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No. 149 September 21, 2000

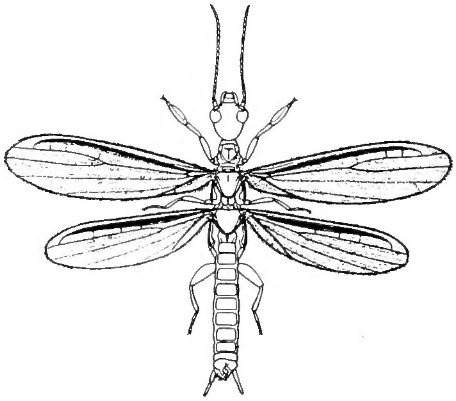
EMBIA

Contributions to the Biosystematics of the Insect Order Embiidina

Part 1
Origin, Relationships and Integumental Anatomy of the Insect Order Embiidina

Part 2
A Review of the Biology of Embiidina

By
Edward S. Ross



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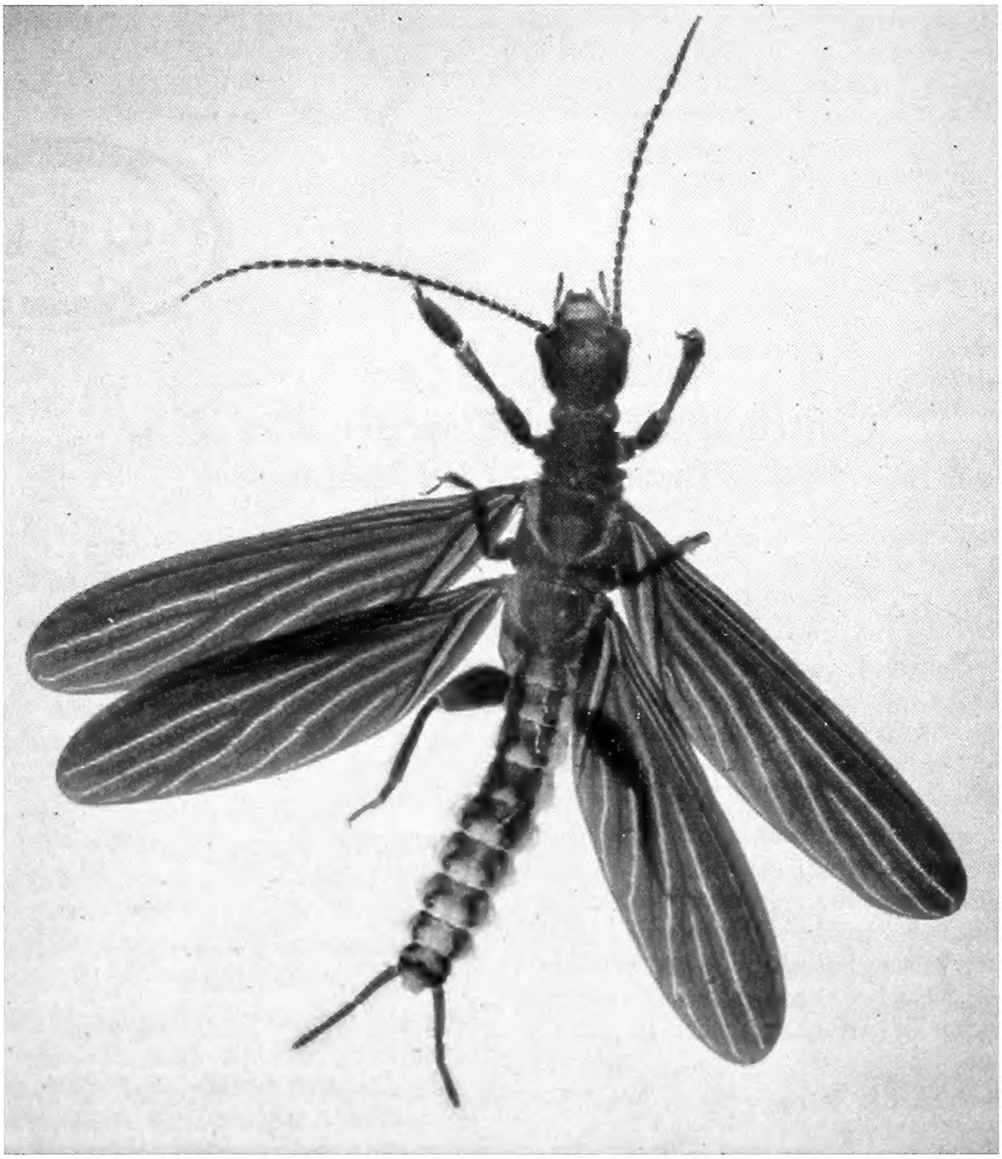

Male *Clothoda* n. sp., (in alcohol, body length 20 mm), related to *C. longicauda* Ross, of Peru, second only to *C. nobilis* (Gerst) as the most plesiomorphic species of the order. Plesiomorphic features include: large size, complex wing venation and almost completely symmetrical terminalia, including exceptionally long cerci. Specimen from upper Napo River region of Ecuador (see Figs. 39A and 40A).

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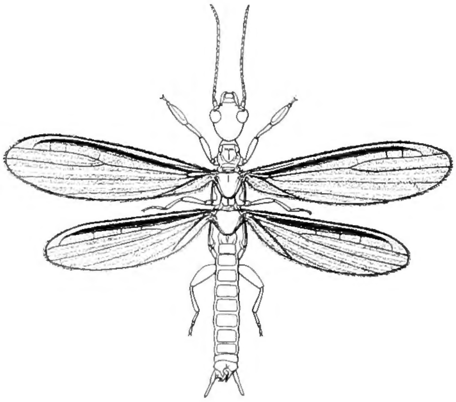

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Part 1

Origin, Relationships and Integumental Anatomy of the Insect Order Embiidina

Preface

This is the first issue of EMBIA, a new publication which, at least initially, will serve as the outlet for my large number of long-shelved manuscripts on Embiidina. Many of these accumulated because I had intended them to be chapters in a series of monographic volumes. However, at this late stage in my life, this will not be possible.

Over the years, of necessity, laboratory research was interrupted by expeditions—one lasting eighteen months—to assemble a meaningful collection of the order. Besides my curatorial duties at the California Academy of Sciences, I was, of course, distracted by many other activities, such as making available to popular and educational media, the rich collection of nature photographs I made during expeditions. Income from such activity paid much of the cost of the fieldwork and, now, a portion required to produce EMBIA.

Recent availability of desktop methods of publishing has encouraged me to discontinue scattering my contributions in a diversity of periodicals. If I live long enough (2000 is my 85th year!), many issues of EMBIA—mostly on systematics—will appear in rapid succession.

I am using Embiidina (Embidina, Hagen, 1861), the first group name applied exclusively to embiids, as the order's name in preference to more recent Embiodea (Kusnezov, 1903) and Embioptera (Shipley, 1904). Embiidina has had important early use in monographs and is now rapidly supplanting the awkward, inappropriate name Embioptera.

Acknowledgments

These will briefly serve this and future issues of EMBIA. This anatomical treatment is in part based on my unpublished Ph.D. dissertation (U.C. Berkeley, 1941). During this early work, I benefited from many contacts with the late G. F. Ferris of Stanford University, as is evident in the style of my drawings. Following four years of Army service in World War II, during which I collected embiids in New Guinea and the Philippines, I began a series of extensive embiid surveys in all major centers of the order's evolution. The resultant collection, now numbering more than 300,000 specimens, representing about 1000 species (75% undescribed) is almost overwhelming.

In this essential fieldwork I was helped by hundreds of individuals, too numerous to mention. Major financial support, in addition to my own funds, came from the John Simon Guggenheim Foundation (Amazon Basin), the National Geographic Society (Africa and Indo-Australia), the National Science Foundation (field and laboratory activities), the Dietz Fund, San Francisco Foundation (Africa), the Schlinger Foundation and Health and Habitat.

Special thanks should be given to my field assistants, who, like myself, participated without salary. They were: Wilda S. Ross, Sandra M. Ross, Evert I. Schlinger (second South American trip), Robin Leech (first African trip), David Cavagnaro and Clark Ross (Indo-Australia), Kenneth Lorenzen (second African trip), Alan Stephen (third African trip) and Mike Irwin (fourth African trip).

Later Robin Leech collected cultures for me especially in southeastern Asia and David Cavagnaro did the same in Central America and Ecuador.

At the California Academy of Sciences, hundreds of embiid cultures were maintained by the late Peter Rubtzoff. Currently, with a Schlinger Foundation grant and my personal funds, the Entomology Department's very able secretary, Julieta Parinas, as off-duty employment, is typing manuscripts for EMBIA and preparing pages for publication. Earlier, also with Schlinger funds, Andrei Sourakov, assisted me in many ways. I am also greatly indebted to Jarmila Kukalová-Peck of Carleton University, Canada for valuable information on wing articulation,venation and Paleozoic relationships of embiids. Norman D. Penny, and Katie Martin, California Academy of Sciences, kindly checked manuscripts and made editorial improvements.

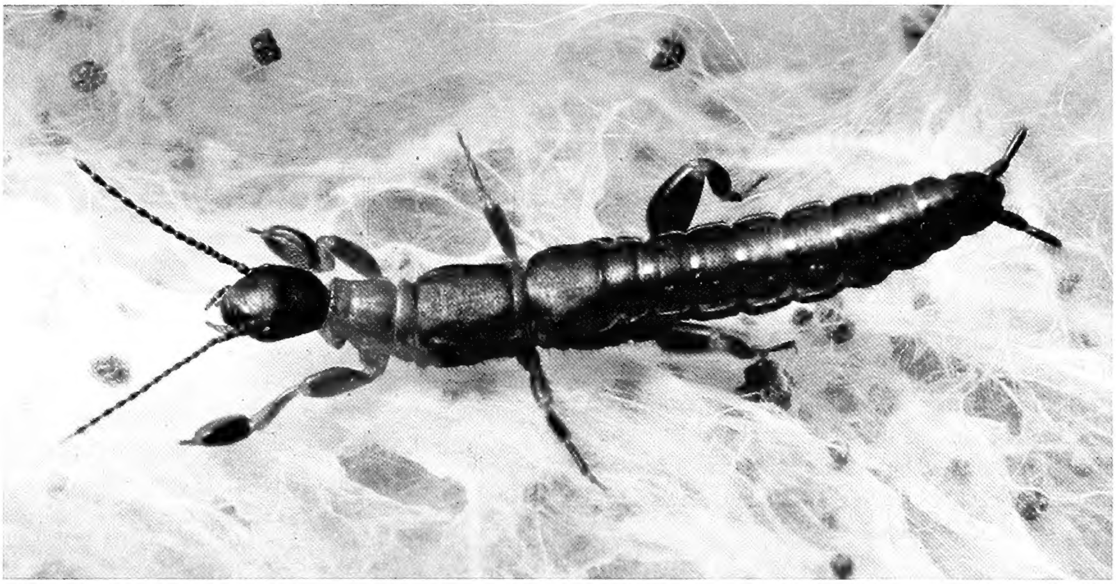


FIGURE A. Except for size and coloration, all female embiids have similar appearance. This photograph clearly shows the spinning foretarsi and the enlarged hind femora within which large tibial flexor muscles motivate quick reverse movement. New genus and species, Oligotomidae. Thailand. Body length 12.0 mm.

FIGURE B. Typical adult male. Like females, alate males are similar in appearance throughout the order. *Antipaluria caribbeana* Ross, Clothodidae. Venezuela. Body length 13.0 mm. Frontispiece shows spread wings.

Origin and Relationships

Summary

No proven pre-Tertiary embiid fossils have been found but, according to Jarmila Kukalová-Peck (pers. com.), there is evidence that Embiidina and what she regards as its sister order, Plecoptera, evolved from a common early Carboniferous ancestor. Tertiary embiid fossils closely resemble extant species—all with the same adaptations easing backward, predator-escape movement in narrow, silk galleries.

This rather "textbookish" treatment of integumental anatomy emphasizes these order-defining structures. Especially important are the peculiar wings of males. To attain ultimate freedom of movement in galleries, females of all species, by the process of neoteny, became apterous (Fig. A).

Much attention is also given to evolution and diversity of the abdominal terminalia of males which are of prime importance in defining species and higher taxonomic categories. Such diversity, as well as other anatomical features, are profusely illustrated. Additional information relating to anatomy will appear in EMBIA, Part 2, "A review of the biology of Embiidina."

Relationships

Based on a phylogenetic assessment of embiid wing venation and articulation, using specimens provided by me, Kukalová-Peck has concluded that embiids comprise a very old order derived from generalized plecopteroid stock and that this stock, represented by Upper Carboniferous fossils, must have served as a stem group for Plecoptera and Embiidina. Incidentally, she regards plecopteroids as the sister group of all other Neoptera.

Earlier, Hennig (1981) speculated that ancestors of Embiidina diverged from the paurometabolan line about the beginning of the Carboniferous period. He believed that the earliest division of Paurometabola was Embiidina and Orthopteromorpha with the latter dividing into Blattopteriformia and Orthopteroidea. Thus, he concluded that embiids have an isolated systematic position and high categorical rank.

Rähle (1970) decided that there is a sister-group relationship between Embiidina and Phasmida. Matsuda (1970) believed that Embiidina and Phasmida are apomorphic sister groups of Plecoptera (Fig. C). Kristensen (1975), while reviewing the phylogeny of all hexapod orders and devoting considerable attention to *Timema* (Fig. D), a generalized phasmid, concluded that determination of the relationship of Embiidina is inconclusive. He believed that further comparative study of the thorax of alate male embiids (Fig. B) and their genitalia might aid determination of the relationship of these orders. Storozhenko (1997) placed Embiidina in the superorder Plecopterodea with orders Plecoptera, Grylloblattida (Fig. E), Dermaptera, and the extinct order Protelytroptera. Phasmids were placed with Orthoptera in the superorder Orthopterodea. The most thorough treatment of orthopteroid relationships is that of Flook and Rowell (1998). They decided that Embiidina is a sister taxon to a clade consisting of Phasmida and Orthoptera.

Origin

Embiid ancestors may have had the following characteristics: (1) A prognathus head with chewing mouthparts and long, filiform antennae, as in extant embiids. (2) Legs moderately long, as in Plecoptera; tarsi five-segmented. (3) Wings present in both sexes, subequal in size and shape except for a relatively large anojugal area in hind wings; veins uniformly sclerotized, none developed as blood sinuses. (4) Male abdominal terminalia symmetrical, cerci more than two segmented. (5) Habitat and food (as today), weathered outer bark and dead leaf litter. (6) Defensive biting weak; repugnant secretions absent. (7) Distribution, equatorial portions of Laurasia, perhaps during the Carboniferous period.

The ancestors probably ventured out of crevices and other protective places to feed and retreated into them to avoid predators and other adversities. It is likely that short hind leg adaptations for rapid backward movement developed during the order's early evolution. Such predator avoidance would have been greatly improved if feeding forays could have occurred beneath a silken cover or within galleries. Such an unlikely adaptation was yet to evolve.

During the Carboniferous period there must have existed embiid stem-group species with the above-described characteristics and habits but, by chance, only in one of them did mutations appear which enabled individuals to spin silken coverways using highly efficient "tools"—the basitarsi of their forelegs.

One may well question, as with many other "threshold innovations," how the initial mutation could have been effective. It may be that a single mutation might have simultaneously modified each of the many secretory pores on the plantar surface of the basal segment of the foretarsi. If this had happened, the quantity of silk immediately might have been sufficient to produce at least crude predator-barriers extending outward from crevice retreats, or for crevice coverage during vulnerable periods such as ecdysis, or brood development.

Offspring of the mutant individuals could have survived to reproduce in greater numbers, especially, as is likely, the brood had remained together and mated incestuously within their parent's "nest." Over time, through natural selection, the secretory cells became multiple, elaborate internal glands while the derm evaginated to produce associated tubular, seta-like ejectors (Figs. 19, 20). This now-universal ensemble has enabled all instars of all species of the order to extend their feeding range within tubular galleries, often enhanced in bark inhabiting species by an additional sheet-like covering.

The tubular form of the galleries, sized to fit the maker, is responsible for specializations which define the order, as follows: (1) A linear, supple body with short legs. (2) Prognathism. (3) Greatly enlarged hind tibial flexor muscles motivating rapid backward movement in galleries. (4) Reduction of wing-snag by flexibility resulting from desclerotization of most wing veins. (5) Compensating ability to stiffen wings for flight by blood pressure in sinus veins—especially in the anterior radius (RBS). (6) Universal apterism of females, and males of some species, through neoteny—the ultimate adaptation for improving backward movement within galleries.

Fossil record

The few fossils which unquestionably represent Embiidina are modern forms from Tertiary formations and, therefore, useless for tracing the origin and early evolution of the order. Fortunately, however, much can be learned from extant, plesiomorphic species such as Amazonia's *Clothoda nobilis* (Gerstaeker) and *C. longicauda* Ross. Also, even without fossils, one can postulate a great age for the order because it must have fully evolved its order-defining features, its major higher taxa, and wide distribution on Pangaea long before its fragmentation. The order's specializations are much too complex to have evolved *de novo* on each separated tectonic plate.

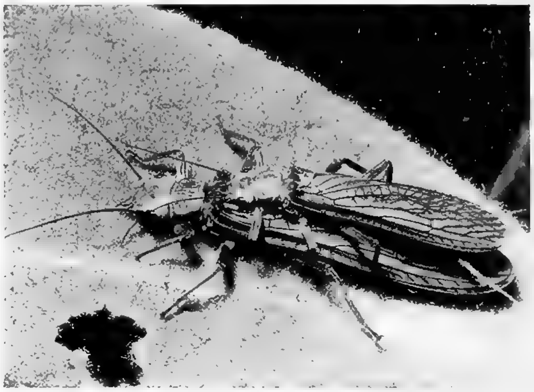


FIGURE C. Paired stoneflies (Plecoptera), *Acroneuria californica* (Banks) from northern California. Although there are vast anatomical and biological differences between modern Plecoptera and Embiidina, it is believed that the two orders diverged from the same stock during the Carboniferous period. The copulatory positions are very similar but in Plecoptera there are no adaptations for reverse or rapid movement.

FIGURE D. Adult male of *Timema californica* Scudder (Phasmida), from central California, on foliage of live oak. Its Paleozoic ancestors have been considered possible relatives of those of Embiidina.

FIGURE E. Adult female of *Grylloblatta campodeiformis occidentalis* Silvestri (Grylloblattida) from Mt. Baker, Washington (1280 m). Kukalová-Peck (pers. com.) on the basis of many characters concluded that grylloblattids belong to the blattoid line.

Pretertiary fossils

Zeuner (1936), treating his *Germanoprisca zimmermanni*, a new species from a European Permian formation, concluded that Embiidina were derived from the family Lemmatophoridae of the Protoperlaria. These fossils belong to the plecopteroid stem group which possess similar, generalized wing venation and attachment. No pretertiary fossil shows blood sinus wing veins which characterize embiids but, of course, much of the order's evolution must predate the appearance of sinus veins.

In 1937 Tillyard established the new suborder Protembiaria (he used Embiaria as the ordinal name) and family Protembiidae to include his *Protembia permiana*, the type specimen of which was found in Elmo deposits, Lower Permian of Kansas. Shortly thereafter, Zalessky (1937) named two additional species in his new genus, *Tillyardembia,* from related Russian Permian deposits. Later, Carpenter (1950), after re-examination of Kansas specimens, decided that they do not represent Embiidina, and assigned *Protembia* to the cumulative order Protorthoptera. His figure of *P. permiana* indicates that it was a rather long-legged insect without any of the specializations characterizing Embiidina.

In 1958 Martynova proposed a new embiid suborder, Sheimiodea, family Sheimiidae and species, *Sheimia sojanensis (*Figs. 1, 2), based on a winged fossil from the Upper Permian of Russia. Through the kindness of Dr. Frank M. Carpenter I was able to closely examine this specimen which, with two apparently conspecific individuals, is preserved in a piece of very hard, light tan rock. Anatomical details are not as clear as represented in Martynova's drawings (Fig. 2) and I can see no evidence that these fossils represent Embiidina. The head and antennae of *Sheimia* are embiid-like but the caudal cranial margin appears to be more transverse, instead of rounded, as in embiids. The apparently quadrate prothorax of *Sheimia* is embiid-like but this character isn't peculiar to embiids. The pterothorax is well sclerotized and broad, not unlike that of embiids, but the scuta, figured as triangular by Martynova, are not clearly so in the type specimen. The meso- and metathorax, however, seem to be nearly equal in size and this embiid feature is associated with wide-spaced, nearly equal (homonomous) wings.

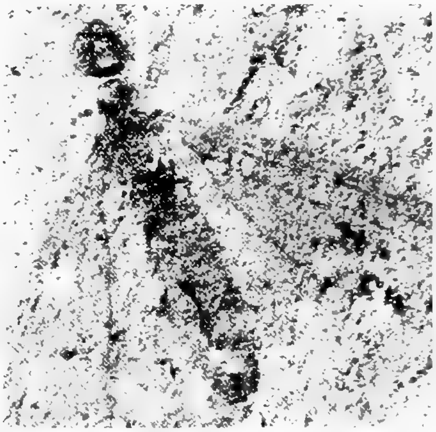


FIGURE 1. Holotype of *Sheimia sojanensis* Martynova, Upper Permian of Russia.

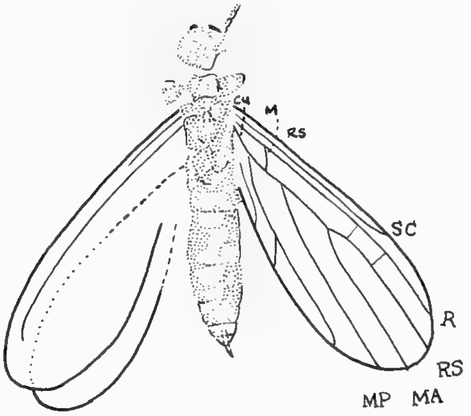


FIGURE 2. Martynova's representation of the holotype of *Sheimia sojanensis* (Redrawn by Ross).

Martynova's drawing (Fig. 2) indicates that the femora of the foreleg are greatly enlarged (an embiid feature), but it is not certain that the faint impressions she regarded as femora are indeed femora. The wings are quite embiid-like but broader than typical. The venation, although delineated as definite in Martynova's drawing, is obscure, yet there is a slight indication in the specimen of the radius-border lines which are peculiar to embiids. If indeed these were present, this would be a strong basis for assigning *Sheimia* to Embiidina, or a related extinct order.

The fossil's abdomen is broad, perhaps due to pressure of fossilization, and appears to be weakly sclerotized with a darker apex. Unlike embiids, this apex tapers to an acute point and Martinova's drawing indicates an ovipositor-like internal (?) structure, but this could simply be a disconnected basal portion of a filament-like cercus. She also indicated what appears to be fragments of multisegmented cerci in the vicinity of the abdomen's apex.

After serious consideration I have concluded that *Sheimia* is not an embiid. Carpenter (in litt, 1965) drew the same conclusion and later (1976) placed Sheimiidae and four other "problem" families in "Families of uncertain ordinal position." However, there is a strong possibility that it belongs to the embiid stem group.

Tertiary fossils

Perhaps the oldest Tertiary embiid fossil, *Burmitembia venosa* Cockerell (1919) is a very small male (body length 4.4 mm) preserved in amber (Burmite), possessed by the Paleontology Department, British Natural History Museum. Some workers, e.g., D. A. Grimaldi (pers. com.), consider Burmite to be clearly Eocene but others, e.g., A. P. Rasnitsyn (pers. com.), believe it to be late Cretaceous. The fossil, definitely an embiid, was treated in detail by Davis (1939). I briefly examined the specimen, didn't have time to study it in detail, but I have decided to assign it to a new family. Contrary to expectations, the species is highly apomorphic.

Several embiid specimens have been encountered in Baltic Amber (Eocene?) and, fortunately, two of these are adult males clearly exhibiting the terminalia. Thanks to the Geologischen Staatsinstitut in Hamburg, I have studied these specimens and suspect that they are the cotypes of *Embia antiqua* Pictet (1854). I assigned the species (Fig. 36) to a new genus, *Electroembia* Ross (1956), and concluded that it is more closely related to *Rhagadochir* Enderlein and related genera of equatorial Africa than to *Embia*. Apterism and melanism of these males suggests that the climate during the period of entrapment in amber was characterized by a long, dry season. In the Mediterranean region there are several species of *Embia* and *Haploembia* with black, apterous males with general appearance almost identical to *E. antiqua* and can be distinguished only by examination of the abdominal terminalia and hind tarsi.

Two small, alate embiids, collected in Chiapas Amber, Mexico, are new species of the large modern genus *Oligembia* Davis, family Teratembiidae, of which there are many species in the American tropics. Chiapas Amber has been "positively dated as Oligocene and Miocene with possibility in some areas of 'Eocene epoch' " (Hurd, Smith and Usinger, 1958).

More recently embiids have been collected in Oligocene amber mines of northern Hispaniola (Dominican Republic). Most of these fossils, some in my collection, are winged males of the genus *Oligembia*. One of these in the American Museum's collection became the holotype of *Oligembia vetusta* Szumik (1994). Other Dominican Amber embiids belong to two new genera in Anisembiidae, one of which is represented today in Hispaniola, southern Mexico and Central America.

Embiids preserved in East African copal, such as *Oligotoma westwoodi* Hagen, represent modern species of the family Teratembiidae.

The Eocene-Oligocene alate male fossil, *Embia florissantensis* Cockerell, found in Florissant (Colorado) volcanic shales, a large alate male of the family Embiidae, has been assigned to a new genus, *Lithembia* Ross (1984). The all-important characters of the male terminalia are indistinguishable.

According to A. P. Rasnitsyn (pers. com.), of Moscow, the Miocene shale fossil *Clothonopsis miocenica* Hong and Wang (1993) isn't an embiid but has proved to be a bibionid fly, perhaps genus *Plecia*.

Integumental Anatomy

> "Anatomy is what you see with your
> eyes, morphology is what you ***think*** you
> see with your mind."
> R. E. Snodgrass

> It follows that the appropriate title of this
> work should be the anatomy ***and***
> morphology of the Embiidina.

Introduction

For this simple exposition of the basic integumental anatomy of Embiidina, a representative species of the order, an *Oligotoma,* was selected because three species of this genus have been widely distributed in commerce and, because adult males are attracted to light, they are most frequently collected and available for comparative study.

Adult females throughout the order are neotenic and thus, except for their paragenital sternites, internal genitalia, size and coloration, are similar to early stage nymphs. Probably due to advantageous endocrinal controls curtailing development, most features of adult females are those of an early instar nymph before even a trace of developing wings appear (Fig. A). As will be discussed later, intermediate stages of neoteny have evolved in adult males of many species, as is shown by all ontogenetic stages of wing development from complete aptery (Figs. 34, 35, 36) through various stages of wing pad growth, brachyptery and microptery. Fully formed wings, however, are the most apparent characteristic of adult males of the majority of species (Figs. B, 53). The alate condition is associated with a full compliment of adult embiid anatomical features, many of which certainly must also have been possessed by adult females during early evolution of the order.

Because of the high degree of specialization for silk gallery life exhibited by adult females, it is safe to assume that such features evolved not especially to foster adult male survival but instead to secure and prolong the lives of the more essential adult females. Being short-lived and needing only to quickly disperse and inseminate females, males faced less selective pressure toward perfect adaptation to gallery life and consequently are most likely to retain structures, such as wings, which are no longer of critical importance in survival.

Among other plesiomorphic characters, adult males also possess structures which aid location of mates and insure successful copulation. Because of their more complex anatomy, and consequent greater value in systematics, I will devote most attention to the anatomy of adult males.

Methods

To fully expose sclerites which are partially or entirely concealed in integumental folds, almost all studied specimens were macerated in heated 10% potassium hydroxide (KOH) and cleared of body contents. Whenever possible drawings were made of specimens positioned in alcohol. At times acid fuchsin stain was used to intensify details. Distortion of position of sclerites is inevitable in KOH-treated specimens and this must be considered during interpretation of certain drawings. Unless otherwise credited, all of these were made by me, based on camera lucida and photographic outlines. I adopted the style of R. E. Snodgrass (1935) with membranous areas stippled and degree of sclerotization represented by thickness of lines and some shading. Usually setae are omitted. The figures are intended to be self-explanatory and the text only a guide and a means of calling attention to the functional or phylogenetic significance of structures. Unless otherwise indicated, they are based on specimens of *Oligotoma nigra* Hagen.

Knowledge of musculature is vital to any study of integumental anatomy, but I haven't had the time nor background to make such a study. Therefore, I asked Edward L Smith to at least investigate the musculature of the abdominal terminalia of adult males and some females. Some of this research has been applied by me in the present paper. Perhaps his complete research will be published separately.

I am indebted to Christine A. Nalepa, a cockroach specialist, for useful suggestions concerning my treatment of embiid wings, their reduction and loss.

While concurrently producing Part 2 of EMBIA which reviews the biology of Embiidina, I became increasingly aware of the difficulty of separating behavior from anatomy—especially in the case of embiids where there is such a close relationship between structure and function, as is most apparent in my treatment of embiid wings. Consequently, some information in this paper will be repeated in my review of embiid biology.

Head

The head of embiids is orthopteroid in type, basically similar in all stages of all species (Fig. 3). Due to the universal vegetative diet of nymphs and adult females, there has been no great need for head specialization and diversification. Only in adult males are there significant cranial and mouthpart specializations and these relate to the habit of males of many, if not all species, to grasp the female's head with the mandibles prior to, or during, copulation. Except in highly neotenic males, guts of adult males are empty and thus their mandibles aren't used for eating, instead being used only as mating claspers and for cutting an entrance into a gallery occupied by a receptive female.

Non-neotenic males also have varied cranial and eye structure as well as longer more sensory antennae (Figs. 4, 34). Such characters probably are related to a male's more frequent movement outside of galleries to disperse and locate a mate. Due to neoteny, adult females retain the nymphoid head anatomy of early instars of both sexes (Fig. 3C, D) but, as

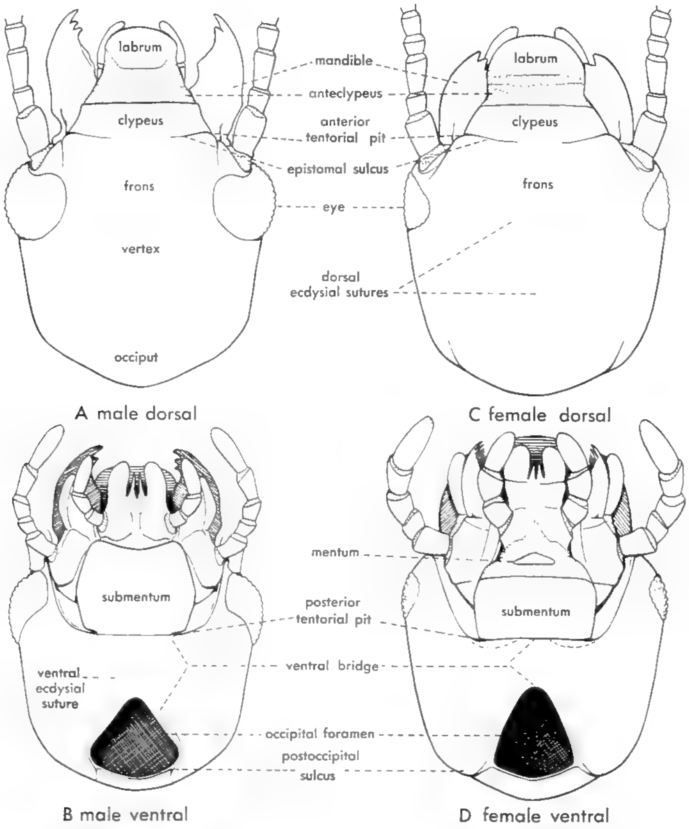


FIGURE 3. General structure of head of A, B adult male and C, D female of *Oligotoma nigra* Hagen.

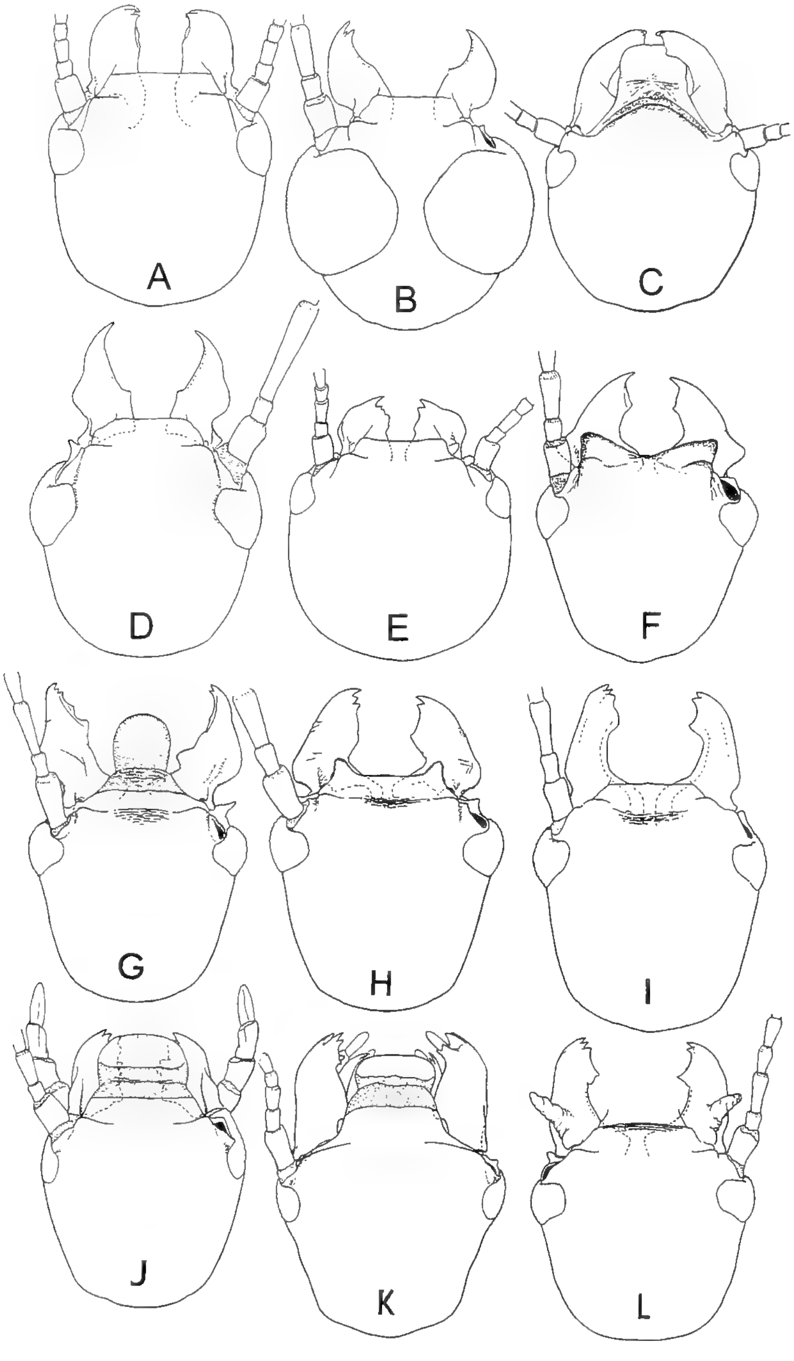


FIGURE 4. Diversity of heads of adult males (labrum not figured in some species). A. *Embia.* B. New genus Embiidae. C. *Enveja.* D and F new genera, Anisembiidae. E. *Pelorembia tumidiceps* Ross, Anisembiidae. G. and H new genera in a new family. I. *Oligembia* n. sp., Teratembiidae. J. *Australembia*, Australembiidae. K. *Metoligotoma*, Australembiidae. L. New genus and species, Oligotomidae.

will be later discussed, males of some species also have similar nymphoid heads due to neoteny. However, at least in one exceptional case, a species of *Metoligotoma* Davis, adult males with completely nymphoid heads appear as intraspecific variants in populations which include males having an adult-type head, normal for the species.

The head of *Oligotoma nigra* Hagen, as in all other species of the order, is strongly prognathous, angled downward at about 35° (Fig. 13). Obviously, prognathism, an adaptation easing movement in narrow galleries, causes eyes, antennae and mouthparts to have a functional forward position. There is also obsolescence of most cranial sutures.

A feature apparently associated with prognathism is the universally-present, broad sclerotic bridge between the posterior tentorial pits and the occipital foramen (Fig. 3B-D). In many species this bridge, here termed "ventral bridge," is so strongly developed that all traces of its origin are lacking. In males of *Oligotoma*, however, and more so in those of certain other genera, there is evidence that much of this bridge is due to postoccipital sclerotization. The possibility that the medial portion represents a true gula (a posterior extension of the submentum) was considered. However, in females and nymphs the submentum is clearly delimited basally by a transverse suture between the posterior tentorial pits and thus the bridge is not continuous with the submentum. A sclerotic bridge behind the posterior tentorial pits frequently occurs in other prognathous insects but in such cases a true gula is present. To my knowledge, the occurrence of a non-gular bridge in this position does not occur in any other order.

