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Comparative anatomy of larvae of the family Leptophlebiidae (Ephemeroptera) based on ventral nerve cord, alimentary canal, malpighian tubules, gonads and tracheal system

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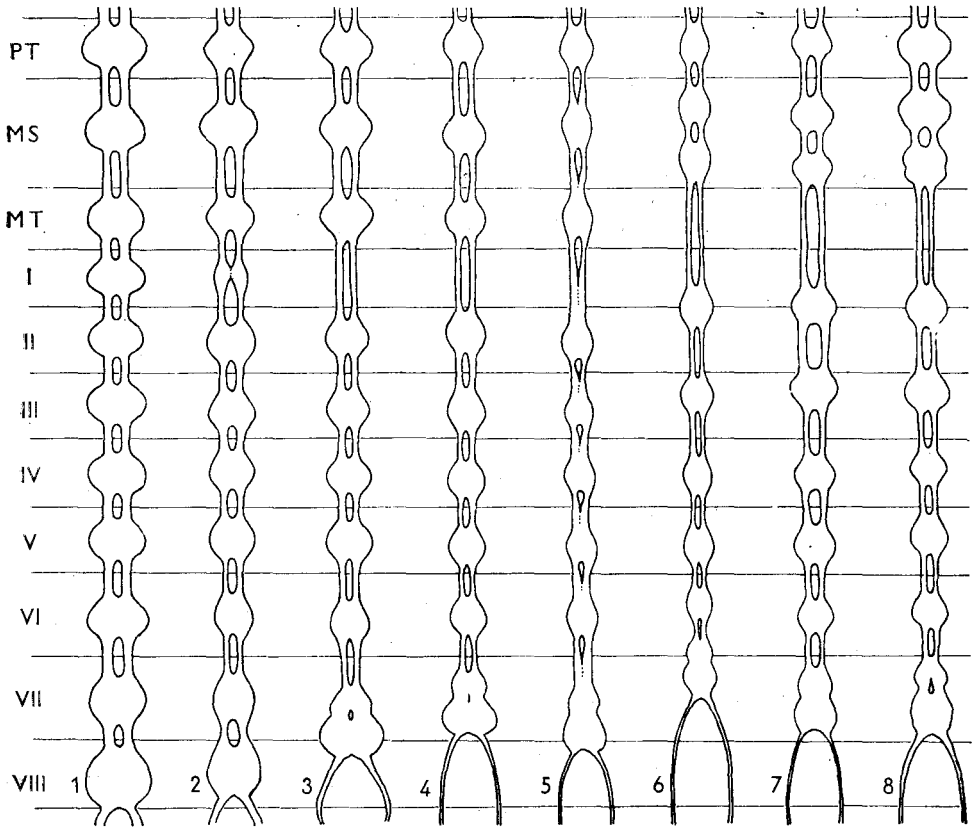
Morphology, internal organs, anagenesis

Abstract. The arrangement of internal organs of larvae of 65 species from 51 genera of the family Leptophlebiidae is studied. The following characters are considered as those of comparative value: position of metathoracic ganglion (A); position of first 4 or 5 abdominal ganglia (B); position and degree of association of last ganglionic centre (C); arrangement of connectives (D); degree of apparent macroscopic differentiation of stomodaeum (E); position of colon and pyloric valve (F); arrangement of anterior portion of rectum (G); number of common trunks of malpighian tubules and their specialization (H); position of gonads in body (I); arrangement of testicular follicles and ovarioles (J); shape of testis and ovary (K); arrangement of visceral tracheae (L); arrangement of ventral tracheal anastomoses (M, N). The anatomical schemes of genera investigated are summarized in tables and the anagenetic trends forming the above characters are discussed.

Our knowledge of the arrangement of internal organs is restricted mostly to the European genera. PALMÉN (1877, 1884) and HEINER (1914) mentioned internal organs of *Leptophlebia* and *Habrophlebia*. MEYER (1931) described the arrangement of the circulatory system and haemolymph circulation of *Leptophlebia marginata* (L.). The alimentary canal and arrangement of malpighian tubules were studied in *Choroterpes picteti* ETN. by GRANDI (1950). Certain particularities in the arrangement of corpora allata, suboesophagial ganglion and pars intercerebralis are dealt with by ARVY & GABE (1952, 1953) in four European species. GRANDI (1962) and BRINCK (1957) mention the anatomy of abdominal muscles and gonads in *Leptophlebia*, *Paraleptophlebia* and *Habrophlebia*. The larval and imaginal endoskeleton (tentorium) of four Ethiopian genera are described by HUDSON (1951). TSUI & PETERS (1972, 1976) published comparative studies dealing with the head and thoracic endoskeleton and thoracic musculature of 21 South Hemisphere genera.

The family Leptophlebiidae represents an unique group of mayflies in many respects. A considerably high number of more or less specialized genera replaces larvae of the other families in water biotopes in the Southern Hemisphere. Approximately 65 genera have been described so far (see list by HUBBARD, 1978) but the family is supposed to have as many as 200 genera. Such a group undoubtedly serves as an excellent subject for comparative anatomy purposes. One of us (V. Landa) started the study of internal anatomy of the Leptophlebiidae more than 10 years ago. Some results were published in several papers (LANDA, 1948, 1969, 1973). Recently we had an opportunity to investigate the larvae of 51 genera from all zoogeographic regions. The results of this study are presented in the present paper.



Figs. 1—8. Comparative anatomy of ventral nerve cord of Leptophlebiidae (sketch, relative length of body segments not followed in Figs. 1—38, 41—52). 1 — scheme of hypothetical ancestral conditions. 2 — *Jappa*. 3 — *Paraleptophlebia*. 4 — *Adenophlebia*. 5 — *Massartella*. 6 — *Zephlebia* (cf. *cruentata*). 7 — *Atalophlebioides sepia*. 8 — *Atalophlebioides* (Australia). PT, MS, MT — pro-, meso-, and metathorax; I—IX — abdominal segments.

MATERIAL AND METHODS

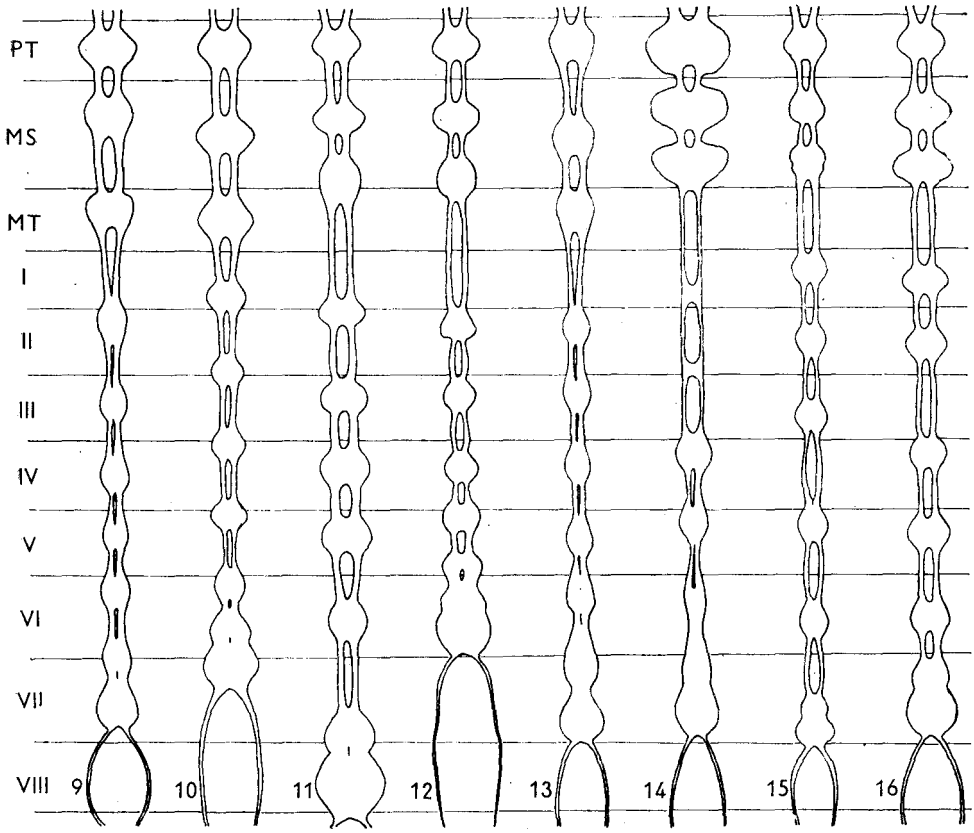
Older larvae, i.e. those from about 10th instar to the last instar (all larval characters fully developed) of the following species were studied (see list by HUBBARD, 1978 for the authors of genera):

Palaearctic region: *Habrophlebia fusca* (CURT.), *H. lauta* ETN., *Habroleptoides modesta* (HAG.), *Choroterpes* (s. str.) *picteti* ETN., *Leptophlebia marginata* (L.), *L. vespertina* (L.), *Paraleptophlebia submarginata* (STEPH.), *Thraulus bellus* ETN.

Nearctic region: *Choroterpes* (s. str.) sp. (USA, Colorado), *Choroterpes* (*Neochoroterpes*) sp. (USA, Texas), *Leptophlebia gravastella* ETN., *Paraleptophlebia bicornuta* (MCDUNN.), *P. gutata* MC DUNN., *Traverella albertana* (MC DUNN.) *Travella* sp. (USA, New Mexico).

Ethiopian region: *Adenophlebia* sp. (Nigeria, S. E. State), *Adenophlebiodes* (s. str.) sp. (Nigeria, S. E. State), *Aprionyx* sp. (South Africa, Western Cape Prov.), *Castanophlebia calida* BARNARD, *Petersophlebia* sp. (Malagasy, Tananarive Prov.), *Polythelais* sp. (Malagasy, Fianar Prov.).

Oriental region: *Choroterpes* (*Euthraulus*) sp. (India, Madras State), *Choroterpides* sp. (Thailand, Chiengmai Prov.), *Habrophlebiodes* sp. (Malaysia, Gombak riv.), *Hagenulodes* sp. (Seychelles), *Indialis badia* PETERS & EDMUNDS, *Isca* (s. str.) sp. (India, Kerala State), *Isca*



Figs. 9—16: Comparative anatomy of ventral nerve cord of Leptophlebiidae (sketsh). 9 — new genus A of Peters. 10 — new genus B of Peters. 11 — *Choroterpides*. 12 — *Miroculis*. 13 — *Lepeorus*. 14 — *Kimminsula*. 15 — *Farrodes*. 16 — *Traverella*. Abbreviations as in Figs. 1—8.

(*Minyphlebia*) sp. (Thailand, Chiengmai Prov.), *Kimminsula* sp. (Srí Lanka, Maratenua Prov.), *Megaglena* sp. (Srí Lanka, Belihuloa Prov.), *Thraulus mariae* PETERS & TSUI.

Neotropical region: *Askola froehlichi* PETERS, *Atalonella ophis* NEEDHAM & MURPHY, *Borinquena* (s. str.) sp. (Puerto Rico, Rio Mariacao), new genus A of Pescador (Argentina), new genus F of Pescador (Chile), *Farrodes* sp. (Trinidad, Arimana Riv.), *Hagenulopsis* sp. (Brazil, Sao Paulo Prov.), *Hagenulus caligatus* ETN., *H. morrisoni* PETERS & ALAYO, *Hapsiphlebia* sp. (Chile, Llanquihue Prov.), *Hermanella* sp. (Brazil, Nova Teutonia), *Homothraulus* sp. (Brazil, Santa Catarina State), *Massartella brieni* LEST., *Massartellopsis* sp. (Chile, Acongagua Prov.), *Meridialaris* sp. (Chile, Osborno Prov.), *Miroculis* sp. (Brazil, Amazonas State), *Penaphlebia chilensis* (ETN.), *P. vinosa* (DEMOULIN), *Terpides* sp. (Brazil, Amazonas State), *Thraulodes* sp. (Panama, Chiquiri Prov.), *Ulmeritus* (s. str.) sp. (Brazil, Nova Teutonia).

