

Internal Anatomy of *Dolania americana* (Ephemeroptera: Behningiidae)¹

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ABSTRACT

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Based on dissections of different aged larvae and adults, the anatomy and developmental changes of the central nervous system, tracheal system, digestive canal and Malpighian tubules, circulatory system, and gonads of *Dolania americana* are presented. The Malpighian tubules are the most plesiomorphic in the Ephemeroidea; affinities with other families of Ephemeroidea are evident in many characters, some with Potamanthidae and Ephemeridae and some with Palingeniidae and Polymitarciidae. Derived conditions are found in the alimentary canal (a result of predatory habits) and in characters associated with the shortened head capsule. Ontogeny of the ovaries is unique within Ephemeroptera: only a single egg matures in an ovariole and some ovarioles disintegrate in older and mature larvae. This type of oögenesis results in extremely low fecundity.

The family Behningiidae Motaş and Băcesco, 1937 consists of 3 recent genera restricted to the Holarctic Region (Edmunds and Traver 1959) and one fossil genus *Archaeobehningia* from the Palearctic Region (Tshernova 1977). While larval habits and adult stages of the genus *Protobehningia* from the Far Eastern U.S.S.R. are unknown (Tshernova and Bajkova 1960), the larvae of the remaining 2 genera are known to live in clean, shifting-sand, lowland rivers (Keffermüller 1959, Peters and Jones 1973, McCafferty 1975). The adult emergence and behavior of *Behningia* are described by Keffermüller (1963), those of *Dolania* by Peters and Peters (1977).

Our knowledge of the internal anatomy and physiology of the Behningiidae is not extensive. The thoracic and abdominal tracheal system, Malpighian tubules, and ventral nerve cord of *Behningia ulmeri* Lestage (a species probably identical with *B. lestagei* Motaş and Băcesco - cf. Keffermüller 1959) have been investigated by Landa (1969). Brodsky (1974) mentions the thoracic musculature of adult *B. ulmeri* adapted for swift speed flight. With the exception of the egg description (Koss and Edmunds 1974), there are no data concerning the internal anatomy of the genus *Dolania*.

The central nervous system, tracheal system, circulatory system, digestive canal and Malpighian tubules, and gonads of *Dolania americana* Edmunds and Traver are described herein.

Material and Methods

In order to study the developmental changes of internal organs, all stages of *D. americana* (i.e., larvae of different sizes, male and female subimagos, male imagos—a total of 52 specimens) were dissected. All material studied was collected in Florida, Okaloosa Co., Blackwater River, Florida A&M Univ. Biol. Stn., 4.5 mi. NW of Holt, in 1977-1978, by W. L. and J. G. Peters and T. Soldán.

Preferably fresh material was studied (larvae); further material (mature larvae and adults) was fixed with 75% EtOH, Carnoy or Bouin. Fresh specimens from which tissues were disintegrated by water at 30°-40°C for 1-2 h were used for study of the tracheal system. Some

important parts of the internal organs were mounted in Canada balsam with Cellosolve. The nomenclature of the tracheal system proposed by Landa (1948, 1949, 1969) is followed.

Results

Central Nervous System

The central nervous system (Fig. 1,5) consists of the following ganglionic centers: brain, subesophageal ganglion, 3 thoracic ganglia, and 7 abdominal ganglia. Both ganglia and connectives of the ventral nerve cord are situated between the alimentary canal and the ventral muscles.

Brain (supraesophageal ganglion) cylindrical, situated between alimentary canal (pharynx) and dorsal head integument (frons). Optical lobes elongated, slightly tapered laterally, with brownish-black stippling. Lobes of ocelli very stout, cylindrical, frontal ocellus directly connected with brain. All parts of brain (proto-, deuto-, and tritocerebrum) completely fused, distinguishable only by means of nerve bases (Fig. 5). Circumesophageal connectives stout, situated laterally around pharynx (esophagus).

Subesophageal ganglion rectangular, situated in cervical region between head and prothorax, below alimentary canal, extended slightly into prothorax. Connectives between subesophageal ganglion and prothoracic ganglion not distinguishable.

All thoracic ganglia of ca. same shape and size, connectives well separated, doubled. Ganglia diamond-shaped, much larger than remaining abdominal ganglia. Three pairs of nerves emerging from pro- and mesothoracic ganglia, 2nd pair of nerves branched near base. Metathoracic ganglion with 3 pairs of nerves from anterior portion (as in meso- and prothoracic ganglia) and with 2 other pairs of nerves from posterior portion (Fig. 5).