Sutures related to original head segmentation are practically obliterated on the venter (posterior portion) of the head. The post-occipital sulcus can be traced, however, by lines on either side of the occipital foramen and these diminish anteriorly. In males there is a slight indication that they parallel the extremities of the mesal extension of the posterior cranial walls on the ventral bridge. They might therefore be postoccipital.

The occipital foramen (Fig. 3B-D) is triangular and its margins, although thickened, are not especially modified for contact with the first cervical sclerites midway on each side. The lateral margins are more thickened posteriorly and gradually form a small internal ridge extending around the posterior end of the head to the dorsal surface where it diminishes. This line coincides with the outer margin of the long lateral maculation of the pattern visible in the young and adults of certain species.

In adult males, the dorsal (frontal) surface of the cranium usually lacks sutures (Fig. 3A), but in females, lines of weakness ("coronal sutures") serving ecdysis, appear as very faint unpigmented lines extending forward to the middle of the dorsum of the head where they fork as two broadly divergent, equally-faint lines (Fig. 3C). These terminate just before reaching the bases of the antennae.

Both dorsally and ventrally, the cranium often has a characteristic pattern which appears to be quite uniform throughout the order and is visible in nymphs, and adults of some species, as lighter pigmented areas. Melanization of most adults generally completely obscures these paler areas, but close examination reveals that they can still be traced as areas lacking setae and reticulate in sculpture. This pattern correlates with interior attachment of bundles of mandibular muscles. Another frequent pattern is a diffused, often golden, transverse "cloud" from eye to eye on an otherwise dark head. This overlays the brain and may have some special function, one perhaps related to light perception, or to mating.

The anterior tentorial pits open dorsally as transverse, short slits situated in the epistomal sulcus just behind the anterior articulation of the mandible. The epistomal sulcus is represented laterally only, but serves to distinguish the clypeus from the frons. The anteclypeus (Fig. 3A, C) is entirely membranous and limited anteriorly by a transverse fold.

The antennal socket is surrounded by a basal flange delimited by an incomplete antennal suture. The space between the eye and the mouth cavity is greatly reduced and its sutures are obsolete.

The tentorium of the male is here figured from the anterior and posterior aspects (Fig. 5). The anterior and posterior arms unite medially and form a thin, quadrate corporotentorium. The anterior arms bear small dorsal branches which appear to be vestigial. The posterior arms are dilated and join the very large crassa, or hypostoma, and the inwardly-slanting lateral flanges of the submentum. In males these lateral flanges are heavily sclerotized, whereas in females they are submembranous. The general structure of the tentorium appears to be constant throughout the order. The posterior tentorial pits are situated on either side of the base of the submentum.

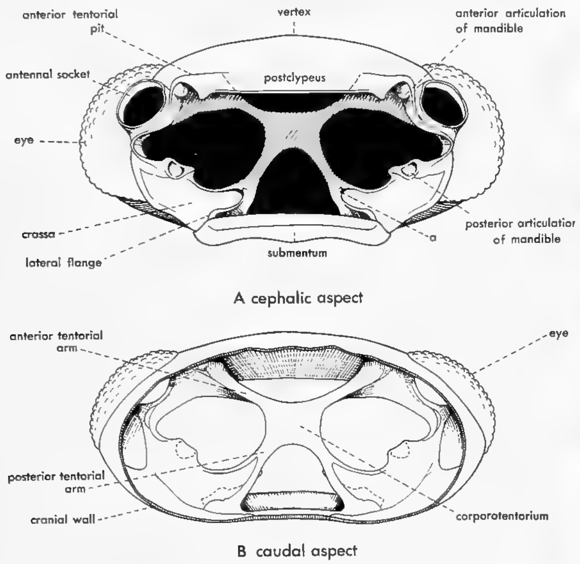


FIGURE 5. Tentorial structure of adult male of *Oligotoma nigra* Hagen.

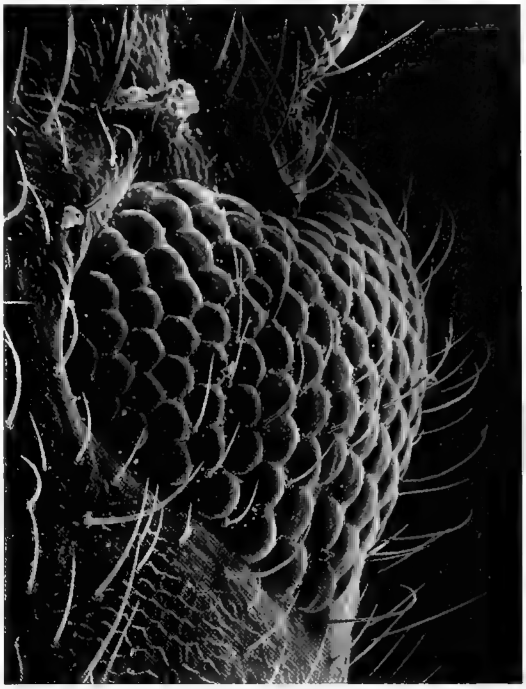


FIGURE 6. Scanning Electron Micrograph photo of eye of adult male of *Oligotoma nigra.*

Eyes

Paired compound eyes are the only organs of sight or light perception, ocelli being absent in all species of the order. The eyes of adult males of *Oligotoma nigra* (Fig. 6), as in those of many other non-neotenic species, are relatively large, inflated, reniform and composed of numerous, large, convex facets. The greater development of eyes in males usually correlates with the presence of wings and thus activity outside of galleries. Some alate males, however, have small eyes. Very large, inflated eyes with prominent facets, occur in males of many pale species which disperse nocturnally. This combination of pale or somber body coloration and large eyes is, of course, a condition found in many nocturnal insects, as well as in nocturnal vertebrates.

In females and nymphs throughout the order the eyes are very small and have relatively few facets. Such a condition in adult females is nymphoid and is associated with almost complete confinement in silk galleries where activities are probably guided more by touch than sight. Males of well-pigmented species, especially those which disperse diurnally, may have smaller eyes often with dark pigment in the facet interstices. In a few species the head is nearly holoptic; the space between the eyes being very narrow and the post-ocular cranial bulk greatly reduced (Fig. 4B).

Antennae

The antennae of both sexes are basically similar throughout the order. They are annulated and filiform, thus similar to those of *Grylloblatta* and numerous other orthopteroid insects.

An antenna consists of a scape, a pedicel and many flagellar segments (flagellomeres). Few specimens can be found with a complete number because terminal segments frequently are broken or bitten off by other embiids. However, these may be partially regenerated if lost during an early nymphal instar. In general, the number of flagellar segments seems to correlate with body size; the largest number, about 32, is present in adults of large species and the smallest number, as few as 11, is found in tiny species of the family Teratembiidae. Adults of average size, such as those of *Oligotoma* spp., tend to have about 19 flagellar segments. Antennae of the first instar of all examined species are nine-segmented, while those of the second are twelve-segmented. This increase is accomplished by the basal flagellar segment dividing into three.

Antennae of adult females are nymphoid and similar throughout the order. However, non-nymphoid adult males show consistent intergeneric and interspecific variation useful in classification. Such characters involve segment proportions, type of vesture and color. In many genera, and in some congeneric species, the apical segments may be abruptly and consistently white in both males and females. In many genera, e.g., *Archembia* Ross, females have white-tipped antennae while males of most species of this genus have uniformly brown segments. Great antennal length in large males is due in part to increased segment-number, but also to segment-elongation.

As is to be expected in insects that venture into open environments to locate a mate, antennae of males have the greatest sensory function. Antennae of males of two species were studied by Slifer and Sekhon (1973) with specimens provided by me. They reported at least five types of sense organs on flagellar segments of *Ptilocerembia* sp. which, incidentally, has the most hirsute antennae found in the order.

They concluded that the large sense organs are "thick-walled chemoreceptors" (or contact chemoreceptors). Each has about five neurones at the base and extend their dendrites to the tip of the hair within a long cuticular sheath, at which point they are exposed to air.

Mouthparts

The mouthparts are typically orthopteroid and need not be described in detail. The labrum (Fig. 7) is a simple, semicircular flap, slightly apically emarginated, and membranous medially along its anterior margin, and clothed with setae. The ventral surface, or epipharynx, is entirely membranous and characterized by two widely spaced, nearly parallel rows of inwardly-directed short setae. The surface between these rows has a fine reticulated structure which continues on the dorsal lining of the esophagus. Well-developed tormae are located near each basal angle of the labrum, and extend well within the anteclypeus. The hypopharynx (Fig. 8) is large, similar to that found in other orthopteroids. Its dorsal (anterior) surface lies against the epipharynx and is clothed with dense, scale-like setae.

Mandibles of nymphs and adult females (Fig. D-F) are stout, asymmetrical, and have large, multidentate grinding surfaces well adapted for chewing coarse food. The points of dorsal (anterior) and ventral (posterior) articulation are located medially in nymphs and females, whereas in adult males they are located near the caudal angle of each mandible.

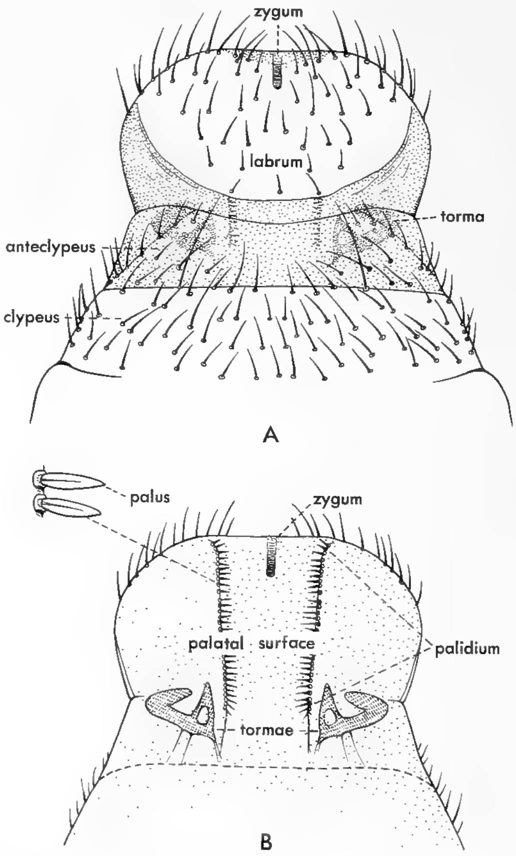


FIGURE 7. Labrum of female *Oligotoma nigra*. A. dorsal B. ventral

The mandibles of adult males (Fig. 9A, C) generally greatly differ from those of females, as well as those of their nymphs the mandibles of which are identical to those of adult females. These differences are quite constant within a taxonomic group and thus important in systematics. Unlike those of females, mandibles of males are often elongate, rather flattened and without grinding surfaces. Their teeth are few in number and located apically, usually with three on the left mandible and two on the right. At times these apical, or incisor teeth, may be fused and/or curled ventrad (as in the genus *Embia* Latr.). In all Anisembiidae, and certain other taxa, there is fusion of the subapical teeth with the apicals.

In males of many species the inner face of each mandible has a prominent, acute point sub-basally. This, which may be the proxadental cusp, separates the incisor area from the molar area, which is often greatly projected mesad. Between the incisor teeth

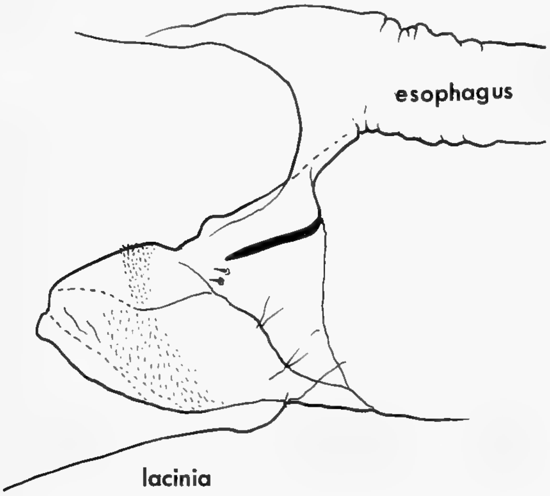


FIGURE 8. Lateral aspect of hypopharynx.

and the proxadental cusp the surface may be smoothly, inwardly arcuate but often it is produced as an obtusely angulated point, here termed medial flange. The outer, sub-basal angle of the mandible is occasionally extensively produced. The diverse forms of male mandibles are illustrated in Figure 4, as well as in my publications dealing with embiid systematics.

Mandibles of adult males usually differ so greatly from a type adapted for a herbivorous diet that some workers erroneously concluded that they must be used for predation. Actually, the peculiar mandibles of many species function as claspers to control the head of females during copulation. Only in a few species with highly neotenic males are the mandibles ever used for mastication of food because males normally stop eating during the penultimate instar. It is possible that the mandibles of males may be effective in warding off small predators and rival males. They are also useful for snipping an entrance into silk galleries likely to contain a prospective mate.

Females and nymphs regularly use their mandibles to pick up and place fecal pellets outside of gallery walls. They are also used by ovipositing females of some species to pulverize feces and habitat materials for inclusion in a paste deposited around eggs. Such pulverizations may also be deposited on the outer surface of a silk labyrinth to enhance or perhaps obscure the protective cover. The mandibles may also be used to gnaw burrows into the habitat—soil, bark, dead twigs, etc.

The maxilla (Fig. 10) have no peculiar features and are similar in both sexes throughout the order. The maxillary palpi of adult males of *Australembia* Ross, however, are exceptionally large and may assist mandibular clasping during copulation. The base of the cardo articulates well within the head.

The labium (Fig. 11), although generalized, exhibits interesting modifications. The glossae once were believed to be supplementary spinning organs (Enderlein, 1912). This is not the case, however, and no trace of labial gland openings have been found associated with them. The mentum is greatly reduced and is almost obsolete in adult males of many species. In neotenic, apterous adult males and females, as well as in nymphs, it is a small triangular sclerite.

The submentum is a well-developed broad plate, weakly sclerotized and uniform in females and young, but in adult males of *Oligotoma* Hagen (Fig. 11A) and those of many other genera, it is heavily sclerotized with the anterior and lateral margins folded inward, or inflexed with lateral flanges and fused basally to the posterior tentorial arms as described before. In some genera, such as *Antipaluria* Enderlein, the submentum of the male is deeply bifoveate and these depressions may be a source of glandular secretions associated with mating. In *Archembia* Ross the surface may be flat and from which tiny pores produce a secretion that becomes a white coagulant around setae in alcohol-preserved specimens. Males of some species of a new southeast Asian genus have a peculiar, rugose, conate submentum but in other species of the genus the structure is normal. The posterior tentorial pits are located at the proximal angles of the submentum and are separated from the occipital foramen by the extensive ventral bridge.

Cervix

The large size of the cervical sclerites (Fig. 12 B, C) appears to be related to vigorous head activity. For example, strong musculature is involved in head-pushing to shape silk galleries as they are spun and adult males of many species need cervical strength to pull a female's head to the right in a mandibular grip prior to copulation. Adult males are also able to turn their heads at surprisingly extreme angles as, in a mantid-like manner, they follow the movements of an observer, most often by males resting on walls under a light.

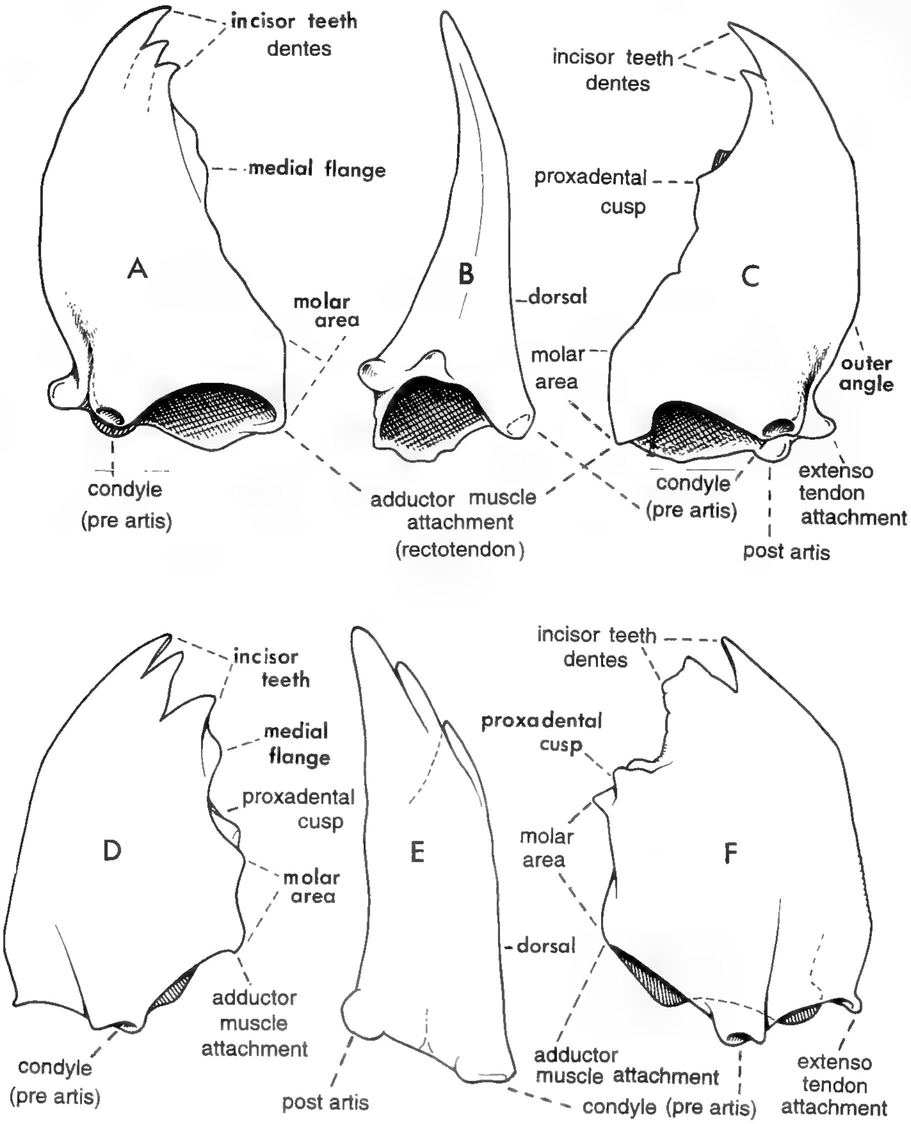


FIGURE 9. Mandibles of adult male (A–C) and adult female (D–F).

The first lateral cervical sclerites contact submedial points on the sides of the occipital foramen but these points are not especially modified to receive such contact. The outer edge of each cervical sclerite is thickened and its anterior apex bears a small hair plate. In the head's normal position, about 35° downward from the horizontal axis (Fig. 13), the second lateral cervical sclerites are almost perpendicular to the longitudinal axis of the first. This angle becomes obtuse as the head projects forward and is thus more horizontal. Each second lateral cervical sclerite articulates with a small, medio-ventral projection of the adjacent pronotal flange.

In the ventral neck membrane, immediately before the prosternum, are located small sclerites; the anterior of which is smaller than the posterior (Fig. 12B). Crampton (1926) designated the first as an intersternite and the second as the presternum (an anterior detachment of the prosternum). In the present work these are simply designated anterior and posterior ventral cervical sclerites. Ahead of these, between apices of the first cervical sclerites, are two membranous domes which are densely setose in *Clothoda* Enderlein. Similar setose domes are found in membranes lateral to these apices. These are termed lateroventral cervical sclerites.

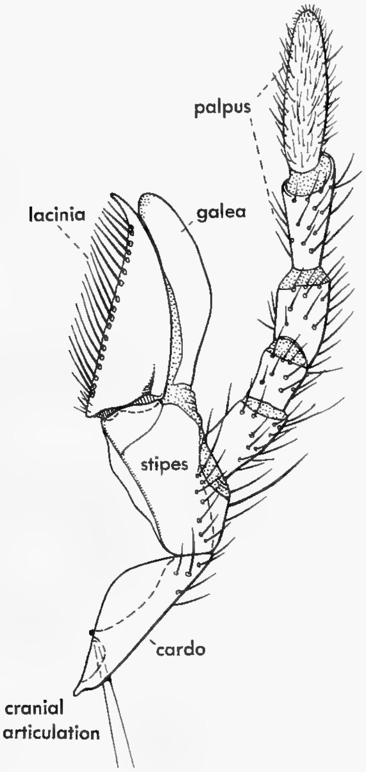


FIGURE 10. Maxilla, adult male.

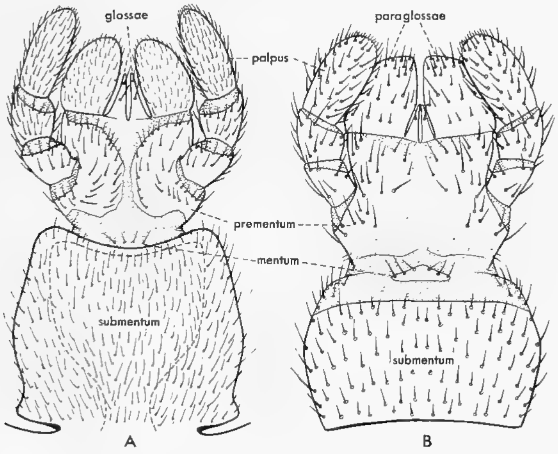


FIGURE 11. Labium, adult male (A), adult female (B).

There is no great intra-ordinal variation in the cervix except in males of certain genera. In *Enveja* Navás the lateral cervical sclerites are especially broadened and this seems to be associated with the need for greater anchorage of large muscles moving an exceptionally large head. In this case the second lateral cervical sclerites are greatly produced mesad, almost touching the presternal sclerite.

Prothorax

The prothorax (Fig. 12A, C), one of the least specialized parts of the body, is similar in both sexes throughout the order; the prothorax of the alate male simply being less robust. The generalized condition reflects a lack of unusual prothoracic involvement in embiid behavior.

The pronotum is unusual, however, in that it is not produced laterally in folds and is usually much narrower than the pterothorax. It is divided across the anterior third by a deep furrow which delimits a narrow anterior part, the prescutum, and a large convex posterior part. The latter is divided medially by a longitudinal suture probably associated with ecdysis. In males the posterior angles are broadly produced caudad as gradually diminishing extensions. Medially, the caudal margin is developed as a small point. In many cases, especially in nymphs and females, the pronotum bears a characteristic pigmented design which lacks setae and is reticulated, as in the head pattern. This design, like that on the cranium's vertex, probably is related to internal muscle attachment. In males of many species the prothorax often is pale in coloration, or reddish in some diurnally dispersing species.

The very clearly-defined straight sutures which form the lateral margins of the pronotum delimit flap-like flanges on either side. These invaginate posteriorly to form two wide-mouthed, pleural apophyseal pits, the apophyses of which are stout, conical and directed caudad at a 45° angle. Submedially, a small ventral lobe is produced against which the base of the second cervical sclerite articulates. Behind this projection a suture extends to the mouth of the apophyseal pit and defines the catepisternite as a distinct sclerite somewhat as in Plecoptera. This sclerite is slightly convex and produced ventrad in the posterior half to form the dorsal coxal articulation. The trochantin is dorsally separated from the catepisternite by a transverse suture.

The prothoracic sternum (Fig. 12B) is a broad, quadrate plate, the posterior angles of which are produced as short truncate processes. Narrow, lateral areas separated by sutures may be subcoxal elements fused to the prosternum. Slit-like openings of the

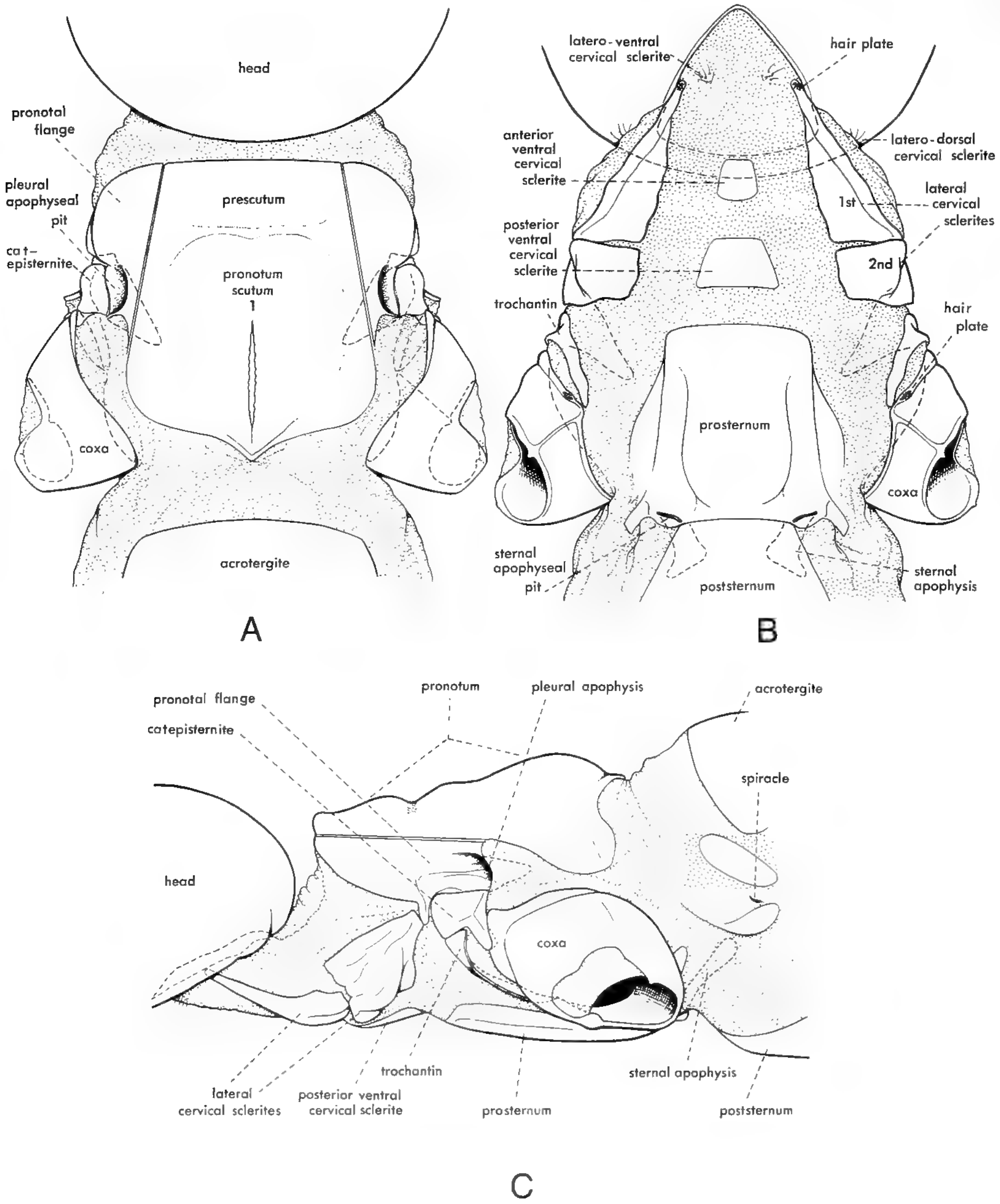


FIGURE 12. Structure of prothorax, adult male. A. Dorsal aspect, B. Ventral aspect, C. Lateral aspect. *Oligotoma nigra* Hagen.

sternum's apophyseal pits are located on either side of the posterior margin. These are transverse and develop internally as short, terminally-dilated, flat apodemes. The broad area between the inner ends of the apophyseal slits represents the point of basal contact of the very large first poststernum which is fused to the prosternum.

A detailed treatment of the prothorax, including its musculature, will be found in Bitsch and Raymond (1970).

Pterothorax of males

The pterothorax of alate males (Figs. 13–16) exhibits a number of very interesting features. Unlike

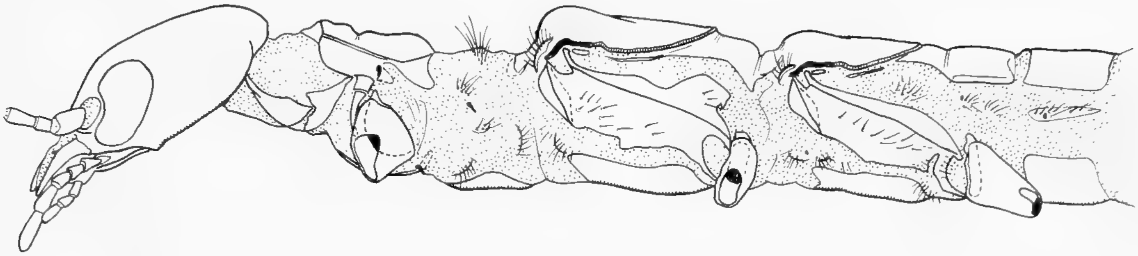


FIGURE 13. Lateral aspect of head and thorax of a male showing angle of head in repose. Somewhat distended as a result of KOH maceration. *Oligotoma nigra* Hagen.

corresponding somites of females which are rounded and distended by a large, food-filled crop, these somites are dorso-ventrally depressed and transversely rectangulate in cross-section in alate males.

Males of *Oligotoma nigra* have a rather apomorphic type of embiid pterothorax but adequately represent general features. Most prominent is the large, elongate, triangular mesonotum (scutum 2) which abruptly arches downward anteriorly forming a nearly vertical prescutum terminating in a short phragma. The acrotergite (anterior notal plate) is quite similar to that of females and nymphs, being separated from the antecostal suture by a membrane. The anterior notal wing processes are prominent, strongly developed, with deep submembranous emarginations behind them. The posterior notal wing processes, located not far behind the former, are nearly obsolete, being represented only by the anterior angles of very weakly-sclerotized lateral flanges of the mesonotum. The mesonotum is rather strongly arched in cross-section and the lateral flanges are limited mesad by a low point of the sides of this arched portion and hence are directed upward. In apomorphic families, such as Oligotomidae, Anisembiidae and Teratembiidae, these lateral areas are very weak. In plesiomorphic groups, such as Clothodidae and Embiidae, they are more heavily sclerotized. When wings are in repose, a certain amount of inward bending occurs along this area and the tendency for its weakness may be an adaptation for life in narrow galleries, for such bending permits the wings to rest more directly over the body (Fig. B). Otherwise, wing-edge projection beyond the body's lateral lines could cause disadvantageous friction with adjacent gallery walls. The most peculiar feature of the pterothorax is the very great reduction of the scutellum which causes the axillary cords to almost meet on the mid-dorsal line. To my knowledge, these are the longest axillary cords to be found among insects.

The acrotergite (anterior notal plate) of the mesothorax is exceptionally large and closely contacts the scutellum and the metathoracic prescutum. It is divided medially by a longitudinal membranous cleft. Small, elongate sclerites located on either side beneath the axillary cord probably represent isolated rudiments of the anterior angles of the acrotergite. Essentially, the metanotum has the same structure as the mesonotum. It differs chiefly in its shorter proportions and the fact that its acrotergite forms a bridge between the scutellum and the first abdominal tergum to which it is fused.

In males the pterothoracic pleura (Fig. 16B) are, of course, more extensively developed than in females. A peculiar feature is the nearly vertical prealar suture near the anterior end of the episternum which delimits a small sclerotic area (prealar sclerite). This area may represent a fusion of one of the anterior precoxal sclerites, which in females is separated from the episternum. Another possibility is that it results from secondary folding. The suture is represented internally as a strong ridge directed caudad. The dorsal end of the prealar suture forms a process separated from the pleural wing process by a membranous area. The basalare bridges the gap between these two processes in the form of a small, elongate, convex arch which is firmly attached at either extremity. The subalar, a small unmodified sclerite, appears to be similar in males throughout the order.

The sternum of the pterothorax (Fig. 15B) is a composite plate resulting from fusion of precoxal sclerites (free in females and young) with the basisternum and furcasternum. This fusion can readily be

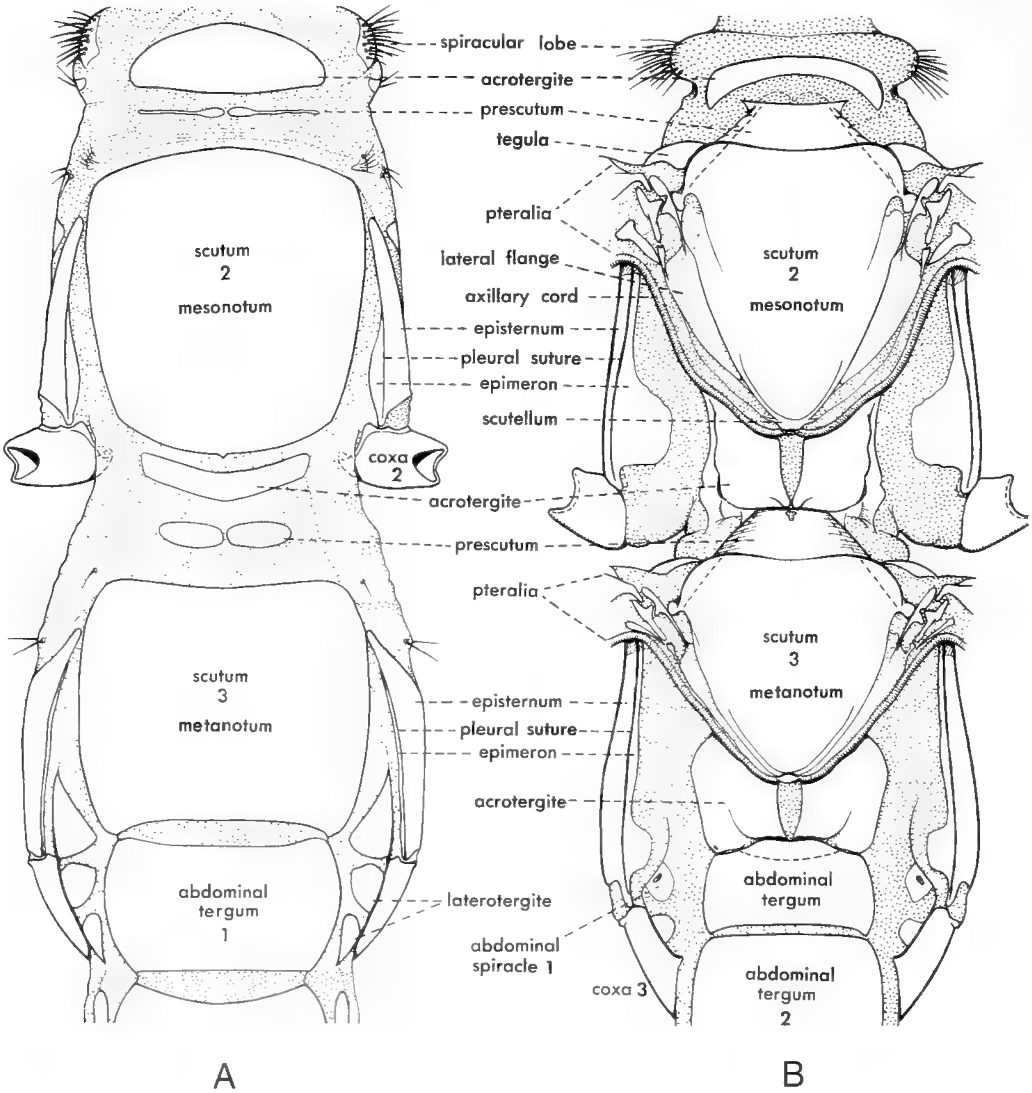


FIGURE 14. Meso- and metathorax, dorsal aspect of A. Adult female, and B. Adult male. *Oligotoma nigra* Hagen.

traced by lines of internal thickening, by the position of the sternal apophyseal pits, and often by distribution of setae. The sternum of a male of *Oligotoma nigra* has been figured alongside that of the female (Fig. 15A, B) and a comparison clearly indicates the homologies of the various areas of the composite sternum. The subcoxal area, very prominent in the mesosternum, is obsolete in the metasternum of this species, but is more evident in more plesiomorphic genera, such as *Embia*.

The pterothorax of more plesiomorphic Embiidina, such as clothodids and embiids, seems to retain many primitive features, e.g., broader and shorter proportions of the scutum with stronger lateral flanges, a broader scutellum, a partially separated prescutum, undivided acrotergites (notal plates), as well as certain features of the sternum.

Meso- and metathorax of females

The meso- and metathoracic anatomy of adult females of *Oligotoma nigra* (Figs. 14A, 15A, 16A) typifies that of adult females and nymphs throughout the order, as well as that of fully neotenic (apterous) males. Adult females unquestionably once possessed wings.