Australian region: *Atalomicria* sp. (Australia, New South Wales), *Atalophlebia* sp. (Australia, Tasmania), *Atalophlebioides* sp. (Australia, Tasmania), *A. cromwelli* PHILLIPS, *A. sepia* PHILLIPS, *A. aucklandensis* PETERS, new genus A of Peters (New Caledonia), *Deleatidium* sp. (New Zealand, Auckland Prov.), *Jappa* sp. (Australia, New South Wales), *Kirrara* sp. (Australia, New South Wales), *Lepeorus calidus* PETERS, PETERS & EDMUNDS, new genus B of Peters (New Caledonia), *Ulmerophlebia* sp. (Australia, New South Wales), *Zephlebia* (s. str.) sp. (cf. *cruentata*) (New Zealand, North Island), *Z.* (s. str.) sp. (cf. *borealis*) (New Zealand, North Island), *Zephlebia* (*Neozephlebia*) sp. (New Zealand, Maturi Bay of Islands).

TABLE 1

Position of metathoracic ganglion and relative length of connectives of thoracic ganglia, (A)

Aa	Metathoracic ganglion in metathorax; connectives between thoracic ganglia equal in length (Figs. 2, 3, 4)	*Adenophlebia, Aprionyx, Hermanella, Jappa, Leptophlebia, Paraleptophlebia, Ulmerophlebia*
Ab	Metathoracic ganglion near anterior margin of metathorax; meta-mesothoracic connectives slightly shorter than meso-prothoracic connectives	
	Ab_1 Metathoracic ganglion at anterior margin of metathorax (Figs. 5, 9, 10, 13)	*Adenophlebiodes, Atalomicria, Atalophlebia, Castanophlebia,* new genus A of Peters, *Habroleptoides, Habrophlebiodes, Habrophlebia, Kirrara, Lepeorus, Massartella,* new genus B of Peters
	Ab_2 Metathoracic ganglion between mesothorax and metathorax (Figs. 11, 12)	*Atalonella, Borinquena, Choroterpes, Ch.* (*Neochoroterpes*), *Choroterpides,* new genus A of Pescador, *Hapsiphlebia, Massartellopsis, Meridialaris, Miroculis, Penaphlebia, Polythelais, Thraulus, Thraulodes, Zephlebia* (*Neozephlebia*)
Ac	Metathoracic ganglion in mesothorax, no ganglion in metathorax; meta-mesothoracic connectives much shorter than pro-mesothoracic connectives (Figs. 6, 7, 8, 14, 15, 16)	*Askola, Atalophlebioides, Choroterpes* (*Euthraulus*), *Deleatidium,* new genus F of Pescador, *Farrodes, Hagenulodes, Hagenulus, Hagenulopsis, Homothraulus, Indialis, Isca, Isca* (*Minyphlebia*), *Kimminsula, Megaglena, Petersophlebia, Terpides, Traverella, Ulmeritus, Zephlebia* (cf. *cruentata*), *Zephlebia* (cf. *borealis*)

TABLE 2

Position of anterior abdominal ganglia (ganglia 2 to 5), (B)

Ba + Bb	Abdominal ganglia 2–5 in abdominal segments II–V	
Ba	Connectives from metathoracic to abdominal ganglion 2 expanded, forming "ganglion" in some specimens (Fig. 2)	*Aprionyx, Jappa, Ulmerophlebia*
Bb	Connectives from metathoracic ganglion to abdominal ganglion 2 not expanded (Figs. 3, 4, 5, 12, 13)	*Adenophlebia, Adenophlebioides, Atalomicria, Atalophlebia,* new genera A and F of Pescador, *Habroleptoides, Habrophlebia, Habrophlebiodes, Hapsiphlebia, Hermanella, Kirrara, Lepeorus, Leptophlebia, Massartella, Massartellopsis, Meridialaris, Miroculis, Zephlebia* (*Neozephlebia*), *Paraleptophlebia, Penaphlebia*
Bc	Abdominal ganglion 2 shifted anteriorly; abdominal ganglia 3–5 in abdominal segments II–V.	
Bc_1	Ganglion 2 between segments I and II; ganglia 3 and 4 shifted to anterior margins of respective segments (III–IV) (Figs. 6, 7, 8, 9, 11)	*Askola, Atalonella, Atalophlebioides, Castanophlebia,* new genus A of Peters, *Choroterpes* (*Choroterpes, Euthraulus, Neochoroterpes*), *Choroterpides, Deleatidium, Hagenulodes, Indialis, Isca* (*Isca, Minyphlebia*), *Megaglena, Petersophlebia, Polythelais, Terpides, Thraulodes, Thraulus, Zephlebia* cf. *borealis,* cf. *cruentata*)
Bc_2	Ganglion II in segment I (recognized by inervation of segments I and II); ganglion 3 in segment II; ganglion 4 – at anterior margin of IV, no ganglion III (Figs. 10, 16) – (ganglia sometimes strongly reduced as in Fig. 14), or – in III, ganglion 5 near anterior margin of V, no ganglion in IV (Fig. 15)	*Hagenulopsis, Homothraulus,* new genus B of Peters, *Traverella Kimminsula* *Borinquena, Farrodes, Hagenulus, Ulmeritus*

Species dissected and a list of material studied are deposited in the collections of Florida A&M University, Tallahassee and the Institute of Entomology, Praha. All specimens were preserved in 75% to 95% alcohol after fixation in Carnoy or Bouin. Permanent mounts were prepared by transferring important parts of the internal organs directly to Canada balsam with Cellosolve. Microphotographs were taken with an automatic camera attached to an interference phase contrast microscope.

RESULTS

Ventral nerve cord

Ventral nerve cord consisting of 3 thoracic ganglia and 6—7 abdominal ganglia. Prothoracic ganglion connected with suboesophageal ganglion in head by a pair of connectives. Thoracic ganglia usually equal in size, metathoracic ganglion sometimes slightly different in shape and size from other thoracic ganglia (Figs. 8, 11, 15; Plate I, Figs. 4, 5).* Abdominal ganglia similar to thoracic ganglia, equal in length and shape (Figs. 2—4) or thoracic ganglia larger (Figs. 9, 13, 14). Connectives of thoracic ganglia always doubled, well separated; connectives from metathoracic ganglion to abdominal ganglion 2 usually separated, sometimes partially fused (Fig. 5) or expanded midway between ganglia as in Fig. 2 (assumed to represent remnants of ganglion 1 but abdominal segment I is at least partially inervated from metathoracic ganglion); connectives of abdominal ganglia (especially the posterior 3—4) sometimes fused (Figs. 13, 14). First abdominal ganglion absent, fused with metathoracic ganglion (recognized by innervation of abdominal segments I and II); abdominal ganglia 8, 9 and 10 recognizable only by emerging nerves; metathoracic and last abdominal ganglia representing true ganglionic centres. A pair of strong caudal nerves innervating last abdominal segment (IX, X) and cerci emerging from last ganglion. Ganglia 7 and 8 (more precisely 8, 9, and 10) fused in various degrees. Ventral nerve cord usually hyaline whitish (translucent in fresh material, Pl. I, Fig. 3); in some genera either thoracic and last abdominal ganglia or all ganglia (not connectives) with a dark brown stippling (*Adenophlebia* — Pl. I, Fig. 1; *Farrodes* — Pl. I, Fig. 2, and others).

Although the fusion of the last abdominal ganglia occurs to varying degrees and could be used in comparative study, necessary detailed histological preparations were not available. Important characters used to describe the comparative anatomy of the ventral nerve cord are given in Tables 1—4: position of metathoracic ganglion (A); position of first 4 or 5 abdominal ganglia (B); position and degree of association of last ganglionic centre (C); and arrangement of connectives, especially in the last abdominal segments (V—VIII) (D).

Alimentary canal

Alimentary canal consisting of stomodaeum, mesenteron and proctodaeum (Fig. 17). Stomodaeum a simple tube extending posteriorly; pharynx and oesophagus indistinguishable (Figs. 18—22, 23, 25, 28) or slightly differentiated in some genera (Figs. 24, 26, 27). Mesenteron and oesophagus with (Figs. 21, 22, 24, 26, 27) or without (Figs. 18—20, 23, 25, 28) apparent macroscopic differentiation (Table 5). Mesenteron a cylindrical or spindle

* Plates I—II will be found at the end of this issue.

TABLE 3

Arrangement of posterior abdominal ganglionic centres (abdominal ganglia 7 and 8), (C)

Ca	Abdominal ganglia 7 and 8 in abdominal segments VII and VIII or shifted to intersegmental area between segments VII and VIII	
	Ganglion 8 in segment VIII	
	Ganglion 7 in VII, ganglia entirely separated (Fig. 2); or	*Jappa*
	Ganglion 7 partially in VIII, ganglia partially fused to entirely fused (Fig. 11)	*Ulmerophlebia* *Choroterpes* (*Choroterpes*, *Euthraulus*, *Neochoroterpes*), *Choroterpides*, *Terpides*
	Ganglia 7 and 8 between segments VII and VIII, ganglia partially to entirely fused (Figs. 3, 5)	*Atalomicria*, *Atalonella*, *Atalophlebia*, new genera A and F of Pescador, *Habroleptoides*, *Habrophlebia*, *Habrophlebiodes*, *Leptophlebia*, *Massartella*, *Massartellopsis*, *Meridialaris*, *Zephlebia* (*Neozephlebia*), *Paraleptophlebia*, *Penaphlebia*
Cb	Abdominal ganglia 7 and 8 in abdominal segment VII or partially shifted to abdominal segment VI; ganglia partially to entirely fused.	
	Cb_1 Ganglia 7 and 8 in abdominal segment VII, usually in the middle of sternum VII (Figs. 4, 7, 8, 15, 16) but	*Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Askola*, *Atalophlebioides*, *Borinquena*, *Castanophlebia*, *Deleatidium*, *Farrodes*, *Hagenulodes*, *Hagenulopsis*, *Hapsiphlebia*, *Homotraulus*, *Indialis*, *Isca* (*Isca*, *Minyphlebia*), *Petersophlebia*, *Polythelais*, *Thraulodes*, *Traverella*, *Ulmeritus*, *Z.* (cf. *cruentata*), new genus A of Peters
	sometimes at anterior margin of sternum VII (Fig. 5)	*Hagenulus*, *Hermanella*, *Megaglena*, *Thraulus*, *Zephlebia* (cf. *borealis*, cf. *cruentata*)
	Cb_2 Ganglia 7 and 8 partially in abdominal segment VI (Figs. 9, 10, 13, 14) to	new A of genus Peters, *Kimminsula*, *Kirrara*, *Lepeorus*, new genus B of Peters
	almost entirely in VI (Fig. 12)	*Miroculis*

TABLE 4

Arrangement of connectives of abdominal ganglia, (D)

Da	Connectives of abdominal ganglia (except 7 and 8) doubled and well separated (Figs. 2, 3, 4, 6, 7, 8, 11, 15, 16) to	all other genera studied
	contiguous (but never fused) (Fig. 9) or	new genus A of Peters, *Hagenulus*, *Thraulus*, *Ulmeritus*
	contiguous and shortened between ganglia 6, 7, and 8 (Fig. 12)	*Miroculis*
Db	Connectives of abdominal ganglia partially fused into a shallow band:	
	Connectives of ganglia 2—7 partially fused posteriorly (Fig. 5); or	*Massartella*
	connectives of ganglia 2—5 separated or partially fused, connectives 6—8 shortened and partially fused (Fig. 10); or	*Kirrara*, *Lepeorus*, new genus B of Peters
	connectives of ganglia 2—3 separated, 4—5 partially fused, 5—8 entirely fused (Fig. 14)	*Kimminsula*

shaped tube, broad in thorax (usually twice as wide as oesophagus), tapered in anterior abdominal segments, broader in posterior segment (but shape depends on amount of food), always tapered in abdominal segments VII—VIII and constricted at malpighian tubules (Figs. 18—28); mesenteron with dark stippling in some genera (*Massartella*, *Habrophlebioides*), without enterogastric caeca. Proctodaeum differentiated into colon and rectum. Colon variable: cylindrical (Figs. 18, 19), subcylindrical, spherical (Fig. 28), pear-shaped, spindle-shaped, constricted caudally (Figs. 26, 28), narrow and elongated (Figs. 22, 26), wide and rounded (Fig. 27), etc; very long (nearly as long as rectum — Fig. 20) to very short; sometimes telescopically connected with rectum (Figs. 23, 28). Rectum broad in abdominal segment VIII and constricted in segment IX; anterior portion rounded to egg-shaped to triangular, with (Figs. 22, 24, 26, 27) or without (Figs. 18—21) a pair of rectal projections; rectal projection hollow at base and extended into lumen of rectum and membraneous tissues extended distally (probably attaching rectum to wall of abdomen); rectal projections simple and elongated, short with broad base (Fig. 22), triangular or branched (Figs. 24, 27; Pl. II, Figs. 7, 8).