Abdominal nerve cord with 7 ganglia situated in abdominal segments II, III, IV, V, VI and VII (2 ganglia). First ganglion either situated in 1st segment or at anterior margin of segment II; 2nd ganglion sometimes situated at anterior margin of segment III; remaining ganglia always situated as mentioned above (Fig. 1). All abdominal ganglia of ca. same shape and size with single pair of nerves. Two ganglia deposited in segment VII, these

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ganglia contiguous but not fused, posterior ganglion with pair of long caudal nerves leading to cerci. Connectives of all abdominal ganglia contiguous, not fused, easily distinguished in most specimens to partially fused in some specimens.

As pointed out by Bazyukina and Brodsky (1975), only the metathoracic and last abdominal ganglia are true ganglionic centers. The metathoracic ganglion contains the fused 1st abdominal ganglion (2 abdominal neuromeres) as is usual in most recent Ephemeroptera; the last abdominal ganglion contains 2 neuromeres also.

No changes were observed between larvae and adults in the arrangement of the central nervous system.

Tracheal System

The tracheae of larvae (Fig. 1,2) and adults consist of a pair of strong lateral trunks situated along the alimentary canal and gonads in the thorax and abdomen. Lateral trunks are directly connected with the gills by 7 pairs of short, slightly curved tracheae (*tracheae arci laterales*).

Thoracic (Meso- and Metathoracic) and Abdominal Tracheation (Tracheae of Stigma 2-10).—Visceral tracheae (*tracheae viscerales*) in mesothorax and abdominal segments III-VII [TV2, TV6, TV7, TV8, TV9, TV10 in Landa's (1969) classification] (Fig. 1,2). Visceral trachea in mesothorax very strong, supplying stomodaeum, thoracic muscles, and, in part, mesenteron; visceral trachea in abdominal segment III (TV6) supplying mesenteron and gonad in 1st abdominal segments; other abdominal visceral tracheae narrow and short. Pedal tracheae (3 pairs) strong, especially those of metathoracic legs. Ventral tracheal anastomoses (*tracheae anastomoses ventrales*) in abdominal segments I-VIII [TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10(VIII), TAV10(IX) in Landa's (1969) classification] (Fig. 1); tracheal anastomoses curved, medially extended forward to previous segment, deposited below ventral nerve cord.

Head and Prothoracic Tracheation (Tracheae of Spiracle I) (Fig. 3).—Common head trachea (*trachea cephalica communis*) very short, practically indistinguishable from lateral trunk. Dorsal head trachea (*trachea cephalica dorsalis*) relatively narrow, lateral trunks ca. 2 times broader; tracheal anastomosis leading to Palmen organ (*trachea anastomotica transversa organi Palmeni*) broad and conspicuously bent. Brain and mouth-part tracheae [no. 7-16 in Landa's (1948) classification] originating at fork of dorsal head trachea and tracheal anastomosis to Palmen body. Ventral head trachea (*trachea cephalica ventralis*) very short, ventral tracheal anastomosis to Palmen body forked from ventral head trachea at same point as propedial trachea (*trachea propedialis*) and trachea supplying prothoracic muscles (*trachea prothoracalis muscularis*) (Fig. 3); propedial trachea branched even in prothorax; prothoracic ganglion trachea as wide as tracheal anastomosis to Palmen body. Mandibular trachea starting near propedial trachea. Tracheal anastomosis (*trachea anastomotica longitudinalis cephalica*) and contact mallet between branches of dorsal and ventral head tracheae (Fig. 3) located near optical lobes of brain.

No changes in the tracheal system were observed during larval development. The changes occurring during the larval-subimaginal molt are the same as mentioned by Landa (1949) for some European genera: loss of gills with consequent closing of respective tracheae and forming of stigmatic tracheae; disappearance of some visceral tracheae or their branches, especially those supplying the alimentary system. It is possible to suppose that these changes occur in mayflies in general.

Alimentary Canal

Stomodaeum (foregut) in head and prothorax only (Fig. 2). Pharynx and esophagus not differentiated, esophagus gradually extended posteriorly. Posterior portion of esophagus rounded or spherical, ca. 2 times broader than anterior portion, both portions telescopically connected. Stomodaeum membranous, colorless, translucent when empty.