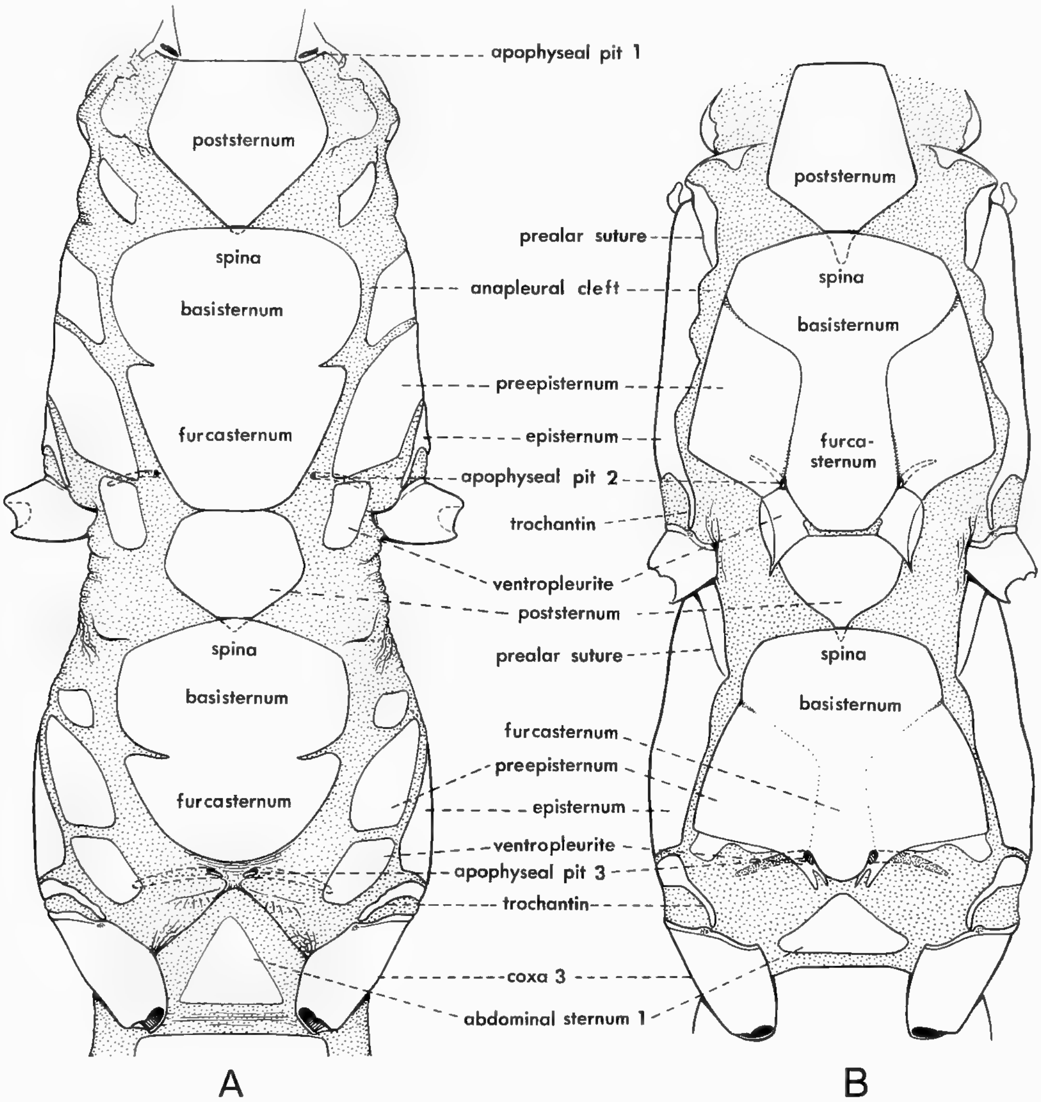


FIGURE 15. Meso- and metathorax, ventral aspect of A. Adult female and B. Adult male. *Oligotoma nigra* Hagen.

Their present simple juvenile thoracic structure strongly contrasts with ancestral complexity retained in the thorax of alate males. Thoracic simplicity in adult females obviously results from neoteny for its sclerotization is nearly identical to that of immature stages of females, and the second instar of males destined to develop wings. Some difficulties in interpretation can perhaps be attributed to the fact that most sclerites are rather soft and are seldom fused along sutural lines. This would appear to make possible distention of the midgut and more supple body movement—the latter a decided advantage in gallery life. The apterous condition of adult females, and the same tendency in males of some species, is undoubtedly an adaptation for life in silk galleries, as will be fully treated in the section dealing with wings.

The meso- and metathoracic scuta of females are simple, large plates, each having a prominent anterior acrotergite. The narrow transverse sclerite in the membrane between the anterior margin of each and its acrotergite is probably homologous to the fully developed prescutum in alate males. There is no great development of phragmata. The posterior margin of the metathoracic scutum closely contacts the first

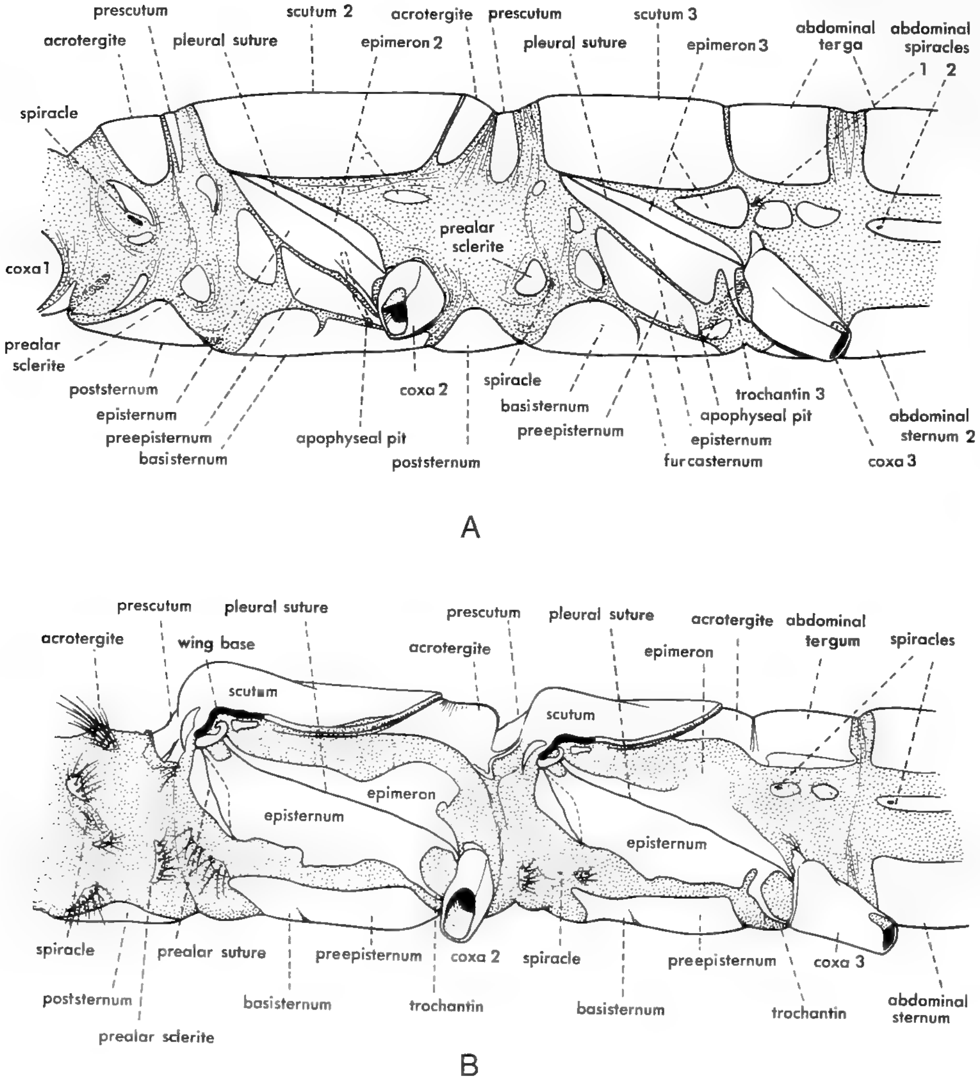


FIGURE 16. Meso- and metathorax, lateral aspect of A. Adult female and B. Adult male.

abdominal tergum without any apparent development of an acrotergite of the latter.

The pleura of both thoracic somites are similar (Fig. 16A). The pleural suture dorsally contacts the anterior angle of the scutum and extends ventro-caudad at an angle of about 30° to form the dorsal articulation point of each coxa. Coxae are located at points directly in line with the posterior angles of the scutum. This dorso-ventral compression, characteristic of all embiids, probably is associated with life in narrow galleries for it results in a lengthening of the body and a decrease in its vertical plane. On either side of each pleural suture is a narrow epimeron and a slightly broader episternum. The mesothoracic episternum produces a ventral trochantin which, in the metathorax, is delimited by a deep cleft extending nearly to the pleural suture. The apices of the tronchantins constitute the ventral articulation of the coxae.

Between the ventral (anterior) margin of the episternum and the basisternum there are large, weakly sclerotized plates which I believe are pleural in origin. In the mesothorax they are rather rhomboid in shape, unequal in size and, as in the metathorax, are two in number, probably as a result of secondary division. In the metathorax they are unequal; the anterior sclerite (pre-episternum) being larger and greatly elongated, the posterior (ventropleurite) smaller. In an alate male's thorax, the ventropleurite is fused to the sides of the furcasternum and the pre-episternum becomes the anterior appendix (prealar area) of the adult male episternum. Beneath each coxa there is a small quadrate sclerite surrounded by membrane which, in adult males, also becomes a part of the sternal plate. Tentatively, I regard this series of three sclerites as the precoxal arc.

The sternal region (Fig. 15A, B) is one of the most interesting portions of the thorax of Embiidina. Matsuda's (1960) interpretation of the thoracic sternites of insects seems to satisfactorily explain the conditions present. The development of the sternum in the order is one of the best examples of the broad type characteristic of orthopteroid orders. This is manifested by widely-spaced sternal apophyseal pits and a consequently large furcasternum between them, as is best exhibited in the mesothorax.

In the mesothorax of females the sternal apophyseal pits are located in the lateral membranes of the sternum and are widely separated by the broad furcasternum which, in combination with a greatly developed basisternum, covers most of the venter of the mesothorax. The sternal apophyses are very slender and project only a short distance inward.

The sternum of the metathorax is similar to that of the preceding somite but shorter, with its apophyseal pits very close together. The pits may have "migrated" caudad from lateral positions comparable to those of the mesosternum. The sternal apophyses are much stouter and longer than those of the mesothorax and are strongly directed dorso-laterad.

The first pair of thoracic spiracles is located in the intersomital membrane behind the prothorax on prominent, setiferous, lateral lobes and they are accompanied by small sclerites. The second pair of spiracles is subventrally located near the anterior angles of the metathoracic basisternum. They are inconspicuous and do not open on prominent lobes.

Barlet (1985) has published a more detailed treatment of the thorax.

Legs

The legs of embiids, remarkably similar in all taxa, are very short relative to body size as best exhibited by nymphs, adult females, and neotenic adult males, which are more perfectly adapted to gallery life than alate, slightly longer-legged, non-neotenic adult males. Also universal is the distinct form and function of each pair of legs. Most significant are the unique foretarsi which produce the peculiar environment and thus the order's associated anatomical and behavioral adaptations. It is noteworthy that all leg features, even the spinning glands, are similar in all instars of all species of the order.

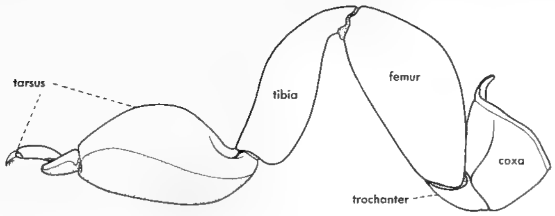
Prothoracic legs

Silk-spinning is the most important function of the forelegs and, accordingly, all of its segments are enlarged, well sclerotized and muscled to serve vigorous activity (Fig. 17). The resting position of the forelegs is forward, tarsi paralleling the sides of the head. During spinning the legs sweep very wide arcs—even back and up to the mid-line of the thorax. This activity includes short strokes in many directions combined with outward pushes of the tarsi and head to shape galleries. Even teneral individuals spin soon after ecdysis. Diminutive forelegs regenerated after loss during a nymphal instar are also capable of spinning.

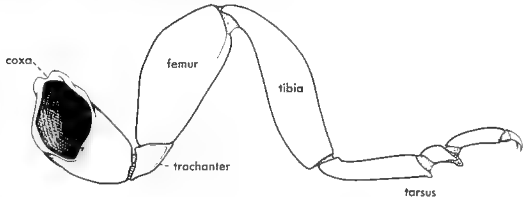
The spinning organs (Figs. 18, 19) have been described several times (e.g., Melander, 1902; Rimsky-Korsakov, 1914; Mukerji, 1928; best by Barth, 1954; and Alberti and Storck, 1976). The contention of Enderlein (1909, 1912), who probably never observed a live embiid, that the silk is produced by labial glands, has long been rejected.

The glands are confined to the greatly enlarged basal segment of foretarsus and number at least 150 per tarsus. Variations according to taxa and instar remain to be studied. Each gland consists of a large lumen enclosed in an irregular layer of syncytial cells. The globular, but often quadrate and irregular shaped glands, are closely appressed to each other. They are sufficiently large to be visible under low magnification, especially through the pale thin derm of the plantar surface. The crowded glands resemble seeds in a pomegranate fruit.

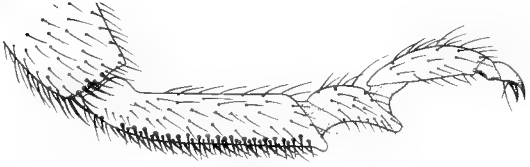
Within each lumen there is a chambered corbiculum (ampulla) with radiating filaments which apparently direct liquid silk secretions of gland cells into a duct (one per gland). Each duct opens distally at the tip of a relatively long, hollow filament, here termed silk-ejector (ejector of Barth, 1954). They are not homologous to setae (Fig. 20A–C).



A prothoracic leg

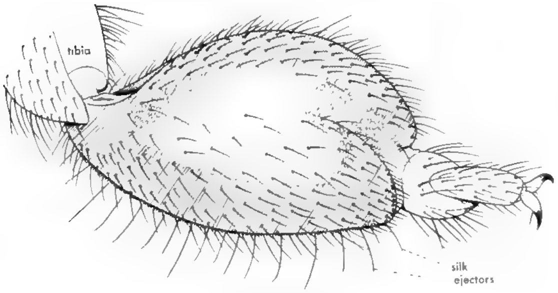


B mesothoracic leg

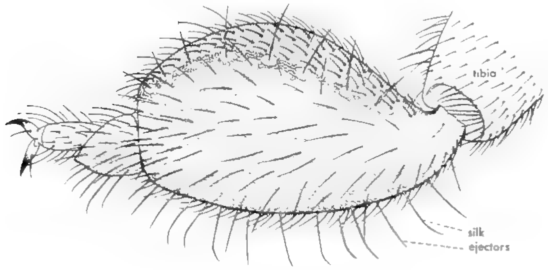


C tarsus of mesothoracic leg

FIGURE 17. A. Prothoracic leg, B. Mesothoracic leg, and C. Its tarsus.



DORSAL



VENTRAL

FIGURE 18. External aspects of foretarsus of a female.

According to Barth's excellent cytological investigation—the first made with the aid of an electron microscope—the silk-ejectors and their glands are unique organs. As shown in my diagrammed hypothesis (Fig. 19A), the glands perhaps evolved from invaginations of secretory cell pores in the ectodermis. Each silk-ejector apparently represents a setae-like, evagination of the exocuticle which might first have been simply a cuticular rim around a pore opening.

It is probable that the early ectodermal glands were hollow "balls" composed of walled secretory cells. The duct, or constriction, leading to each primordial silk-ejector must at first have been fully cell-lined. The inner walls of these duct cells appear to have gradually thickened and fused to become the elaborate ducts which now extend from the silk glands to the ejectors. Similar ectodermal glands are treated and illustrated by Snodgrass (1935: 62, fig. 32).

Cells of the ectodermal gland and the duct later became syncytial. Only a small amount of nucleated cytoplasm persists on the outer wall of a duct. The ducts are thread-like and wend their way between the glands with never more than one duct per gland and its ejector. The evolution of such unique, complex organs is difficult to comprehend unless one considers the probability that even small mutations must have had simultaneous expression on all glands. Under such circumstances, even minute, favorable modifications could have had almost immediate significance in the survival of the possessor.

The basal tarsal segment (Fig. 18) is elongate-oval. In alate males it is narrower and more cylindrical in cross-section than in females, nymphs and nymphoid apterous males. In females and nymphs the segment is almost triangular in cross-section due to slant of the inner-dorsal surface. The outer side is almost vertical. The inner-dorsal surface is almost entirely submembranous, finely reticulate in texture and almost lacks setae. A medial, longitudinal depression which extends the length of the surface gradually becomes stronger terminally. The area immediately inward of this depression often pulsates. Dorsal surfaces adjacent to this membrane are darker and clothed with moderately long setae of the usual type.

The ventral, or plantar, surface of the basal segment (Fig. 20A) is entirely membranous, pale, often pinkish in color, and densely covered with short,

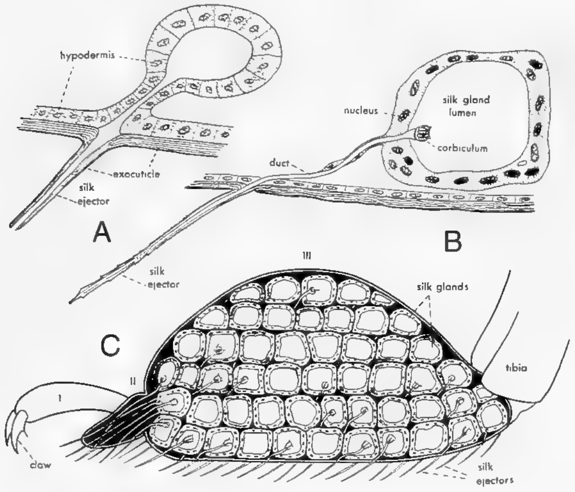


FIGURE 19. A. Hypothetical origin of silk gland. B. Definitive structure of a single gland and its ejector. C. Glandular content of foretarsus of a female.

acutely-tapered microspicules which may function as combs. Silk-ejectors on the outer edge arise within small, circular areas lacking such microspicules. The ejectors are characterized by a lack of basal sockets and are thin walled, fragile and whitish— conditions apparently associated with their hollow nature. They are variable in form and length but are straight except for occasional abrupt curvature of their complex apices (Fig. 20B, C).

Along the lateral margins of the plantar surface the microspicules are much shorter and the bare spots from which the ejectors arise are more conspicuous. Ejectors arising from these lateral borders appear to be much longer than elsewhere and probably are the most important silk-strand ejectors.

The mid-segment of the foretarsus is a small triangular pad with a membranous ventral surface clothed with both microspicules and silk-ejectors; the latter being denser but, of course, less numerous than on the basal segment. These ejectors are served by ducts arising in glands located within the basal segment. The distal segment of the foretarsus is smaller than those on the mid- and hindlegs but otherwise anatomically similar. During spinning it is elevated to prevent its claws from hooking into the webs.

Nature of embiid silk

Using specimens provided by me, K. M. Rudall of the Department of Biophysics, University of Leeds, England, made brief studies of the silk during 1973–78 and in letters to me, conveyed the following information.

Double X-ray diffraction pattern shows embiid silk to be of the classic Group I fibroin silk characteristic of *Bombyx mori* and *Beria* sp. (Cymbidae). This silk group isn't found in most other Lepidoptera, therefore, its occurrence in an embiid is "most exciting." He regarded the dermal tarsal glands of embiids as perhaps simpler secretory systems than the long salivary glands of Lepidoptera larvae. The diffraction pattern has been interpreted (by universal agreement) to be due to alternative residues along extended polypeptide chains of glycene and alanine. Some of the alanine positions are reflected by serine (serine is nearly the same size as alanine). Rudall noted that the main difference between *Bombyx mori* silk and that of embiids is that the serine to alanine ratio is reversed, there being a much greater content of serine. The ratios in the embiid sample was 197 glycine to 40 alanine to 130 serine.

Mesothoracic legs

The mesothoracic legs (Fig. 17B, C) are the least specialized of the three pairs. Their most notable feature is a relatively great reduction in size and they do not seem to have much locomotor importance in or out of galleries. In their normal position they extend laterad and span a gallery's interior. They are capable of great upward movement and frequently the tarsus of one of the pair is able to contact the upper surface of a gallery while the body is in a normal position. It is possible that these legs aid rotation of the body within a gallery.

The tarsi consist of elongated, unmodified segments (Fig. 17C). The basal segment is evenly clothed ventrally with stout setae. The mid-tarsal segment is small and has a distal papilla. In adult females and nymphs of many species, the ventral membrane of this papilla is clothed with very small, basally-directed peg-setae which must aid reverse traction on the silk substrate. In adult males this surface never is echinulate and perhaps this is another indication of the male's poorer adaptation to gallery life.

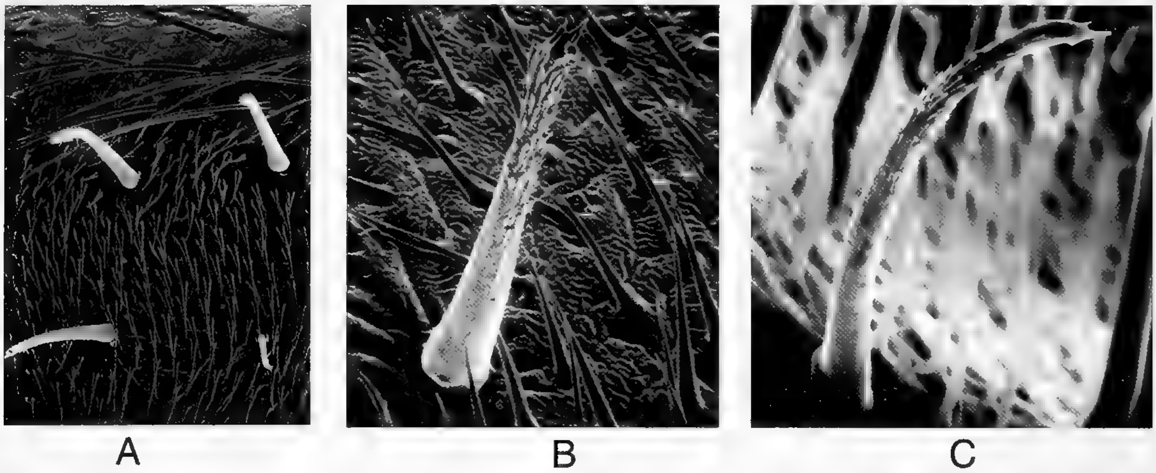


FIGURE 20. A. Silk-ejectors (white) and "combs" of female *Embia* (SEM 440×). B. and C. Silk-ejectors and "combs of female *Embia* (SEM 1750×). Ejectors are highly variable in length and distal structure.

Metathoracic legs

Formerly, there was some question as to the function of the greatly enlarged femora of the hind legs (Fig. 21). It was assumed that their enlargement indicated a saltatorial function. Davis (1936) examined the tibial muscles and noted that, unlike saltatorial insects which have large hind tibial extensor or levator muscles, the flexor or depressor muscle is greatly enlarged and thus accounts for the large size of the femora. The extensor, or levator, muscle is much reduced and fits into a groove atop the flexor (Fig. 21C, D).

Such tibial musculature obviously facilitates backward movement in the galleries—an activity requiring strong muscles to flex the hind legs. Rapid reverse movement in narrow galleries has been a major factor in the evolution of many adaptive characteristics of the order, notably wing modifications and, ultimately, wing elimination in all females as well as in males of many species. This will be more fully discussed in the section dealing with wings.

Reverse movement can be rapid, very smooth, the body axis remaining straight. In contrast, an embiid's forward movement usually is rather awkward and slow but, with stimulation, it can be very fleet especially within the galleries. The resting position of the hind legs is straight back, closely paralleling the sides of the abdomen. In walking, the terminal segment of the hind tarsus is elevated and doesn't contact the web and, obviously, this avoids a snagging of the claws in the silk. Thus, substrate contact of the tarsus is with the basal and middle segments.

The basal segment, or basitarsus, probably a composite of three fused ancestral segments, is slender in adult males, stout in nymphs and adult females (Fig. 22). In both sexes the plantar surface bears large, irregular, peg-like setae which are more slender in males. In some females the setae are directed basad in the distal half of the segment. The upper and lateral surfaces are clothed with long, slender setae which, like many others on the legs, have the outer curvature finely serrate. Scanning electronic microscope images show each serration as the apex of one of the fibers composing a seta.

The distal end of the plantar surface of the basitarsus is always produced as a membranous "bladder," or papilla. Many species, however— often all species of a taxon— have a submedial, second papilla on the ventral surface (Fig. 22B). This may represent one of the papillae of the three segments which fused to form the basitarsus. If so, its presence may be plesiomorphic. Two papillae are possessed by species of *Clothoda*, the order's most plesiomorphic genus. However, a second papilla may appear sporadically throughout the order as a specific or even generic character without any phylogenetic significance. In spite of this, the presence or absence of a second papilla is constant in all instars of a species, usually so within a genus and thus serves as an im-

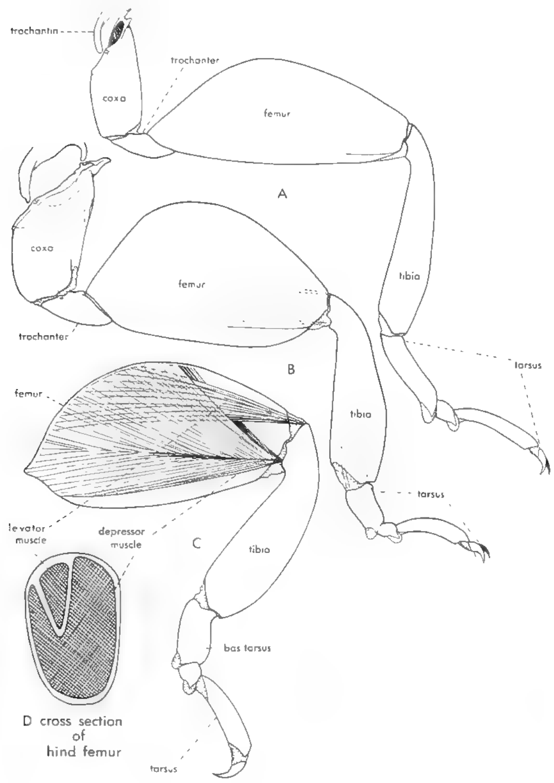


FIGURE 21. A. Hind leg of male. B. Hind leg of female, C and D. Tibial musculature.

portant character in systematics. In a few species, males have only one papilla, females two. Occasionally, the second papilla is much reduced, often simply a small, unprotruded, clear spot. Such papillae appear to be homologous to arolia of the tarsi of grasshoppers and other insects and were so designated by Imms (1913). Snodgrass (1935:198) called them tarsal pulvilli, or euplantulae.

Wings

Ancestral embiids must have possessed fairly inflexible wings similar in texture to those of most other alate insects. However, with increasing dependence on quick reverse movement in silk galleries as a principle means of evading predators, the apices of such relatively stiff wings must have frequently snagged against opposing gallery walls and slowed or prevented escape. To overcome such a problem, and to increase suppleness during U-turns, embiids long ago evolved extraordinary wing flexibility. As a result, when in repose over the back, the wings of all modern embiids readily fold transversely and slide forward toward the head (Fig. 23), thereby reducing likelihood of a snag, or "barb-effect."

Although the wings usually fold upward and cephalad across their midline, they can bend at almost any point and may even irregularly crumple. Such flexibility appears to have been accomplished through desclerotization of most of the longitudinal veins behind the radial blood sinus (RBS), notably the media (M) and cubitus (Cu). Perhaps reduction of plication is also involved, as suggested by the fact that vein cuticularization is almost entirely confined to the dorsal membrane with only blood sinus veins evident on both wing surfaces.

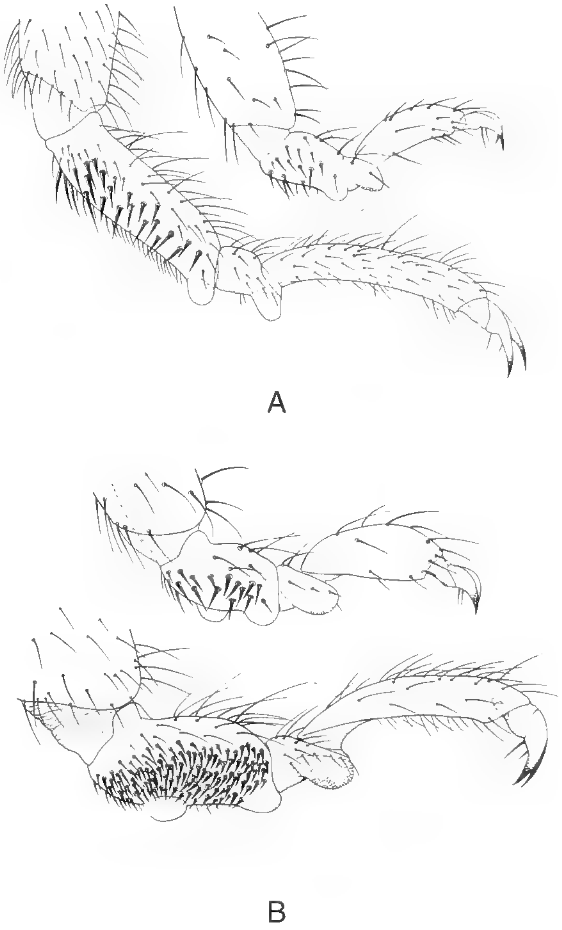


FIGURE 22. A. Hind tarsus of first instar and adult of male *Oligotoma nigra*. B. First instar and adult hind tarsus of female *Haploembia solieri* (both showing medial papilla, lacking in *O. nigra*).

FIGURE 23. Wing flip of a reverse-moving male. New genus and species, Oligotomidae. Thailand.

The great flexibility of such wings leads one to question how they could serve as flight organs. The answer seems to lie in the functioning of four blood sinus veins, the most important of which follows the course of the anterior radius (RBS = RA). Secondary blood sinuses include the subcostal (ScBS = Sc), the cubital (CuBS), and the anal (ABS = A) (Fig. 24). These sinuses correspond in position to the associated veins except for the terminal halves of CuBS and ABS which do not contain tracheae. Throughout the order the sinus veins are cuticularized on both the dorsal and ventral wing membranes.

In effect, each sinus vein is a dark, glossy, dorsoventrally-flattened sac that is tapered and perhaps closed distally. When wings are in repose, sinus surfaces are flat but during "excitement" preceding flight, hemocoelic pressure must increase and, as the wings extend laterally preparatory to flight, hemolymph ("blood") flows into the sinuses causing their surfaces to become convex. Microscopic examination of a turgid sinus shows that hemocytes synchronously pulsate with the beat of the dorsal blood vessel and do not perceptibly move distad.

Together, the turgid subcostal, cubital and anal sinuses appear to function as tines of a fork that stiffen the wing's base, while the radial blood sinus (RBS) stiffens almost the entire length of the wing's lead edge. When an embiid alights, and the wings return to repose over the body, it is probable that a crimping of the blood sinuses occurs in the axillary region. Hemolymph then gradually oozes back into the body cavity.

One could regard, especially the longitudinal wing veins of all insects, as narrow sinuses into which coelomic blood pressure extends as a means of expanding wings from pad to adult form. Following a teneral period, during which these veins gradually cuticularize, blood pressure into them must decrease, or completely cease except for pressure in the axillary area which remains to extend wings for flight ("take-off"), or defensive, or sexual, display, among insects which fold their wings over the body when they are not in use.

In contrast, blood sinus veins of embiids enable blood pressure to continue on and off throughout the adult life of all species with alate males. Over time, such veins broadened and sclerotized to become distally-closed sinuses characterizing wings of all species of the order. Embiids apparently are the only insects—indeed the only animals on Earth—capable of temporarily stiffening, otherwise flexible, wings.

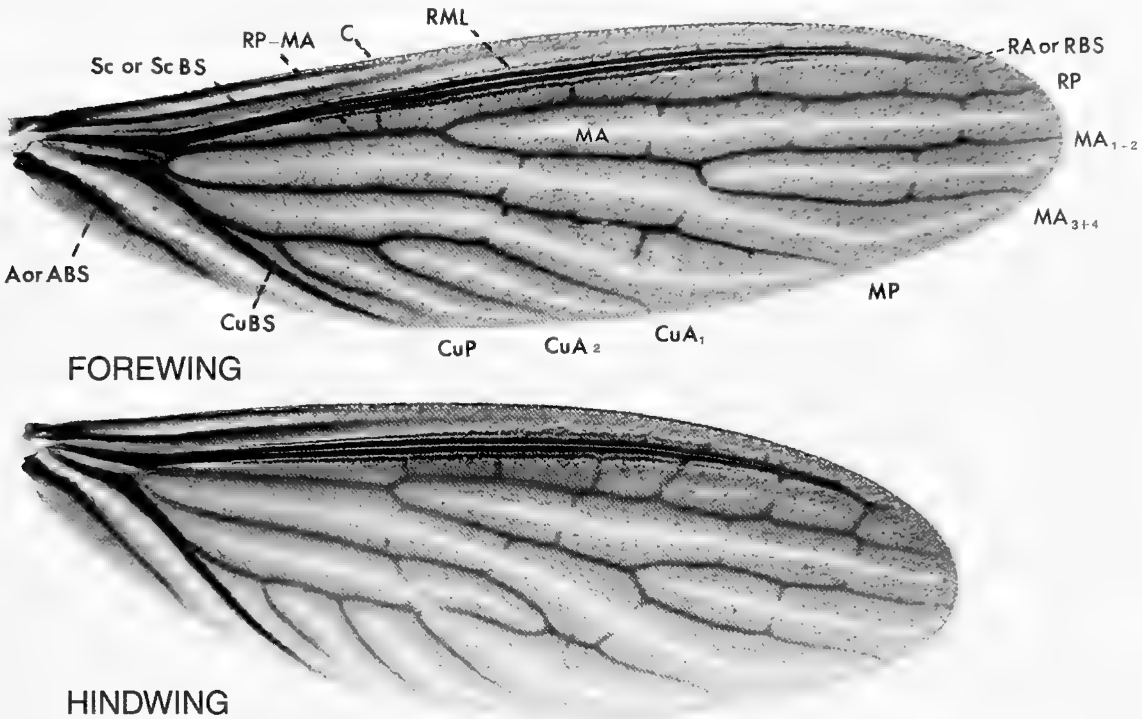


FIGURE 24. Wing venation of a plesiomorphic embiid, *Clothoda longicauda* Ross (Clothodidae). ScBS, RBS, CuBS and ABS are symbols for blood sinus veins. RML = radius marginal line. Note: MP vein is anomalous in hindwing.

The fact that the sinus veins are similarly-developed throughout the order indicates a great antiquity for the specialization, but one preceded by evolution of the silk-spinning ability and increased survival associated with the complete confinement in silk galleries. Such unusual wing adaptations must have been initially perfected in a single species for it seems unlikely that they could have evolved with identical complexity more than once. Furthermore, primary selection pressure for wing flexibility was most likely on adult females, not adult males, to adapt them more perfectly to gallery life. The adult life of a male is too short and its prime biological function—simply a non-feeding "vehicle" for delivery of sperm and genetic diversity—is performed so quickly that there would not seem to be sufficient selective advantage for males to have been the primary target for this remarkable wing specialization. Adult females, however, must live long enough to mature eggs, oviposit and guard eggs and early-instar nymphs. Thus, a species more significantly benefits from adaptations which foster quick, predator-avoiding movement of females in narrow silk galleries. The evolution of alternating wing flexibility and stiffening represents one of the order's first "attempts" to ease backward movement.

Venation

Strength (cuticularization) and completeness of venation (plesiomorphic features), are greatest in species with largest body size (also plesiomorphic). Complex venation apparently is related to the obvious need for more extensive blood and air distribution in larger wings, especially in the pads of large nymphs during development.

Wings of *Clothoda longicauda* Ross (Fig. 24), one of the order's most plesiomorphic species, may be used for interpreting venation. Most past work on Embiidina, including mine, used Comstock-Needham nomenclature of veins, as summarized by Comstock (1918). Based on tracheation, a modified nomenclature is here adopted. I am aware that many entomologists since Comstock have rejected tracheation as a basis for interpretation; however, in embiids there is consistent correlation between tracheation and venation, both in pads and in fully developed wings. It should be noted that tracheae aren't easily seen, if at all, in wings of dead, dry specimens but are most apparent in freshly killed individuals, especially those still teneral (Fig. 25A, B).

The costa (C) forms the anterior wing margin and terminates at the apex of the anterior radius (RA). The subcosta (Sc) is short, cuticularized, terminates within the wing's basal fourth, and probably functions as a blood sinus, hence the symbol ScBS. The anterior radius (RA), the wing's most prominent vein and, most significant blood sinus (RBS), stiffens the wing's lead edge. It originates strongly near the wing base and parallels the costal margin almost to the wing's apex, at which point it tapers and usually curves downward to join RP. Especially in apomorphic species of Anisembiidae, RA slants toward the costal margin well before the wing's distal curvature.

Throughout most of its length RBS is exceptionally broad, sclerotized, glossy, darkly melanized and bordered, except at basal fourth, by peculiar streaks (radius margin lines, RML), having a fleshy, granular appearance, and usually are brick red in color. Images taken by SEM show the surface of these lines to be irregularly wrinkled, perhaps to accommodate alternate turgescence and flattening of RBS. The radial blood sinus and its margins would be an interesting subject for detailed study.