Characters used to describe the comparative anatomy of the alimentary canal are given in Tables 5—7: degree of apparent macroscopic differentiation of stomodaeum (E); position of colon and pyloric valve (F); and arrangement of anterior portion of rectum (G).

Malpighian tubules

Malpighian tubules attached to mesenteron or partly to anterior portion of colon, position depending on position of colon; tubules usually in abdominal segments VII—VIII but may extend to segments II—III (*Cho-*

TABLE 5

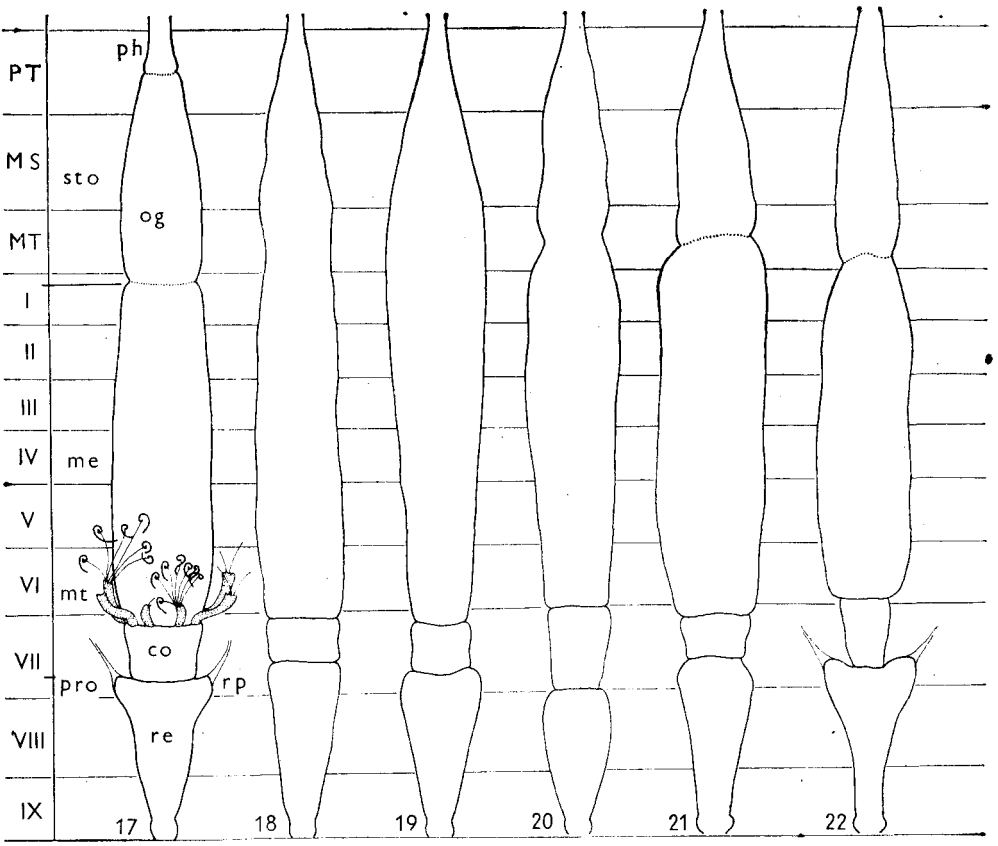
Degree of apparent macroscopic differentiation of stomodaeum, (E)

Ea	Stomodaeum not differentiated from mesenteron; mesenteron and posterior part of oesophagus about equal in width; cardiac valve absent or very weakly indicated (Figs. 18, 19, 23, 25, 28)	*Adenophlebia, Adenophlebiodes, Aprionyx, Atalomicria, Atalophlebia, Castanophlebia,* new genus A of Pescador, *Hapsiphlebia, Hermanella, Indialis, Isca, Jappa, Leptophlebia, Miroculis, Paraleptophlebia, Penaphlebia, Thraulus, Ulmeritus*
Eb	Stomodaeum differentiated from mesenteron.	
	Eb_1 Mesenteron usually broader than posterior part of oesophagus; cardiac valve represented by constriction in thorax (Fig. 20)	*Atalonella, Choroterpes, Choroterpes (Euthraulus), Choroterpes (Neochoroterpes),* new genus F of Pescador, *Habroleptoides, Habrophlebia, Habrophlebiodes, Hagenulodes, Homothraulus, Isca (Minyphlebia), Megaglena, Ulmerophlebia, Zephlebia (Neozephlebia)*
	Eb_2 Mesenteron very broad; constriction of cardiac valve very conspicuous (Fig. 21, 22, 27), and	*Askola, Atalophlebioides, Borinquena,* new genus A of Peters, *Choroterpides, Deleatidium, Farrodes, Hagenulus, Hagenulopsis, Kimminsula, Lepeorus, Massartella, Massartellopsis, Meridialaris, Petersophlebia, Terpides, Thraulodes, Traverella,* new genus B of Peters, *Zephlebia* (cf. *cruentata*), *Zephlebia* (cf. *borealis*), *Polythelais*
	pharynx occasionally differentiated from oesophagus in head or prothorax (Figs. 24, 26)	*Atalophlebioides, Kirrara*

TABLE 6

Position of colon and pyloric valve, (F)

Fa	Colon in abdominal segments VII, VI–VII, or VI. Pyloric valve at anterior margin of segment VII, colon in middle or anterior part of segment VII (Figs. 18–21, 24, 26, 27); or	*Adenophlebia, Adenophlebiodes, Aprionyx, Askola, Atalomicria, Atalophlebia, Atalophlebioides, Borinquena, Castanophlebia,* new genus A of Pescador, *Deleatidium,* new genus F of Pescador, *Farrodes, Habroleptoides, Habrophlebia, Hagenulodes, Hagenulus, Hagenulopsis, Hapsiphlebia, Homothraulus, Jappa, Kirrara, Lepeorus, Leptophlebia, Megaglena, Massartella, Meridialaris, Paraleptophlebia, Polythelais, Penaphlebia, Petersophlebia, Thraulus, Thraulodes,* new genus B of Peters, *Ulmerophlebia, Zephlebia* (*Neozephlebia*), *Zephlebia* (cf. *cruentata*), *Zephlebia* (cf. *borealis*), *Massartellopsis, Ulmeritus*
	pyloric valve in VI, colon between VII and VI (Figs. 22), to colon entirely in VI (Fig. 25, 25)	*Atalonella,* new genus A of Peters, *Kimminsula, Miroculis*
Fb	Color shifted caudally, pyloric valve in segment VII or VII. Colon partially in VIII (Figs. 23, 27), to	*Choroterpes, Choroterpes* (*Euthraulus*), *Choroterpes* (*Neochoroterpes*), *Choroterpides, Habrophlebiodes, Indialis, Isca, Isca* (*Minyphlebia*), *Terpides, Traverella,*
	colon entirely in VIII (Fig. 28)	*Hermanella*



Figs. 17—22. Comparative anatomy of alimentary canal of Leptophlebiidae (sketch). 17 — scheme of apomorphic situation showing all existing structures. 18 — *Castanophlebia*. 19 — *Paraleptophlebia*. 20 — *Ulmerophlebia*. 21 — *Massartella*. 22 — *Kimminsula*. PT, MS, MT — pro-meso-, and metathorax; I—IX — abdominal segments; ph — pharynx; sto — stomodaeum; og — oesophagus; me — mesenteron; mt — malpighian tubules; co — colon; pro — proctodaeum; re — rectum; rp — rectal projections.

roterpides). Number of tubules ranging from 40—70 in *Isca* (body length 4 mm) to 200—300 in *Massartella* (body length 30 mm), averaging about 100 tubules, number apparently correlated with size of specimen. Malpighian tubules consisting of proximal tubular portion and coiled or curved distal portion. Proximal portion uniform in structure varying only in length; distal portion variable (Pl. II, Figs. 9—15). Distal portion basally can be uncoiled and curved into broad base (*Aprionyx*), coiled and broad, or discoid; apically, distal portion straight, slightly bent or narrow, slightly bent with s-curve, coiled apically, coiled into a spiral and sometimes slightly or strongly expanded at apex (Pl. II, Fig. 13). Tubules entering unbranched buds (Figs. 30, 31) or paired common trunks (Figs. 32—40, Table 8) on alimentary canal. Common trunks simple and unbranched (Pl. II, Fig. 12), apically expanded forming cup-like structure (Pl. II, Fig. 10), or dichotomously branched (*Ulmeritus*); trunks can also be branched irregularly, but branching is not

TABLE 7

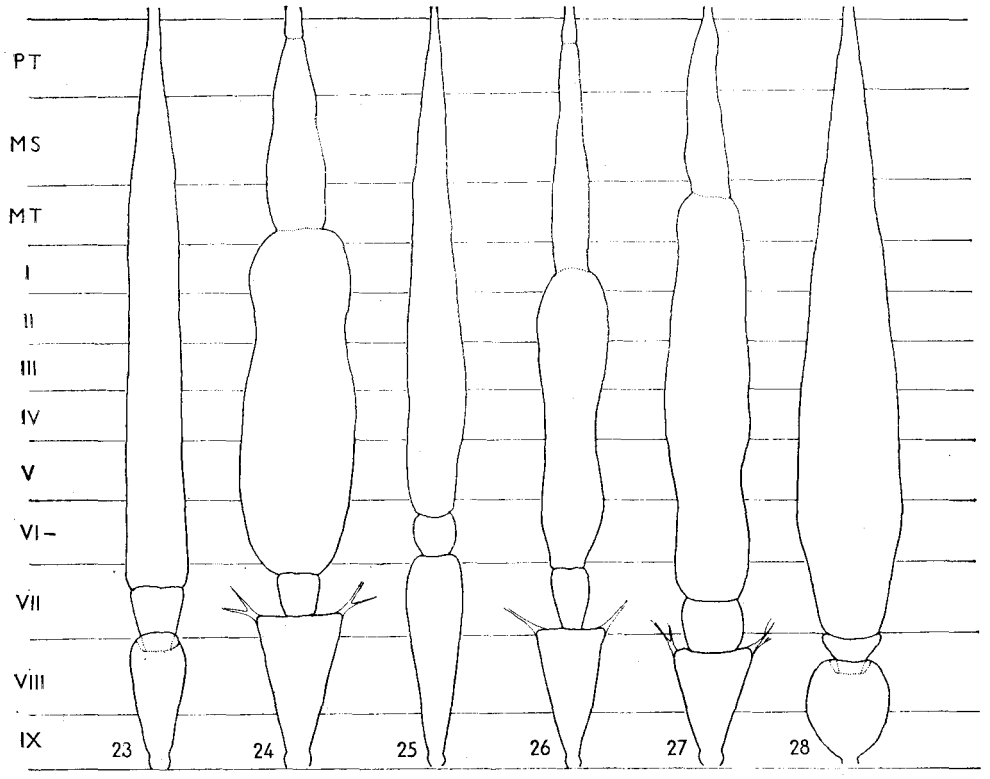
Arrangement of anterior portion of rectum, (G)

ga	Anterior portion of rectum smooth and rounded without any projections (Fig. 18, 19, 20, 21, 23, 25)	*Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Askola*, *Atalomicria*, *Atalonella*, *Atalophlebia*, *Boringuena*, *Castanophlebia*, new genus A of Pescador, new genus F of Pescador, *Farrodes*, *Habroleptoides*, *Habrophlebia*, *Habrophlebiodes*, *Hagenulodes*, *Hagenulus*, *Hagenulopsis*, *Hermanella*, *Hapsiphlebia*, *Homotraulus*, *Indialis*, *Isca*, *Isca* (*Minyphlebia*) *Jappa*, *Leptophlebia*, *Massartella*, *Massartellopsis*, *Megaglena*, *Meridialaris*, *Miroculis*, *Paraleptophlebia*, *Penaphlebia*, *Thraulus*, *Thraulodes*, new genus B of Peters, *Ulmerophlebia*
Gb	Anterior portion of rectum with pair of anterolateral rectal projections (Fig. 22, 24, 26, 27)	*Atalophlebioides*, new genus A of Peters, *Choroterpes*, *Choroterpes* (*Euthraulus*), *Choroterpes* (*Neochoroterpes*), *Choroterpides*, *Deleatidium*, *Kimminsula*, *Kirrara*, *Lepeorus*, *Petersophlebia*, *Polythelais*, *Terpides*, *Traverella*, *Ulmeritus*, *Zephlebia* (*Neozephlebia*), *Zephlebia* (cf. *cruentata*), *Zephlebia* (cf. *borealis*)