Mesenteron (midgut) in pro-, meso-, metathorax, and abdominal segments I-VI, slightly extended into segment VII, cylindrical, ca. 2-3 times broader than posterior part of stomodaeum (Fig. 2). Although shape dependent on amount of food, mesenteron usually slightly tapered in meso- and metathorax and extended in abdominal segments I-IV, considerably constricted in segments VI and VII. Mesenteron with dark brownish stippling, apparent through dorsal integument in living larvae.

Proctodaeum (hind gut) apparently differentiated in colon and rectum, Malpighian tubules entering the alimentary canal between mesenteron and colon. Colon subcylindrical, situated in abdominal segment VII, slightly tapered backwards (Fig. 6). Rectum in segments VIII and IX and extended into segment VII, its proximal portion rounded and extended, without any rectal projections. Rectum tapered posteriorly (Fig. 6) and extended again near posterior margin of segment IX forming anal papillae. Proctodaeum membranous, whitish or translucent, without stippling.

Larvae of *Dolania* are predaceous (Tsui and Hubbard 1979). Although the mouthparts of *Dolania* lack the conspicuous modifications of other predaceous mayfly larvae (Siphonuridae, Ameletopsinae), the bulbous posterior portion of the stomodaeum more or less apparent in both younger and older larvae resembles a similar structure (crop, ingluvies) found in some carnivorous Siphonuridae. This structure is not the proventriculus (neither strong musculature nor inner chitinous elements were observed) but it probably is used for storing ingested food before passing food to the mesenteron. [I have found whole insects (small stonefly larvae and chironomids) in the crop of larvae of *Ameletopsis*.]

The developmental changes in the alimentary canal during the larval-subimaginal molt are as described by Pickles (1931) and Grandi (1950) for other mayflies. The alimentary canal of mature larvae is filled with air bubbles and the stomodaeum is hardly recognizable. In adults, the anterior part of the gut (stomodaeum and mesenteron in the thorax) disappears; only membranous remnants remain. The posterior parts (mesenteron in the abdomen and the proctodaeum bearing Malpighian tubules) are usually recognizable.

