some prospect of the future may be drawn. A number of species are known still from only the original collection, with perhaps one or two subsequent records. These are not unexpected circumstances for remote parts of the globe. It seems likely, for example, that the present fragmentary knowledge of the life history and range of the Himalayan species of *Eubasilissa* and *Neurocyta* will grow in time. Indeed, adaptation of many phryganeid species to aquatic habitats of higher latitude and elevation in remote areas may shelter them to some degree from environmental degradation. And some species, such as the common and widespread *Banksiola crotchii* in North America, are successful ecological generalists.

For some other species the future seems less assured. In Japan, *Eubasilissa imperialis* and *Agrypnia ulmeri* are known only by the original collection and may now be extinct. In Korea, *Eubasilissa signata*, a species previously unrecognized, is known by only a single specimen. In China, to my knowledge, only a single specimen of *Oligostomis soochowica* (q.v.) has been recorded since the first collection of two specimens in 1930. This is a species of unusual evolutionary interest, probably living in cool streams although unknown in the larval stage, and we may hope that somewhere it still survives. These exceedingly rare species may still persist where fortune has conspired to protect a piece of the habitat, as happened for Ginkgo trees. For the insects themselves, no matter how remarkable they may be, there is little understanding or interest.