TABLE 8

Number and degree of specialization of common trunks of malpighian tubules, (H)

Ha	No common trunks. Tubules enter 8 low flat buds on digestive tube.	
	Buds small, egg-shaped (Fig. 30)	*Leptophlebia, Paraleptophlebia,*
	or elongated, cylindrical (Fig. 31)	*Penaphlebia chilensis*
Hb	Eight trunks (1 lateral, 2 dorsal, and 1 ventral pair). Trunks branched or expanded, straight and cylindrical or bent.	
	Hb_1 All trunks equal in length and shape (Fig. 32)	*Adenophlebia, Adenophlebiodes, Aprionyx, Atalomicria, Atalophlebia, Atalophlebioides, Castanophlebia,* new genus A of Pescador, *Deleatidium, Hapsiphlebia, Jappa, Kimminsula, Lepeorus, Penaphlebia vinosa, Habrophlebia, Polythelais, Thraulodes, Ulmerophlebia, Zephlebia* (*Neozephlebia,* cf. *borealis,* cf. *cruentata*)
	Hb_2 Lateral pair of trunk longer than other pairs (Fig. 35)	new genus A of Peters, new genus F of Pescador, *Kirrara, Messartellopsis, Meridialaris, Petersophlebia*
Hc	More than 8 trunks (5 or 6 pairs).	
	Twelve trunks, trunks slightly branched at apex (Fig. 33),	*Ulmeritus*
	lateral pairs may be twice as long as other pairs; or	*Atalonella*
	ten trunks with 3 lateral pairs branched at mid length and dorsal and ventral pairs branched or separated at base (Fig. 34)	*Massartella*
Hd	Six trunks (3 pairs). Trunks unbranched or branched near apex.	
	Hd_1 All trunks equal in length (Fig. 37)	*Askola, Borinquena, Farrodes, Hagenulodes, Indialis, Isca* (*Isca, Minyphlebia*), *Megaglena, Miroculis, Thraulus, Choroterpes* (*Choroterpes*)
	Hd_2 Trunks unequal: lateral pair long, cup-like, extended anteriorly; ventral and dorsal pairs cylindrical, bent, usually directed posteriorly. Length of lateral trunks in relation to others may be	
	slightly longer	*Choroterpes* (*Euthraulus, Neochoreterpes*)
	slightly longer with dorsal trunks branched at apex (Fig. 36)	*Hermanella*
	$1^1/_2$ times longer, or 2—3 times longer and robust (Fig. 38)	*Homothraulus, Traverella,* new genus B of Peters, *Choroterpides, Terpides*
He	Four trunks (lateral and dorsal pairs). Trunks unbranched, directed anteriorly	
	Lateral pair strong and twice length of dorsal pair (Fig. 39)	*Hagenulopsis*
Hf	Two trunks (lateral pair). Trunks slightly bent, directed anteriorly.	
	Both trunks strong (Fig. 40)	*Hagenulus*



Figs. 23—28. Comparative anatomy of alimentary canal of Leptophlebiidae (sketch). 23 — *Indialis*. 24 — *Kirrara*. 25 — *Miroculis*. 26 — *Atalophlebioides* (Australia). 27 — *Choroterpides*. 28 — *Hermanella*. Abbreviations as in Figs. 17—22.

a constant character within species or populations and unbranched trunks occur in some individuals. Lateral pairs of trunks usually directed anteriorly, ventral and dorsal pairs posteriorly, but direction variable within genus; specialized lateral trunks (Hb_2, Hd_2) and all trunks if only 2—4 present (He, Hf) always directed anteriorly.

Additional study of the distal portion of the malpighian tubules (using specialized techniques) or branching of common trunks may yield other characters for comparative study. At present, however, we use only one character: the number of common trunks and their degree of specialization (H) (Table 8).

Gonads

Testes usually cylindrical parallel and lateral to mesenteron; testes consisting of numerous follicles directly connected dorsally and laterally to ducts. Vas deferens simple, tubiform, extended from apex of testes to abdominal segment IX forming seminal vesicle in segments VII—IX. Seminal vesicle: inconspicuous, formed from slightly expanded ducts in segments VII (VIII) to IX (*Leptophlebia*, *Atalophlebia*, *Adenophlebia*, *Penaphlebia*); or con-

TABLE 9

Position of gonads, (I)

Ia	Ovaries (Figs. 48, 49) extend from metathorax or abdominal segment I to segment VI; testes in abdominal segments only.	
	Ia_1 Testes in abdominal segments I—VI (Figs. 42, 43)	*Atalomicria, Atalophlebia, Jappa, Miroculis, Penaphlebia, Petersophlebia, Polythelais, Ulmerophlebia*
	Ia_2 Testes in segments III—VI, or in segments II—VII (Fig. 44)	*Kimminsula* *Meridialaris, Massartellopsis, Thraulus*
Ib	Ovaries extend from mesothorax to abdominal segment VI; testes from metathorax to segment VI (Figs. 45, 50)	*Adenophlebia, Atalonella, Atalophlebioides*, new genus A of Peters, new genus A of Pescador, new genus F of Pescador, *Habroleptoides, Habrophlebia, Habrophlebiodes, Kirrara, Lepeorus, Leptophlebia, Paraleptophlebia*, new genus B of Peters, *Zephlebia* (*Neozephlebia*)
Is	Ovaries extend from prothorax to abdominal segment VI; testes from pro- or mesothorax to segments VI—VII (Figs. 46, 51, 52)	*Choroterpes, Choroterpes* (*Euthraulus*), *Choroterpes* (*Neochoroterpes*), *Choroterpides, Deleatidium, Hagenulus, Hagenulopsis, Hermanella, Terpides, Traverella*

TABLE 10

Arrangement of testicular follicles and ovarioles, (J)

Ja	Follicles strong, at right angle to seminal duct. Ja_1 Follicles almost round, with slight size differences; ovarioles straight, at right angle to oviduct (Figs. 42, 48) Ja_2 Follicles round, equal in size; ovarioles slightly bent, at oblique angle to oviduct Figs. 43, 49)	*Atalomicria, Atalophlebia, Jappa, Kimminsula* new genus A of Pescador, new genus F of Pescador, *Massartellopsis Meridialaris Penaphlebia, Petersophlebia, Polythelais, Ulmerophlebia*
Jb	Follicles small and numerous, cylindrical with length 2—3 times width, equal in size, at right angle to seminal duct; ovarioles bent, at oblique angle to oviduct (Figs. 44, 45, 50. 51)	*Adenophlebia, Atalonella, Atalophlebioides*, new genus A of Peters, *Deleatidium, Habroleptoides, Habrophlebia, Habrophlebiodes, Hermanella, Kirrara, Lepeorus, Leptophlebia, Miroculis, Paraleptophlebia, Thraulus*, new genus B of Peters, *Zephlebia* (*Neozephlebia*)
Jc	Follicles very numerous, cylindrical with length 2—4 times width, equal in size, at oblique angle to seminal duct; ovarioles curved anteriorly, strongly oblique. (Figs. 46, 52)	*Choroterpes, Choroterpes* (*Euthraulus*), *Choroterpes*(*Neochoroterpes*), *Choroterpides, Hagenulus, Hagenulopsis, Terpides, Traverella*

spicuous, rounded, occurring only in segment IX (*Hagenulus*, *Thraulus*) (this latter condition evidently derived from simple ducts).

Ovaries similar in structure to testes. Ovarioles consisting of germarium and vitellarium with developing eggs, approximately 3—7 oocytes in each ovariole (Pl. I, Fig. 6). Oviducts simple, directly connected with all ovarioles (no pedicel developed), extended from apex of ovaries to posterior part of segment VII (Fig. 47), sometimes bent in segment VII (occasionally, oviducts fused posteriorly into a short common oviduct).

Important characters for comparative study of gonads are given in Tables 9—11: position of gonads in body (I); arrangement of testicular follicles and ovarioles (J); and shape of testis and ovary (K). The shape and position of the seminal vesicles was not investigated because of the poor state of preservation of this structure in male larvae of most genera studied.

Tracheal system

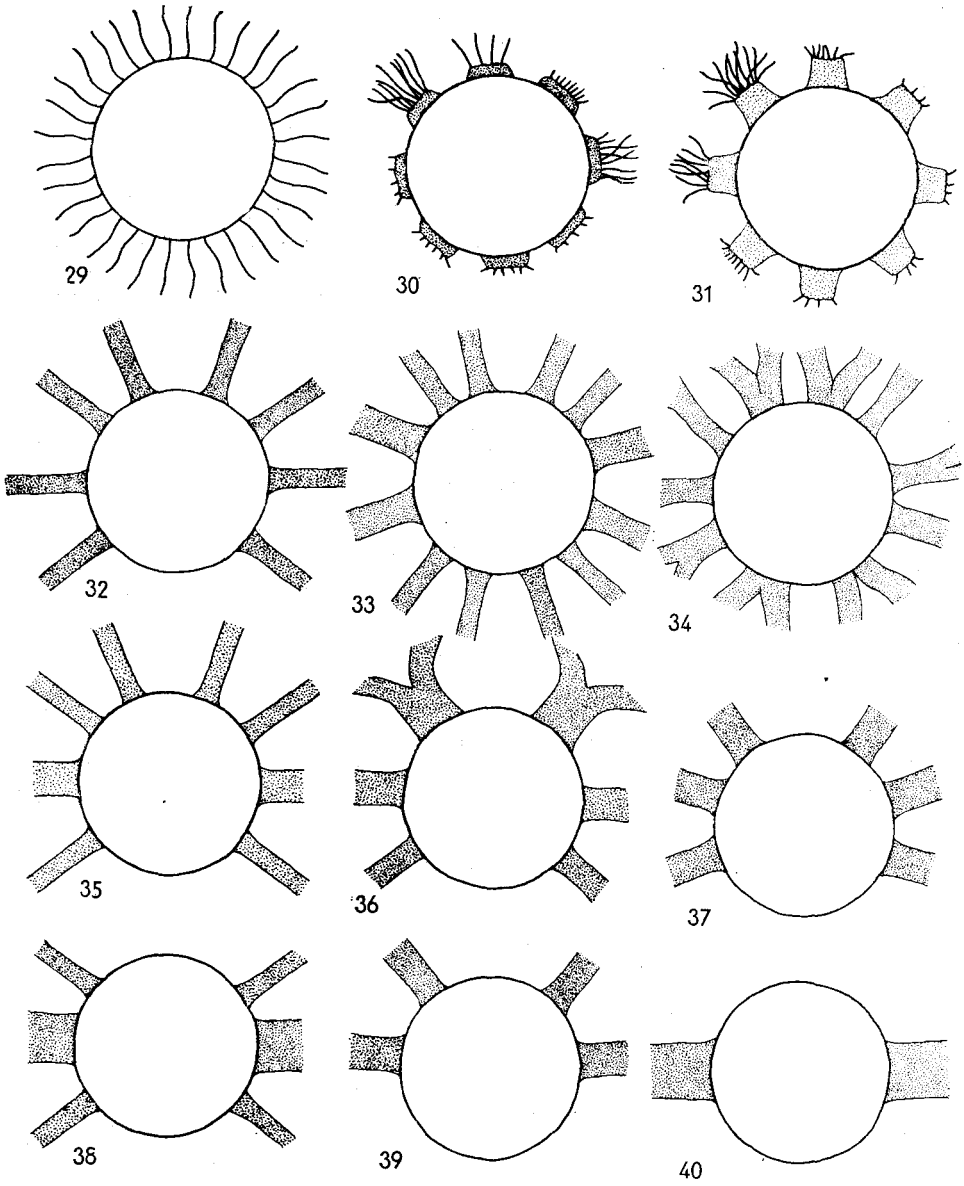
While the tracheation of the mayfly head is very complicated, being dependant on the arrangement of mouthparts (see LANDA, 1948 for details), that of the thorax and abdomen is relatively simple and provides useful data for comparative study.