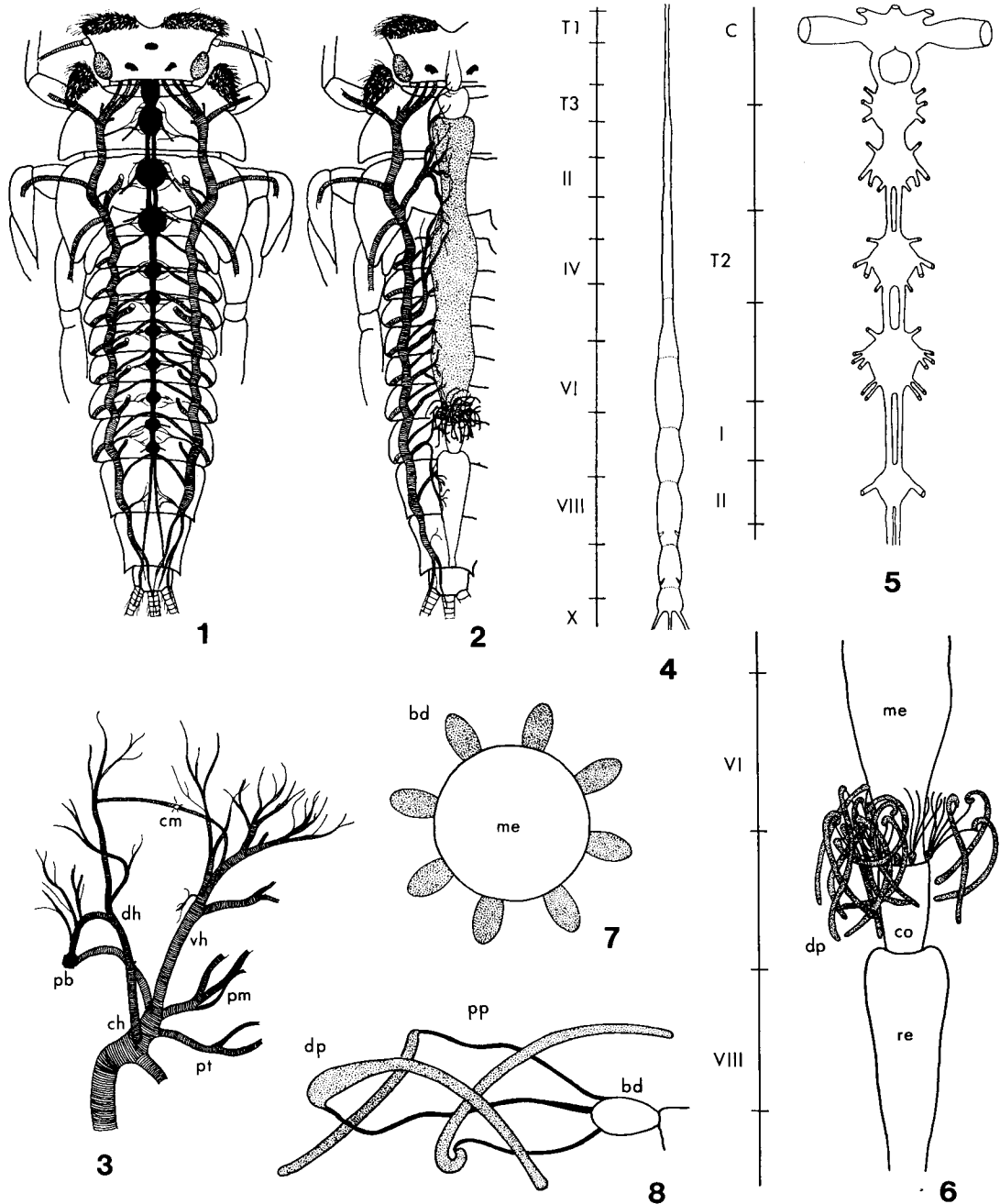


FIG. 1-8.—Internal organs of *D. americana*. 1, 2, tracheation of body, ventral nerve cord, alimentary canal (mesenteron dotted); 3, head tracheation; 4, dorsal vessel; 5, head and thoracic central nervous system; 6, posterior part of alimentary canal; 7, schema of Malpighian tubule bases; 8, detail of Malpighian tubules. Abbreviations: C, T 1-3, I-IX—head, thoracic and abdominal segments; ch, dh, vh—common, dorsal and ventral head trachea; pt—propedial trachea; pm—trachea of prothoracic muscles; pb—Palmen body; cm—contact mallet; me, co, re—mesenteron, colon, rectum; bd—Malpighian tubule buds; dp, pp—distal and proximal portion of tubules.

Malpighian Tubules

Malpighian tubules attached to alimentary canal in abdominal segment VII (Fig. 6), some extended into segments V and VIII. Tubules entering 8 (4 pairs) buds (Fig. 7, 8) connected with alimentary canal; buds egg-shaped, evenly distributed around alimentary canal (2 pairs situated dorsally, a pair laterally or ventrolaterally,

a pair ventrally) (Fig. 7). Tubules apparently differentiated into proximal and distal portions (Fig. 8); proximal portion tubular, hair-like, sometimes slightly extended at base, connected directly with buds; distal portion tubular, either coiled or uncoiled but extended at base, usually slightly bent; distal portion ca. 2-3 times broader than and longer (to equal in length) than proximal

mal portion. Total number of tubules 53–92 (avg 75, 8 specimens examined); apparently, total number not dependent on size of larvae.

There are practically no developmental changes of the Malpighian tubules during the larval stages. Both the distal and proximal parts are recognizable even after degeneration of the alimentary canal. Tubules are also present in subimagos and imagos, but probably have no function since the mesenteron and colon have disintegrated.

No anatomical evidence for secretory activity was found (cf. Sattler 1967).

Circulatory System

From dissections of fixed and fresh specimens, it is only possible to describe the dorsal vessel. Detailed histological examination will be necessary to study the dorsal diaphragm and pulsative organ and to determine the exact number of ostia.

Dorsal vessel (Fig. 4) situated dorsally in thorax and abdominal segments I–IX above alimentary canal. Anterior portion of dorsal vessel (aorta), discharging hemolymph apparently only to head (no extensions or additional arteries of aorta evident), represented by simple narrow tube, apparently unsegmented in thorax, extended only slightly to head. Posterior portion of dorsal vessel (heart) situated in abdominal segments I–X, probably extended into thorax. Heart in 1st abdominal segments not distinguishable from aorta, being of same width and structure without macroscopically apparent segmentation. Heart considerably extended in segments VI(V)–X, showing respective segmentation. Two pairs of ostia macroscopically recognizable in segments IX and VIII, but other pairs of ostia can occur in segments V–VII (4 pairs of ostia occur in *Ephemera vulgata*); both pairs of ostia considered to be incurrent. Heart in segment X bulbous, broadly connected with heart in IX anteriorly and with 3 caudal arteries posteriorly. From dissections of living material, ca. 45–70 pulses/min represented by systolic wave proceeding towards head.