Near the base of RBS a short stem juts caudad and then immediately extends distad (RP + MA) for almost a third of the wing's length, at which point it appears to fork. However, the anterior branch of the "fork" is simply a continuation of RP, which never is forked in any species of the order. Thus, the basal portion of this "vein" really represents a fusion of RP and MA. Superficially, especially in long dead specimens, this composite stem appears to be a single, cuticularized vein; however, two parallel tracheae within it have separate wing-base origins, a condition which prevails in wings and wing pads of all species of the order (Fig. 26). The posterior branch of the fork, once designated R_{4+5}, is here regarded as a continuation of the anterior branch of the media (MA). This vein usually is forked, forming MA_{1+2} and MA_{3+4}, especially in plesiomorphic taxa of the order.

The stem of the "media" is fused to the anterior edge of the sclerotic base of the cubital blood sinus (CuBS). Separate tracheae, within this stem angle abruptly forward toward the stem of RP and then separate to form MA and MP. MP then extends to the mid-margin of the wing and is very rarely forked.

The trachea of the cubitus (Cu) at first parallels those of MA and MP within the extreme base of the cubital blood sinus (CuBS), but then angles caudad within the sinus. At the sinus' mid-length the trachea and its vein emerge from the sinus and parallels MP to the wing margin. In plesiomorphic embiids, or those with exceptionally large wings, the cubitus may be multibranched. I tentatively regard the basal branch of Cu as CuP.

Beyond this diversion of Cu, the cubital blood sinus continues its broad, tapered, diagonal course to the wing's hind margin. No trachea follows the distal half of the sinus. The hyaline stripe between CuBS and the anal blood sinus (ABS) tends to crease and this suggests that it may be equivalent to the claval suture which delimits the anal fold in wings of certain other insect orders. It tends to fold upward and forward in embiids.

As stated before, the anal (or vannal) area of embiid wings is much reduced, but it has a dark central line, an anal blood sinus (ABS), within which one can see the unbranched trachea of the anal vein (A). Kukalová-Peck (pers. com.) prefers to designate A as AA because, in many other insects, there is a posterior branch of A, therefore an AP vein. There is always a cross-vein between A and the base of the cubital blood sinus. Kukalová-Peck regards this as an "anal brace."

The hindwing is similar to the forewing but always is shorter, broader and certain veins, such as MP and Cu, may be less strongly represented. In some species of *Archembia* Ross, the anal area is slightly more expanded than in the forewing (Fig. 27).

Cross-veins may be highly variable in position and number within a species and may even differ in the left and right wings of a single individual. However, their general positions and number is rather constant within a species, or even a genus. In *Oligotoma*, for example, cross-veins seldom if ever are present behind RP. There seems to be no regularity of cross-vein position which would justify nomenclature for cells they delimit.

The upper and lower wing surfaces are densely clothed with small, short hairs commonly called microtrichiae which, having no apparent basal sockets, appear to arise as direct outgrowths of the wing membrane. The entire outer margins of the wing and

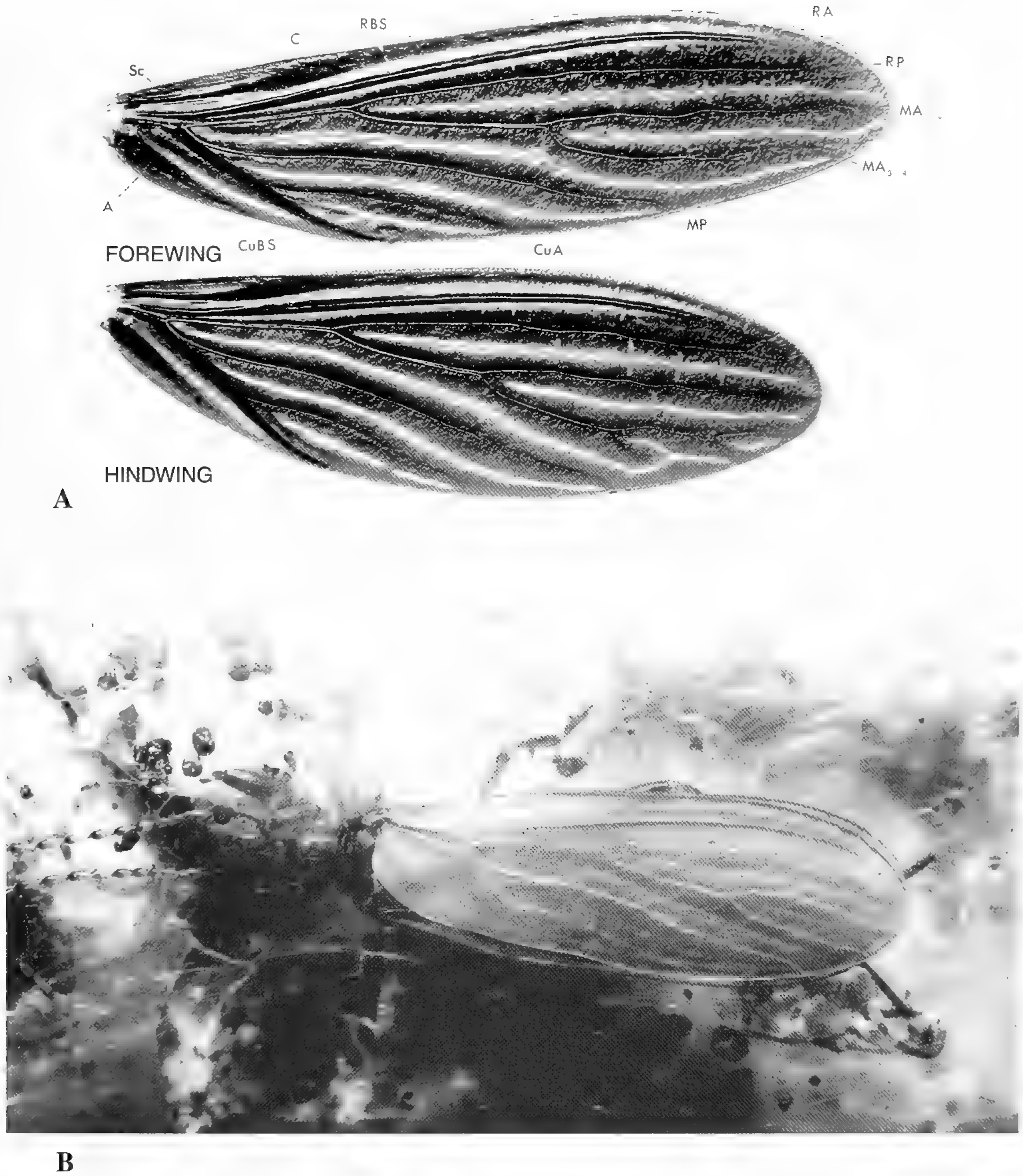


FIGURE 25. A. Dark field illumination of wings of freshly killed *"Embia" surcoufi* Navás (Embiidae) showing tracheae (not visible in "dead" wings). B. Tracheation of teneral *Archembia batesi* (McLachlan) (Embiidae). Photo also shows enlarged anal area of the wing occurring in some species of *Archembia* Ross.

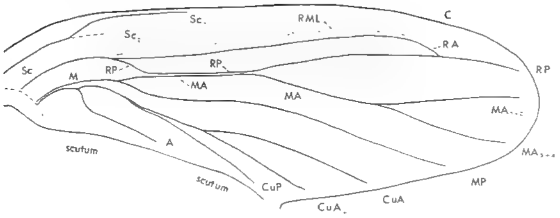


FIGURE 26. Tracheation of forewing pad of penultimate instar *"Embia" surcoufi* Navás.

courses of all veins, even those unsclerotized, bear rather large setae (macrotrichiae) arising from prominent sockets. They are particularly large along the costal margin. Large setae are also present on the ventral wing membrane but are fewer in number and without definite arrangement.

The wings of *Pararhagadochir* Davis (Fig. 28) of the Embiidae exemplify the more apomorphic (= reduced) wing venation found in most Embiidina. In such venation the apex of MA_{1+2} and MA_{3+4} and all of MP are unsclerotized, each vein traceable only by its row of macrotrichiae and pigment stripe.

The wings of *Enveja bequaerti* Navás (Fig. 29) represent contrasting, perhaps plesiomorphic, venation in which all veins are heavily sclerotized, but the cubitus isn't forked.

In some species of the apomorphic family Teratembiidae, as well as in other taxa, small body size correlates with vein reduction, including all veins except those functioning as blood sinuses (Fig. 31).

In a common type of reduction, MA always is simple (Fig. 30). All species of unrelated families Anisembiidae and Oligotomidae have such reduction, a reduction which sporadically occurs in several other distinct evolutionary lines, such as within Embiidae, Notoligotomidae and Teratembiidae.

The most apomorphic wing of the order is found in a South African new species of Teratembiidae. Its wings are very small, slender, with all veins except the blood sinuses obsolete, and the wing margins have especially long setae. Such thysanoptery parallels the tendency of the smallest species of various insect orders (e.g., certain parasitic wasps, small Trichoptera, some microlepidoptera and ptiliid beetles) to have slender, fringed wings.

Although there is much convergence in wing venation in embiids, venational characters have important, supplemental value in the definition of species, genera, and even families. It is doubtful, however, if wing characters can ever be used as the primary basis of phylogenetic conclusions.

Perhaps, because of the unimportance of flight in evasion of predators, embiid wings exhibit considerable random, often anomalous, intraspecific variation. The most extreme, yet consistent, wing anomaly occurs in an Amazonian new species of *Oligembia* Davis, which has normal forewings but, not even a trace of hindwings (Fig. 32), and the metathorax is reduced to the size of an abdominal segment. However, very closely related species from the same region have normal hindwings and thus the hindwing atrophy is of no significance in systematics. If, however, a comparable character appeared in certain other insect orders, it might become the basis for proposing a distinct higher taxon.

Embiid wing anomalies seem to illustrate a law in biology which may be expressed, as follows: if an anatomical feature is not vital to survival or reproduction, it may be subject to much anomalous variation within a taxon. Thus, in flight-dependent insects, such as most Diptera and Hymenoptera, wing features are relatively constant and are, therefore, dependable characters in systematics. The converse appears to be the case in embiids because their flight has little or no adaptive value.

Wing pigmentation

Apparently pigmentation of embiid wings always is confined to the upper membrane, the ventral being completely hyaline except for dark "imprints" of the blood sinuses. Alternating longitudinal dark stripes and hyaline intervals, although faint in some species, are characteristic features of the upper membrane of all embiid wings except possibly those of *Burmitembia venosa* Cockerell, an Eocene (?) amber fossil from Burma.

The veins and/or their macrotrichiae are centered in the dark stripes; the intensity, width and marginal definition of which are consistent within a species. In turn, such melanization correlates with the overall pigmentation of the male. In arid regions many species disperse nocturnally and generally are pale tan with wings correspondingly pale with faint venal stripes and broad hyaline intervals, the margins of which are often indefinite and irregular.

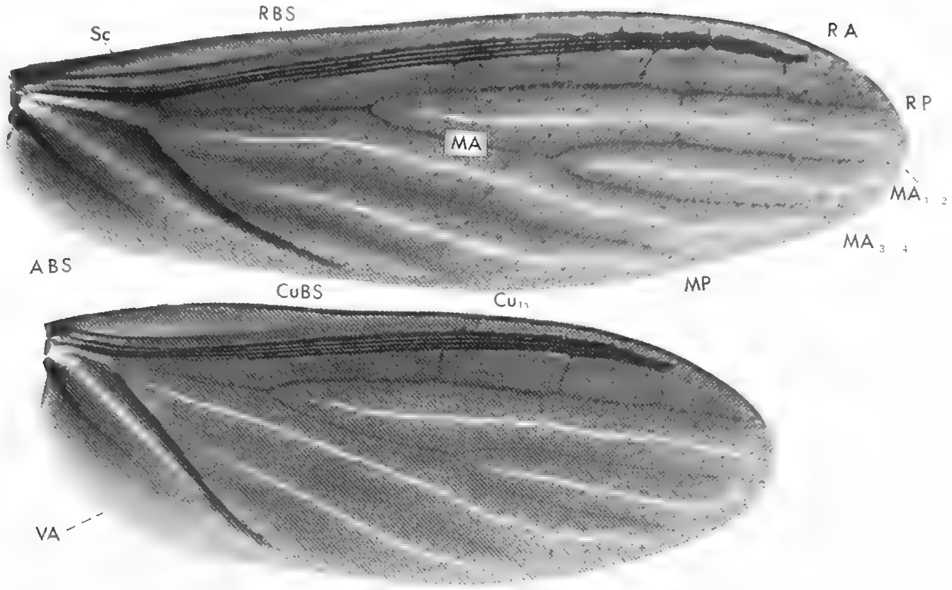


FIGURE 27. Wings of *Archembia* n. sp. (Embiidae) showing narrow hyaline stripes and broad anal area (a plesiomorphic condition).

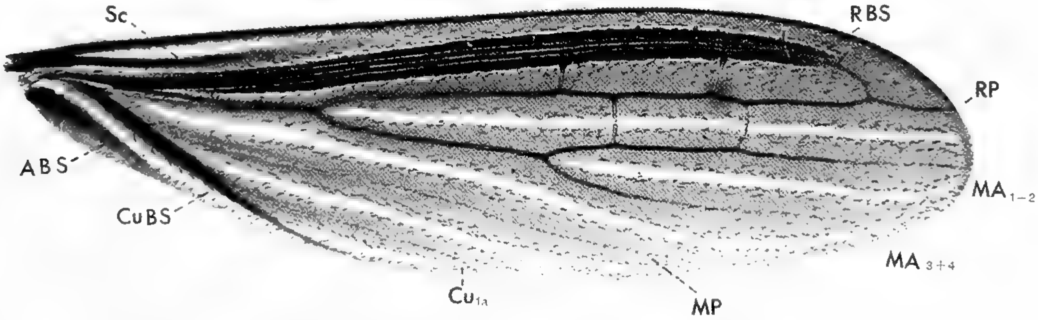


FIGURE 28. Forewing of *Pararhagadochir trinitatis* (Embiidae) showing reduced anal area.

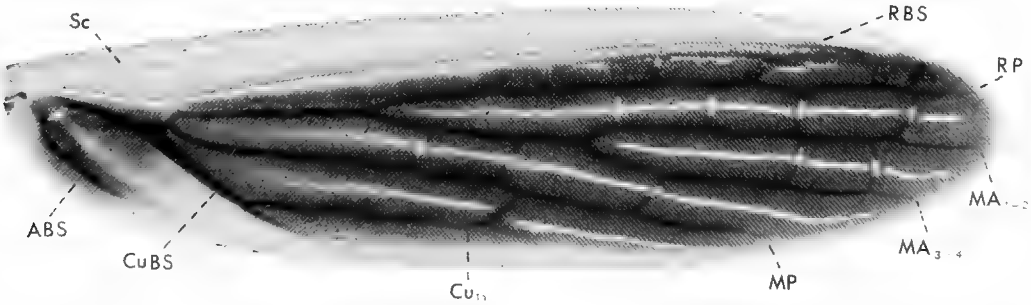


FIGURE 29. Forewing of *Enveja bequarti* showing strong venation and white cross-veins. The wing's costal and hind margins are golden.

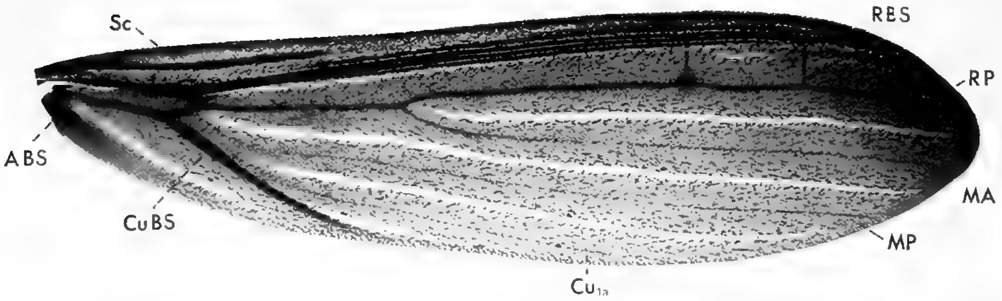


FIGURE 30. Reduced vein-strength of the forewing and venation of a species of *Chelicerca* (Anisembiidae). The unforked MA vein characterizes many species and entire families, e.g., Anisembiidae and Oligotomidae.

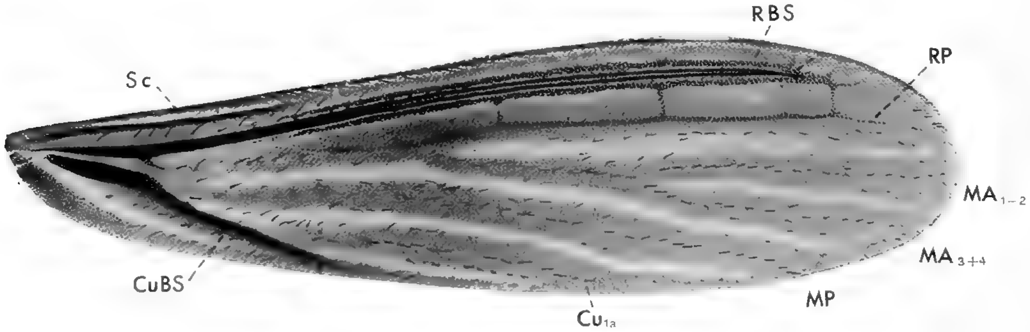


FIGURE 31. Reduced vein-strength of the forewing of *Teratembia geniculata* (Teratembiidae). Many African species of this family have vein MA unforked.

FIGURE 32. Complete atrophy of metathorax and hindwing loss in a new Brazilian species of *Oligembia* (Teratembiidae). Terminalia characters indicate, however, that this isn't a very distinct species.

There are exceptions to this, however, for melanism of some species occurring in certain seasonally-arid regions (e.g., *Embia* Latreille spp., in the Mediterranean region) is often associated with nuptial dispersal during cool weather following winter and early spring rainfall. In such cases melanism may foster rapid body warming in the sun, enabling more rapid dispersal movement, thereby reducing predation hazard.

Especially in the humid tropics, wings of darkly-pigmented males (e.g., *Ptilocerembia* Friederichs spp.) often have a beautiful, metallic blue or lavender luster. This is especially intense on the veins and diminishes toward the hyaline stripes.

In some species wing pigmentation may contribute to a mimetic appearance. Blackness causes the wings to resemble elytra of aposematic beetles, such as Pyrochroidae, which, like their embiid mimics, usually have a reddish prothorax and black elytra. In another type of mimicry, extensive golden margins of the wings (e.g., *Enveja* Navás spp.) result in a resemblance to chemically-repugnant lycid beetles occurring in the same habitats.

Curiously, cross-veins often are conspicuously white when crossing hyaline intervals and darkly pigmented while crossing the dark stripes. The resultant white, cross-slashing of embiid wings is characteristic of richly-pigmented, diurnal males occurring in humid environments.

As mentioned before, brick red or pink, "granular" lines (RML = radius marginal lines) bordering the radius blood sinus characterize all embiid wings. This subcutaneous granular pigmentation may also be present in the costal margin and in veins RP and MA, as in *Pararhagadochir* Davis (Fig. 28). Each side of a radius margin line may be pale. Sometimes the granular red lines extend into adjacent longitudinal veins and cross-veins.

Reflecting on the signifance of the universal striping of embiid wings, I have concluded that wings of ancestral species must have been uniformly dark and that the hyaline intervals evolved in lines of weakness which fostered longitudinal plication. Observed obliquely, embiid wings display slight ridges corresponding to the veins, and furrows correlated with the hyaline intervals. Unlike most insect wings, those of embiids do not have a pattern of positive and negative longitudinal veins; the ventral membrane lacks cuticularized veins. However, at least in some genera, e.g., *Clothoda* Enderlein, veins are pale in color on the ventral membrane.

In some clothodids, such as *Clothoda nobilis* Enderlein and *Antipaluria marginata* Ross, the wing's costal margin is white. In some species of Anisembiidae and Teratembiidae extreme apices of the wings are white.

Wing expansion following ecdysis

During most of the penultimate instar, wing pads of males are flat with venation identical to that of adults (not zig-zagged, for example, as in some Plecoptera). Nearing ecdysis, the pads become thickened, convex and opaque white. When the exuviae is shed, the pads at first retain the fleshy shape and jut out from the thorax at about a 30° angle. This probably assists flow of blood into the pads.

Within ten minutes the projected pads begin to flatten and expand from the costal to anal margins. Then they gradually assume the normal, repose position over the dorsum of the thorax. Periodically, the embiid wriggles and rotates its body. Concurrently, the abdominal terminalia are distended and the cerci project laterad at 45°—perhaps due to an increase in hemocoelic pressure throughout the body.

In about twenty minutes the basal half of each wing has fully expanded and flattened, the distal half remaining as narrow and as fleshy as at the time of ecdysis. In about thirty additional minutes the entire costal margin has expanded and only the distal extremity of the posterior margin remains fleshy. This condition prevails for another thirty minutes after which the wings are fully expanded but remain white with veins paler than the intervening membranes.

About two hours after ecdysis the wings have attained their definitive shape and thickness and their pigment stripes and hyaline intervals are faintly apparent. Seven hours after ecdysis the wings are gray in tone and the body and leg pigmentation is well developed. After about twenty-four hours wing pigmentation, or cuticularization, is completed and the male has ingested his exuviae. The male tends to remain in one position for at least another day following ecdysis.

Wing articulation

I am indebted to Jarmila Kukalová-Peck who, during a visit to my laboratory (1999), greatly improved my treatment of wing articulation. Details, presented in Figure 33A, will be elaborated and possibly corrected, in one of her future publications.

Articulation of the hindwings is similar to that of forewings. There is, however, a trend toward a slightly weaker representation of sclerites which is undoubtedly correlated with the wing's smaller size.

Flexion of wings

In repose the wings lie flat over the back (Fig. B) much as in termites, zorapterans and stoneflies. The anal area of the wing is nearly obsolete and is represented only by a small, basal, posterior corner which, in a fully-flexed wing, folds inward beneath the wing surface. The important fold occurs at the wing base. I have observed the mechanism of this basal flexion in both living and dead specimens of *Oligotoma nigra* and noted movements of the sclerites, as follows: the fulcrum, or pivot, of the flexion is anterior; being at the point of articulation of the anterior part of the first axillary sclerite with the base of the subcosta. An imaginary line drawn from this point through the basal articulation of the third axillary, and still another from it through the point of contact of the apex of the third axillary with the posterior angle of the anal band, delimit a narrow triangular area. As the wing returns from the completely extended position to rest over the back, folds occur along these lines and the area becomes completely inverted. During this movement (or the reverse) only the three axillary sclerites change position while the other parts of the wing-base remain stationary. During flexion the first axillary rotates against the anterior wing process through a 90° arc. The second axillary becomes upright and the third is entirely inverted. The anterior membrane is stretched around the fulcral point and, finally, at least half of it comes to lie parallel with the side of the body.

The flexion of the wing thus seems to correspond to that of many other insects. One point requiring further investigation, in the light of the order's wing peculiarities, is the possible control of blood circulation in the large radial blood-sinus (RBS), and other blood-sinus veins by means of movements in the wing base. This may occur, at least in the case of RBS, by simple pressure of the anterior membrane against the fulcral point. There is a small strengthened point in the membrane opposite this fulcral point which may fit across the place of strongest contact.

Flight

Because predator-avoidance especially depends on remaining within silk galleries, flight did not evolve as an important means of defense or dispersal. Adult males are slow to take flight and do not readily fly away from a disturbance. They are more likely to run away. In preparation for flight, a male rises high on his forelegs, at times lifting them off of the substrate, the head may bob up and down, and the antennae may vibrate and rapidly twirl. Flight distance usually is short, perhaps seldom exceeding a meter and, soon after alighting, there may be a repetition of the pre-flight and flight behavior. At times take-off follows a short run or a hop.

Flight is a swirling, aimless, fluttering with apparently no more directional control than that of nuptials of most species of termites. However, males of nocturnally-dispersing species fly toward artificial lights. It may also be assumed that they can direct their flight to a gallery containing a receptive female. Especially in flight, diurnally-dispersing males of certain species can easily be mistaken for various aposematic beetles, such as some lycids, and pyrochroids, which also serve as models for mimicry of many other insects.

Reduction and elimination of wings

Obviously, the ultimate adaptation for rapid reverse movement in galleries is complete wing elimination, now universal in females, through neoteny. This also has occurred independently in males on almost every evolutionary line within the order. A similar neotenic "solution" developed among worker and soldier termites. Alate termites, however, break off no-longer-needed wings prior to copulation and a return to gallery life.

Due to friction, it is probable that more winged embiid males are caught by predators at the extremities of galleries than are apterous, or subapterous, members of a colony. Thus, mutations resulting in wing-loss, or reduction in their size, are likely to be selected. Another, and perhaps more significant factor, is that alate individuals are more likely to make hazardous flights out of protective galleries and thereby become exposed to predation and other hazards, such as desiccation. The fact that aptery is not yet universal in males may be explained, as follows:

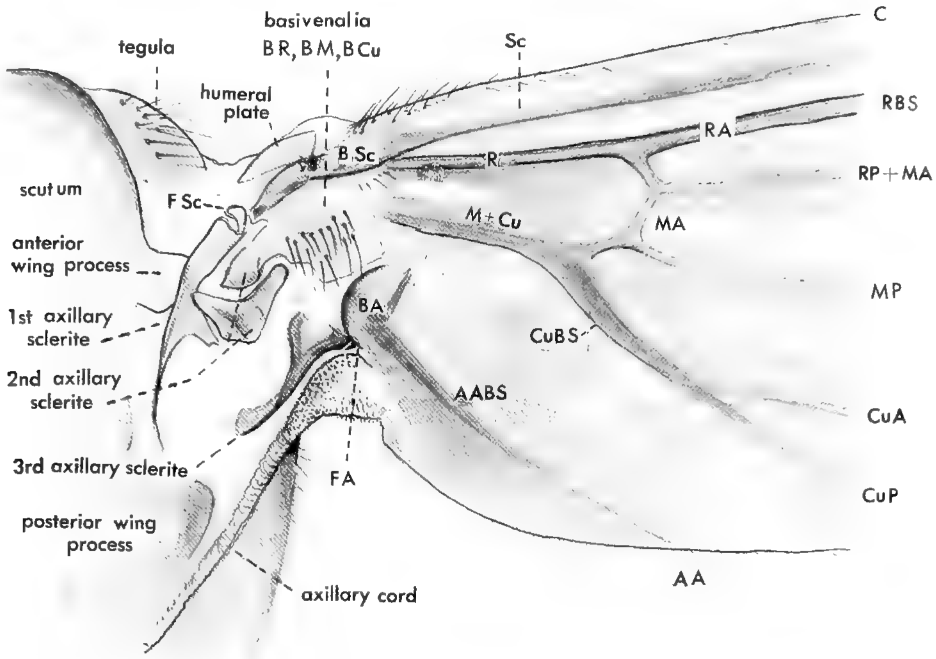


FIGURE 33. A. Wing attachment of forewing of a plesiomorphic embiid, *Archembia kotzbaueri* (Navás), Embiidae. Nomenclature based on studies of Dr. Kukalová-Peck (pers. com.). Explanation of symbols: Sc = subcosta; BSc,BR, BM, BCu, BA = subcostal, radial, medial, cubital, and anal basivenales; medial plate including medial (FM) and cubital (FCu) fulcalares, is almost completely reduced. FA = minute anal arm of third axillary sclerite. The symbol AA (anterior anal vein) is used because there is a tiny anal vein just caudad of the base of AA (not expressed in this species). AABS = anterior anal blood sinus; CuBS = cubital blood sinus; RBS = radial blood sinus. Note that in this drawing the axillaries are somewhat spread apart and that the distance between CuBS and AABS is exaggerated.

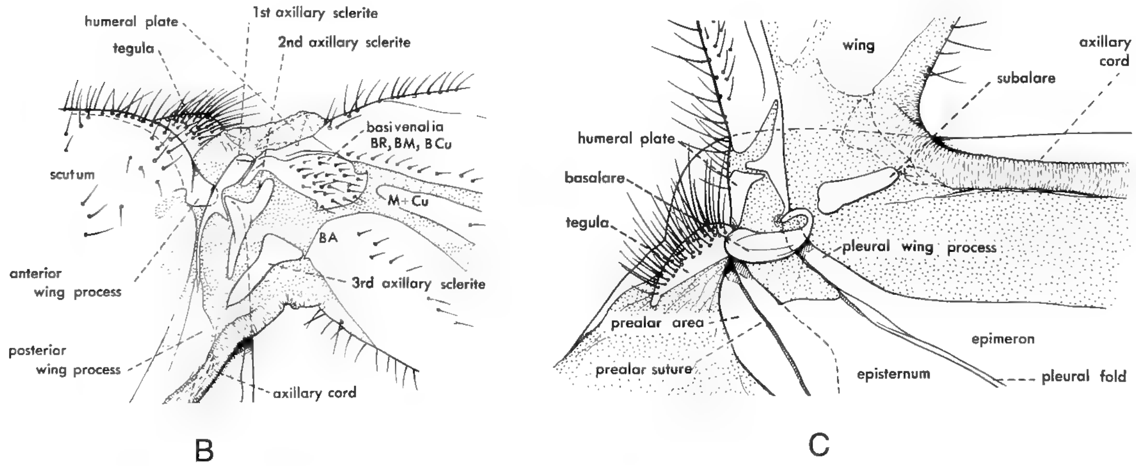


FIGURE 33. B. Dorsal aspect of wing attachment of *Oligotoma nigra*. C. Pleural aspect of wing attachment.

1. Selective pressures favoring wing-loss mutations are too short in duration to be effective. Life of adult males is undoubtedly short (alate males take no food) and they probably mate before the disadvantage of wings is fully felt. In other words, imperfect adaptation of alate males to gallery life is of no importance to a species once males have mated.

2. It is also possible that factors which might result in brachypterism, or apterism, of males have not yet appeared for test in all species.

3. Wing possession may be less disadvantageous in favorable environments, such as tropical rainforests. In such habitats apterism of males is very rare, whereas it is very common in regions with a long dry season. It is thus likely that alate males dispersing in arid regions not only face exposure to adverse climatic conditions, but also are more visible to predators seeking prey in exposed arid habitats.

4. Wide dispersal of advantageous genes is selected through retention of wings.

It may be that universal wing-loss in females was not entirely due to selection against wing-possession per se, but instead for a need to also eliminate projecting ovipositor structures which might have had an even greater barb-effect than wings in reverse movement. One could say that females lost their wings as part of a nymphalization "package" that resulted in a loss of most protruding adult appendages by cessation of development at an early nymphal instar, perhaps not later than the second, before even buds of such appendages make their appearance. This neotenization was probably effected by mutations influencing the secretion of the juvenile hormone.

Such a major specialization of wing structure and function must have occurred long after the order evolved most of its other peculiar specializations before fragmentation of Pangaea. It would be difficult to explain the present widespread distribution of the order if females had been apterous and needed to hazardously extend their range afoot outside of protective galleries. Both sexes must have been alate during the major evolutionary and distributional history of the order and female apterism must have later convergently occurred on all evolutionary lines. The appearance of more aggressive predators, such as ants, could have been a factor favoring apterism and confinement to galleries.

Apterism in males (Figs. 34, 35, 36) also has independently appeared many times within the order, but in varying degrees. Females can deposit eggs in galleries without specialized oviposition structures; males, however, with the exception of those of a new family from Afghanistan, must have well-developed genitalia and mandibles (often used as head claspers) to insure copulation. Thus, even in highly neotenic males, such as those of the Australian family Australembiidae, neoteny mostly retards wing development while, apparently through "tissue competence," the genitalia and head (to a lesser extent), become fully adult. In some species of Australembiidae, however, the head of adult males is variable, an occasional individual within a population has a head indistinguishable from that of a nymph, or of an adult female, and continues to feed.

Males of many species gain advantages of apterism through degrees of thoracic neoteny. As a result, males of some species have only wing buds, or pads, in various states between the extremes of

FIGURE 34. Adult neotenic, apterous male (left) and female of a new species of *Neorhagadochir* Ross (Embiidae) from an arid region of Nicaragua. Unlike its blackish congeners, this species is pale ferrugineous due to its subterranean habits.

FIGURE 35. Neotenic, completely apterous adult male of *Haploembia solieri* (Oligotomidae) (slide preparation, body length 10.0 mm). Endemic to the Mediterranean region. Note: tong-like mandibles for grasping head of females during mating.

FIGURE 36. Neotenic apterous adult male of *Electroembia antiqua* (Pictet) (Embiidae). Baltic Amber, Hamburg Geological Museum, body length about 10.0 mm. This fossil demonstrates antiquity of neoteny in males and close resemblance to modern species.

full wing pad development and no trace of pads whatsoever. All this is probably due to different levels of secretion and timing of juvenile hormone. In some species there may be percentages of apterous, subapterous, micropterous and alate males within a species' population, or in those of certain geographic populations of a single species.

In arid environments apterous males are more likely to remain within the parent colony, mate with a sister, and thereby inbreed the wingless trend or condition. Because of their greater ease of movement, apterous males should survive in greater numbers and eventually male apterism could become universal within a given population. Conversely, in damper, more benign environments, any trend toward male apterism might be swamped out by random matings of alate individuals which are more likely to survive flights from colony to colony.

Some families include genera and species which have radiated into marginal environments and thus have apterous, or subapterous males. Therefore, apterism in males must be used with great caution as a character in systematic studies for it is most often environmentally related. It is interesting to note that one of the oldest known fossil species, *Electroembia antiqua* (Pictet) of Baltic Amber (Ross, 1956), is completely apterous (Fig. 36) and this suggests that the ancient land surface which supported the "amber forest" might have experienced a long dry season. It is possible that it was once in what is now a Mediterranean, seasonally-dry global position, a terrain which has since drifted northward into a colder, wetter latitude.

Ultimate in the trend toward almost complete neotenization of males is in a peculiar, undescribed, subterranean species occurring in the desert steppes of western Afghanistan. In this species males not only have lost all traces of wings but also have completely nymphoid bodies and abdominal terminalia (except for tiny rudiments).

There is an interesting correlation between wing size and body proportions. Relatively large wings are characteristic of light-bodied, slender, small-headed males of species occurring at higher elevations of damp, equatorial mountains. In contrast, shorter, narrower wings are possessed by robust, larger-headed males living at lower altitudes and in semi-arid regions. Except for slight venational diversity, often involving vein-desclerotization, the wings of embiids are remarkably similar in all species.

Abdomen

The abdomen is slender, usually as long as head and thorax combined. In nymphs, adult females, and apterous adult males of some species, it is circular in cross-section. However, in alate adult males of most species it is dorso-ventrally flattened due to reduced content, all food having been excreted during the penultimate nymphal stage. Fat storage is limited, and internal reproductive organs are much smaller than those of females.

Ten abdominal somites are conspicuous in both sexes but vestiges of the 11th and 12th persist. Basic somatization is most apparent in nymphs and adult females whereas that of adult males is confused by complexity of external genitalia, especially in apomorphic taxa, as illustrated (Figs. 44–53).

The first abdominal tergum of nymphs and adult females, a simple plate without an acrotergite, closely contacts the metathoracic scutum. In alate males an extensive, medially-cleft acrotergite is fused to the metathoracic scutum. Terga of somites two through eight are similar to each other but the ninth is much shorter, broader, extends ventrad down each side of the abdomen and almost contacts the outer margins of the ninth sternum, or hypandrium (H). In nymphs and females the tenth tergum is large, triangular, and its outer basal angles extend ventrad to the sides of the ninth sternum (Figs. 37, 38).

Matsuda (1976) regarded the produced apex of the tenth tergum as the supra-anal lobe fused to the tenth tergum. I have concluded that only the small, weakly sclerotized area just beneath the apex of the tenth tergum is a vestige of the eleventh (labelled epiproct in Figs. 37 and 38). In females of some species this vestige is separated from the apex of the tenth by a transversely wrinkled, non-setose, intersomital membrane and the vestige bears its own setae. Edward L. Smith informs me that intertergal muscles are attached to this sclerite. It, and the apex of the tenth tergum, develop into significant terminalia structures, e.g., the epiproct (EP) and the medial flap (MF), prominent in adult males of many species.

Located just beneath the lateral margins of the first eight abdominal terga are elongate laterotergites, each of which has a spiracle in the anterior end. In many species the laterotergites of these somites are divided into two sections, the posterior of which usually is much smaller (Fig. 38). Spiracles and laterotergites are absent on somites nine and ten, the positions of the latter being filled by latero-ventro extensions of the terga.

In many apomorphic embiids, such as species of *Oligotoma*, the first sternum is small and triangular but in plesiomorphic genera, such as *Clothoda* and *Embia*, it is larger and more transverse. Sternites of somites two through seven are nearly equal in size and form, each being subquadrate with a narrower base. In adult females sternites of somites eight and nine, which are associated with the vulva, are variously modified and will be separately discussed.