Tracheal system in thorax and abdomen consisting of a pair of lateral trunks parallel with alimentary canal. Lateral trunks directly connected with gills by 7 pairs of tracheae in abdominal segments I—VII and with pedal tracheae in thorax (Pl. III, IV, Figs. 53—62). Lateral trunks connected by ventral tracheal anastomoses (TAV) in abdominal segments. Anastomoses usually developed in segments III—IX (TAV 5, TAV 6, TAV 7, TAV 8, TAV 9, TAV 10, VIII and TAV 10, IX in LANDA's (1969) classification), rarely also in segments I—II (Pl. III, Fig. 55). Anastomosis in segment IX (TAV 10, IX) absent in some genera (Pl. IV, Fig. 59), Visceral tracheal system consisting usually of 5—6 pairs of visceral tracheae (TV) in abdomen (TV 5 to TV 10 in LANDA's (1969) classification T). TV 4 (in abdominal segment II present only exceptionally (Pl. IV, Fig. 62). TV 2 (in metathorax) very strong, sometimes connected with pedal trachea (*Choroterpes*, *Euthraulus*). First abdominal visceral trachea also strong, usually consisting of two branches (Pl. III, IV, Figs. 54, 61). Last abdominal visceral trachea (TV 10) in segment VIII (Pl. III, IV, Figs. 54, 59, 61, 62), or between segments VIII and IX (*Choroterpes*) or entirely shifted to segment IX (*Leptophlebia*, some species).

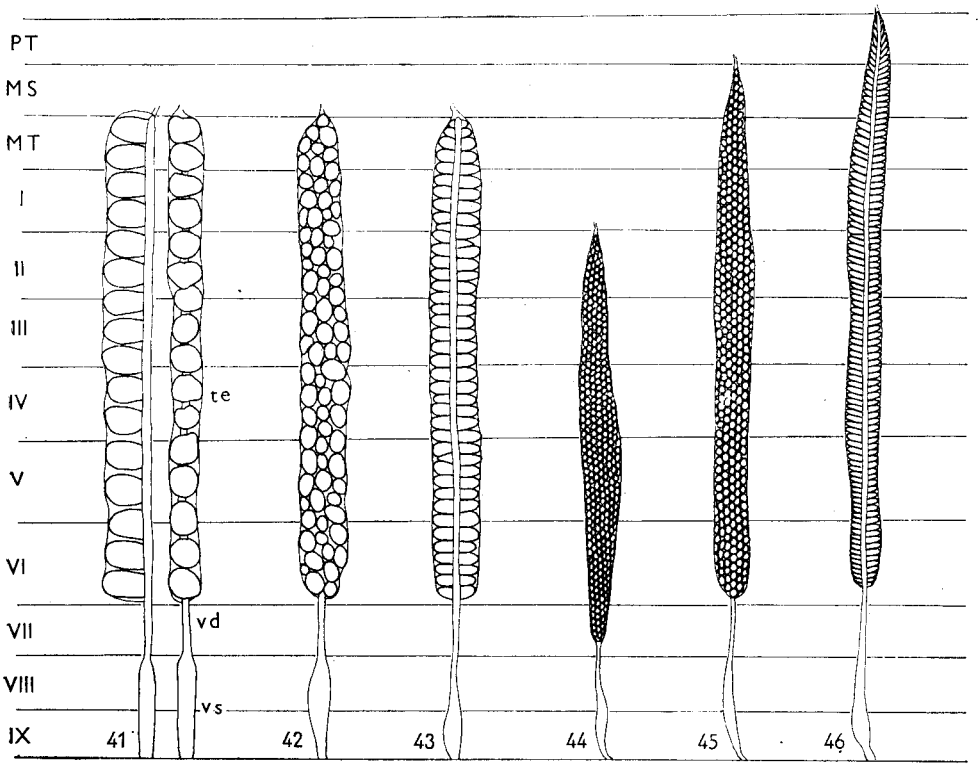
Important characters used to describe the comparative anatomy of the tracheal system are given in Tables 12—14: arrangement of visceral tracheae (L); arrangement of ventral tracheal anastomoses in abdominal segments III—VII (M); and arrangement of ventral tracheal anastomoses in abdominal segments VIII and IX. (N).

DISCUSSION AND CONCLUSIONS

In the following paragraphs an attempt to determine major anagenetic trends in the arrangement of internal organs in ephemeropterous larvae has been made. Although the data obtained could be used in comments on evolution and taxonomy of Leptophlebiidae we appreciate that an evolutionary line cannot be constructed solely according to a few characters, however



Figs. 29—40. Comparative anatomy of malpighian tubules of Leptophlebiidae (sketch of buds or common trunks attached to alimentary canal). 29 — scheme of hypothetical ancestral condition (tubules entering alimentary canal individually). 30 — 8 lower buds (*Paraleptophlebia*). 31 — 8 produced buds (*Penaphlebia chilensis*). 32 — 4 pairs of unspecialized trunks (*Jappa*). 33 — 6 pairs of trunks (*Ulmeritus*). 34 — 5 pairs of trunks (*Massartella*). 35 — 4 pairs of trunks, lateral specialized (*Meridialaris*). 36 — 3 pairs of trunks, dorsal branched (*Hermanella*). 37 — 3 pairs of trunks (*Miroculis*). 38 — 3 pairs of trunks, lateral specialized (*Choroterpides*). 39 — 2 pairs of trunks (*Hagenulopsis*). 40 — 1 pair of trunks (*Hagenulus*). Buds and common trunks dotted.



Figs. 41—46. Comparative anatomy of gonads of Leptophlebiidae (sketch). 41 — testis, scheme of hypothetical ancestral condition. 42 — *Atalophlebia*, testis, dorsal view. 43 — *Petersophlebia*, testis, ventral view. 44 — *Thraulus*, testis, dorsal view. 45 — new genus B of Peters, testis, ventral view. PT, MS, MT — pro-, meso-, and metathorax; I—IX — abdominal segments; te — testicular follicles; vd — vas deferens; vs — seminal vesicle.

comparative anatomy point of view. Preliminary results of the study of the endocrines, haemolymph and chromosomes promise useful new information. carefully studied. Moreover, some organ systems remain unknown from the

The ventral nerve cord of the Leptophlebiidae (and that of Ephemeroptera in general) could easily be derived from nerve cord of an insect ancestor that was subjected to association of original pairs of ganglia and fusion of last 4—5 ganglia (Fig. 1). In recent Ephemeroptera, except the Ametropodidae, the first ganglion is fused with the metathoracic one (synapomorphic character within Leptophlebiidae) and except in *Prosopistoma* and *Baetisca* the abdominal ganglia 2—5 remain separated (symplesiomorphic within Leptophlebiidae). Considering the hypothetical nerve cord (Fig. 1) as that of a preleptophlebiid ancestor, several anagenetic trends leading to further association of central nervous system can be recognized: (i) shifting of metathoracic ganglion to mesothorax; (ii) shifting of abdominal ganglia 2, 3, 4 and 5 to abdominal segments I, II, III and IV); (iii) further fusion and shifting of last ganglion (ganglionic center) to abdominal segments VII or VI; (iv) fusion of originally separated connectives to form a shallow band especially in abdominal segments V—VIII.

TABLE 11

Shape of testis and ovary, (K)

Ka	Testis rounded anteriorly; ovary rounded to bluntly pointed apically. Testis cylindrical; ovary cylindrical to slightly flattened bilaterally. (Figs. 42, 48, 49)	*Adenophlebia, Atalomicria, Atalophlebia, Jappa, Penaphlebia, Ulmerophlebia*
Kb	Testis and ovary bluntly to acutely pointed apically.	
	Kb_1 Testis and ovary bluntly pointed to pointed apically; testis cylindrical to slightly flattened bilaterally; ovary flattened. (Figs. 43, 50, 51)	*Atalonella, Atalophlebioides*, new genus A of Pescador, *Deleatidium* new genus F of Pescador, *Habroleptoides, Habrophlebia, Habrophlebiodes, Hermanella, Kimminsula, Kirrara, Lepeorus, Leptophlebia, Massartellopsis, Meridialaris, Miroculis, Paraleptophlebia, Polythelais, Zephlebia* (*Neozephlebia*)
	Kb_2 Testis and ovary pointed to acutely pointed apically; testis spindle-shaped; ovary tongue-shaped. (Figs. 44, 45, 46, 52)	new genus A of Peters, *Choroterpes, Choroterpes* (*Neochoroterpes*), *Choroterpes* (*Euthraulus*), *Choroterpides, Hagenulus, Hagenulopsis, Terpides, Thraulus, Traverella*, new genus B of Peters

TABLE 12

Arrangement of visceral tracheae, (L)

La	TV 5 (visceral trachea in 2nd abdominal segment) present (Pl. III, IV, Figs. 54, 62)	*Adenophlebia, Adenophlebiodes, Atalomicria, Atalophlebia, Atalophlebioides, Castanophlebia, Deleatidium*, new genus F of Pescador, *Habroleptoides, Habrophlebia, Habrophlebiodes, Hagenulus, Hagenulopsis, Hapsiphlebia, Jappa, Kimminsula, Kirrara, Lepeorus, Leptophlebia, Massartella, Massartellopsis, Meridialaris, Paraleptophlebia, Penaphlebia, Petersophlebia, Polythelais, Traverella*
Lb	TV 5 (visceral trachea in 2nd abdominal segment) absent (Pl. IV, Figs. 59, 61)	*Choroterpes* (*Choroterpes, Euthraulus, Neochoropters*), *Choroterpides, Indialis, Isca, Minyphlebia*), *Megaglena, Thraulus*

TABLE 13

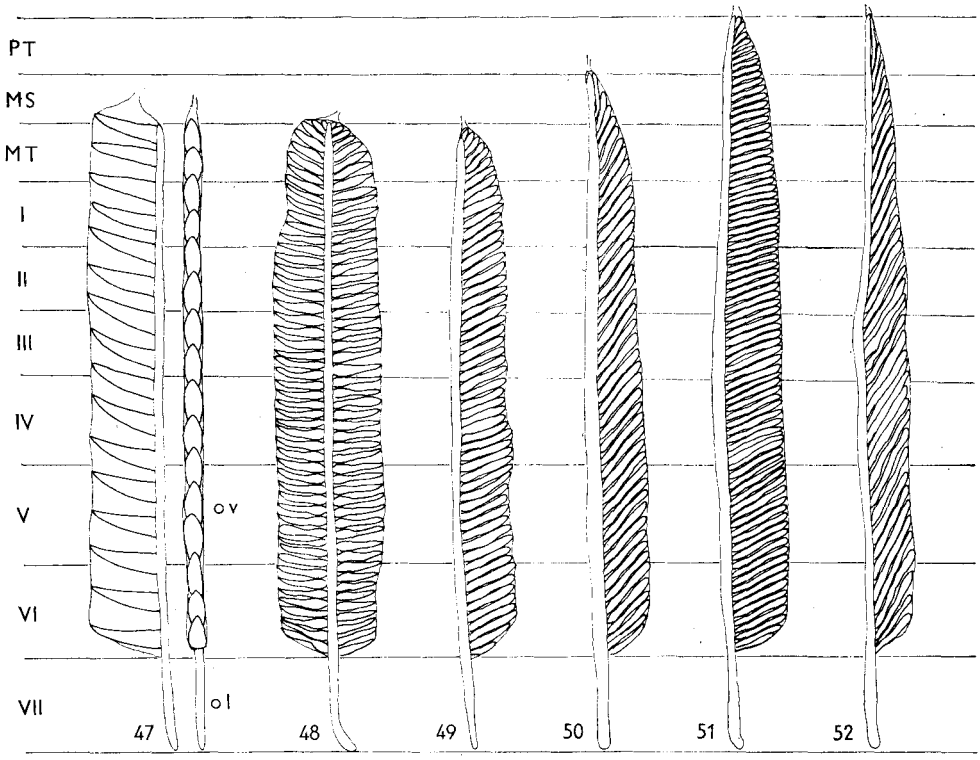
Arrangement of ventral tracheal anastomoses in segments III–VII, (M)