Testes

Testes paired, deposited in abdomen along alimentary canal and tracheal trunks. In young larvae, testes in segments II–V; in half-grown and older larvae, testes in segments I–VI. Testis cylindrical, rounded or bluntly pointed in segments I and II, not flattened or slightly flattened bilaterally. Testis with ca. 200–300 testicular follicles surrounding seminal ducts dorsally and laterally. All follicles equal in shape and length, cylindrical, 2–3 times longer than broad, connected directly with seminal ducts; seminal ducts at right angles to follicles (Fig. 9). Seminal duct (vas deferens) simple and narrow, extending from apex of testis in segment I and II to posterior margin of segment IX. Vas deferens connected with pair of hollow ampullae in younger and half-grown larvae, with penial Anlagen in older and mature larvae. Seminal vesicle (vesicula seminalis) simple, formed by extension of seminal ducts in segments VIII and IX (Fig. 11).

Ontogenetic development of the testis is connected with changes in the arrangement of the seminal vesicle and follicles. Follicles differentiate in younger larvae from primordial cells, then shrink and collapse in more mature larvae when spermateliosis occurs (Fig. 10). The size of the seminal vesicle depends on the amount of mature spermatozoa (Fig. 11, 12). In mature larvae and adults, the testis is barely evident; the follicles are shrunken and hardly recognizable (Fig. 10) in the last abdominal segments; only the seminal vesicles are evident.

Ovaries

Ovaries only in abdomen. Ovary bilaterally flattened, in 1st abdominal segment rounded or bluntly pointed. Ovarioles entirely differentiated in young larvae, in half-grown larvae ovarioles club-shaped; lateral oviduct at angle of ca. 45° to ovarioles, with long terminal filament directed forward (Fig. 13). Ligament of ovary formed from terminal filaments of anterior ovarioles, attached to thoracic endoskeleton. Oviducts straight, slightly curved in segment VII; in younger and half-grown larvae

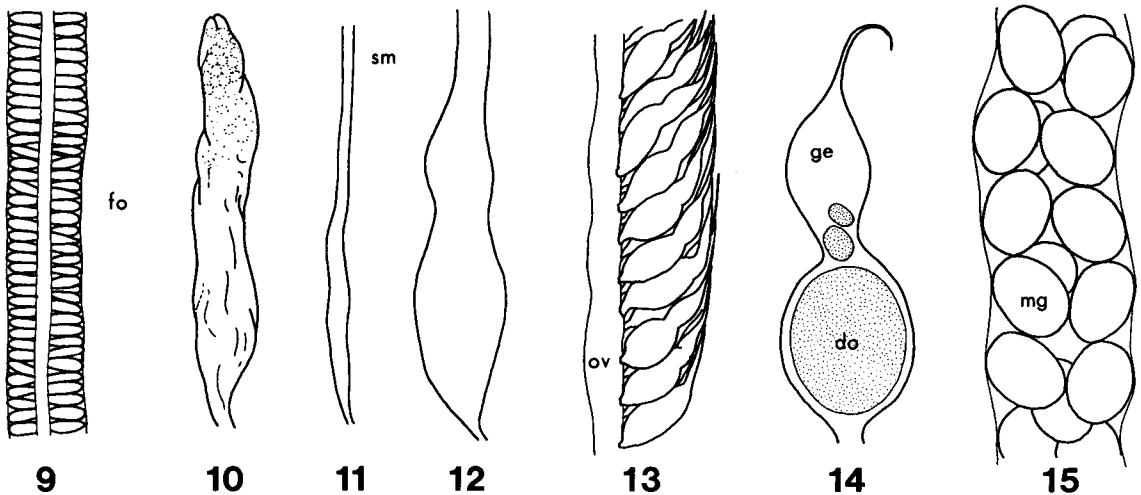


FIG. 9–15.—Gonads of *D. americana*. 9, testis, ventral view, half-grown larva; 10, testis, dorsal view, mature larva; 11, seminal vesicle in half-grown larva; 12, seminal vesicle in subimago; 13, ovary, lateral view, half-grown larva; 14, ovariole, half-grown larva; 15, ovary, subimago. Abbreviations: sm—seminal duct; fo—testicular follicles; ov—oviduct; ge—germarium; do—distal oöcyte; mg—mature eggs.

oviducts connected to pair of hollow ampullae near future external openings of oviducts, in adults oviducts with separate openings. Openings of oviducts without modifications (as usual in Ephemeroidea) representing the most plesiomorphic situation in mayflies (cf. Grandi 1955, Brinck 1957).