On either side of sternites three through eight there are narrow, elongate sclerites similar in shape to the laterotergites. Apparently these are abdominal pleurites. They are almost entirely absent on the first two somites, being represented only by two setae adjacent to the sternite of the second somite. Pleurites are absent on somites nine and ten. Inevitably, there are difficulties in interpreting terminal abdominal somites. Using Snodgrass (1935) as an authority, I have decided that the paraprocts are structures of somite nine. Edward L. Smith (pers. com.) believes that the paraprocts are hemisternites of somite ten. Matsuda (1976), however, regarded them as structures of somite twelve, suggesting that somite eleven is greatly reduced with cerci remaining as its only elements and, therefore, that structures of somite twelve immediately follow those of somite ten. I am not prepared to question these conclusions and will simply endeavor to correctly homologize terminalia characters without being overly concerned with their somital associations.

The cerci of nymphs and adult females are similar throughout the order and seemingly comprise only two segments (I realize that these are properly termed flagellomeres but, for simplicity, I use the term segment). Cercus-basipodites, or coxites, may be regarded as basal segments of three-segmented cerci. Each basipodite forms an almost complete fleshy ring around the base of a cercus. The cercus segments usually are elongate, cylindrical and often unevenly sclerotized. Except for a relatively large nerve, most of the content of a segment appears to be fat. The cercus muscles are attached to the basipodites which, in the left cerci of adult males of many species, become fused to the base of the basal segment. In plesiomorphic species the derm of the cerci is evenly sclerotized, but in some apomorphic taxa it may be almost entirely membranous. As a species character the distal segment may be contrastingly pale or white due to the color of tissue within a transparent derm.

The cerci bear setae of two types. Most numerous are ordinary, tapered setae of various sizes which arise from simple, circular sockets. These occur on all surfaces but may be especially dense on the inner faces of the basal segments. In males such density may augment copulatory grip. The second type of seta is finer, less tapered, arises from a rosette-type of socket, or pit, and is most common on the usually-less-sclerotized outer side of the basal segments. Invariably throughout the order, the distal segment has only one such seta on its inner side in a species-characteristic position. Such setae are present in many other arthropods and are often called trichobothria. Probably both types of setae are mechano-receptors providing tactile guidance, especially during reverse movement in the galleries.

External genitalia of females

Because of neoteny, the external genitalia of females are underdeveloped. However, some species possess buds of gonopophyses which might attain adult form if females completed development, as they did during their pre-neotenic evolutionary period.

Reduction of genitalia is possible because of the simplicity of oviposition. A female merely attaches eggs to a surface within the galleries, or on a silk substrate, therefore no special structures are required to insert them into a substrate. Furthermore, vital reverse movements to escape predators would be slowed, or arrested, if ovipositing structures protruded and snagged against silk gallery walls.

The terminal abdominal terga, paraprocts, and cerci of adult females (Figs. 37, 38) are identical to those of nymphal instars. The only external evidences of maturity, besides the open vulva, are slight modifications of the eighth and ninth sternites. In *Oligotoma* (Fig. 33), and many other genera, there is no trace of valvulae, but between the eighth and ninth sternites there is a slight, transverse, translucent ridge, or carina. This elevation is subject to much modification within the order; for example, in many species of *Embia* its caudal side has two deep fossae with glossy, sclerotic surfaces. The ninth sternite usually has a baso-medial notch which varies from a membranous condition to the dark, glossy, concave sclerite found in some species of *Embia*.

In other genera, notably *Metoligotoma* Davis, rudiments of valvulae are quite conspicuous. In *Metoligotoma* (Fig. 38) the eighth sternite is small and lies beneath two blunt, fleshy lobes, or pads, which bear small, rudimentary sclerites. These appear to be rudiments of the first valvulae. Overlapping the anterior margin of the ninth sternite, a prominent, bilobed, non-setose ridge (probably a homolog of the membranous ridge described for *Oligotoma*) is present which may be a specialized rudiment of the second valvulae. The lobes themselves may be rudiments of the second valvulae and the low connecting ridge represents anterior intervalvula. The ninth sternite is small and has a large, quadrate membranous area in the basal half. The pouch-like development of this area, described for *Oligotoma*, is well developed in *Metoligotoma* and is partially concealed by a vestige of the base of the second valvulae. The aperture of the accessory gland may be located in this pouch (Snodgrass, 1935, fig. 314B).

Although species of *Clothoda* have the most plesiomorphic males of the order, adult females of the genus lack even traces of valvulae, the ninth sternum being simple and lacking a basal pouch. Throughout the order interspecific variation occurs in sclerotization, pigmentation, and vestiture of female genitalia and is of potential value in systematic studies, at least at the species level.

Internal genitalia of males

Probably the distal portion of the ejaculatory duct is projected into the vulva during copulation but it rarely, if ever, has sclerotic rigidity—an aedeagus. Exceptions to this are especially apparent in the genus *Enveja* Navás (Fig. 50), and to a lesser degree in most genera of Anisembiidae, and in some species of Oligotomidae; but this is merely limited to sclerotization of the duct walls. In my figures, labelled

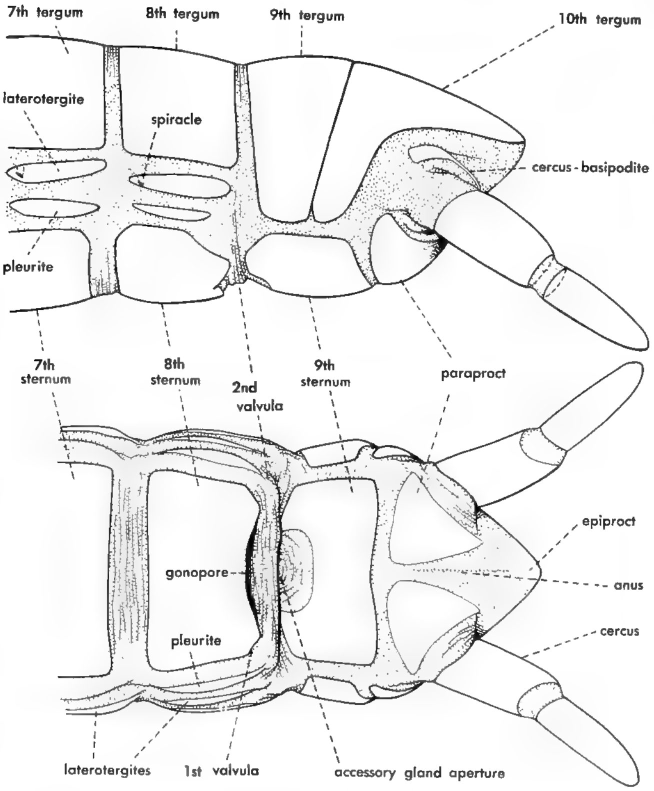


FIGURE 37. Abdominal terminalia of adult female *Oligotoma nigra* Hagen (Oligotomidae). Upper, lateral aspect. Lower, ventral aspect.

gonapophyses, they appear as a pair of rod-like structures fused beneath the duct's apex, the orifice of which is microspiculate in many species. The sclerotic portions of such structures are most apparent in cleared, slide preparations.

The need for a well-developed intermittent organ is lessened by the fact that copulatory union is accomplished and prolonged by use of processes, lobes and hooks on the ninth, tenth and eleventh somites and, in many species by a clasping action of the left cercus and/or its basipodite. These, the primary characters used in classification, must, however, be used with caution because of frequency of convergence. For example, fusion of segments of the left cercus occurs in many unrelated taxa and, in some cases, as a variable within a species.

External genitalia of males

("Terminalia")

Complex, often bewildering, male abdominal terminalia distinctions, often complicated by convergences, are fundamental characters in systematic studies.

Early in its penultimate instar a male's abdominal apex is identical to that of other nymphal stages. Accordingly, the tenth tergum is triangular and unmodified; the eleventh (epiproct) is represented by a small, rudimentary sclerite (EP) just beneath the acute apex of the tenth; the ninth sternite is transversely quadrate; the anus is flanked by large, triangular, convex paraprocts (LPPT and RPPT); the cerci and their fleshy basipodites (LCB and RCB) are symmetrical. Later in the penultimate instar future changes are presaged by distortions due to developments within; the tenth tergum may enlarge toward its left side, the ninth sternite (H) may develop a small medial lobe (HP),

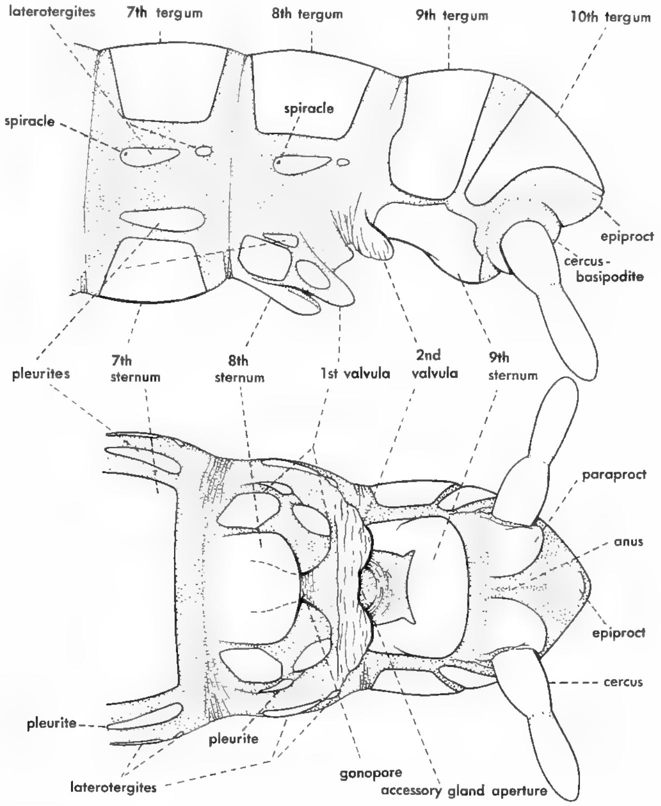


FIGURE 38. Abdominal terminalia of adult female *Metoligotoma ingens* Davis (Australembiidae). Upper, lateral aspect. Lower, ventral aspect.

and its left cercus-basipodite often exhibits signs of profound changes. The appearance of highly modified adult structures following ecdysis and reduction of some nymphal structures, e.g., the right paraproct, is most interesting.

The terminalia usually are intricately developed to insure prolonged copulation and perhaps owe such complexity to sperm competition within the species to improve sexual union and thereby assurance that the contents of a particular male's spermatophore will have time to enter the spermatheca.

In many genera the basal margins of terga of subterminal abdominal somites are extended forward as especially large apodemes anchoring intertergal muscles which elevate the terminalia during copulation. Such males often move about outside of galleries with the terminalia curled forward in the manner of male scorpionflies and earwigs.

In *Clothoda*, the order's most plesiomorphic genus (Frontispiece and Figs. 39–41), the terminalia are almost perfectly symmetrical and basically similar to those of nymphs and females. In *C. nobilis* (Gerst.), the most plesiomorphic species of the order, the tenth tergum (10) is short, narrowly transverse, and medially uncleft. The tergite's caudal apex is turned upward as a thin somewhat translucent medial flap (MF). The medio-basal portion of the tergite is non-setose, weakly sclerotized, shallowly depressed and projected cephalad as an area I have termed medial sclerite (MS). This is a neutral area separating the more vaulted, sclerotic, setose, incipient hemitergites (10 L and 10 R) to which the cercus-basipodite muscles are attached.

In *Clothoda longicauda* Ross (Figs. 39A, 40B), a slightly more apomorphic species, the medial area of the tergite is partially membranous, forming a branched medial cleft which, in adult males of most other species of the order, divides the tenth tergum into well-defined hemitergites (10 L and 10 R), each of which has a distinct copulatory function.

Viewed from the caudal aspect (Fig. 39A) it is apparent that the medial flap (MF) of *C. longicauda* bears a small sclerite on its ventral surface (perhaps a vestige of the eleventh tergite). Also visible is a fleshy lobe above the anus which apparently is the epiproct (EP), a rudiment of somite eleven. This conclusion is confirmed when one views the caudal aspect of *Archembia batesi* (McLachlan) (Fig. 39B) and notes that the ventral sclerite of the medial flap (MF) has elongated and is extended onto the epiproct which has become an extensive supra-anal pad (EP). A transverse fold, or hinge, occurs where the epiproct levels off.

In *C. longicauda*, indistinct, small lobes, visible on either side of the medial flap (MF) appear to be precursors of hemitergal processes (10 LP and 10 RP). In *Archembia batesi* (Fig. 39B), these lobes are distinct processes (10 LP and 10 RP) while the medial flap (MF) remains prominent. This condition prevails in many genera, as exemplified by *Dihybocercus lunaris* (Navás) (Fig. 39C). In most of these genera the medial flap (MF) has rotated clockwise so as to almost parallel the longitudinal axis of the medial cleft. Incidentally, in *Dihybocercus* and other Embiidae, there is a small pouch at the forward end of the medial flap. It is likely that this end of MF produces glandular secretions of significance during copulation. This deserves investigation. However, in at least one major section of Embiidae, the flap (MF) usually is reduced to a longitudinal, sclerotic ridge, or it may have completely atrophied.

In all genera of Clothodidae, except *Clothoda*, the medial flap (MF), or at least its caudal angle, seems to assume the function of the right process (10 RP), for there is no flap-like structure in the normal position of the medial flap. In these genera the epiproct (EP) is a broad, supra-anal pad, often with a narrow, but prominent, longitudinal sclerite. Such conditions, especially that of at least portions of the medial flap (MF) serving as a process, are characteristic of *Enveja*, Oligotomidae, Teratembiidae and other taxa. Interestingly, *Chromatoclothoda nana* Ross is well on its way toward becoming oligotomoid in terminalia structure (Ross, 1987:34).

If this tentative interpretation is correct, then at least portions of the right tergal process (10 RP) are analogous, not homologous. It is therefore possible that a major taxonomic division of the order begins **within** the family Clothodidae. It will be noted that the longitudinal membranous area between the medial flap (MF) and the right hemitergite (10 R) of most Embiidae has become transverse in Oligotomidae and Teratembiidae and partially to completely separates MF + 10 RP from an often much-reduced 10 R. This enables MF and 10 RP to hinge directly ventrad, or even forward, beneath the hypandrium (H) during copulation.

Because of observation limitations within silk galleries, copulation is difficult to observe. However, in a male specimen of *Aposthonia* (Oligotomidae) preserved in alcohol, copulatory positions of various structures were fixed. In this specimen the probably-composite 10 RP (MF + 10 RP) is folded down and forward completely beneath the hypandium (H). The epiproct (EP) is also pulled down so that neither of the two structures is visible from above. Apparently contraction of strong inter-tergal muscles attached to EP is the force that moves the composite right tergal process (which apparently lacks muscles). The specimen also exhibits 10 LP pressed against the inner side of the basal segment of the left cercus with its complex apex vertical and faced to the right. The hypandrium process (HP), forming a rigid trough for the gonopophysis, is directed upward, like an erect human penis and is pressed against the sclerotic margins of 10 L and 10 LP.

Throughout the order, the left hemitergite (10 L) is well defined, its margins usually sclerotic and inflexed and its surface vaulted to provide especially strong anchorage for large muscles serving the important clasper function of the left cercus, or its basipodite.

The left hemitergite's process (10 LP) often consists of an inner talon and an outer flange which often is thin, or fleshy. In many species, however, the outer flange is greatly reduced, or absent. The left hemitergite's process assumes many forms consistent within a species and thus is especially useful in systematic studies. It probably is the most important structure for providing rigid guidance of the apex of the endophallus into the vulva.

Often the left hemitergite (10 L) is clearly separated from other portions of the tenth tergite by a submedial, membranous cleft which may extend to the basal margin of the tergite. In many other species, however, the basal portions of the cleft is absent due to fusion of the inner-basal margin of 10 L

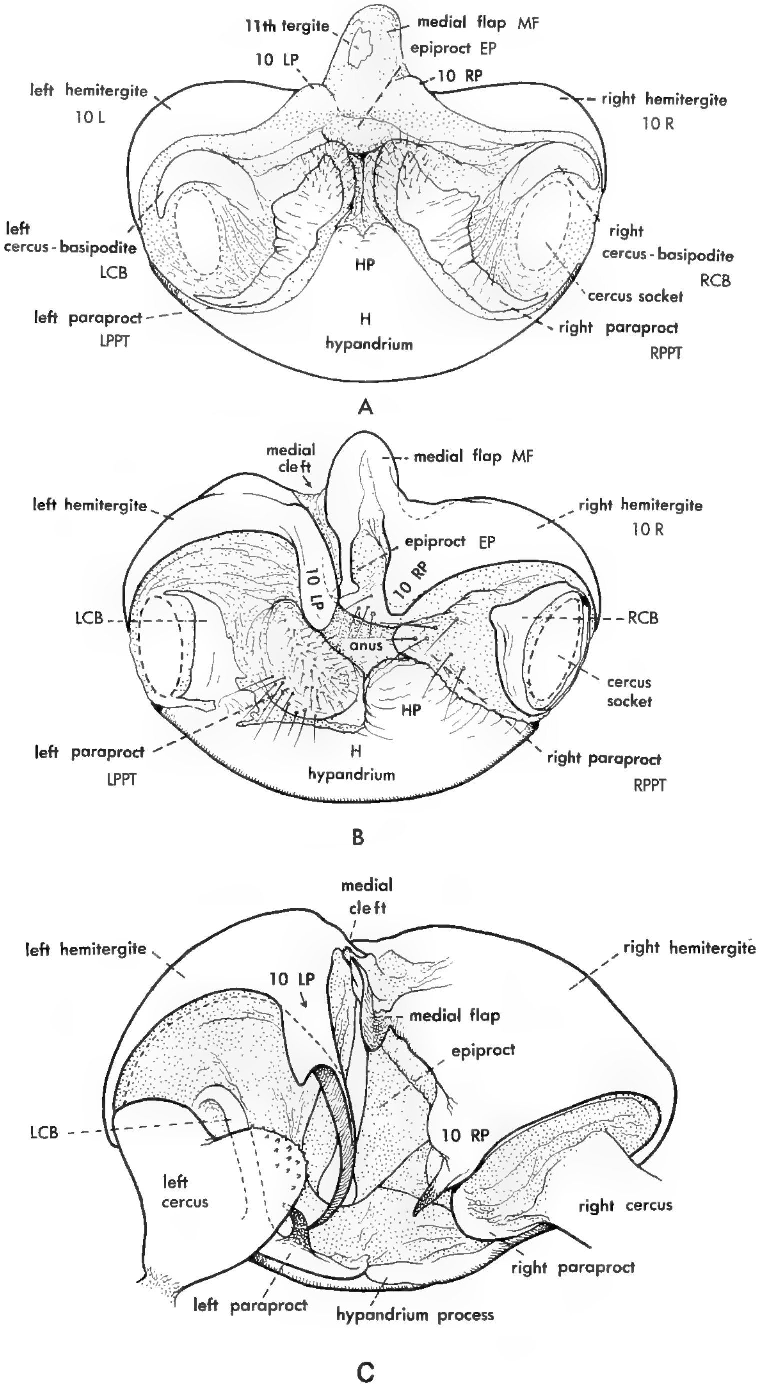


FIGURE 39. A. Caudal aspect of male terminalia of *Clothoda longicauda* Ross (Clothodidae). B. Caudal aspect of *Archembia batesi* McL.) (Embiidae). C. Caudal aspect of *Dihybocercus lunaris* (Navás) (Embiidae). These drawings show increasing complexity of the terminalia.

with the medial sclerite (MS), as in most Teratembiidae (Figs. 52, 53). The medial sclerite (MS) often is obscure, or absent, but in Teratembiidae it is extensive, fused to the inner-base of 10 L and usually projects (often acute in form) beneath the entire left half of the ninth tergite (9). The fold of its left side is continuous with that of the outer side of the left hemitergite (10 L) and thus provides especially strong muscle anchorage.

The ninth sternite, or hypandrium (H), is a broad, quadrate, subgenital plate which usually has a weak basal margin but often has strong lateral margins. In plesiomorphic species it is symmetrically produced medially as a caudal process (HP) which subtends the apex of the endophallus. In apomorphic species it often is angled leftward and complexly modified, as in *Dactylocerca* Ross (Anisembiidae) (Fig. 47). The basal, non-setose, sclerotic portion of the paraprocts (LPPT and RPPT) often are closely associated, or fused, with the caudal angles of H. Indeed, the left paraproct (LPPT) may fuse to become the sclerotic, left-caudal margin of H and, in some species of Teratembiidae, the hypandrium process (HP) is completely atrophied and the left paraproct becomes the sole subgenital support (Fig. 42).

Primitively, the paraprocts (LPPT and RPPT) are equal in size and form. Each consists of a fleshy, setose, distal portion flanking the anus, and a basal, sclerotized, non-setose portion. In *Archembia* (Fig. 39B), the distal (caudal) portion of the paraproct may be membranous and setose and may atrophy while the basal portion may fuse with adjacent structures. This figure also illustrates the beginning of leftward asymmetry of the paraprocts.

The basal segment of the left cercus (LC_1) may be unlobed, as in clothodids, but more often it has a prominent inner lobe bearing numerous, small, conate, peg-like setae ("echinulations") which enhance the segment's copulatory grip. As further improvement of this "tool," especially in some Anisembiidae, the distal segment is "absorbed" into the basal to form an unjointed clasper. The extreme example is in *Dactylocerca* Ross in which the segment is long, arcuate and "embraces" the females left side (Fig. 47). Such composite left cerci have independently developed on many unrelated evolutionary lines.

On a distinct evolutionary tangent, especially in Teratembiidae, the copulatory grip is performed by the extreme base of the basal segment, perhaps by

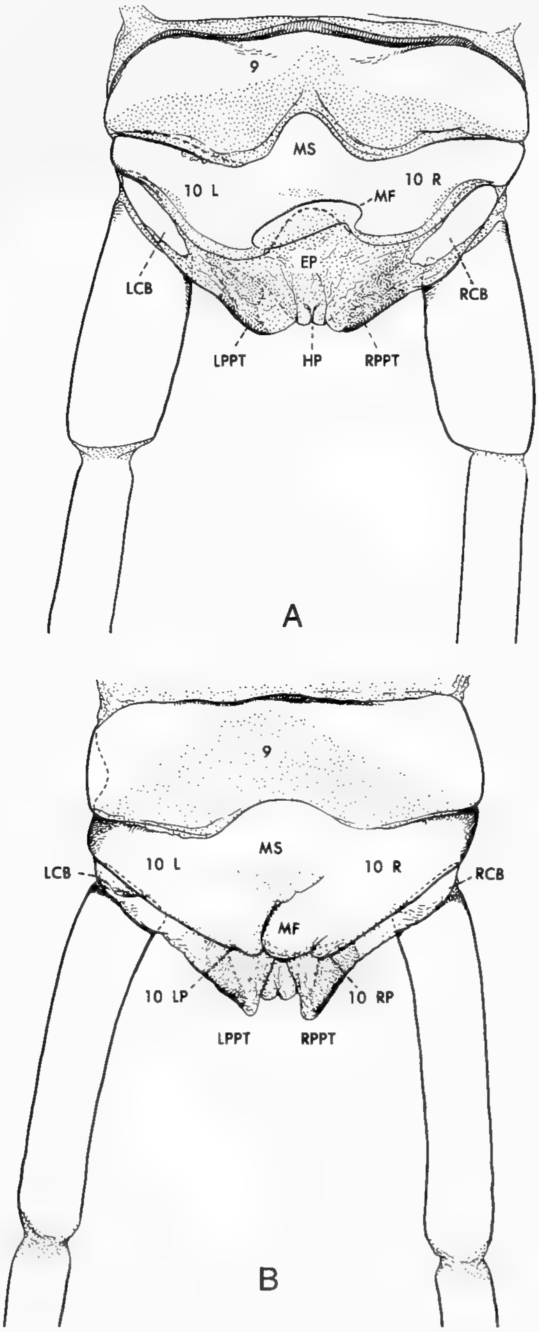


FIGURE 40. A. Dorsal aspect of male terminalia of *Clothoda nobilis* (Gerst.), the most plesiomorphic species of the order. B. Dorsal aspect of terminalia of *Clothoda longicauda* Ross, a slightly more aposematic species of Clothodidae.

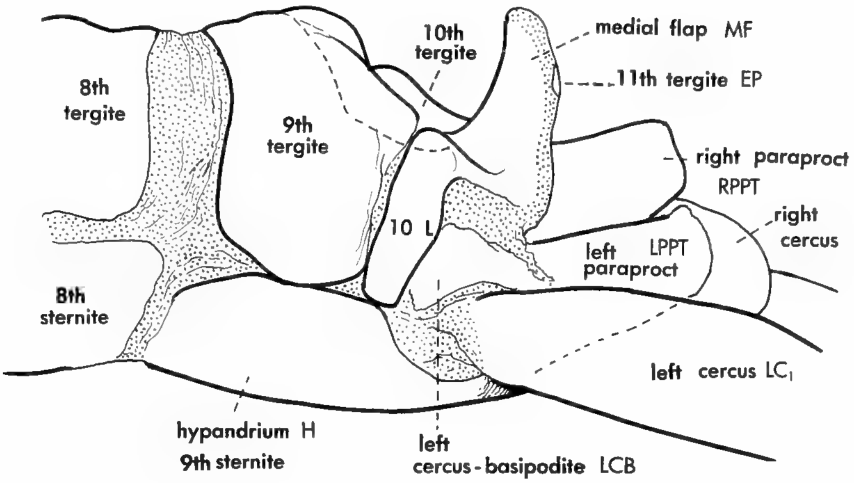


FIGURE 41. Lateral aspect of terminalia of *Clothoda nobilis* showing upturned apex of the tenth tergite which becomes the medial flap (MF), and the rudimentary eleventh tergite which becomes part of the epiproct (EP).

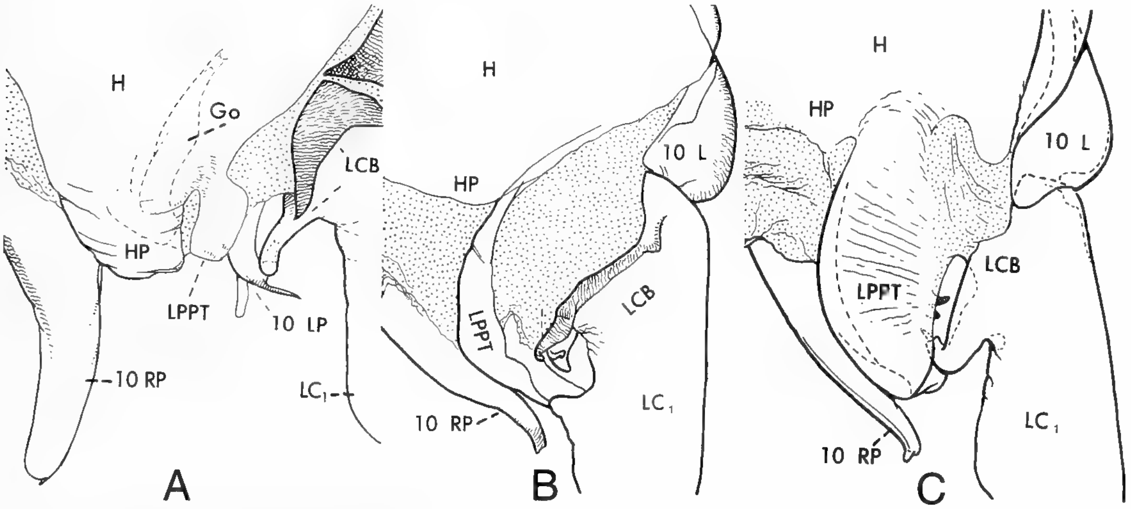


FIGURE 42. Atrophy of hypandrium process (HP) as the ventral support of the ejaculatory duct and assumption of this function by the left paraproct (LPPT) in males of two new genera of Teratembiidae. A. New species from Kenya with HP still serving as ventral support. B. New species from India. C. New species from Nigeria. Also shown in Figs. 51-52.

the left cercus basipodite (LCB) which has varied mesal processes (Figs. 52, 53).

The right cercus of males rarely is modified as it apparently has limited, or no function, in clasping the female and, in many cases, at least the basal segment is partially or entirely desclerotized. In very few species, however, the inner face of the basal segment is sclerotic and even more rarely distally inwardly lobed. Such lobes never are echinulate. In the Australian family Australembiidae the basal segment always is globular.

There are probably many other factors and structures prolonging copulatory union. For example, males often grasp the female's head with highly modified mandibles. Dense, large setae on the hemitergites and inner sides of the cerci, as in *Pachylembia* Ross, may assist. The reader should refer to Figures 44–53, a "portfolio" of terminalia figures at the close of this section, which show some of the diversity of terminalia within the order.

Anomalous male terminalia

A small percentage of males have anomalous, "mirror-image," terminalia in which normally developed structures are completely reversed left-to-right(Fig. 43A). In other anomalous specimens, structures of the left side are symmetrically repeated on the right side (Fig. 43B), or those of the right are repeated on the left (Fig. 43C). There also are occasional bilateral gynandromorphs. These are conspicuous in the case of winged species—the female side, of course, being wingless.

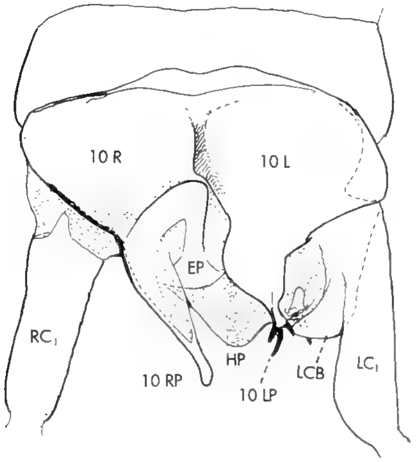


FIGURE 43A. Anomalous terminalia of *Oligotoma greeniana* Enderlein of India, "mirror-image."

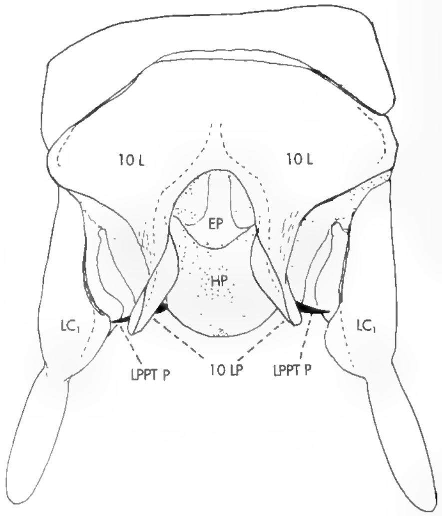


FIGURE 43B. Anomalous *Aposthonia minuscula* (Enderlein) of India. Left side repeated on right side.

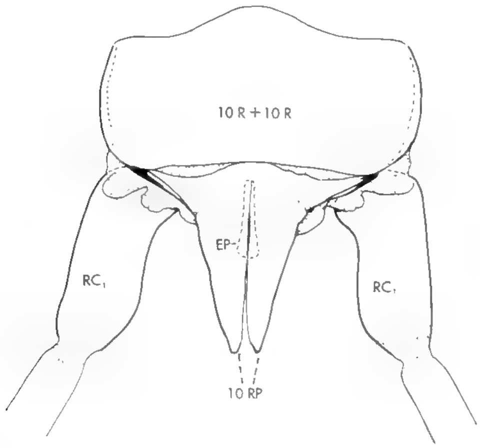


FIGURE 43C. Anomalous *Diradius plaumanni* (Ross) of S. Brazil. Right side repeated on left side.

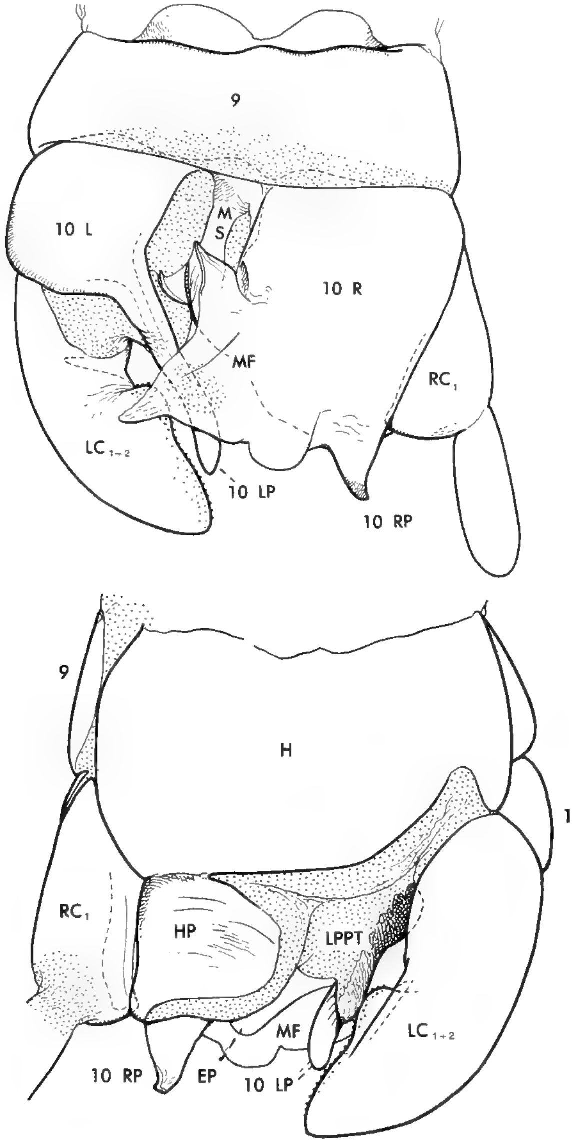


FIGURE 48. *Metoligotoma illawarrae* Davis Australembiidae). Eastern Australia.

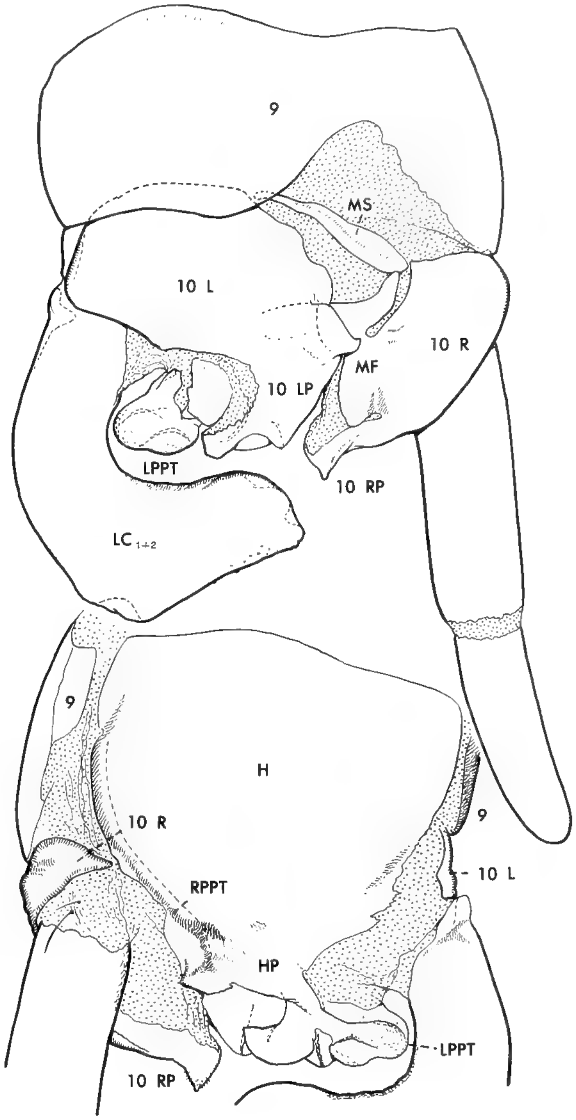


FIGURE 49. *Embonycha interrupta* Navás (Embonychidae). Chapa, northern Vietnam.

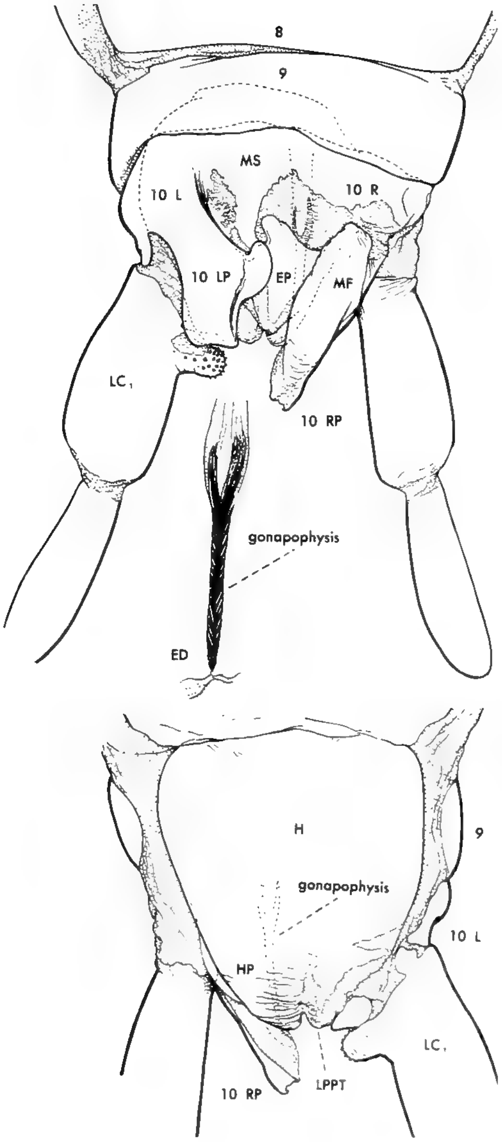


FIGURE 50. *Enveja bequaerti* Navás. Central Africa.