Ma	Anastomoses present in abdominal segments III–VII (TAV 5 present) (Pl. III, Figs. 53, 55, 57, 58)	*Adenophlebia, Adenophlebiodes, Atalomicria, Atalonella, Atalophlebia, Castanophlebia, Hapsiphlebia, Indialis, Jappa, Leptophlebia, Massartella, Penaphlebia*
Mb	Anastomoses present in abdominal segments IV–VII (TAV 5 absent) (Pl. III, IV, Figs. 56, 60)	*Atalophlebioides, Choroterpes* (*Choroterpes, Euthraulus, Neochoroterpes*), *Choroterpides, Deleatidium*, new genus F of Pescador, *Hagenulus, Hagenulopsis, Habroleptoides, Habrophlebia, Habrophlebiodes, Isca* (*Isca, Minyphlebia*), *Kimminsula, Kirrara, Lepeorus, Massartellopsis, Megaglena, Meridialaris, Paraleptophlebia, Petersophlebia, Polythelais, Thraulus, Traverella*

TABLE 14

Arrangement of ventral tracheal anastomoses in segments VIII and IX, (N)

Na	Anastomosis present only in segment VIII (TAV 10, IX absent) (Pl. III, Fig. 53)	*Habrophlebia, Habroleptoides, Habrophlebiodes*
Nb	Anastomoses present in segments VIII and IX (TAV 10, IX present) (Pl. III, IV, Figs. 55–58, 60)	*Adenophlebia, Adenophlebiodes, Atalomicria, Atalophlebioides, Castanophlebia, Choroterpes* (*Choroterpes, Euthraulus, Neochoroterpes*), *Choroterpides, Deleatidium*, new genus F of Pescador, *Hagenulus, Hagenulopsis, Hapsiphlebia, Ibdialis, Isca* (*Isca, Minyphlebia*), *Jappa, Kimminsula, Kirrara, Lepeorus, Massartella, Massartellopsis, Megaglena, Meridialaris, Penaphlebia, Petersophlebia,Polythelais, Thraulus, Traverella*



Figs. 47—52: Comparative anatomy of gonads of Leptophlebiidae (sketch). 47 — ovary, scheme of hypothetical ancestral condition. 48 — *Atalophlebia*, ovary, ventral view. 49 — *Ulmerophlebia*, ovary, lateral view. 50 — *Lepeorus*, ovary, lateral view. 51 — *Deleatidium*, ovary, lateral view. 52 — *Hagenulus*, ovary, lateral view. PT, MS, MT — pro-, meso-, and metathorax; I—VII — abdominal segments; ov — ovarioles; ol — lateral oviduct.

As is apparent from Tables 1—4 there are a large number of interstages between very primitive nerve cord of *Jappa* or *Paraleptophlebia* (Aa, Ba, Ca, Da; Aa, Ba, Cb1, Da) and derived nerve cord of e.g. *Farrodes*, *Hagenulus*, *Traverella* (Ac, Bc2, Cb, Da) or *Kimminsula* (Ac, Bc1, Cb2, Db). A relatively high number of characters investigated in nerve cord showed apparently mosaic-like distribution of characters in most genera, e.g. fusion of connectives in relatively primitive nerve cord of *Massartella* (Ab1, Bb, Ca, Db) or connectives fully separated in highly derived nerve cord of *Farrodes*, *Hagenulus*, and *Traverella*. In *Choroterpides*, despite relatively derived arrangement of abdominal ganglia (Ab2, Bc1), last ganglion remains in segment VIII.

Our knowledge of the alimentary canal of the ancestral mayfly is very fragmentary. Taking into account the only slightly differentiated alimentary canal of primitive mayflies, the Leptophlebiid genera with macroscopically manifestly differentiated stomodaeum are supposed to be more specialized than those with macroscopically hardly distinguishable cardiac valve. Except for a weak differentiation of the pharynx in some genera, the stomodaeum does not show further differentiation (synplesiomorphic character within the family) as in some carnivorous mayflies. Rectal projections of Leptophlebiidae

are probably not homologic with those of Caenidae and Prosopistomatidae. They are much smaller, always connected with connective tissues and probably not storing gut content as in the above families. The question of original position of colon remains open. Judging from the position of colon and rectum in primitive Ephemeroptera (Siphlonurinae) and from anagenetic trends of other organs, the colon was originally situated in segment VIII or VII.

The following anagenetic trends in the arrangement of alimentary canal of the Leptophlebiidae were recognized: (i) gradual differentiation of stomodaeum, extension of mesenteron and elongation of oesophagus; (ii) emergence of rectal projections and tendency to their branching; (iii) shortening of colon, shortening of rectum and their shifting. There are two main anagenetic lines within the genera investigated. Primitive arrangement of the alimentary canal is characterized by only slightly differentiated stomodaeum and absence of rectal projection (*Jappa*, *Adenophlebia*, *Atalophlebia*, *Paraleptophlebia* and others), derived arrangement by advanced macroscopic differentiation of stomodaeum and presence of rectal projections (*Atalophlebioides*, *Choroterpes*, *Choroterpides* and others).

As far as the malpighian tubules are concerned, their anagenesis can be well understood. Taking into consideration the arrangement of malpighian tubules in primitive Ephemeroptera, there is no doubt that plesiomorphic arrangement occurs by the large number of tubules attached individually to the alimentary canal (Fig. 29). In all genera investigated either buds or common trunks are present (synapomorphic character within the Leptophlebiidae). The following tendencies were recognized in anagenesis of malpighian tubules of the Leptophlebiidae: (i) tendency to elongating of buds to form the common trunks; (ii) tendency to specialization of some pairs (usually lateral) of common trunks; (iii) tendency to reduction of number of trunk pairs; (iv) tendency to branching of trunks or to their multiplying. Although the shape of distal part of tubule was not investigated in detail, there is also an apparent tendency to further coiling of originally straight distal part of tubule or to forming of discoidal plate from originally coiled distal part.

There are a large number of interstages between most primitive types with 4 pairs of buds (*Paraleptophlebia*, *Leptophlebia*) or with 4 pairs of unspecialized trunks (*Adenophlebia*, *Hapsiphlebia* and others) and highly derived *Hagenulus* with only a single pair of long, specialized trunks (see Table 8). Multiplied common trunks (5—6 branched pairs) occurring in some genera (*Massartella*, *Ulmeritus*, *Atalonella*) could be easily derived from types with 8 unspecialized trunks by their branching at basis.

The arrangement of the gonads and anagenesis of testes and ovaries are discussed elsewhere (Soldán, in prep.) in detail. Gonads could be derived from metamerically arranged organs. Multiplied follicles were originally arranged in only a single longitudinal row (Figs. 41, 47). The plesiomorphic characters of mayfly gonads are: follicles relatively large and less numerous (testicular follicles sometimes different in size), follicles situated perpendicularly to ducts, gonads deposited only in abdomen. The following anagenetic tendencies were observed in the genera investigated: (i) increasing number of follicles; (ii) extension of gonad to head and their bilateral flattening; (iii) elongation of follicles; (iv) specialization of seminal vesicle (not

TABLE 15

Anatomical schemes and frequency of characters in ancestral state in genera investigated

Genus/Subgenus	Anatomical scheme	Frequency of ancestral state
Adenophlebia	Aa, Bd, Cbl, Da, Ea, Fa, Ga, Hbl, Ib, Jb, Ka, La, Ma, Nb	8
**Adenophlebiodes* (s. str.)	Abl, Bd, Cbl, Da, Ea, Fa, Ga, Hbl, La, Ma, Nb	(6)**
**Aprionyx*	Aa, Ba, Cbl, Da, Ea, Fa, Ga, Hbl	(6)
**Askola*	Ac, Bcl, Cbl, Da, Eb2, Fa, Ga, Hdl	(3)
Atalomicria	Abl, Bd, Ca, Da, Ea, Fa, Ga, Hbl, Ial, Jal, Ka, La, Ma, Nb	10
Atalonella	Ab2, Bcl, Ca, Da, Ebl, Fa, Ga, Hc, Ib, Jb, Kbl, La, Ma, Nb	6
Atalophlebia	Abl, Bb, Ca, Da, Ea, Fa, Ga, Hbl, Ial, Jal, Ka, La, Ma, Nb	10
Atalophlebioides (Australia)	Ac, Bcl, Cbl, Da, Eb2, Fa, Gb, Hbl, Ib, Jb, Kbl, La, Mb, Nb	3
Atalophlebioides	Ac, Bcl, Cbl, Da, Eb2, Fa, Gb, Hbl, Ib, Jb, Kbl, La, Mb, Nb	3
Borinquena (s. str.)	Ab2, Bc2, Cbl, Da, Eb2, Fa, Ga, Hal	(3)
**Castanophlebia*	Abl, Bcl, Cb2, Da, Ea, Fa, Ga, Hbl, La, Ma, Nb	(6)
New genus A of Peters	Abl, Bcl, Cbl, Da, Eb2, Fa, Gb, Hbl, Ib, Jb, Kb2	(2)
Choroterpes (s. str.)	Ab2, Bcl, Ca, Da, Ebl, Fb, Gb, Hdl, Ic, Jc, Kb2, Lb, Mb, Nb	2
Ch. (*Euthraulus*)	Ac, Bcl, Ca, Da, Ebl, Fb, Gb, Hd2, Ic, Jc, Kb2, Lb, Mb, Nb	2
Ch. (*Neochoroterpes*)	Ab2, Bcl, Ca, Da, Ebl, Fb, Gb, Hd2, Ic, Jc, Kb2, Lb, Mb, Nb	2
Choroterpides	Ab2, Bcl, Ca, Da, Eb2, Fb, Gb, Hd2, Ic, Jc, Kb2, Lb, Mb, Nb	2
New genus A of Pescador	Ab2, Bb, Ca, Da, Ea, Fa, Ga, Hbl, Ib, Ja2, Kbl	(5)
Deleatidium	Ac, Bcl, Cbl, Da, Eb2, Fa, Gb, Hbl, Ic, Jb, Kbl, La, Mb, Nb	3
New genus F of Pescador	Ac, Bb, Ca, Da, Ebl, Fa, Ga, Hbl, Ib, Jb, Kbl, La, Mb, Nb	5
**Farrodes*	Ac, Bc2, Cbl, Da, Eb2, Fa, Ga, Hdl	(3)
Habroleptoides	Abl, Bb, Ca, Da, Eb2, Fa, Ga, Hbl, Ib, Jb, Kbl, La, Mb, Na	6
Habrophlebia	Abl, Bb, Ca, Da, Ebl, Fa, Ga, Hbl, Ib, Jb, Kbl, La, Mb, Na	6
Habrophlebiodes	Abl, Bb, Ca, Da, Ebl, Fb, Ga, Hbl, Ib, Jb, Kbl, La, Mb, Na	5
**Hagenulodes*	Ac, Bcl, Cbl, Da, Ebl, Fa, Ga, Hdl	(3)
Hagenulus	Ac, Bc2, Cbl, Da, Eb2, Fa, Ga, Hg, Ic, Jc, Kb2, La, Mb, Nb	4
Hagenulopsis	Ac, Bc2, Cbl, Da, Eb2, Fa, Ga, Hf, Ic, Jc, Kb2, La, Mb, Nb	4
**Hapsiphlebia*	Ab2, Bb, Cbl, Da, Ea, Fa, Ga, Hbl, La, Ma, Nb	(6)