Oögenesis, like spermatogenesis, is completed before the subimaginal molt, with the descent of all mature eggs into extended oviducts (Fig. 15). Although the anatomical arrangement of ovaries in *Dolania* does not differ substantially from that of other Ephemeroidea (in Ephemeroidea the ovaries may extend to the thorax), oögenesis, descent of mature eggs, and developmental changes of ovaries in mature larvae represent a unique type not only within the Ephemeroidea but within Ephemeroptera in general. Egg number in mayflies usually ranges from ca. 150 eggs in *Prosopistoma* (De-grange 1960) to 12,000 eggs in *Palingenia* (Kosova 1967). *Dolania* females have the lowest fecundity described so far for mayflies, ranging 24–161 eggs/female (avg 91, Peters and Peters 1977). Despite this, the ovary of *Dolania* consists of 80–120 ovarioles (avg number 98 ovarioles, 8 half-grown larvae from a different population examined), so that each female has ca. 200 ovarioles in the half-grown larval stage. Taking into account the fact that usually 5–8 oöcytes mature in a single ovariole in Ephemeroidea (*Ephemerella*, *Palingenia*), the theoretical fecundity of *Dolania* is 1000–1600 eggs/female. However, although the vitellarium is formed by 1–3 oöcytes and another 2–3 oöcytes from the previtellarium, only a single oöcyte (proximal, Fig. 14) actually matures. The other oöcytes in the vitellarium and previtellarium, and the germarium as a whole, degenerate and are probably resorbed before descent of the proximal oöcytes with chorion. Moreover, some of the ovarioles (ca. $\frac{1}{3}$ – $\frac{1}{2}$ of the total number) disintegrate and do not give rise to any mature eggs.

The surprisingly low fecundity of *Dolania* and most probably *Behningia* is undoubtedly related to the large size of eggs (Keffermüller 1959, Koss and Edmunds 1974, Peters and Peters 1977). Examining eggs, I found large egg size related to very high yolk content. Histological and embryological treatment of ovaries and developing eggs could elucidate the proper role of these conspicuous phenomena.

Discussion

The central nervous systems of *Dolania* and *Behningia* are similar in all characters but one: abdominal connectives of *Dolania* are more plesiomorphic in that they are contiguous instead of fused into a shallow band as in *Behningia* (Landa 1969). The central nervous system is similar to that of the Potamanthidae, except for the fusing of the subesophageal ganglion with the prothoracic ganglion (ganglia are usually separated). This fusion of ganglia, unique among Ephemeroidea, undoubtedly results from the shortening of the head. In Ephemeroidea, Euthyplociidae, Palingeniidae, and Polymitarciidae the last abdominal ganglion is situated in abdominal segment VIII (Landa 1969, Bazyukina and Brodsky 1975); in *Dolania* it is in segment VII. In this character, Behningiidae are similar to some Leptophlebiidae.

Although the head and prothoracic tracheation were not studied in detail and only the main head tracheae are described, the tracheal system of the first spiracle can be compared with that of *Potamanthus* (Potamanthidae), *Ephoron* (Polymitarciidae), and *Ephemerella* (Ephemeroidea), described in detail by Landa (1948). Head tracheation of *Dolania* is quite different from that of Heptageniidae (in arrangement of the ventral head tracheae) and Oligoneuriidae (in branching of lateral trunks), and it seems to differ from Leptophlebiidae as well. Although the head tracheation of *Ephoron* is similar to that of *Dolania*, it differs markedly in possessing stigmatic visceral tracheae and 6 pairs of air sacs (these also occur in Asthenopodinae and Campsurinae). Apart from minor differences in the arrangement of final tracheae, probably resulting from a different arrangement of other organs of the head (especially mouthparts), the head tracheation of *Dolania* is closely related to that of *Potamanthus* and *Ephemerella*. These genera, however, lack the considerable shortening of the common head trachea in the prothorax which occurs in *Dolania*. Moreover, the dorsal head trachea, propedial trachea, and trachea of the prothoracic muscles are shifted posteriorly to the prothorax or between the pro- and mesothorax in *Dolania*. This modification of the lateral trunk branching is probably due to the shortening and extension of the head capsule. Judging from the morphological similarities between *Dolania* and *Behningia*, the head tracheal system of *Behningia* must be closely related.