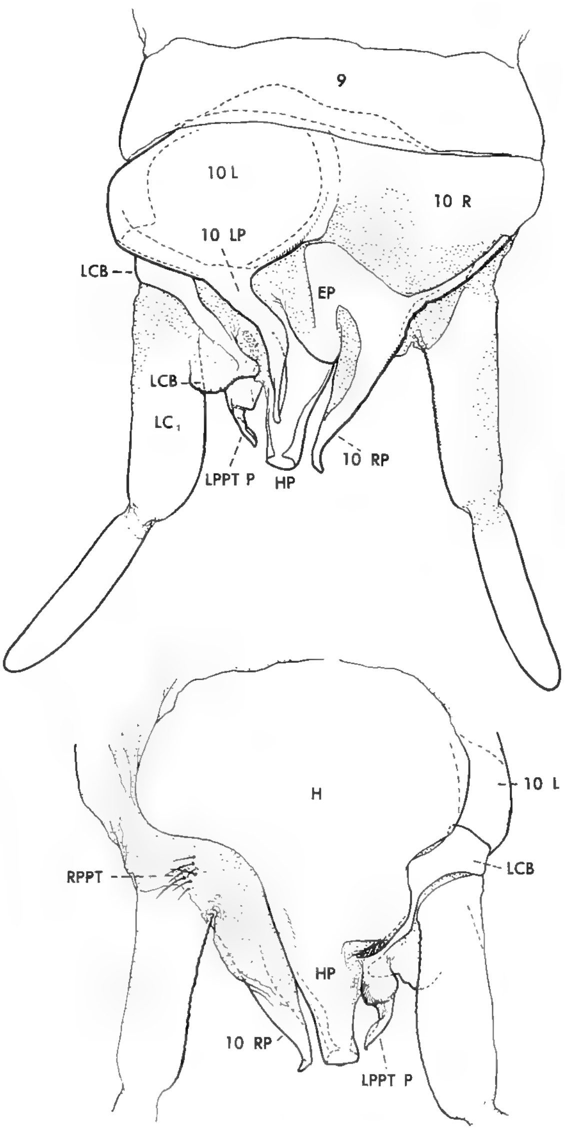


FIGURE 51. *Oligotoma nigra* Hagen (Oligotomidae). Middle East, introduced into southwestern USA and Australia.

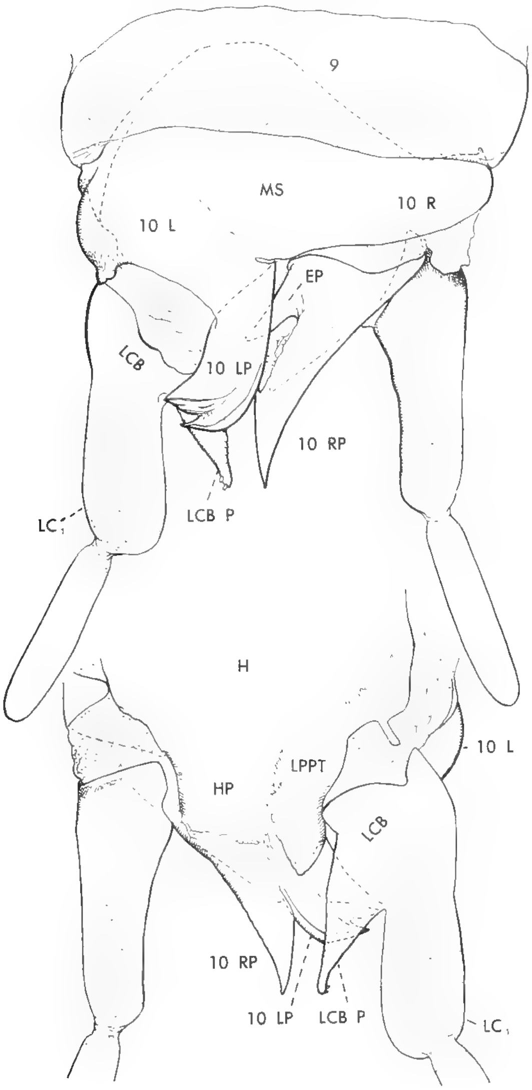


FIGURE 52. *Oligembia capensis* Ross (Teratembiidae). Cape Region, Baja California, Mexico.

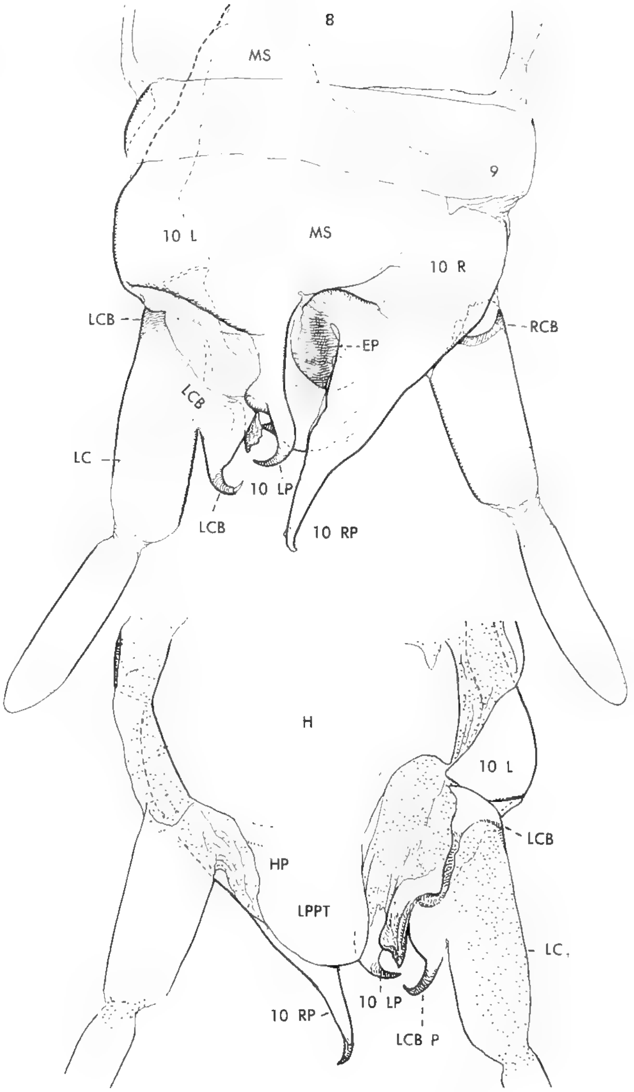


FIGURE 53. *Paroligembia* n. sp. (Teratembiidae). Ethiopian highlands.

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Part 2

A Review of the Biology of Embiidina

Summary

The biology of Embiidina is reviewed and illustrated with many of my photographs. Stressed are the evolutionary restrictions imposed by life almost completely confined to self-produced, narrow, silk galleries. This review also covers diverse topics, such as: diet, locomotion, social behavior, mating, eggs and their protection, development, ecological and geographic ranges, natural enemies, and diseases.

In writing EMBIA Part 1, on anatomy of the order, it was necessary to discuss the relationship of structure to function, especially in reference to the wings. Therefore, the reader must expect some repetition of information in the two parts.

Methods

To secure specimens for a comprehensive, world scope coverage of embiid taxa, I made many, often extensive, collecting trips throughout the order's range. For example, almost all countries of Africa were visited during eight excursions covering about four years in all. Nine months were spent in India, Bangladesh and Pakistan, several months in southeastern Asia, Australia and many months in significant regions of the Americas, and other places.

To be effective, and to avoid wasting time and funds in hotels, major trips were made in personally-designed camping vehicles (see National Geographic articles in March 1961 and September 1965 issues). To get a broad representation of higher taxa, vegetation and life zone maps were used to determine routes of travel.

Such extensive fieldwork over a fifty-year period, offered opportunities to observe embiid biology, but only briefly, for life histories are often a year in length. Prolonged observations had to be made in cultures maintained in my Academy and home laboratories (Fig. 43). However, because as many as 800 cultures resulted from a single eighteen-month expedition, it wasn't possible to make an in-depth study of any one species.

General biology

In spite of presumed great antiquity and isolation of taxa on long-separated continents, the biology of embiids is remarkably uniform, as it is in several other ancient arthropod groups, such as scorpions and cockroaches. In embiids, order-defining characters and biological uniformity result from perfection of evasive movement in a self-produced micro-environment, one which literally and figuratively has "channeled," or limited diversification of the order's anatomy and biology. The key factor, of course, is life almost entirely confined to narrow silk galleries (Figs. 1, 2 and 3).

The galleries are produced by unique foretarsi swollen by numerous, perhaps hundreds, of globular, blastula-like, syncytial glands within the basal segment (Fig. 2). Viscous silk is conducted from each gland via a narrow duct to an opening at the tip of a hollow, seta-like silk-ejector. These are located mostly on the thin, ventral surface of the basal segment and to a much lesser extent on the mid-tarsal segment. In *Oligotoma nigra* Hagen, for example, there are approximately 150 such ejectors on each tarsus and thus a corresponding number of silk strands may simultaneously issue with each tarsal stroke. As both legs spin, silk webbing is produced with remarkable rapidity. Indeed, considering production speed and quantity, embiids may rival spiders as the most efficient silk-producing organisms on Earth.

Except perhaps for their number, it is assumed that the glands are similar in all developmental stages of all species of the order. Even first instar and teneral individuals are able to spin and, remarkably, the ability continues throughout adult life.

The galleries compose an expanding labyrinth usually produced and occupied by the brood of a parent female. In some species, however, it is necessary for early stage nymphs to disperse and establish independent galleries so as to avoid injury, or death, due to sibling hostility. It should be noted, however, that such hazards are likely to be intensified in crowded laboratory cultures in which most of my observations were made.

FIGURE 1. Adult *Pararhagadochir birabeni* (Navás) (Embiidae) of Argentina, showing typical appearance and posture of all female embiids. Pale bands between thoracic somites characterize many species of the order.

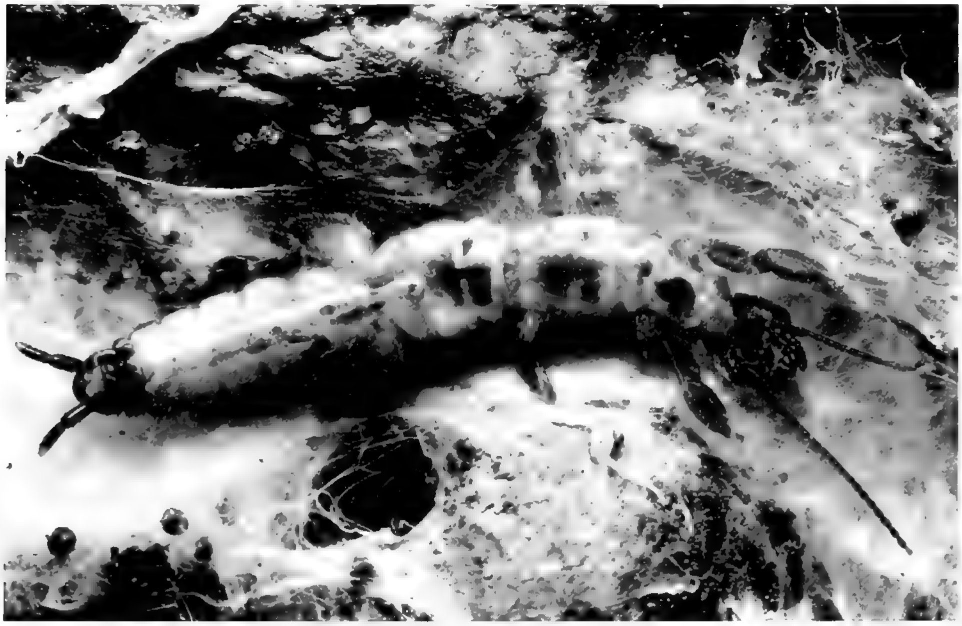


FIGURE 2. Adult female of *Ptiloceremb ia* n. sp. (Notoligotomidae) from Malaya exhibits universal spinning foretarsi, large hind femora and short, two segmented cerci. The vulva opens between the dark, sclerotic eighth and ninth abdominal sterna.

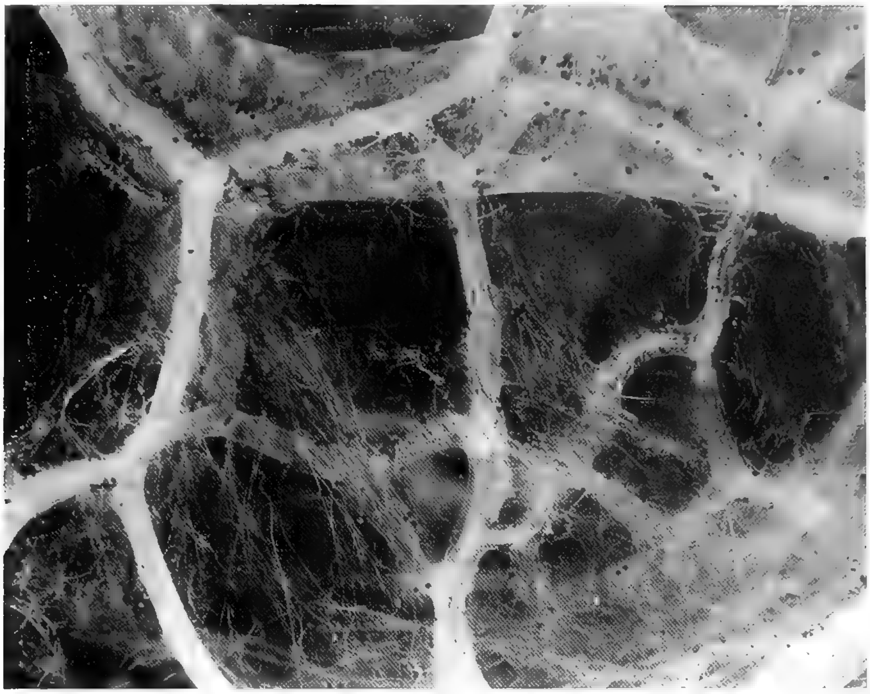


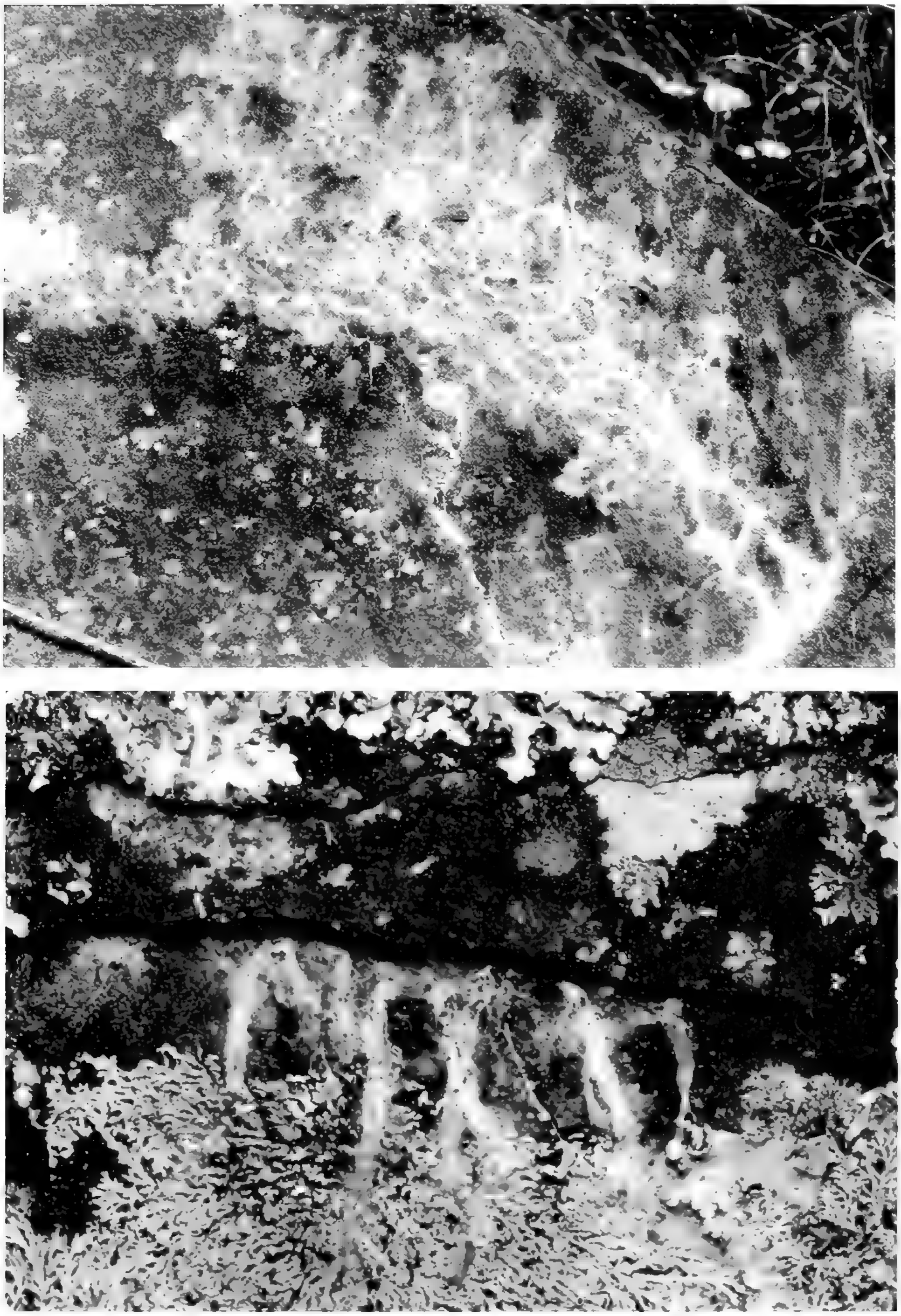
FIGURE 3. Nymphs radiate in galleries, often used in common, which fit their body size. A portion of the parent's larger gallery crosses the top of this photograph, *Donaconethis* n. sp. (Embiidae), Eritrea.

Embiids are highly thigmotactic and produce galleries just narrow enough to maintain constant contact of body vestiture with walls. Advantageous confinement within galleries apparently has governed anatomical and behavioral trends over a long period of evolutionary time. Thus, the spinning organs appear to antedate and to have regulated the evolution of all order-defining characters. Such characters must have become fixed in Upper Paleozoic or Lower Mesozoic times and fully distributed within the order before the breakup of Pangaea.

Gallery diameter correlates with the size of the embiid frequenting the particular section of a colony. In most species first and second instar nymphs, after clustering for several days near their mother (Fig. 4) commence to radiate outward in their own galleries which are increased in diameter and extent as the maker grows. Because offspring of most species hatch from a single egg mass and develop in unison, the galleries of a brood usually become interconnected and used in common.

In addition to the tarsal silk glands, ordinal characters include an elongate, supple body; a prognathus

FIGURE 4. First and second instar nymphs usually cluster near the parent female, *Embia* sp.



FIGURES 5 and 6. Especially in arid regions, parent females often find refuge in rock crevices. Following rains, galleries of the brood radiate on the rock's surface as lichens are "grazed." During excessive heat, or bush fires, the embiids crowd back into the crevice. *Scelembia* n. sp., (Embiidae), Angola.

head with a sclerotic, ventral bridge; short legs, efficient backward movement; equal wings with reduced vein strength except for sinus veins which temporarily can be stiffened with blood pressure; tactile, two-segmented cerci; universal neoteny in females, partially or entirely so in males of some species.

These, and other features treated elsewhere in this work, maximize survival almost entirely dependent on confinement in narrow galleries. Such galleries are constantly extended within or on edible surfaces. Therefore, embiids can feed without leaving their galleries. Food is very simple. All species are primarily phyto-scavengers but some may also occasionally eat live mosses, lichens, etc. There are no predatory species.

Some researchers have suggested that the galleries control humidity, others, including me, have concluded that their primary function is protection from predators and parasites. Although it seems unlikely that the galleries can regulate humidity to any appreciable extent, I have observed the dense gallery walls are at least temporarily impervious to water and thus may protect the occupants, especially soil-inhabiting species, from short-term flooding or habitat saturation after heavy rainfall.

Embiids, such as *Haploembia* spp., inhabiting regions with cold periods, even those temporarily blanketed in snow, completely enclose themselves in a cocoon spun within the galleries. I have noted them in the introduced species, *Haploembia solieri* (Rambur), in California, as well as in Mediterranean and Turkish regions. The habit may be widespread in species living in seasonally-cold regions. As with cocoons of moths, and other insects, the enclosures must function primarily as predator barriers. This is especially important to embiids in seasonally-cold regions because potential enemies, such as predaceous beetles, may be able to hunt prey at low temperatures which immobilize embiids.

The primary advantage of gallery life seems to be predator-avoidance and this is increased when galleries extend beneath or within, solid objects (Figs. 5, 6). Protection in exposed galleries may be somewhat indirect because the silk isn't strong enough to wall off most predators. A predator's initial contact with a web surface probably broadcasts a tactile warning which stimulates rapid, usually reverse, movement into a deeper, more rigid recess within the labyrinth. Edgerly's study (1997) of ant entrance holes in gallery walls, based on *Antipaluria urichi* in Trinidad, appears to contradict this conclusion, at least in her study area. While collecting embiids throughout the order's geographic and ecological range, I have frequently encountered embiid colonies in direct contact with those of ants, often under the same stone, without any apparent molestation by the ants. Ants, however, are probably the principal predators of embiids whenever they leave their galleries.

The value of rapid silk web production was appreciated by me when, experimentally, I released embiids on tropical tree trunks. An exposed embiid immediately retreats into the nearest bark crevice and at once begins to cover it with a silk web. This barrier is steadily improved and extended and, if favorably located, may become the locus of a new labyrinth. It is more likely, however, that the exposed embiid will immediately be seized by an ant or other predator before it can get into a crevice and spin a barrier. It may be said that an embiid outside of its gallery is almost as much out of its element as a fish out of water.

Life in silk galleries may offer other benefits. It is probable that embiids conserve energy by having pre-constructed, smooth-surfaced runways to and from a food source. Silk itself may be an excretory by-product put to good physiological use. There is also the advantage of being able to silk-partition fecal pellets from within the galleries, thereby maintaining debris-free avenues of movement. After excreting a pellet, an embiid snips a hole in the adjacent gallery wall and, using its mandibles as tongs, places the pellet outside and then closes the opening with silk. Fecal pellets accumulated between galleries tend to strengthen their walls (Fig. 7A) and, when deliberately placed atop a labyrinth's surface on a tropical tree trunk, serve as a medium for growth of a microflora enhancing the cover. The habit of protecting, or not protecting, exposed galleries with a surface covering may characterize a species, or even a genus. In addition to fecal pellets, some species pulverize outer bark and cause gallery surfaces to become dusted with chewed powdery debris which may almost completely conceal the colony (Figs. 8, 9). In contrast, species of many other genera never cover their galleries and thus they can be seen from a considerable distance (Figs. 25, 26).

Another type of feces disposal involves their accumulation in low mounds here and there on the la-

FIGURE 7A. Embiids place their dry fecal pellets outside of their galleries, thereby insuring debris-free avenues of movement and a strengthening of gallery walls. *Archembia batesi* (McL.) (Embiidae) in an Amazon rainforest. Surface layer of silk removed.

FIGURE 8. In contrast to *Archembia*, many embiids, as a generic habit, deposit feces on exposed surfaces of their galleries. *Chromatoclothoda* n. sp., (Clothodidae). Ecuadorian montaña.

FIGURE 7B. Galleries of *Archembia batesi* are conspicuously white and, in this case, aligned with bark crevices.

FIGURE 9. Galleries of a new genus and species from southeastern Asia's Golden Triangle, are completely concealed beneath pulverized bark particles and feces. Doi Pue, Thailand.

byrinth's substrate. These are then progressively covered with layers of silk and appear as low white mounds similar to those covering egg masses of some species (Fig. 42).

In tropical forest habitats another type of protection involves prolonged use of old galleries as a surface cover over those spun beneath by successive broods. Thus they can function somewhat as a layer of bark. Galleries themselves may also have prolonged use and consequently silk becomes increasingly dense and obscured by surface debris. Thus, in Amazonia, galleries of species of *Chromatoclothoda* Ross (Fig. 8), in contrast to the conspicuous, white galleries of more plesiomorphic *Clothoda* Enderlein (Fig. 23), both family Clothodidae, can be located only by random tweezer-scraping of likely surfaces, such as the underside of laterally projected branches or ledge overhangs.

The presence or absence of wings and their peculiarities are directly related to predator-avoiding reverse movement in silk galleries—the need to reduce or overcome wing friction, or snag, against gallery walls through flexibility (vein atrophy) and alternating stiffening for flight by blood pressure in sinus veins. The ultimate accommodation is wing size reduction, or complete loss, through neoteny (or paedomorphosis).

These wing specializations are so complex and universal that it is inconceivable that they evolved solely to increase survivability of adult males. Instead, they must have developed ages ago when the order was confined to tropical zones of Pangaea as a means of increasing predator-avoidance by adult females which must live long enough to produce and guard eggs and early instar broods. In contrast, males are short-lived and contribute only sperm to the reproductive process. Later, however, more effective reverse locomotion of females was achieved through complete apterism by means of neoteny. In a sense, females of all extant species are second or third instar reproductive nymphs increased in size. Although males of most species possess wings, there is a tendency on almost all evolutionary lines for them to become completely apterous or brachypterous through neoteny.

FIGURE 10. Adult male during defensive backward movement. Temporarily flexible wings bend forward, thereby reducing friction which could slow escape. Actually, wings when not used in flight can bend at any point—even crumple. New genus and species of Oligotomidae, Thailand.

Embiid wings are non-deciduous, nearly equal in size and shape, wide spaced in thoracic attachment, flat and unfolded when in repose over the dorsum, have pigmented stripes separated by hyaline intervals following the courses of all longitudinal veins, and, most important—indeed unique—some veins are broad, glossy, cuticularized, longitudinal, blood sinuses. Except for slight anal (vannal) lobing in wings of certain species of the rather plesiomorphic genus *Archembia* Ross, the anal area of embiid wings is greatly reduced. Such reduction even occurs in *Clothoda* Enderlein, the order's most plesiomorphic genus. It is probable, however, that embiids had ancient ancestors with a well-developed anal area in the hindwings comparable to that of Plecoptera and *Mastotermes* in Isoptera.

Thus the principal evolutionary trend in embiid wings wasn't improvement for flight but, instead, toward rendering their possession less of a handicap during movement within galleries. The ultimate accommodation is complete aptery of all females as well as of males of many taxa. A similar disadvantage of wing possession was faced by sexual termites adapting toward easier movement in galleries in earth and wood. In this case, however, the disadvantage is eliminated by wing break-off by nuptial adults prior to copulation. Also, lifelong aptery of most individuals in a termite colony is caused by endocrinal retardation of the appearance of adult structures and functions (neoteny). A similar retardation is probably responsible for the universal aptery of adult female embiids, as well as varying degrees of brachyptery to complete aptery in males of many embiid species, genera, and even an entire family (Australembiidae).

The trend toward apterism in males is presently active and has been so for at least the entire Tertiary period, as evidenced by complete apterism of males of *Electroembia antiqua* (Pictet), Baltic Amber (Eocene?). Degrees of male aptery and brachyptery occur on most evolutionary lines, such as: (1) males with robust (nymphoid) bodies and short wings; (2) males with wing pads similar to those of various ontogenic stages from buds (gemmae) to full pads; (3) complete aptery without even traces of wing buds. In some species, such as *Anisembia texana* (Mel.), a percentage of adult males in a population have normal wings, but most possess only tiny wing buds. In Oklahoma, at the northern range of *A. texana*, all males are completely apterous without traces of wing buds.

Because females are universally apterous, flight of males cannot increase geographic range of a species, or enable a population to move away from environments uninhabitable as a result of sudden or gradual adverse ecological changes. Range extension and relocation can be effected only by females surviving hazardous movement afoot outside of their protective galleries, or by being carried in materials transported by wind, water or human commerce. Male flight, however, fosters random mating and thereby reduces potentially disadvantageous incestuous matings so likely in gregarious, subsocial populations. The complex subject of embiid wings is more fully treated in my review of the order's anatomy (EMBIA Part 1).

Social behavior

A typical embiid colony is a "gynopaedium"—a parent female and her brood living together. Often galleries of broods of adjacent females become interconnected and the nymphs intermingle without hostility.

Although there is no evidence of a division of labor, or castes, some social advantages could result from utilization, by some species, of preexisting galleries produced by previous generations which had occupied the same bark surface. In rainforests a mat of such galleries may thus serve like a layer of bark protecting new galleries spun beneath by succeeding generations of nymphs. However, to reach ungrazed edible surfaces, most species produce new labyrinths radiating out from such initial coverings. Incidentally, the silk of new galleries of some species is lavender in color.

The most important social activity is guarding eggs and young by parent females in a manner similar to that of Dermaptera (Figs. 18, 42) (Edgerly, 1987a and b; 1988). Early instar nymphs usually congregate near their mother and perhaps benefit from her presence for at least two instars (Fig. 4). As I service laboratory cultures, young are often inadvertently disassociated from their parent but, in a short time manage to reassemble in spite of the disadvantage of having to spin new galleries to do so. An aggregation pheromone may be involved in this.

Food provisioning in arid regions by subterranean species can also be regarded as social activity for it tends to insure dependable, readily accessible, food for the brood. It also avoids energy loss and risks consequential to making repeated forays to an often inclement and hazardous surface environment.

Embiids may be termed subsocial communal insects. In this category females remain with their offspring for a period of time and members of the same generation use the same composite nest without cooperating in brood care. Such an interaction is an inevitable consequence of gallery life. A lone female simply lays eggs in a favorable place—often within existing galleries, or in a new site, and her offspring having no need to disperse, extend individual galleries no farther than needed to reach food. Upon maturity, her offpspring do not need to disperse to find food or a mate. Therefore, females are likely to deposit eggs not far from their own place of origin.

In communal species, especially those occupying tree trunks, or rock and road bank surfaces in the tropics, a colony may grow to great size and even envelope a huge tree trunk (Fig. 26). Theoretically, such growth is radial—expanding at the periphery as edible surfaces are sought. In jar cultures and under other artificial conditions, colony growth is three-dimensional, as reported by Friederichs (1913) in reference to an outbreak of *Aposthonia gurneyi* (Froggatt) in a sugar refinery in Australia, or of *Oligotoma saundersii* (Westwood) in piles of stored peanuts in Senegal.

There are exceptions to a gregarious habit, however. In some species, especially those found in the savanna woodlands of central Africa (e.g., *Dinembia* Davis spp.), nymphs are intolerant to one another and must disperse soon after hatching and develop in individual galleries to avoid injury.

It is conceivable that if ever a form of reciprocal or proctodeal feeding, or body licking should evolve which would permit transmission of maturity-inhibiting pheromones, a worker caste might develop in embiids. There is, however, absolutely no indication or need of such behavior in Embiidina. Food exchange between embiids has never been observed and proctodaeal feeding potentials are lessened because excrement consists of dry pellets which are deliberately placed or partitioned outside of the galleries immediately following defecation. Nymphs hatching from eggs don't even eat the hardened pulverized material, which in part may be fecal, placed around the eggs by females of most species. Covering and side-by-side placement of eggs appears to reduce oviposition by parasitoid wasps (Figs. 19, 42).

Female embiids could be likened to nymphoid reproductives in termites, but it is most likely that their neotenization is programmed by regulation of juvenile hormone rather than exchanges between individuals.

Behavior of adult males

Upon maturity an adult male usually remains inactive for a few days in the gallery section where final ecdysis took place (Fig. 12). During this time its derm hardens and becomes fully melanized, or pigmented. Concurrently, its nymphal pelt slowly passes through the gut and is excreted. Later a male may wander about within the galleries and may mate with a receptive female, perhaps a sister, particularly in species with apterous males which are more likely to remain in a colony with sisters. Sister-mating is likely in laboratory cultures and in gregarious species but, in some species, males and females develop in separate galleries. In such cases a male must vacate his "personal" gallery, locate and bite his way into one occupied by a female (Fig. 15).

In cultures, usually during warm afternoons, adults of both sexes often move to uppermost levels of a culture, protrude their forebodies from gallery openings (Fig. 14) and, with their heads often hypognathously angled, they rapidly vibrate their antennae. It is assumed that such activity encourages sexual contact. No investigations have been made to determine if "calling" pheromones are released during such exposure, but this is likely.

Under certain meteorological conditions, often just after the first rains ending a dry season, adult males usually leave their galleries and take flight (Fig. 11), or, if apterous, simply run about on the ground. In arid regions males of pale species have large, coarsely-faceted eyes and tend to fly during warm, humid nights when many other insects, notably nuptial termites, also fly. During such periods collectors should always search for male embiids attracted to lights, not only to collect specimens, but also as a means of determining what nocturnal species of the order have colonies in the vicinity. At least a portion of a light sheet should be on the ground inasmuch as males of some pale, nocturnal species are apterous and can only run to lights. In some species, such as *Aposthonia tillyardi* (Davis) of western Australia, apterous and alate males may occur in a single locality.

Color of adult males

Adult males of most species are melanized, at times with a reddish prothorax, and/or a golden pterothorax and metallic blue wing veins and sheen (Fig. 13). Dispersal of colorful males is diurnal and one may see alate males of such species in flight, or resting on vegetation but, more likely, yet rarely, they will be collected by random sweeping. Probably mortality of diurnally dispersing males is very high due to increased exposure to birds, or the elements. Some protection against predation may involve Batesian mimetic resemblance to chemically-protected diurnal beetles and stinging ants.

In various, usually unrelated taxa, the distal antennal segments may be abruptly white, as also are one or both cercus segments. In many species pale intersomatic thoracic bands are present, as well as longitudinal, pale, pleural abdominal stripes. All such characteristics are due to white fat visible through a transparent integument.

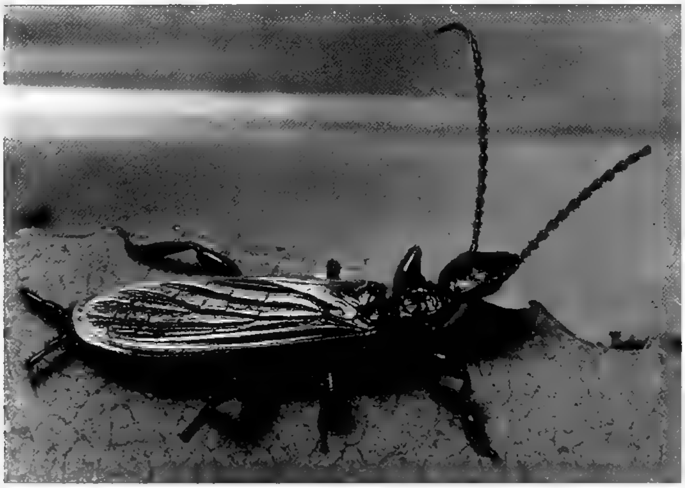


FIGURE 11. Alert posture of an adult male about to take flight. The strongly cuticularized wing veins of this genus are prominent in this photograph. *Enveja bequaerti* Navás. Katanga, central Africa.

FIGURE 12. This teneral male will remain for a long time in one place until fully hardened. Incidentally, it has especially large wings, a characteristic of high altitude species. *Pararhagadochir* n. sp., (Embiidae). Machu Picchu, Peru.

FIGURE 13. Adult female and penultimate male of new genus and species of Oligotomidae from Thailand. The prothorax of both sexes of this dark brown species is bright orange. Body length of female 18 mm.

FIGURE 14. Epigamic females may protrude their forebodies from galleries, possibly emitting pheromones to attract males. "*Embia*" *surcoufi* Navás, (Embiidae). Mozambique.

Mating

When a male locates a gallery containing a receptive female, he bites an opening (Fig. 15), enters, and approaches the female head-on, rapidly jerking his body and vibrating his antennae. If the female is unreceptive, her reaction, perhaps varying according to species, may be antagonistic and dangerous. In some encounters a female may attempt to eat, or at least bite an approaching male. She lunges toward the male with the same motions used in defending eggs, or young brood. Often there is antagonism or fighting between males.