**Hermanella*	Aa, Bb, Cb1, Da, Ea, Fb, Ga, Hd2, Ic, Jb, Kb1	(4)
**Homothraulus*	Ac, Bc2, Cb1, Da, Eb1, Fa, Ga, Hd2	(3)
**Indialis*	Ac, Bc1, Cb1, Da, Ea, Fb, Ga, Hd1, Lb, Ma, Nb	(4)
**Isca* (s. str.)	Ac, Bc1, Cb1, Da, Ea, Fb, Ga, Hd1, Lb, Mb, Nb	(3)
**I.* (*Minyphlebia*)	Ac, Bc1, Cb1, Da, Eb1, Fb, Ga, Hd1, Lb, Mb, Nb	(2)
Jappa	Aa, Ba, Ca, Da, Ea, Fa, Ga, Hb1, Ia1, Ja1, Ka, La, Ma, Nb	12
Kimminsula	Ac, Bc2, Cb2, Db, Eb2, Fa, Gb, Hb1, Ia2, Ja1, Kb1, La, Mb, Nb	3
Kirrara	Ab1, Bb, Cb2, Db, Eb2, Fa, Gb, Hb1, Ib, Jb, Kb1, La, Mb, Nb	2
Lepeorus	Ab1, Bb, Cb2, Dd, Eb2, Fa, Gb, Hb1, Ib, Jb, Kb1, La, Mb, Nb	2
Leptophlebia	Aa, Bb, Ca, Da, Ea, Fa, Ga, Ha, Ib, Jb, Kb1, La, Ma, Na	10
**Massartella*	Ab1, Bb, Ca, Db, Eb2, Fa, Ga, Hc, La, Ma, Nb	(5)
Massartellopsis	Ab2, Bb, Ca, Da, Eb2, Fa, Ga, Hb2, Ia2, Ja2, Kb1, La, Mb, Nb	5
**Megaglena*	Ac, Bc1, Cb1, Da, Eb1, Fa, Ga, Hd1, Lb, Mb, Nb	(3)
Meridialaris	Ab2, Bb, Ca, Da, Eb2, Fa, Ga, Hb2, Ia2, Ja2, Kb1, La, Mb, Nb	5
**Miroculis*	Ab2, Bb, Cb2, Da, Ea, Fa, Ga, Hd1, Ia2, Jb, Kb1	(5)
Paraleptophlebia	Aa, Bb, Ca, Da, Ea, Fa, Ga, Ha, Ib, Jb, Ka, La, Mb, Na	9
Penaphlebia	Ab2, Bb, Ca, Da, Ea, Fa, Ga, Ha, Hb1, Ia1, Ja2, Ka, La, Ma, Nb	10[1] (11)[2]
Petersophlebia	Ac, Bc1, Cb1, Da, Eb2, Fa, Gb, Hb2, Ia1, Ja2, Kb1, La, Mb, Nb	4
Polythelais	Ab2, Bc1, Cb1, Da, Eb2, Fa, Gb, Hb1, Ia1, Ja2, Kb1, La, Mb, Nb	4
**Terpides*	Ac, Bc1, Ca, Da, Eb2, Fb, Gb, Hd2, Ic, Jc, Kb2	(2)
**Thraulodes*	Ab2, Bc1, Cb1, Da, Eb2, Fa, Ga, Hb1	(3)
Thraulus	Ab2, Bc1, Cb1, Da, Ea, Fa, Ga, Hd1, Ia2, Jb, Kb2, Lb, Mb, Nb	4
Traverella	Ac, Bc2, Cb1, Da, Eb2, Fb, Gb, Hd2, Ic, Jc, Kb2, La, Mb, Nb	2
New genus B of Peters	Ab1, Bc2, Cb2, Db, Eb2, Fa, Ga, Hd2, Ib, Jb, Kb2	(2)
**Ulmeritus* (s. str.)	Ac, Bc2, Cb1, Da, Ea, Fa, Gb, Hc	(3)
**Ulmerophlebia*	Aa, Ba, Ca, Da, Eb1, Fa, Ga, Hb1, Ia1, Ja2, Ka	(8)
**Zephlebia* cf. *cruentata*	Ac, Bc1, Cb1, Da, Eb2, Fa, Gb, Hb1	(2)
**Z.* cf. *borealis*	Ac, Bc1, Cb1, Da, Eb2, Fa, Gb, Hb1	(2)
Z. (*Neozephlebia*)	Ab2, Bb, Ca, Da, Eb1, Fa, Gb, Hb1, Ib, Jb, Kb1, La, Mb, Nb	4

*) Gonads and/or tracheal system not preserved; **) genera without preserved gonads and/or tracheal system indicated in brackets; [1]) *P.chilensis*; [2]) *P. vinosa*.

investigated in most genera because of poor preserving of ducts). Primitive arrangement of gonads was found in *Atalophlebia*, *Atalomicria*, *Jappa* and others (Ia1, Ja1, Ka), highly derived arrangement in *Choroterpes*, *Hagenulus*, *Hagenulopsis* *Traverella* (Ic, Jc, Kb). Various interstages and cases of mosaic--like occurrence of characters are apparent from Tables 9—11.

The anagenesis of the tracheal system of Ephemeroptera is outlined by LANDA (1948, 1969). The following trends were observed in genera investigated: (i) reduction of visceral trachea (TV 5, in abdominal segment III; (ii) decreasing number of ventral tracheal anastomoses in first abdominal segments; (iii) appearance of anastomosis in abdominal segment IX (TAV 10, IX). More primitive types of arrangement of tracheal system are represented by genera *Leptophlebia*, *Paraleptophlebia*, *Habrophlebia*, *Adenophlebia* and others, more derived genera by *Choroterpes*, *Indialis*, *Megaglena*, *Thraulus*. In some genera (e.g. *Adenophlebia*) highly derived characters (anastomoses in first abdominal segments) were observed although other characters are primitive. Weak anastomoses in abdominal segments I—II would probably be found in fresh material of several further genera.

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Сравнительная анатомия личинок семейства Leptophlebiidae (Ephemeroptera) на основании строения брюшной цепочки, кишечного канала, мальпигиевых сосудов, гонад и трахейной системы

Морфология, внутренние органы, анагенез

Резюме. Изучалось строение внутренних органов личинок 65 видов из 51 рода семейства Leptophlebiidae. Следующие признаки считаются важными для сравнения: положение заднегрудного ганглия (A); положение первых 4—5 абдоминальных ганглиев (B); положение и степень слияния ганглиев заднего центра (C); строение коннективов (D); степень видимой макроскопической дифференциации передней кишки (E); положение толстой кишки и пилорического клапана (F); строение передней части прямой кишки (G); количество общих стволов мальпигиевых сосудов и их специализация (H); положение гонад в теле (I); строение семенных фолликулов и яйцевых трубочек (K); форма семенников и яичников (K); строение висцеральных трахей (L); строение комиссур между брюшиными трахейными стволами (M, N). Анатомические схемы исследованных родов приведены в виде таблиц и обсуждаются направления анагенеза, лежащие в основе формирования указанных признаков.

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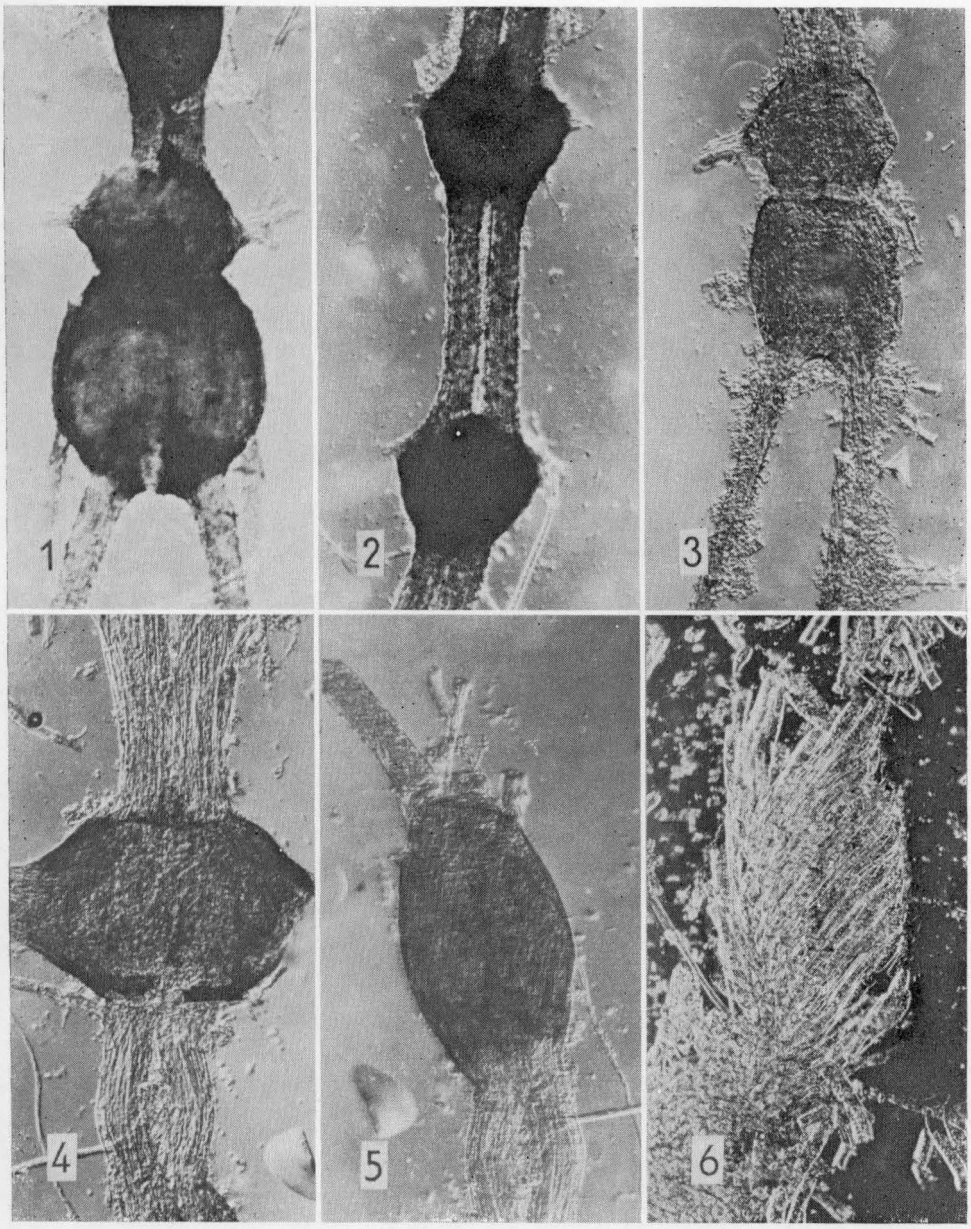

PLATE I, 1–5: 1 — *Adenophlebia*, last ganglionic centre. 2 — *Farrodes*, abdominal ganglia 3 and 4. 3 — *Neozephlebia*, last ganglionic centre. 4 — *Thraulus*, mesothoracic ganglion. 5 — *Thraulus*, metathoracic ganglion. 6 — *Meridialaris*, ovarioles. Figs. 1–5 — objective 25×, projection 8×.