The thoracic and abdominal tracheal system resembles that of *Behningia*. *Dolania* differs from *Behningia* only in possessing a ventral anastomosis in abdominal segment I (TAV4). In this character, *Dolania* is similar to the Euthyplociidae, Polymitarciidae, and plesiomorphic Ephemeroidea (*Ephemerella*, *Ichthybotus*), while *Behningia* is similar to the Potamanthidae.

The alimentary canal of *Dolania* (and probably *Behningia*) differs from that of related families (Ephemeroidea) in the relative length of the stomodaeum. The stomodaeum is very short, shorter by $\frac{2}{3}$ than the proctodaeum; in most mayflies, the stomodaeum is at least as long as the proctodaeum. Analogous to the arrangement of the nervous and tracheal systems, this modification is probably due to the relative length of the body segments. The last 3 abdominal segments of *Dolania* and *Behningia* are at least twice as long as the head.

Among Ephemeroidea, the Malpighian tubules of *Dolania* (like those of *Behningia*) represent the most plesiomorphic type. The Malpighian tubules do not form common trunks and the Malpighian tubule buds can be derived directly from simple tubules entering the gut individually (Siphonuridae) by the fusion of the bases of several tubules. Some plesiomorphic genera of Leptophlebiidae have the same arrangement. Malpighian tubules of other Ephemeroidea enter 4 trunks with bush-like branching (Potamanthidae, Polymitarciidae, Palingeniidae) or 6 trunks with extensive branching (Euthyplociidae, Ephemeroidea, Campsurinae, Asthenopodinae) (Landa 1969).

Our knowledge of the comparative anatomy of the circulatory system of Ephemeroptera is fragmentary. Ac-

ording to Popovici-Bazosanu (1905) and Meyer (1931), the mayfly dorsal vessel is segmented in both the thorax and abdomen and there are 1–4 pairs of ostiae in segments VI–IX (*Caenis* 3; *Cloeon* 2; *Baetis* 1; *Heptagenia*, *Ephemerella* 4). The dorsal vessel of *Dolania* probably has an arrangement similar to that of *Ephemerella*, from which it differs by the specialized posterior portion of the heart (anterior portion of heart is as wide as posterior portion in *Hexagenia*, *Ephemerella*, *Ephoron*, and *Palingenia*). Reduced segmentation of the heart in the 1st abdominal segments may occur in *Dolania*. Histological examination of the dorsal vessel is needed to recognize a degree of specialization.

The testes of *Dolania* do not differ substantially from those of related families. *Dolania* is similar to Polymitarcyidae and Palingeniidae in that the testes are found in the abdomen only instead of extending into the thorax (Ephemeridae and Potamanthidae). Also, as usual in genera with short adult stages (*Ephoron*, *Palingenia*), spermatogenesis in *Dolania* is fully shifted to the larval stage; no change takes place between male subimagos and imagos. Morphological changes connected with the final phase of spermatogenesis (spermateliosis and descent of mature spermatozoa into the seminal vesicles) occur in *Dolania* much earlier than Potamanthidae or Ephemeridae (spermateliosis is completed during the subimaginal stage in *Ephemerella*).

While spermatogenesis in *Dolania* is of a type common in Ephemeroptera, oögenesis is unique for the order and can be considered very apomorphic. A similar type of oögenesis occurs in viviparous species of the genus *Cloeon* (Baetidae) and probably in some species of *Calibaetis* as well. In *Cloeon* only a single or at most 2 oöcytes develop in one ovariole, but no disintegration of ovarioles or parts of ovarioles have been observed before the descent of eggs to the oviduct and a relatively higher fecundity is preserved: 400–600 eggs were produced by *C. dipterum* (L.) (Degrange 1960). In *Cloeon* these changes are considered to be associated with ovoviviparity. Ovoviviparity does not occur in *Dolania*, so other reasons must be found for the large egg size and small egg number. In this regard, embryological studies should be particularly interesting.

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