When a female is receptive, there is mutual quivering of the antennae, head and prothorax and, alternately, forward darting and retreat. Inasmuch as there may remain a threat to the male, males of many species reduce danger by grasping the fore portion of the female's head with the mandibles. Mandibles of males exhibit varying degrees of specialization for such a grasp, the most extreme of which are the large, elongate, arcuate type characterizing some species of *Enveja* Navás. Mandibles of males may also be used to gently nibble the female's body. Because the mandibles of adult males are not used for grinding food, but primarily seem to be secondary sexual organs, they have greatly diversified and are thus useful characters in systematics. The short, robust, nymphoid mandibles of adult females, used for food-grinding, vary little throughout the order.

FIGURE 15. Adult male (new genus and species, Oligotomidae) biting an entrance into a gallery presumably occupied by a receptive female. Thailand.

Usually, a male grips a female's head across the frontal region but there are variations. In one abnormal case, I observed a male holding the dorsal cervical region instead of the head. Once secure in a mandibular grip, the female's head usually is pulled to the right and the tip of the male's abdomen probes down her right side, thence leftward and upward beneath her genital opening. It is remarkable that a right-side approach is constant in all species of the order. In any event, it explains the almost universal leftward asymmetry of the male terminalia (to extend its "reach") and why the specialized left cercus functions in many species as a clasper against the female's left side

Because mating occurs obscurely within galleries, it is difficult to observe. However, Stefani (1953a, c) made detailed descriptions of copulation in *Embia ramburi* R. K., *Cleomia guareschii* Stefani, and *Haploembia solieri* (Rambur). Earlier, Friederichs (1934) made brief observations of *Embia ramburi* and *Oligotoma nigra* Hagen.

FIGURE 16. Copulating *Pachylembia chapalae* Ross of western Mexico preserved in alcohol. As generic characters, the male (left) lacks lobing on the left cercus and has a greatly reduced left tergal process. The copulatory grip appears to be increased by pressure of the dense, bristle-like setae borne on the left and right hemitergites.

A few of my observations are recorded as follows:

(1) *Archembia lacombea* Ross (Embiidae). Brazil: Rio de Janeiro. A male was observed rubbing his submentum against the vertex of a female's head. In this species, and congeners, there are relatively dense, often parallel, setal clumps, as well as foveae on the submentum in and around which white secretions collect. During this rubbing the male's antennae extended on either side of the female's body. She wriggled sinuously and continued a limited spinning movement of her forelegs. Females of *Archembia* Ross, and related genera, have a transverse, pale, often golden, eye-to-eye band above the brain. One should investigate the function of this pale maculation. Is it associated with mating, or does it have a light-perception function?

(2) *Machadoembia* Ross, n. sp., (Embiidae) Angola: near Quilenda.

Male grasped female's head (face to face) with his mandibles across her clypeus. The female frequently lurched but the male maintained his grip for at least a minute. During this time the male's genitalia united with those of the female. These disconnected before the male released his grip on the head. When freed the female walked off unharmed by the male's mandibular grip.

During other matings, males of this species grasped heads of females from several frontal angles, as well as the cervix. The female's head was twisted to the right as the male's genitalia quickly sought contact. In spite of much tugging, females seemed receptive to mating. One copulation lasted about 60 seconds.

(3) *Parembia major* (Imms), (Embiidae). India: Mussourie U.P.

Male gripped female's head frontally.

(4) *Embia* n. sp., (Embiidae). Ethiopia: Nazareth.

Male faced female and gripped her head with his mandibles behind her eyes. The male twisted so that most of his body paralleled the right side of the female and the tip of his abdomen crossed beneath the female's genitalia. Actual genital union wasn't observed.

(5) *Embia mauritanica* Lucas (Embiidae). Algeria: 27 mi. N. M'Sila.

Ventral concavity of median flap (MF) covered inner curvature of left tergal process (10 LP). Process of left paraproct (LPPT) pressed into dorsal depression of left cercus lobe. Ventral nodule of LPPT prevented left cercus lobe from moving ventrad.

(6) "*Parembia*" *dobhali* Ross, (Embiidae). India: Dehra Dun.

Female began to eat copulating male while the genitalia were still joined.

(7) "*Parembia*" n. sp., (Embiidae). India: Badamtan Forest Res. W. Bengal.

A male attempted to mate with another male while holding its head in his jaws (behind the eyes) and pushing his genitalia beneath the other male's wings, apparently mistaking this surface for that of a female's abdominal venter. Such abnormal approaches were observed on several occasions.

(8) *Enveja bequaerti* Navás, Zaire: 12 mi. S. Sampwe.

Grip of head with jaws not observed but the remarkably large mandibles suggest that they are adapted for head-clasping. During one mating the sexes remained parallel; the male on the right side of the female with his terminalia angled leftward and upward to join the female's genitalia. They remained united for about thirty minutes. Close examination revealed that the male's right tergal process was folded ventrad against the surface of its hypandrium and pressed against the female's second valvifer. After the pair separated, a hard, irregular, gelatinous object, probably a spermatophore, protruded from the vulva.

(9) *Dactylocerca* Ross, n. sp. (Anisembiidae), Mexico: Alamos, Sonora.

The male's long, arcuate, one-segmented, left cercus embraced the left side of the female's abdominal apex from beneath. The grip was so tight that membranes at the base of the female's right cercus became distended. At no time did the heads connect although this might have occurred before the observation began. Males of the genus have very small mandibles.

(10) *Australembia nodosa* (Davis) (Australembiidae). Queensland: Millstream Falls. Mating fixed in alcohol.

Male terminalia centered beneath female. The apex of LC_{1+2} depressed membranes between left basal corner of H and between caudal tips of pleurite and laterotergite of somite 8. The hypandrium process (HP) and tenth tergite (10 RP) pushed into vulva. After separation, a spermatophore wasn't visible in the vulva. Perhaps the pair was killed in alcohol before copulation was completed.

(11) New genus and species (Teratembiidae), Transvaal: 18 mi. S. Louis Trichardt.

Mates faced the same direction. The male did not grip female's head and was somewhat beneath her, his terminalia turned upward to the vulva, well centered. Because it is unlobed, the left cercus did not seem to be used as a clasper.

Later the female walked forward causing the two insects to face opposite directions. The female continued to walk out of sight into a gallery dragging the male backward as the genital union continued.

(12) *Aposthonia* Krauss, n. sp. (Oligotomidae). Queensland: Brookdale (coastal plain).

In a male specimen preserved in alcohol, the right tergal process (10 RP) was folded down and completely pressed against his hypandrium (H). The epiproct (EP) was also pulled down and provided musculature for movement of 10 RP. The left tergal process (10 LP) paralleled the inner face of the basal segment of the left cercus (LC_1) with its complex apex vertical, its dorsal surface facing toward right; its left side was appressed on the inner apex of LC_1. The hypandrium process (HP) and the gonopophysis were projected dorsad (almost vertical, like an erect penis) and, pressed by the inner angle of the sclerotic left hemitergite (10 L) and its process, provided rigid enclosure for the ejaculatory duct.

These "mechanics" are probably universal in the Oligotomidae, Teratembiidae, and other taxa which, by convergence, have a transverse, membranous separation of EP and 10 RP from 10 R which serves as a hinge permitting downward movement of 10 RP.

Eggs and their protection

Eggs of all species are remarkably similar (Fig. 17). They are tubular in form, basally rounded, slightly curved, and have a large, slanted, strongly-rimmed operculum. Their general appearance is similar to that of bedbug eggs.

Eggs issue from the vulva with the operculum inward and are deposited within the galleries, usually attached to a substrate. However, in some species they are loosely clustered in the galleries and not imbedded in a hardened paste. In some species uncovered eggs may form a tunnel within which the guarding female rests. Most often, however, eggs are laid in a single-layered cluster and are imbedded in a hardened paste of habitat material pulverized by the female and deliberately placed as the eggs are laid (Figs. 19, 20). It is probable that fecal pellets are also pulverized for this purpose. I have counted more than two hundred eggs in a cluster laid over a period of several days in one species, but the numbers may be much less in other species. Egg size may be constant regardless of the size of the female, i.e., those laid in small numbers by minute species of *Oligembia* appear to be as large as those laid by relatively huge *Antipaluria* females.

FIGURE 17. All embiid eggs are similar in shape, have a rimmed operculum, and are laid on their back. *Haploembia solieri* (Rambur) (Oligotomidae) endemic to the Mediterranean region.

The tightly clumped eggs are slightly slanted with the opercula exposed. Many species spin a dense covering of silk over the mass. Obviously, such coverings, and parental guarding, reduce the percentage of eggs parasitized by scelionid wasps. It is likely that the habit of covering eggs is related to the geographic occurrence of the wasps. For example, in the Mediterranean region where such wasps apparently do not occur, the eggs of *Haploembia* spp. and *Embia* spp. are uncovered and loosely clumped.

Species within unrelated Amazonian genera enclose eggs in a sawdust-like matrix of chewed habitat particles which is densely covered with silk, thus forming a low mound on which the female rests (Fig. 42), ready to challenge approaching parasites and

FIGURE 18. As females guard their eggs, they lunge toward enemies—particularly egg parasites. *Dinembia* sp. (Embiidae). Northern Zambia.

predators. However, such protection, like most defenses in nature, is imperfect. For example, I found within a mass containing 51 eggs, 12 fully developed scelionid wasps clearly visible through transparent egg shells.

Additional information on maternal protection of eggs and young is provided by Edgerly (1987a, b; 1988, 1994) in her detailed study of plesiomorphic *Antipaluria urichi* (Saussure) (Clothodidae) in Trinidad.

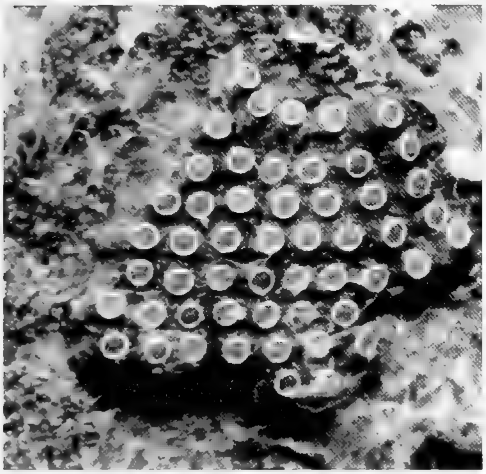


FIGURE 19. Most embiids, such as *Antipaluria* Enderlein (Clothodidae), reduce oviposition of wasp egg parasites by packing a paste of pulverized material around their eggs. Venezuela.

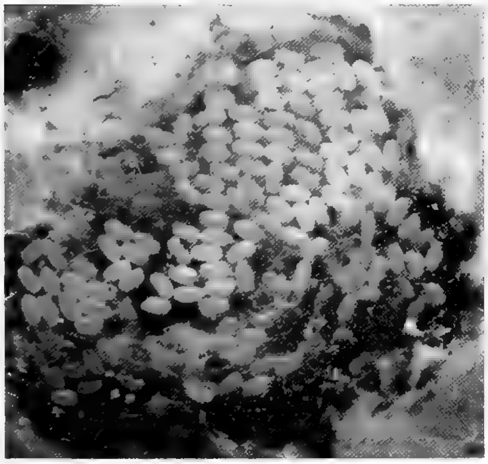


FIGURE 20. As eggs are laid on the sides of culture jars, their number and imbedding sequence can be observed. *"Embia" surcoufi* Navás, Mozambique.

Development

Adult female embiids exhibit little change in appearance from first instar nymphs except, of course, for increased size and coloration. Ventrally, the eighth and ninth abdominal paragenital sternites adjacent to the vulva's opening are modified, as is, of course, maturation of internal reproductive organs. Neotenic apterous males usually are similarly nymphoid but, as adults, are more melanic, or pigmented, and have distinct cranial and abdominal terminalia characters.

Males destined to have wings show the first external evidences during an early nymphal instar. At first they are merely very slight extensions of the posterior angles of the meso- and metascuta (Fig. 21A). These are accompanied by increased development of certain setae near, and on, the lateral margins of the nota. The enlarged angles somewhat increase in size during the stadium.

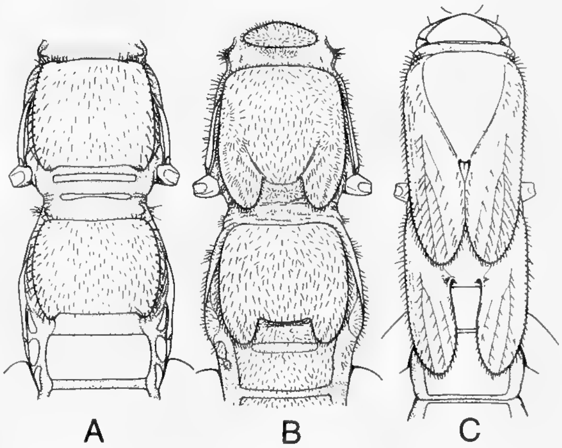


FIGURE 21. Wing development of a typical male embiid. *Oligotoma nigra* Hagen.

In the next instar definite wing pads appear (Fig. 21B). Those of the mesothorax nearly reach the anterior margin of the metanotum. The lateral notal setae now have increased in number and mark courses of future wing veins. Development of the special radius blood sinus vein (RBS) is indicated in some specimens by faint "fleshy," reddish lines which border RBS in the adult wing. As in the previous instar, there is pad enlargement during the stadium.

In the next (penultimate) instar (fifth?) (Figs. 13, 21C , 22), the wing pads are well developed and greatly elongated; those of the mesothorax overlap most of the metascutum, the pads of which extend caudally over most of the second abdominal scutum. They are broadly attached to their respective scuta. However, these lines of attachment do not represent definitive wing bases for they are actually part of the posterior wing margin.

Definitive veins are indicated by their setae and RBS by even greater pigmentation of its marginal bands. Tracheae follow the same courses as the setae. It is significant that venation of the pads conforms to that of the adult; MA being unbranched, for example, in all oligotomid and anisembiid wings. The observation by Melander (1903) that MA (his R_{4+5}) in *Anisembia texana*, as evidenced by the tracheation in the pads, is forked in the nymph and not in the adult was probably an error, or anomalous.

Expansion of wings

During most of the penultimate nymph stage of males destined to be fully alate, the wing pads are clear, thin, and flat. Later they become thick, opaque, cream white in color, and the dark lines bordering the radial blood sinuses are conspicuous (Fig. 22). Incidentally, at this time divisions of the tenth abdominal tergite are visible through the derm and the adult cerci are withdrawing basad. Finally, the nymph ceases movement and in a short time it is possible to observe ecdysis, and wing expansion. The following is my account of these events in a species of Embiidae from Africa's Ruwenzori Mountains.

2:40 PM Nymph emerged from its last nymphal exuvium. The unexpanded wings at first were slender, strongly convex, thick, and cream white in color.

2:50 PM Starting from the costal and basal margins, the wings began to flatten and expand. Periodically, the soft adult wriggled and rotated its body. The abdominal terminalia were distended, all structures were swollen, and the cerci projected laterad at 45°.

3:00 PM Entire basal half of the wings now broadened and flattened. The distal half remained as small and as narrow and fleshy as at 2:40 PM. At 3:10 PM the entire costal margin had expanded with only the apical end of the hind margin remaining fleshy. This condition prevailed until 3:30 PM.

3:50 PM Left pair of wings now completely ex-

FIGURE 22. Late penultimate instar of a male. Note that the wing pads have thickened and that cerci of the adult are withdrawing from the nymphal skin. *Antipaluria caribbeana* Ross.

panded, right pair remain fleshy ventrally at apices. Wing veins paler than membranes.

4:10 PM All wings completely expanded, definitive in form and thickness. Hyaline stripes had appeared.

9:40 PM Wings now gray in tone. Body and leg pigment developing.

7:30 AM (next day) Wings now smoke black. Exuviae eaten during the night.

1:00 PM Male remains in same place in gallery. Much darker in color.

9:00 AM (third day) Male still in same position. Darker in color.

The above appears to typify wing expansion of all Embiidina. Sequences have been observed on several occasions in distantly related species. However, a number of variations were noted, as follows: In an embiid from Takoradi, Ghana, a male nymph about to transform to an adult, was isolated at 2 PM. As late as 8 PM it continued to spin silk even though subdermal adult structures were well advanced and in spite of the fact that it was destined to shed its nymphal skin within two hours. During ecdysis the head bowed downward and under towards the prosternum until the abdomen completely withdrew from the exuviae. The apex of the abdomen thrashed from side to side to shake off the pelt. The unexpanded wings were held out and away from the thorax and bent caudad parallel to, but not touching, the sides of the thorax. By 10:20 PM the wings reached the fourth segment. The expanded bases were cream white while the unexpanded apices remained smoke black.

In a new species of *Dactylocerca* from Alamos, Mexico, an adult emerged at 10:40 PM and by 11:15 PM its wings had already assumed their definitive shape. They were pure white and no veins or pattern were evident. The exuviae was not yet consumed. Surprisingly, while still teneral, the adult was able to resume its silk spinning. By 8:00 AM the next day the male was semi-hardened but the wings were still pale. By this time the exuviae was almost entirely ingested. At 8:00 AM, the third day, the male was still in the same place, fully pigmented, and the exuviae had been completely consumed.

Parthenogenesis

Parthenogenesis probably occurs sporadically throughout the order but only a few cases, involving Mediterranean and equatorial African species, have been studied. One of these, *Parthenembia reclusa* Ross (1961), is widespread in western Africa. More recently, I have decided that a number of undescribed bisexual species from Angola and southeastern Zaire must be assigned to *Parthenembia*, therefore, this generic name is inappropriate. *Scelembia virgo* Ross (1960) from Angola and Zaire also is parthenogenetic. Other species of this potentially large genus are bisexual. Caryiology of the above two species was investigated by Renzo Stefani of Sardinia (1961).

Parthenogenesis of *Haploembia solieri* (Rambur), indigenous to the Mediterranean region, was intensively researched by Stefani and reported in a series of papers cited in his bibliography. Rosanna Giordano of the University of Vermont, who is fluent in Italian, kindly provided the basis for the following summary of Stefani's conclusions on the bisexual and parthenogenetic forms of *H. solieri*:

Stefani noted that bisexual *H. solieri* has only 20 chromosomes whereas the parthenogenetic form has 22. He assumed that the sex chromosome had been replicated.

Haploembia solieri, like many other insects, suffers infection by the gregarine sporozoan parasite, *Diplocystis clerci*. Such infections aren't well tolerated in bisexual populations of *H. solieri* for, although both sexes are debilitated, the influence on males is critical for they become ineffective mates due to damaged sperm and lowered vitality. In contrast, a minority of females in a population which can reproduce parthenogenetically, tolerate infection and, even though they produce fewer eggs, they can at least reproduce. As a result, parthenogenetic females supplant sexual populations, as has happened on Sardinia and Corsica.

During the 1960s when Stefani conducted his research, small islands, such as Elba, had both sexual and parthenogenetic individuals. He predicted that with time only parthenogenetic populations would exist on these islands. Perhaps by now this transformation has occurred.

Because the parthenogenetic form tolerates infection, and thereby permits *D. clerci* to mature and complete its life cycle, *H. solieri* can serve as a vector for the parasite.

Another of Stefani's interesting observations was that virgin females of the bisexual form of *H. solieri*, unlike those of two other species of *Haploembia* he checked, have the habit of eating their unfertilized eggs. Very few eggs escape this cannibalism.

Strangely, 22-chromosome females (parthenogenetic), unlike 20-chromosome females (sexual), do not eat their own unfertilized eggs. Sometimes parasites alter behavior of their hosts. However, infected parthenogenetic females aren't thus influenced. Stefani was inclined to conclude that this results from a duplication of the sex chromosomes, or perhaps a combination of both—an interesting question to investigate.

Obviously, Stefani wished to determine how parthenogenetic females could have arisen from sexual females. As an experiment he deliberately infected a sexual female (20 chromosomes) with *Diplocystis*. It managed to lay an egg in 1959, but this didn't hatch until 1961! The egg produced an adult female that began to oviposit without mating. Much to his surprise her progeny had a chromosome number of 22. In effect, he had artificially produced parthenogenesis. He must have been amazed! [End of Giordano's abstract, somewhat reworded by me.]

Because every individual is reproductive, the parthenogenetic form of *Haploembia solieri* readily becomes a "weed"; one rapidly spread and established in new lands by human commerce. From California where it was perhaps introduced in early Spanish "Hides and Tallow" commerce, including dumping ashore of sailing ship ballast, *H. solieri* is now a very widespread species in warmer habitats of southwestern United States and northwestern Mexico. I have also found the parthenogenetic form common in many Mediterranean mainland localities. Bisexual *H. solieri*, and related species, or races, also occur, but these apparently have not yet become parthenogenetic as a result of *Diplocystis clerci* infection.

Much to my surprise, a bisexual population of *H. solieri* was found in a garden (isolated from natural environments) south of San Francisco, California. I assumed that it resulted from a recent introduction in nursery stock, perhaps from Spain. I attempted to mate males with the very common parthenogenetic females well established in nearby hills. The culture produced only parthenogenetic broods. I didn't observe copulation but, even if this had occurred, it is likely that the parthenogenetic females were already "self-fertilized." This crossing attempt was made in 1976. It is possible that the sexual population has since been eliminated by infection with *D. clerci*.

Diet

In nature embiids primarily eat weathered outer bark of trees and decomposing leaf litter. They may also eat mosses and lichens growing on bark, rocks, termite mounds and soil surfaces. Undoubtedly, many old substrates are coated or permeated with live microorganisms, such as algae, which are also nutritious. There is no evidence that digestion is dependent on symbiotic intestinal organisms.

It is likely that the diet of embiids is primordial and that during the entire evolutionary history of the order there has always been a certainty of food wherever the insects choose to live on the basis of other environmental factors, such as availability of crevice retreats. Trees with exfoliating bark flakes, or vertical crevices, are most likely to have embiid colonies on them even though the nutritive value of the outer bark of other tree species in the environment might be the same.

Embiids seem to have no host plant preferences, but one may expect that freshly-fallen leaf litter of plants with strong antiherbivore chemicals, as in *Asclepias*, *Euphorbia*, and *Eucalyptus*, will be avoided. However, such litter can be assimilated if decomposing. For example, species of Australembiidae feed almost exclusively on a diet of layered, aging *Eucalyptus* leaf litter which also serves as the habitat (Fig. 23). In *Antipaluria intermedia* (Davis) of Venezuela, the dry season may be spent in leaf litter and the wet season in sheet-like colonies on the bark of adjacent trees.

A highly neotenic new genus and species from the desert steppes of western Afghanistan extends foraging galleries upward from subterranean retreats into *Artemesia* shrubs to reach live foliage. In this case, the small, chemically-protected, aromatic leaves are transported into deep subterranean galleries as a food supply during periods when the surface environment is intolerably hot and dry. It can be assumed that similar provisioning occurs in other species of embiids inhabiting arid environments.

The universal acceptance of any non-toxic dead leaves as food is demonstrated by my success in culturing hundreds of usually-unrelated species from all regions of the world on the same diet—dead California live oak leaves and a supplement of fresh Romaine lettuce. Although not an essential element in the diet, frequent replenishment of lettuce to the surface of a laboratory culture increases carrying capacity in a limited culture space while also moisturizing the diet.

Adult females simply continue the diet of nymphs of both sexes. Adult males, however—at least of all non-neotenic species—never feed. This conclusion is based on examination of thousands of adult male specimens of hundreds of species during KOH maceration while making microscope slides. These observations show that the gut of non-neotenic males is invariably empty except during the short, teneral period when it only contains fragments of its own penultimate nymphal exuviae which it ingested shortly after the final ecdysis. This pelt gradually moves caudad in the otherwise empty gut and eventually is voided. Earlier workers, discovering such fragments in the gut, erroneously concluded that embiid males are predaceous. It is likely that all embiids, as do many other insects with chewing mouthparts, invariably ingest their exuviae after each moult. Some physiologists believe that this insures a beneficial recycling of sugars and nitrogen for chiton is a nitrogen-containing polysaccharide.

Apparently, males of almost all species cease normal feeding during the penultimate instar and completely empty the gut prior to the final moult. This, together with a reduced, or arrested, accumulation of fat, results in a lighter, more vagile organism, but one with shorter life expectancy

Neotenic, apterous, adult males of certain species may, or may not, have the intestinal tract filled with food in the usual stages of assimilation. Ingested exuviae would be less discernible in such accumulations. Males which continue to eat as adults are found in several new genera in central Africa and in a race of *Metoligotoma reducta* Davis of Queensland. Such males, having a more pronounced intraspecific degree of neoteny, have mandibles similar or identical to those of nymphs and females and thus they are suited for chewing food and apparently not for gripping a female's head during copulation.

FIGURE 23. Decomposing leaf litter of *Eucalyptus* is the typical habitat and food of the numerous species and races of Australia's family Australembiidae. Such galleries apparently don't extend deeply into soil beneath the litter. *Metoligotoma ingens* Davis. Black Mtn., Canberra, Australia.

Perhaps due to genetically-fixed, behavioral traits, there is usually a correlation of taxon and specific habitat and its particular food resources. For example, in any suitable Queensland locality one encounters at least one species of each of the three families occurring in Australia. Notoligotomids will be found on rock, ledge, and bark surfaces without gallery extensions into soil; australembiids will be encountered between layers of dead leaves (usually *Eucalyptus*) and, likewise, never extend galleries into soil; and oligotomids, having a more widespread Australian distribution, will be the only species dependent on soil retreats. However, in the laboratory, species of all three families thrive under identical cultural conditions and eat the same food. Comparable correlations of taxa and habitat may exist in any environment inhabited by embiids. Therefore, an experienced collector routinely examines each characteristic microhabitat as a means of securing cultures of all species in the region.

It is probable that embiids seldom face food or habitat limitations and this accounts in part for the absence of striking biological and anatomical diversity within the order. It is apparent that embiids are never able to fully exploit local environments, or to spread out into all suitable habitats. Typically, occurrence in any environment is spotty and many an apparently satisfactory habitat, or even a major region, seemingly lacks representation of the order.

Such apparent absence may be attributed to hazardous dispersal. Flight, because it is limited to males, cannot extend a species' range and the almost completely gallery-dependent, apterous females and nymphs can walk only short distances outside of the parent colony before encountering a predator—most likely an ant. Unlike nuptial termites, ants, mayflies, etc., embiids are unable to overwhelm the predation-potential of an environment by concurrent bursts of thousands of dispersing nuptual individuals in a limited time and space.

Another factor is the lack of a need to disperse because of exhaustion of the food supply, or crowding. This is especially apparent in tropical evergreen forests. For example, because food in the form of weathered bark and surface growths would be restored very soon after consumption, it is possible that successive generations of one or more species of embiids could remain indefinitely on a single, large tree trunk. The activities of parasitoids, diseases, and other natural hazards would also tend to limit embiid populations.

Because of reduction in dispersal incentives and limited vagility, embiids promise to serve as excellent indicators of zoogeographic regions and continental drift.

Movement

Embiids are especially adapted for movement in narrow galleries. Shortness of legs, probably a plesiomorphic feature retained from a Paleozoic archetype, is especially important. Such ancestors probably depended on bark, rock, plant crevices, or layered leaf litter, as refuges from predators. Because such retreats usually are edible, embiids didn't have to venture far afoot, or in flight, to reach food. However, even short forays to extend "grazing" were made safer by evolution of an ability to produce silk coverways.

Although wings were once possessed by adults of both sexes, rapid flight probably never was important as a means of avoiding predators. However, aerial dispersal of alate females of ancestral species must have fostered spread of taxa over a long period of geological time, thus extending the order's range throughout warm portions of Panagea. Later, however, except for sporadic movement of gallery substrate objects by storms, bird plumage, or in commerce, dispersal is severly limited by universal female apterism. Therefore, walking by females is the only way an embiid can move to a new location if the one presently occupied becomes intolerably wet, dry, exposed, or "overgrazed."

Ordinarily, nymphs remain within their galleries unless they are torn open by predators, such as birds, mammals, or army ants. Adults of both sexes, however, may concurrently leave their galleries soon after the first rains following a long dry season, or during what appears to be primordial, prenuptual excitement comparable to that causing simultaneous nest-exodus of nuptual termites and ants. However, because embiid colonies are less populous and scattered, nuptual embiids never create noticeable swarms. Dispersal of individual embiids are therefore probably more vulnerable to predators. Consequently, some diurnal species of embiids have evolved a degree of protection by mimicking appearance and movement of unpalatable or dangerous models, such as ponerine ants, paederine Staphylinidae, or lycid or pyrochroid beetles.

Forward walking, either within or outside of the galleries, is steady, slightly sinous, with all legs involved. Stimulation of the cerci triggers rapid forward bursts of speed. However, the most important defensive movement is rapidly backward, powered by the enlarged tibial flexor (depressor) muscles that almost fill the large hind femora. A firm tread, especially on a silk surface, is insured by numerous, stout setae on the plantar surface of the hind basitarsi. Backward movement has had a profound influence on wing specializations, as well as being the primary cause of neotenic apterism and subapterism.

During casual forward movement outside of galleries, adult females often walk with their genital segments arched upwards as though to "welcome" insertion of a male's terminalia. Adult males of many species often walk with the abdominal apex bent forward on the dorsum of the abdomen. In alate species this apex may even press tightly against a corresponding forward fold of wing apices and must be an additional means of reducing the adverse barb effect of both wings and terminalia during reverse movement within galleries. Such forward bending of the abdominal apex also occurs in apterous males of some species.

Males outside of galleries are very lively and alert. Often they stand high on the forelegs, thus elevating the usually large-eyed head, and the prothorax. A male's head is very mobile and capable of turning at least 45° from the longitudinal axis. Especially while resting on walls beneath artificial lights, males often twist the head in a mantid-like fashion as they follow the movements of an observer. Just before flight, a male's body may tremble, antennae vibrate and twirl, and the forebody bobs up and down (Fig. 11). Alate males thus retain much of the activity and sensitivity of free-living ancestors while the nymphs and adult females, perhaps because they are secluded in galleries, are less alert.

Embiids are highly sensitive to vibration, as may be observed in laboratory cultures kept in jars. In these, adults often rest for long periods in upper gallery levels. In reaction to human approach, or vibration, even as much as ten feet away, embiids suddenly, often in unison, back downward into the depths of the culture. Because of this, a person wishing to collect such individuals, must approach a culture jar slowly, gently open its lid, and trap the desired individual by blocking the gallery behind it. At times embiids feign death, even during handling, and then suddenly burst into activity.

Habitats

1. TROPICAL EVERGREEN FORESTS. Such forests appear to be the basic, or primordial environment of the order. Most species occurring in wet forests are arboreal, or colonize sheltered surfaces, such as undersides of ledges, logs or branches which remain relatively dry during frequent rains. Even on well-drained, vertical tree trunks, or road banks, the sheltered slant-side is preferred (Fig. 24).

In spite of the great number of species potentially present in a particular forest with its profusion of microhabitats and food, an experienced collector may, after hours, even days of concentrated search in a virgin forest, fail to find a single colony. This difficulty apparently results from the abundance of ant predators, diffusion, and an inability of embiids to fully exploit or reach potential habitats.

An entomologist, regardless of his specialty, is well aware that the best general insect collecting is found in recently disturbed forests and this is particularly the case with embiids. One soon learns that embiid colonies are most frequently encountered on residual trees, stumps and logs left in forest lands partially cleared (but not burned) for plantations, such as those of cocoa and coffee. Also, clearance and trails provide easier collector access to potential sites.

Natural and artificial habitats within tropical forests are listed as follows:

(a) ***Surfaces of trunks, limbs and lianas***. Some embiid species spin conspicuous galleries of clean silk fully exposed to view (Figs. 25, 26). As weathered outer bark is consumed, galleries are extended over fresh surfaces. Occasionally, an entire tree trunk is matted with the silk of apparently merged galleries of separate broods (Fig. 26). It is conceivable that regrowth of an edible substrate is delayed by such cover and that portions of a trunk will have to be abandoned. While large colonies are active, the matting of silk constitutes a protective cover, which, as stated before, is almost as effective as a layer of bark for it not only protects new galleries, but also other organisms taking advantage of the cover.

Often, for some distance around a large colony, small satellite colonies will be found on adjacent trees. Farther out, the forest may lack additional colonies until another concentration occurs. In some species gallery silk on bark is made inconspicuous by a covering of pulverized fecal pellets and bark fragments deliberately placed on the surface by the embiids (Figs. 8, 9). Often minute plant life will grow on this and render the silk even more obscure while also enhancing the protective cover.

(b) ***Bark crevices and flakes***. At times galleries of small species are not visible without removal of bark flakes. However, presence of a colony is often indicated by a slight extension of silk beyond the edge of a flake.

(c) ***Roots of orchids and other epiphytes***. Vines and their leaves appressed to tree trunks often shelter colonies. For example, the flat, circular leaves of *Peperomia* rooted to tree bark provide excellent cover for colonies of *Saussurembia* Davis in Costa Rica.

(d) ***Undersides of elevated logs often criss-crossed in clearing and selectively-logged forests***. Recently-felled trees provide access to colonies normally out of reach on standing trees. Because of changed exposure, the colonies may shift to the undersides of levelled trunks and branches, thereby gaining greater shelter than that afforded on upright trees.

(e) ***Fence and stockade posts***. Especially those recently cut which still have loose bark, are frequent sites of colonies.

(f) ***Surfaces of ledges and earthen banks***. Especially if somewhat under-slanted and favorably exposed toward or away from the sun, these surfaces tend to serve much like tree bark in that they offer many retreat crevices and a food supply in the form of surface growths.

(g) ***Surfaces and crevices of structures***. Even mossy, steel girders of bridges.

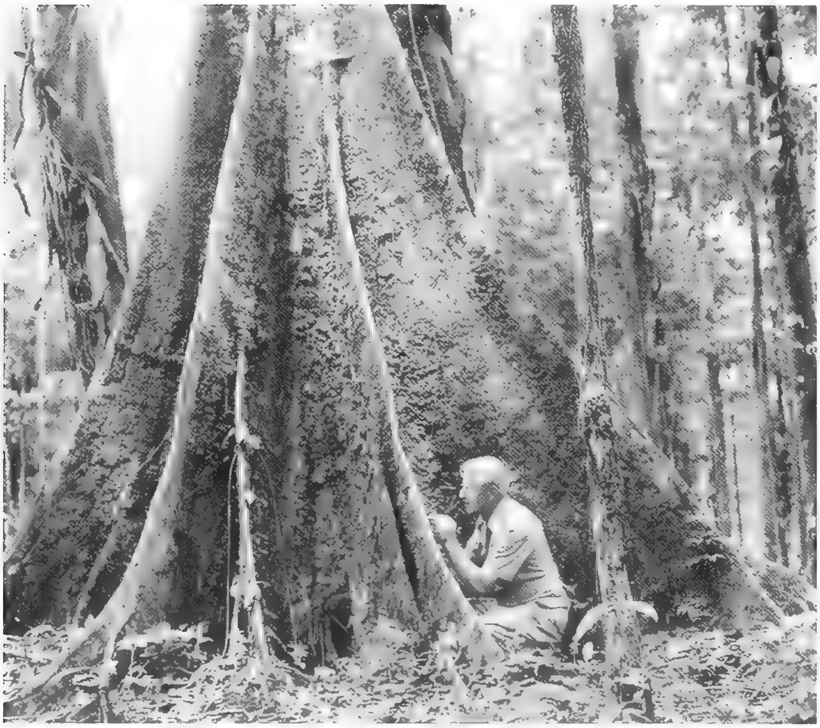


FIGURE 24. Typical rainforest habitat (semicleared). Several embiid species may be found on such a trunk. Near Belém, Brazil.

2. TROPICAL CLOUD FORESTS. These occur at various altitudes, usually starting at 3,000 meters on wet, often windward slopes of tropical peaks and ranges. Embiids reach their highest known altitude in this zone—about 3,500 meters in the Ecuadorian Andes. In spite of cold nights and proximity to snow, each day is warm in equatorial latitudes. Therefore, there is no need for the special, low temperature, physiological adaptations, required in temperate regions with prolonged cold periods.

Males of many cloud forest species are slender-bodied, have disproportionately long legs and large wings (Fig. 12). All are difficult to culture and it is advisable to secure adequate series of adults in the field by persistent collecting rather than to depend on culturing. Late instar nymphs may survive long enough to mature, however.

All habitats listed for lowland rain forests should be searched for embiids. However, colonies are not only less conspicuous, but also less accessible, because of steep terrain, usually impenetrable vegetation (especially bamboo), and dense coverings of mosses and epiphytes on most surfaces. Because of such disadvantages, the best collecting opportunities are in agricultural clearings and in edges of residual gallery forest.

The most characteristic cloud forest embiid habitat is moss festooning from tree limbs and trail banks. Such moss is often thoroughly bound together with embiid galleries (Fig. 27).

Because of better drainage, shelter, and accessibility, road and trail banks are the best places to search for embiids in cloud forests. At times galleries on road banks can even be seen from a moving vehicle.

3. SEASONALLY-DRY GRASSY WOODLAND. In the rainy season these forests are lush and green, but the long dry season and repeated fires tend to reduce epiphytic growth and thus suitability of most tree trunk surfaces as embiid habitats. However, this zone—especially the savanna woodlands of central Africa and the deciduous woodlands of India and southeast Asia (Fig. 28)—is home to some of the most interesting species of the order. It should be noted that evergreen groundwater forests frequently occur

FIGURE 25. In rainforests, colonies often are conspicuous. It is surprising that they are so often neglected by entomologists. *Clothoda longicauda* Ross. Tingo María, Peru.