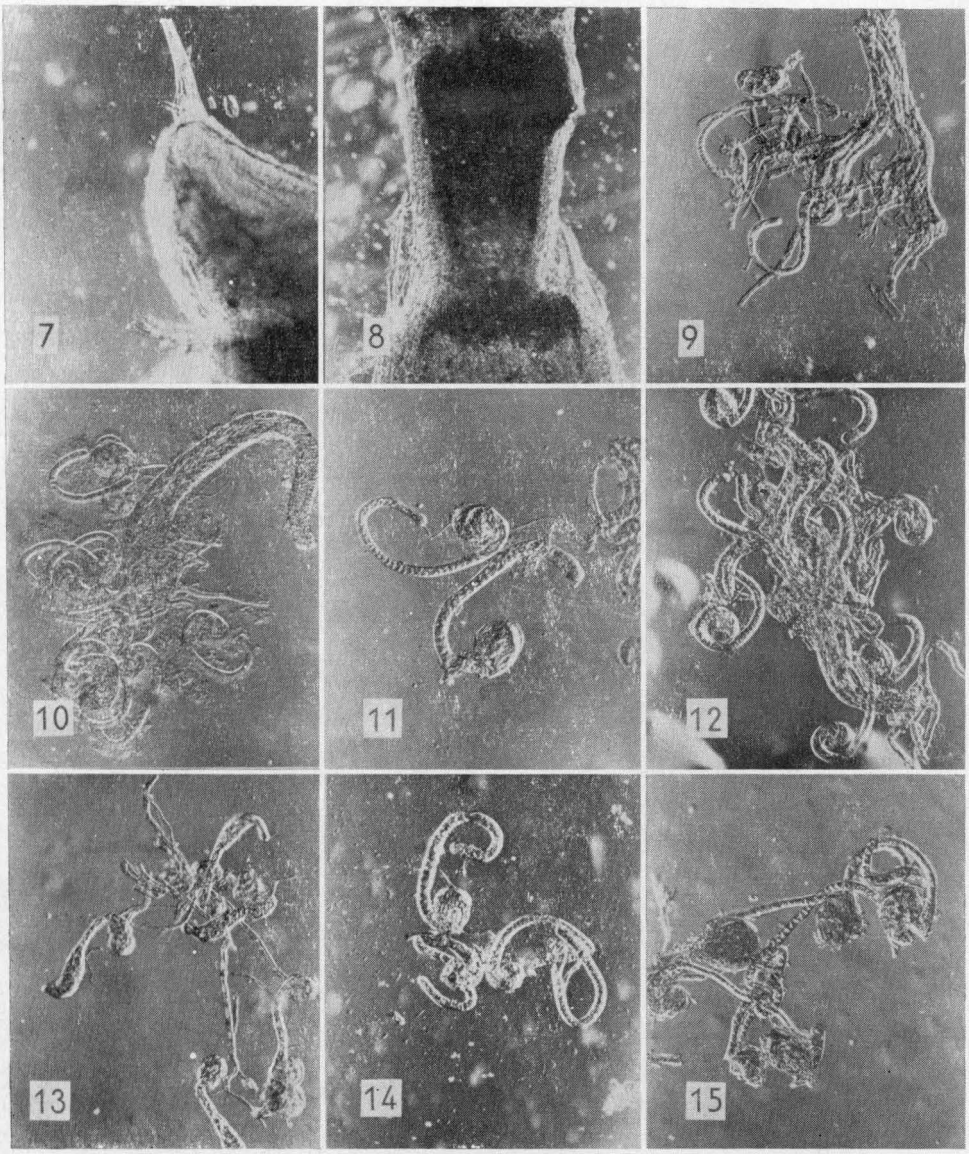

PLATE II, 7—15: 7 — *Kimminsula*, rectal projection. 8 — *Lepeorus* — colon and rectal projections. 9 — *Hermanella*, branched common trunk. 10 — *Choroterpides*, malpighian tubules. 11 — *Massartella*. malpighian tubules. 12 — *Lepeorus*, common trunk and malpighian tubules. 13 — *Paraleptophlebia bicornuta*, malpighian tubules. 14 — *Neozephlebia*, malpighian tubules. 15 — *Meridialis*, malpighian tubules. Figs. 7—15 — objective 25×, projection 8×.

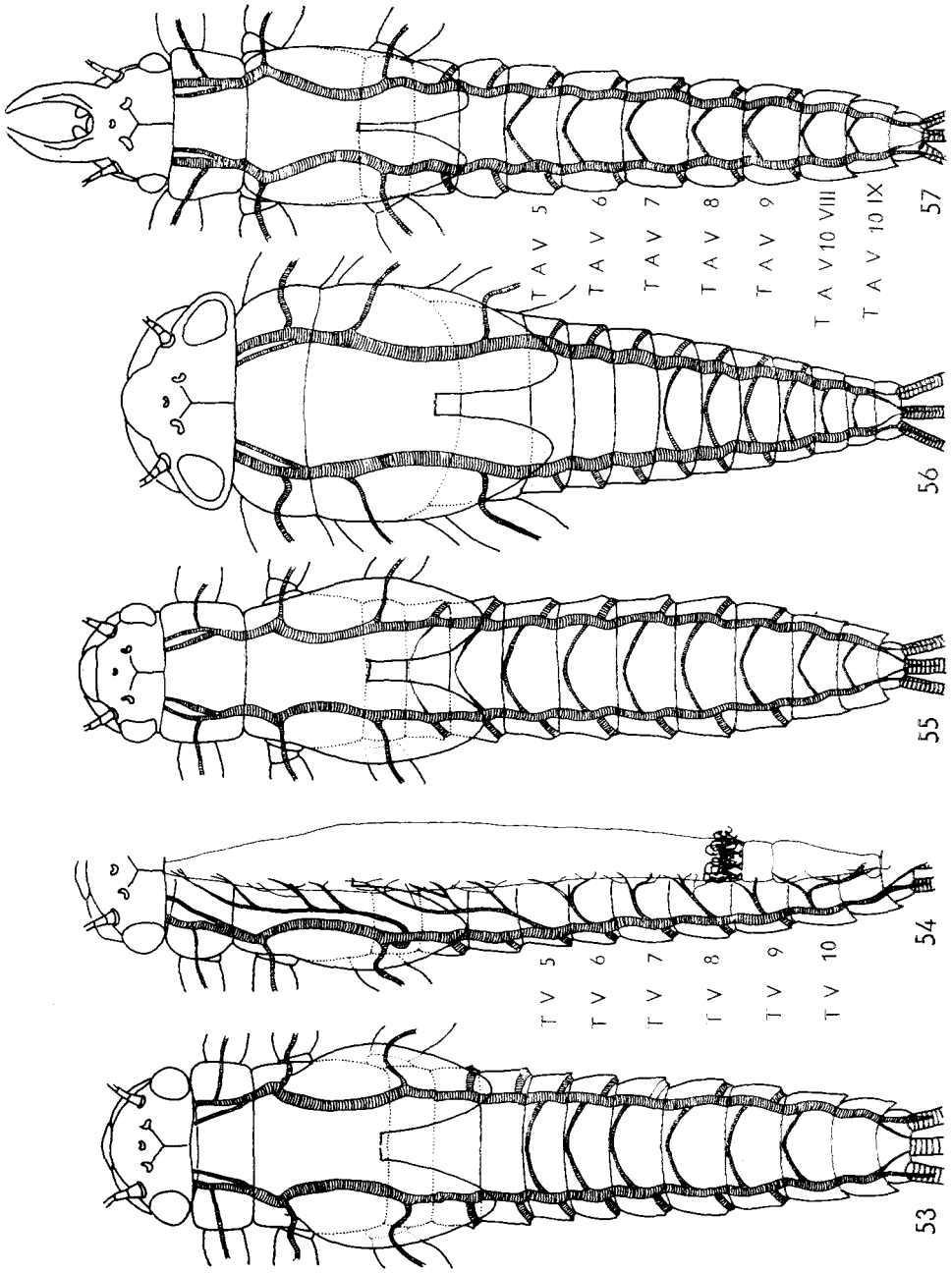

PLATE III, Figs. 53—57: Comparative anatomy of tracheal system of Leptophlebiidae. 53 — *Leptophlebia*, ventral anastomoses. 54 — *Paraleptophlebia*, visceral tracheae. 55 — *Adenophlebia*, ventral anastomoses. 56 — *Kimminsula*, ventral anastomoses. 57 — *Jappa*, ventral anastomoses. TAV 5—9, TAV 10, VIII, TAV 10, IX — ventral anastomoses in abdominal segments III—IX; TV 5—10 — visceral tracheae in abdominal segments III—IX.

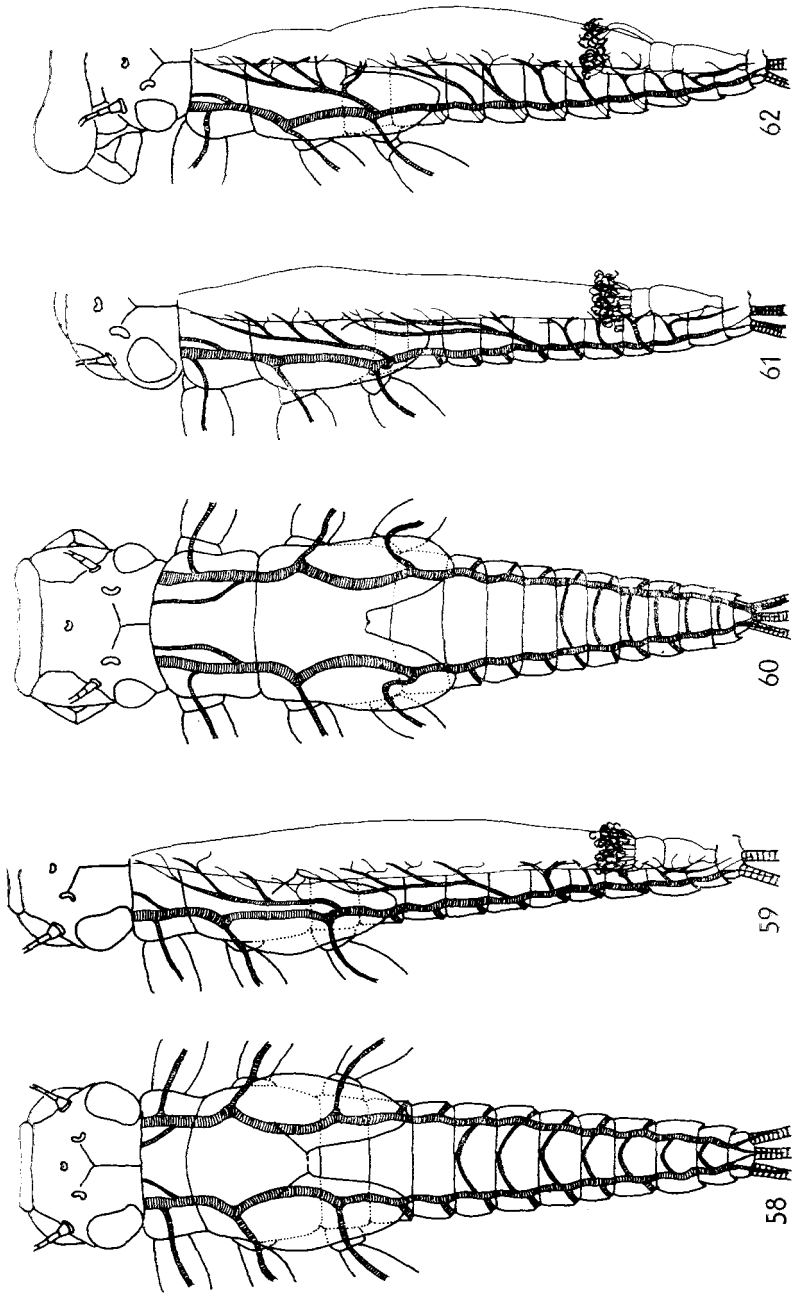

PLATE IV, Figs. 58—62: Comparative anatomy of tracheal system of Leptophlebiidae. 58 — *Indialis*, visceral tracheae. 59 — *Indialis*, ventral anastomoses. 60 — *Choroterpes* (*Euthraulus*), ventral anastomoses. 61 — *Thraulus*, visceral tracheae. 62 — *Hagenulus*, visceral tracheae.