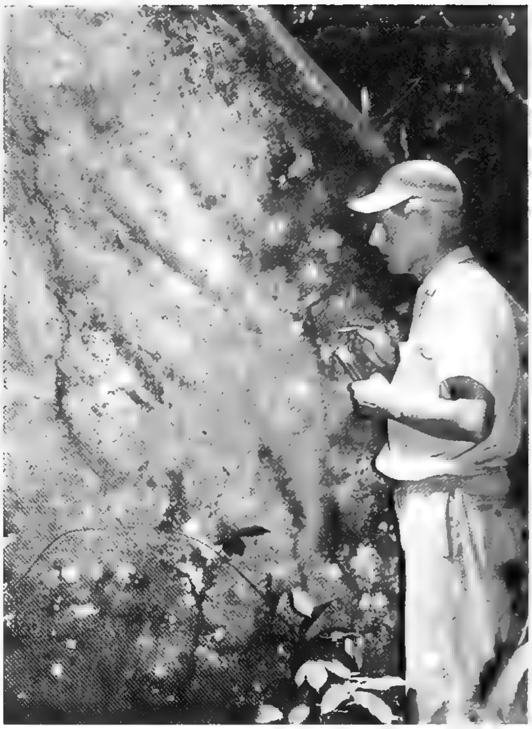


FIGURE 26. Interconnected galleries of many broods of *Machadoembia* n.sp. almost cover buttresses of huge trees in Congo rainforests. Such concentrations occasionally are ripped open and plundered by vertebrate predators.

within this type of woodland along rivers and on shaded slopes. The characteristic dry woodland habitats are:

(a) ***Tree bark crevices and flakes***. Several large, pale species are found in bark, but tend to develop in individual galleries, nymphs having dispersed soon after hatching. At certain seasons only tiny nymphs of potentially-large-bodied species will be found only after careful search. Species of African genera, *Berlandembia* Davis and *Dinembia* Davis, are examples. Occasionally, seemingly-empty, prior-season galleries will be found, but close examination will reveal unattended live egg masses or tiny nymphs enduring the dry season, above the height of bush fires.

(b) ***Dead branches attached to trees***. These are especially important habitats. In them, man-made splinter-cracks, beetle burrows, pithy twigs and loose bark serve as refuges from predators, temperature extremes, and dessication.

(c) ***Dead branches and logs on ground***. Especially those recently cut or fallen should be rolled over and their undersides carefully examined. Galleries once connected with those in thus-exposed leaf litter and soil crevices should also be searched.

(d) ***Leaf litter on forest floor***. Embiid galleries from deep, protective, soil crevices may extend into such cover during the wet season, or cooler periods of the day or night. Species of the Australian family Australembiidae almost exclusively occur amongst matted leaves and apparently do not utilize soil retreats (Fig. 23).

(e) ***Crevices in surfaces of rocks, ledges and termite mounds***. The latter offer almost rock-hard protective retreats, good drainage in the wet season, and the weathered surfaces are often rich in nutrients (Figs. 5, 6).

(f.) ***Leaf clusters in understory of savanna woodland*** (Figs. 28; 29A, B).

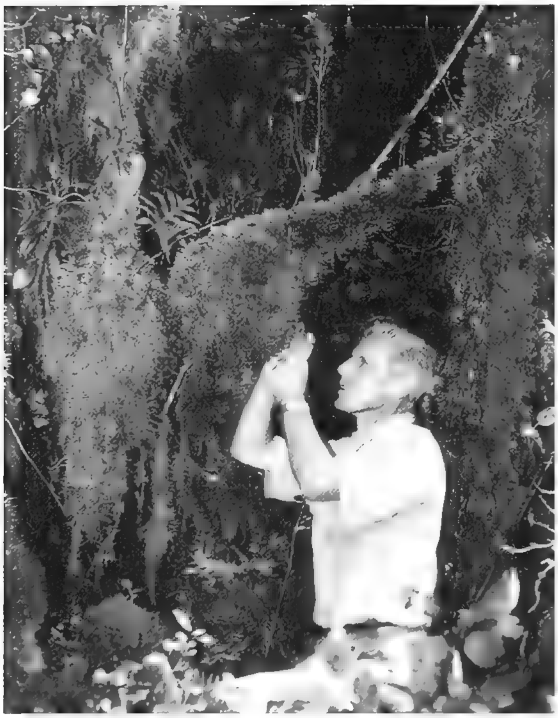


FIGURE 27. In cloud forests many unrelated species utilize well-drained, festooned moss both as habitat and food. New genus and species (Oligotomidae). Gunong Batu Brinchong, Malaya.

4. SEMI-ARID, OPEN GRASSLANDS. Whenever present, all previously mentioned habitats should be searched in this zone. Forest habitats may be localized along river courses and around springs.

(a) ***Stones***. Most grassland species are best encountered under stones (Figs. 30, 31) but it should be realized that the turned stone simply exposes a soil profile (Fig. 32) for it is likely that most grassland embiids are widely distributed in the sod and are not necessarily stone-cover-dependent. Very little surface activity will be seen in the dry season and excavations may be required to secure cultures (Fig. 33). However, there is a chance of encountering embiids in surface galleries at night or early in the morning. Their attraction to the surface could be increased by artificially wetting soil around galleries expected to contain embiids.

(b) ***Dead branches and limbs riddled with beetle borings.*** Some embiids utilize these retreats to survive the long dry season and fires.

(c) ***Leaf litter and soil***. At the bases of large trees and beneath clumped shrubs.

(d) ***Soil crevices in open ground***. In western Australia, immediately after rains, species of *Aposthonia* extend galleries in soil crevices upward

FIGURE 28. The savanna (*Brachystegia*) woodlands of the Congo-Zambezi divide have the greatest diversity of higher embiid taxa. "Nests" of female *Enveja* (Fig. 29A) were present on low shrubs in this scene.

FIGURE 29A. Silk webs in a leaf cluster. Such leaves may be dead or alive on low understory vegetation. This habitat is chiefly used by species of *Enveja* Navás occurring in certain portions of Africa's *Brachystegia* woodlands. By occupation of leaf clusters, females and their early brood escape excessive soil moisture in the rainy season. With rainfall decline, the embiids move down into leaf litter and, finally, into soil cracks to escape dry conditions and fires.

FIGURE 29B. Opened *Enveja* nest revealing female guarding eggs. Unlike those of most embiids, the eggs are loosely covered with fibrous debris—perhaps her fragmented fecal pellets.

to reach leaf litter food. Fragments may be carried down into subterranean galleries to serve as food provisions. With a return to complete aridity, temporary surface galleries may soon weather away and thus no evidence of embiid occurrence may remain. An exceptional species in western Afghanistan extends galleries upward into low shrubs (*Artemesia*) to collect leaf fragments.

5. DESERT AREAS. An embiid fauna is considerably reduced by extreme aridity and may be confined to oases, drainage lines and foggy coastal deserts. A lack of significant precipitation almost completely eliminates occupation of all above-ground habitats. However, palm trees, such as the date palm, provide safe retreat in leaf bases of the trunk which tend to collect abundant embiid food in the form of leaf debris. In the Nile Delta two species of the order, *Embia savignyi* Westood, and *Haploembia solieri* (Rambur), occur in nest material deep in the underground burrows of rats of the genus *Arvicanthus* (Hoogstraal, pers. com.) (Figs. 34–36).

6. HUMAN HABITATS. Cities may have large embiid populations on the bark of shade trees. Most often these are introduced species of the India-centered genus *Oligotoma: O. saundersii* (Westwood), *O. humbertiana* (Saussure), and *O. nigra* (Hagen). Native species may also be found, especially if the highly disturbed areas are near natural environments. In Trinidad extensive webs of a native species, *Antipaluria urichi* (Saussure), are conspicuous on trees along streets and in parks.

Occasionally, embiids eat stored products. For example, species have been reported in sugar refineries in Australia.

In Perth, Australia, *Notoligotoma hardyi* (Friederichs) inhabits old wood fences in residential areas utilizing crevices as retreats and weathered wood surfaces as food. In southern California galleries of *Oligotoma nigra* Hagen occasionally extend from the ground up the sides of residential foundations, but embiids do no damage to structures.

In vineyards embiids may extend their webs into bunches of grapes near the ground, but probably feed only on dead material and detritus accumulated in interstices, not the grapes. In Senegal, *Oligotoma saundersii* (Westwood) may produce colonies in piles of harvested peanuts accumulated prior to export.

FIGURE 30. An excellent stony, seasonally-dry embiid habitat in southern India. (David Cavagnaro, assistant during Indo-Australian expedition).

FIGURE 31. This dry slope in central Algeria, too stony for plowing, is the type locality of *Embia silvestrii* Davis (Embiidae).

FIGURE 32. A removed stone exposes a sod profile with galleries of *Haploembia solieri* (Rambur) (Oligotomidae) in Californian seasonally-dry grasslands. From cool moist depths, embiids move upward to feed on dead plant litter, perhaps at night or other cool periods.

FIGURE 33. In arid Baja California, Mexico, *Bulbocerca sini* (Chamberlin) (Anisembiidae), feed at night and during the rainy season, on leaf litter accumulated between desert stones. Dense silk galleries extend downward in the silty soil.

FIGURE 34. Numerous galleries of *Notoligotoma* n. sp. (Notoligotomidae) are found, but not exclusively, on undersurfaces of exfoliating slabs on "granite islands" in southwestern Australia. Wind-blown plant debris caught beneath such slabs is the basis of an ecosystem which includes many embiid colonies.

FIGURE 35. Deserts near sea coasts may have a special embiid fauna supported by fog precipitation. For example, in the almost rainless coastal fog zones of Peru and southwestern Angola, embiids may extensively colonize fog-supported lichens growing on rock and ground surfaces. Retreats beneath rocks and into soil and rock crevices provide escape from the excessive dryness of certain seasons and/or hot periods of the day. Illustrated is the habitat of *Chelicerca* n. sp. (Anisembiidae) in the Peruvian Desert north of Callao.

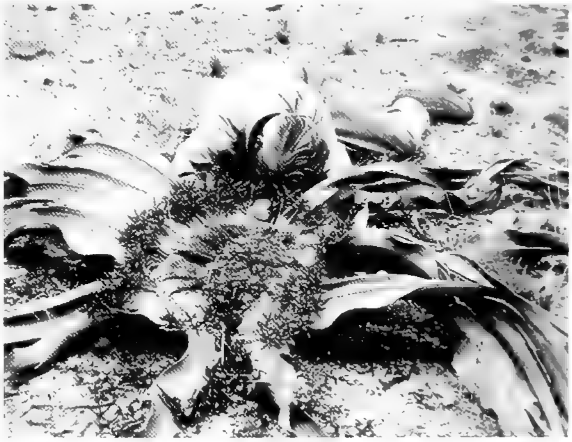


FIGURE 36. Galleries of some species occur on the surfaces of roots of perennial shrubs as well as of trees. An interesting new genus and species was thus found in Africa's Namib Desert following the roots of *Welwitschia* plants. However, the species probably isn't restricted to a host.

Geographic range

Embiids are warm-climate-adapted insects whose natural occurrence is almost universal in all suitable environments on any continent, or continental island, which has a tropical or warm-temperate climate. The order's distribution roughly coincides, for example, with that of phasmids and termites but the latter extend farther into colder latitudes, perhaps because of deeper penetration into habitats, such as soil, logs, and buildings. But, as with termites, embiid occurrence in temperate regions is reduced. In western North America the most northerly record of an endemic species, *Dactylocerca rubra* (Ross), is in central Utah, lat. 39°N. Non-endemic *Haploembia solieri* (Rambur) occurs farther north into eastern Washington. In eastern North America, represented by *Diradius vandykei* (Ross), the order reaches about 35° N in coastal Virginia.

In South America the southern limit has not been determined. The most southern occurrence known to me is *Pararhagadochir trachelia* (Navás) in a desert habitat west of Mendoza, Argentina, at about 35° S. West of the Andes, the southern range appears to be limited by the extreme aridity of the Atacama Desert of northern Chile, rather than by latitudinal cold. An undescribed species of *Chelicerca* Ross probably extends well southward in the coastal fog belt (lomas) of northern Chile, but, to date, I have found it only as far south as Mollendo, Peru. The northern Chilean lomas aren't very accessible to a collector. There is absolutely no evidence of a Southern Hemisphere, or Patagonian, origin of any species.

In the Old World, endemic species of the order occur in warm portions of all continents and continental islands even including Tasmania [*Metoligotoma tasmanica* Davis and *Aposthonia gurneyi* (Froggatt)]. New Zealand and Madagascar, which apparently could not be reached by natural spread of any species, evidently do not have endemic representation of the order. The northern extremity of range in western Eurasia is in the Crimea, about 45°N, with *Haploembia solieri* (Rambur). In the Middle East, *Parembia persica* (McLachlan) ranges into northern Iran, Afghanistan, and Turkestan (about 38°N). In eastern Asia, *Aposthonia japonica* (Okajima) reaches about 32°N in southern Japan, but this may be a species introduced from a south-Asian locality. It is assumed that the order ranges to comparable latitudes along the coast of mainland China.

Oceanic islands of the Pacific appear to have no endemic species, those present having been introduced by movements of ancient and modern man. *Aposthonia oceania* (Ross) is widespread in Oceania as far south as Easter Island 27°S and New Caledonia (20°S), at first by dispersal of Polynesians.

The fossil record indicates occurrences far to the north of present ranges, but this may be due to drift of land surfaces northward from warmer zones subsequent to fossilization. In the case of the Florissant fossil, *Lithembia florissantensis* (Cockerell), the fossil beds probably drifted northwestward and were lifted an additional 5,000 feet in altitude by elevation of the Rocky Mountain Range. I speculated that Baltic Amber fossil, *Electroembia antiqua* (Pictet), lived when the Baltic land surface was in a warm, dry Mediterranean latitude (Ross, 1956).

Ecological range

Within the extremes of geographic range, embiids are confined to regions lacking prolonged cold periods; the more equatorial the location, the greater the potential altitudinal range. Aridity can also be a limiting factor, but some practically rainless deserts, such as the Peruvian and Namib, have one or more embiid species in habitats regularly dampened by sea fog.

The primordial habitat of the order appears to be tropical rain forests. Those of the Amazon Basin retain the order's most "primitive" species. From such forest centers, embiids appear to have radiated and become adapted to many other types of environments. In this movement the trend has been toward an evasion of adverse ecological conditions rather than physiological adaptation to them. Thus, in regions experiencing prolonged dry seasons, embiids escape heat, dessication and fires by retreating downward in silken galleries following cracks, which provide access to cooler, more moist soil depths. Others may find refuge in burrows produced by beetle larvae in dead limbs of trees. Under such circumstances the activities of the embiids are confined to the rainy season or to periods of the day or night when the surface temperature and moisture are favorable.

In equatorial regions embiids spreading from optimum lowland zones have adapted to higher elevations. The highest known altitudinal record of the order is that of a new genus and species found in cloud forests and paramos above Cuenca, Ecuador at about 3,500 meters elevation. The order is present in most of the cloud forests I have visited, e.g., Andean, central African, and Malaysian. In such high zones the low temperature extreme may not be much more severe than that of many warm-temperate regions at sea level. The zones are also subject to almost daily intense equatorial, solar heat at all seasons. A few endurable hours of cold occur one night at a time rather than for weeks and months, as in cold latitudes.

Low temperature, however, appears to be the most critical ecological factor limiting the order's occurrence. Perhaps this is due to an absence of a truly cold resisting or hibernating life stage. No species is known to utilize the egg stage as a means of surviving cold periods, and, of course, there is no dormant pupal stage. Three species endure rather severe winter cold: *Dactylocerca rubra* (Ross) in central Utah, *Anisembia texana* (Mel.) in northern Texas and southern Oklahoma, and *Haploembia solieri* (Rambur) in Crimea and, by introduction into eastern Washington. *Haploembia solieri* overwinters as half-developed nymphs which, during cold periods, are protected in dense cocoon-like silk enclosures. Such a protection probably is characteristic of all cold-enduring species of the order. These "cocoons" probably are a means by which predation is reduced during the embiid's torpid state for, in cold environments, potential predators, such as carabid beetles, are likely to be adapted for movement during cold periods and therefore can easily catch unprotected prey.

Natural dispersal

The major distribution of the order must have occurred on portions of Pangaea during the long period when both sexes possessed wings. After females became universally apterous, natural dispersal outside of galleries became slow and hazardous, especially after ants evolved to become significant predators. It is possible, however, that the natural spread of small species, such as teratembiids, could have occurred as substrate objects, such as twigs and branches, were moved by wind, and rafting. On or in such objects survival and transport of embiids would have been insured by enclosure in securely attached silk galleries. When continents, such as South America and Africa, were still separated by a narrow sea, aerial movement and rafting would have been more likely considering the long time periods available.

Another, yet rare means of dispersal could be in bird plumage, as is likely to have happened in the case of *Chelicerca galapagoensis* Ross. Colonies of this anisembiid frequently web the general environment and nests of birds in higher elevations in larger islands of the Galapagos. It would seem to be a simple matter for embiids to extend their galleries into the feathers of birds resting on a nest and, although many of these would be groomed out of the plumage, a certain percentage over the ages, could be carried from place to place and thus experience an extension of range. *Chelicerca galapagoensis* is related to a Peruvian and Ecuadorian loma (fog zone) *Chelicerca* and it is likely that a limited gene pool of a future new species was carried to the islands from the mainland as "passengers" in the plumage of birds (Ross, 1966).

Dispersal by man

Because of the use of crevice retreats and the adherence of silk galleries to logs, plant materials, ship's ballast and cargo, the range of some species has been, and will continue to be, extended when such objects are moved either by natural or artificial means. In warmer regions, especially where man has engaged in commerce for thousands of years, it is probable that species which appear to be endemic, were actually unintentionally introduced by humans. This is particularly likely in southern Asia and the Mediterranean region. It is to be expected that the greater speed and volume of modern commerce will accelerate artificial spread of additional species.

Embiidina are able, at least temporarily, to become established in greenhouses located in temperate regions. One of the earliest known species, "*Embia*" *michaeli* McLachlan, 1877, was collected in an orchid house in England and is known only from its incomplete type specimen. The origin of the orchid appears to have been northeast India, or Burma.

The establishment of a South American teratembiid, apparently *Diradius intricatus* (Davis), in an orchid greenhouse near Wageningen, Netherlands was reported to me by R. H. Cobben. It was first noted about 1970 and, in spite of several intensive insecticidal treatments, the infestation persisted many years until the greenhouse was removed for other reasons. It is unlikely, however, that such an introduction would have economic significance. Undoubtedly the insects were unintentionally introduced on live plants, perhaps orchids, from Suriname.

For many years embiids were frequently intercepted by U. S. plant quarantine inspectors in orchid plants from various Neotropical sources—particularly Colombia. It is unlikely that any of these would have survived very long, even if they slipped past inspection.

Some embiid species are more successful than others in becoming established abroad and it is significant that most of these belong to the family Oligotomidae. Certain species of this family often have a high survival potential and reproductive vigor as indicated by the fact that they are the easiest to propagate in laboratory cultures. They also tend to produce overlapping generations throughout the year.

In order of importance, species whose range is steadily being extended by man are listed, as follows (Species 1–9 are in Oligotomidae):

1. *Oligotoma saundersii* (Westwood).

Endemic to northern India. Now likely to be found in any warm, moist tropical or warm-temperate region. This is the species most often collected in settled areas by the non-specialist. Males frequently are attracted to lights.

2. *Oligotoma humbertiana* (Saussure).

Endemic to India. Now very common in Indonesia, Philippines, China, western Mexico (probably introduced from the Philippines in galleon trade to Acapulco). Unfortunately, this species is becoming distributed in natural areas of western Mexico, especially in the states of Sinaloa and Nayarit. Males frequently appear at lights.

3. *Oligotoma nigra* Hagen.

Probably endemic to northern India, *O. nigra* has spread westward and northwestward in ancient caravan traffic and now is well established in Arabia, the Middle East and the valley of the Nile. It was apparently introduced into southern United States in date palm cuttings (Ross, 1957) and now extends into eastern Texas and northwestern Mexico. It has also been collected in inland NSW Australia. It is now occupying natural habitats. Males frequent at lights.

4. *Oligotoma greeniana* Enderlein.

Probably endemic to India. Now established in Malaya, Taiwan, Mindanao, Hong Kong, Macao (probably from Goa), and China's southwestern interior.

5. *Aposthonia borneensis* (Hagen).

Probably endemic to continental southeastern Asia, or Indonesia. Now also occurs in southern China, Vietnam, Philippines, New Guinea and Indonesia.

6. *Aposthonia oceania* (Ross).

Possibly endemic to continental southeastern Asia, or Indonesia. Apparently was spread by early Polynesians to various portions of Micronesia and Polynesia, including Easter Island and New Caledonia. In at least one case, *Aposthonia micronesiae* (Ross), from Mariana Island, speciation may have since occurred but there is a possibility that this is a species introduced from a source-region distinct from that of *A. oceania*.

7. *Aposthonia ceylonica* (Enderlein).

Probably endemic to southern India and Sri Lanka. Now spread to Mauritius, Madagascar, Malaya, Thailand and Laos.

8. *Aposthonia minuscula* (Enderlein).

Probably endemic to India. Now spread to East African coast and Madagascar.

9. *Haploembia solieri* (Rambur).

Endemic to some undetermined Mediterranean area. Now common almost throughout Mediterranean shores and Black Sea region. This wide range perhaps resulted from ancient land and sea commerce. A parthenogenetic form occurs in scattered Mediterranean regions, especially on certain islands, and has since been spread to southern Spain, northwestern Africa, Asia Minor, Afghanistan, the Canary Islands and western United States—especially California.

10. *Embia savignyi* Westwood.

Probably endemic to southern Sudan and adjacent regions. Now spread westward as far as northern Nigeria and north into the Nile Delta, Israel, and Crete. Males fly to light.

11. *Parembia persica* (McLachlan).

Probably endemic to northwestern India, or Pakistan. Now spread, perhaps at first by ancient commerce, as far north as Russian Turkestan and as far west as Israel, Jordan and Arabia. The damaged type of *Parembia producta* Davis from Somalia appears to represent *P. persica* (Ross, 1981).

12. *Pararhagadochir trinitatis* (Saussure).

Probably endemic to northeastern South America and Trinidad. Now sporadically common on tree trunks around San Jose, Guatemala; northern Costa Rica; Panama; and probably elsewhere.

13. Some South American species, such as *Archembia batesi* (Mc.L.) and *Pararhagadochir bicingillata* (Enderlein), appear to have extended their range in river commerce.

Natural hazards

PREDATORS: Outside of their galleries embiids are easy prey to predators, especially ants, as well as spiders, beetles, centipedes, and small vertebrates. Predation appears to be the prime factor limiting establishment of colonies in new places. Out of their galleries it is difficult to think of creatures more vulnerable to predation than embiids. They cannot run or fly very well, they lack biting or stinging defenses, repugnant secretions, body armor, irritating vestiture, or defense through high reproductive potential. There is indication, however, that some diurnally-dispersing species may reduce predation by mimicking the coloration and movement of repugnant or dangerous models. For example, in the Neotropical region many species, especially females, resemble notoriously aggressive, stinging ponerine ants. Most spectacular is the orange-and-black pattern, especially of nymphs and females, of several species of *Dihybocercus* Enderlein in south-central Africa. Combined with a similar body form, such embiids strongly resemble aposematic, highly irritating staphylinid beetles of the genus *Paederus*.

The most significant defense, although not complete, is confinement in silk galleries. The importance of silk gallery protection was clearly evident during a brief field experiment conducted by me in Singapore with colonies of *Oligotoma saundersii* (Westw.). The colonies occurred on bark of shade trees on which swarmed large, vicious *Oecophylla* ants. These ants ran over the silk webs apparently unable to detect embiids underfoot. However, when I opened some webs, the exposed embiids were immediately detected and carried off by the ants. Under such circumstances the spread of the embiids would be possible only by gallery extension, or by movement outside of galleries during inactive periods of predators. It is likely that ants are the most significant predators of embiids and that the major extension of embiid occurrence on Earth took place before ants evolved and became abundant. Of course, during the pre-ant period, wide dispersal was augmented by presence of wings in both sexes.

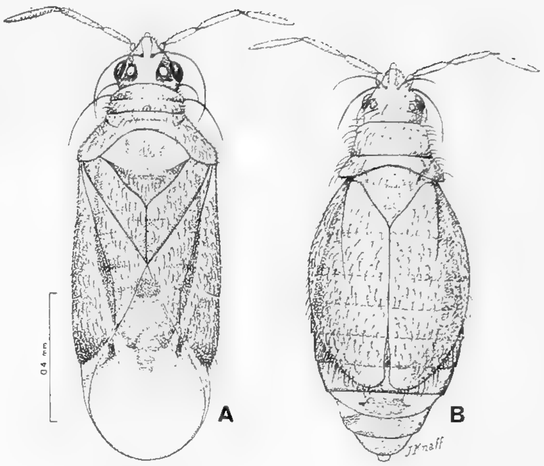


FIGURE 37. Mirid-like appearance of a species of Plokiophilidae bug, *Embiophila (Acladina) africana* Carayon, I collected in Katanga, central Africa. A. Male. B. Brachypterous female. (After Carayon)

In addition to arthropod predation, colonies may be ripped open and plundered by birds, rodents, lemurs, monkeys, and other vertebrates. This is most evident in tropical forests where one occasionally encounters sheet-like mats of galleries torn open and devoid of occupants following discovery by an insectivore.

As is to be expected in any ancient group of insects, embiids provide both habitat and food for parasitoids and parasites, some exclusive to the order. Included are various species of tiny, brown, anthocorid-like Hemiptera of the little-known family Plokiophilidae (Figs. 37, 38). All members of this tropical family live on silk webs; those of the subfamily Plokiophilinae appear to be confined to spider webs and the Embiophilinae to galleries of Embiidina. Apparently, however, a substrate of silk and available food is more important than actual association with spider and embiid hosts for Carayon reared the bugs for several generations on a diet of mites. Carayon's work (1974) is the best reference.

FIGURE 38. Plokiophilid bug nymph sucking fluids from the basitarsus of a dead embiid (*Archembia* n. sp., Tingo Mariá, Peru).

I have encountered the bugs sporadically in colonies of many species of embiids in both Old and New World tropics. The family appears to be absent in Australia. Often they are inadvertently collected as silk galleries and other habitat material is included in a field culture. As embiid cultures grow, embiophilines usually thrive, but apparently do not always kill their hosts. The bugs are most numerous in the vicinity of embiid egg masses and broods of young nymphs. Carayon (1974) reported that they regularly suck fluids from eggs and young nymphs. Tyroglyphid mites are always present in embiid cultures and must supplement the bug's diet. I have also observed them sucking shriveled, recently dead, embiids. Unless salivary toxins are introduced in their feeding, the bugs should not adversely affect the embiids unless several individuals simultaneously feed on a single egg or a small nymph.

The following arthropods are also encountered within embiid galleries:

Acarina. Predatory mites frequently infest cultures and can seriously reduce their vitality. Larval mites of the family Trombiculidae attached to embiids have been encountered. Scavenger mites are also abundant in most colonies.

Rhaphidioptera. The sinuous, predaceous larvae of snake flies frequently are encountered in under-stone galleries of *Haploembia solieri* (Rambur) in California.

Coleoptera. On one occasion (*Embia sabulosa* group, S.W. Africa) I encountered numerous larvae of a species of Lampyridae which had consumed all of the embiids in an under-stone colony. I found a beetle of the family Monommidae in galleries of *Clothoda longicauda* Ross at Tingo Mariá, Peru. Myers (1928) reported numerous monommids, *Hyporrhagus marginatus* (Fab.), within extensive, mat-like webs of *Mesembia hospes* (Myers) in Cuba.

Diptera. Larva of *Leptopteromyia* Williston (Leptogastridae) have been reared on several occasions in embiid cultures from widespread Neotropical localities. In the labyrinth of a culture it is difficult to determine the exact relationship of these slender fly larvae to embiids. However, frequency of emergence of adults from my cultures suggests that their larvae regularly utilize cover, and embiids as food, in field colonies. Carrera (1947) reported a puparium of the genus in embiid galleries in the botanical garden in Rio de Janeiro.

ECTOPARASITOIDS: The most interesting ectophagic parasitoids are larvae of wasps of the family Sclerogibbidae (Chrysidoidea). The only recorded hosts of this family are Embiidina. Male sclerogibbids are black, slender, alate, 1–4 mm in length. Females (Fig. 39) are always apterous and move with great swiftness within the galleries, however, like their hosts, they spend much time resting motionless in upper levels of the galleries spun in culture jars.

First instar larvae of sclerogibbids are legless, but otherwise resemble meloid triungulins. They are sclerotic, well-segmented, and attach themselves to membranes in various parts of the host's body and, soon after beginning to feed, become maggot-like. As a rule, only one larva is attached to a host (Fig. 40), but as many as four larvae of a large species have been found attached to a single embiid (Fig. 41). Larvae of certain small species of sclerogibbids may be more numerous on a single host; a dozen or more may be attached in a neat row on each side of the venter of the abdomen.

When a sclerogibbid larva completes its feeding, it drops off of the host and spins an elongate whitish cocoon within a gallery, and pupates. Cocoons of some species are coated with debris, which must have been added by an embiid because they characteristically eject or cover foreign objects encountered in their galleries. The cocoon is attached to the gallery wall near the shrivelled, dead body of the host.

The sclerogibbids were revised by Richards (1939) and there have been more recent papers dealing with the systematics and biology of several species. Scores of host-associated new species await description in California Academy of Sciences as a result of my fieldwork and culturing activity. I have had no success in continuous rearing of the wasps in laboratory cultures but this may be due to absence in a culture of both sexes at the same time to insure mating. Shetlar (1973) succeeded in getting unmated females of *Probethylus schwarzi* to reproduce, but, of course, the progeny were males. In another example, fifteen males, but no females, emerged from a culture of *Archembia* n. sp., from Santa Catarina state, Brazil.

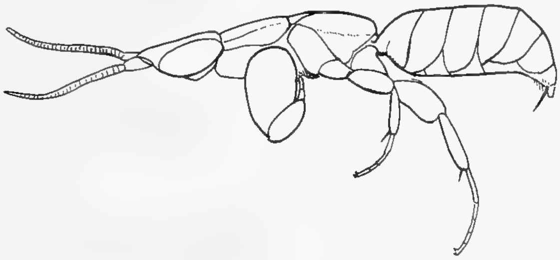


FIGURE 39. Universal appearance of female sclerogibbids. Note peculiar enlarged forelegs. Superficially, species differ only in size and coloration. Body length 3.0 mm.

Sclerogibbids are themselves parasitized by wasps of the chalcidoid family Perilampidae, as evidenced by the emergence of five *Perilampus philembia* Burks from as many cocoons of a sclerogibbid parasitoid of *Archembia* n. sp. in Tingo Maríá, Peru. More recently, apparently the same species emerged in a large culture of *Gibocercus* n. sp. from Ecuador's Rio Napo region. A pupa of the Tingo Maríá sclerogibbid also yielded a male chalcidoid of the genus *Mondontemerus* (Torymidae).

It is possible that sclerogibbids may be attacked by their hosts. Three large males collected in a culture of *Neorhagadochir* Ross from Nicaragua suffered extensive loss of antennal segments and this

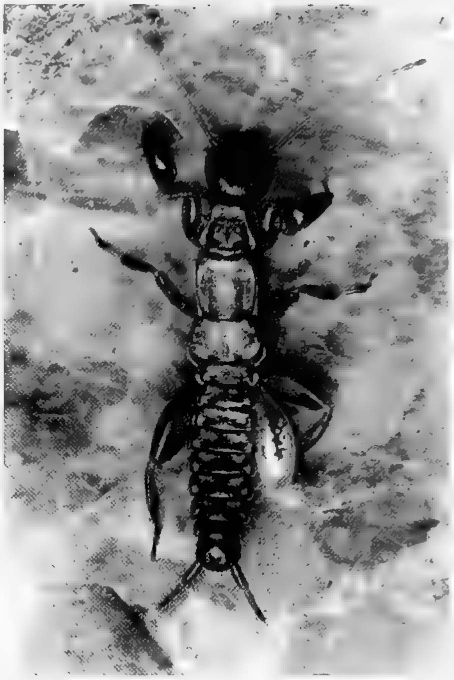


FIGURE 40. Single sclerogibbid wasp larva feeding on adult female of a new genus and species of Anisembiidae occurring in upper Amazon of Brazil and Peru.

FIGURE 41. Mature sclerogibid larvae attached to adult female of *Archembia* n. sp. Tingo Mariá, Peru.

could only have resulted from nibbling by the host embiids.

Another type of ectophagy involves larvae of small cecidomyid gnats of the genera *Feltiella*, or *Lestodiplosis* (Ross 1944:491). These are similar to sclerogibbid larvae both in appearance and method of feeding. They were encountered on one occasion only, in northern Florida, on *Diradius vandykei* (Ross).

ENDOPARASITOIDS: Embiids, at least in Neotropical regions, apparently are hosts to braconid wasps of the genus *Sericobracon* (Doryctinae). Studies of such wasps were conducted by Scott R. Shaw and Janice S. Edgerly (1985).

Embiidina are hosts to larvae of unusual tachinid flies as evidenced by collections I have made in widely separated geographic regions. Only two of the several new species have been described. *Rossimyiopsis whiteheadi* Mesnil, 1953, was reared from *Apterembia cercocyrta* (Krauss) in South Africa and E. I. Schlinger and I reared another series, *Perumyia embiaphaga* Arnaud (1963), from *Clothoda longicauda* Ross in Tingo Maríá, Peru. Series I reared from various embiid hosts occurring in Central America, Africa and tropical Asia await study. These tachinids are small, averaging about 3 mm in length; with shiny, not densely setose, black bodies, and usually smoky wings. As they walk they rotate their wings.

EGG PARASITOIDS: Tiny wasps developing within embiid eggs belong to genera *Embidobia* Ashmead and *Palaeogryon* Masner, tribe Embidobiini, family Scelionidae. They occur almost throughout the range of Embiidina. The writer has reared and preserved numerous host-associated lots of specimens which should represent many new species. This collection is being studied by L. Masner. The females of some species are pale ferrugineous and often apterous or subalate (brachypterous). Successive generations can be reared in embiid cultures. At times only one sex of the wasps, usually males, appear in a particular culture.

The tendency of most embiid species to coat their eggs with a hardened paste of chewed debris and their feces, may reduce oviposition by the wasps. Guarding by the parent female may also protect a large percentage of the eggs in a mass (Fig. 42).

PATHOLOGICAL HAZARDS: Disease epidemics may weaken and even kill all individuals in a culture. It is assumed that such diseases also occur in nature but probably do not have such a catastrophic effect due to scattered occurrence of host colonies and consequent reduced contagion.

FIGURE 42. Adult female of *Gibocercus* n. sp. from Ecuador resting on her mass of eggs covered with layers of silk. Note egg parasite approaching from her rear.

No studies specific to embiids have been made of these diseases but one can speculate that they are caused by viral, bacterial and fungal pathogens not necessarily restricted to embiids. In some cases activity of the victim will slow and eventually cease, the body turning reddish as its tissues liquefy. In cases of fungal infection, white mycelia begin to outline somites and sclerites of the embiid victim and later its entire body becomes a fuzzy, moldy mass. Gerald M. Thomas of the University of California identified the pathogen of one such epidemic, in a culture of an oligotomid from northwest Thailand, as *Beauveria bassiana.* He commented that this is the most commonly occurring insect pathogenic fungus in the world, and has a very wide host range on terrestrial and aquatic arthropods.

The most important epidemics, however, are caused by sporozoan parasites of the genera *Adelina* (*A. transita* according to J. P. Kramer, pers. com.), *Gregarina*, and *Diplocystis*. An infected culture exhibits gradually reduced vitality, no new galleries are spun and eventually all the occupants die. Stefani (1959, 1960) made special studies of *Diplocystis clerci* parasitizing *Haploembia solieri* in the Mediterranean region. He noted that the protozoa may damage sperm and weaken all males and thereby limit a species' reproduction to a residual minority of females capable of reproducing parthenogenetically. Perhaps the consistently parthenogenetic form of *H. solieri* developed this way in populations on islands on the Tyrrhenean Sea on which all males had been exterminated by repeated epidemics (see section on parthenogenesis for details).

Undoubtedly, numerous other microorganisms infect embiids throughout the order's range; however, the only important investigations to date, are limited to Sardinian hosts studied by Stefani who also reported the parasitic nematode, *Hexamermis*, in two species of *Embia*.

FIGURE 43. Culturing is a way of studying embiid biology and securing specimens for study. Those from Australia were maintained in my home laboratory. Each (left) had an associated jar (right) in which "harvested" series were preserved in alcohol jars.

FIGURE 44 Left, a gallon-sized culture (cover removed) produced hundreds of adult specimens of *Dihybocercus* n. sp. from Zambia. These half-grown, orange-and-black nymphs mimic poisonous paederine staphylinid beetles.

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