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with the author's good wishes
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II.

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Contributions to the Anatomy of Ephemerids Larvae.

I.

Topography and Anatomy of Tracheal System.

VLADIMÍR LANDA.

I. HISTORY AND LITERATURE.

The first reference to the tracheal system of may-fly larvae can be found in Swammerdam's work „Biblia Naturae" (32, 1752)*) where the author describes on three pages the tracheal tubes which he calls „fistulae pulmonales". This work, which was brilliant in its time, has now only a historical value. The basic work on the topography and anatomy of the tracheal system was done by Palmen (43, 1887), whose work has not been surpassed so far. Its only shortcoming is bad weighing of the results and excessive generalisation of them: Palmén studies the larvae of seventeen species, the result is not a description of the tracheal system of various genus with corresponding figures, but a generalised description, where the differences either completely disappear or where they are mentioned only as points of interest. He finds that the tracheal gills are in a quite different place than where in the imago-stage the spiracles open. He first finds the bands which already in the larva lead to the spots of the future spiracles of the imago and recognises their importance during the moulting of the tracheas. Drenkelfort (12, 1910) devotes in his anatomical study of the species *Siphlurus lacustris* one chapter to the tracheal system. In the same way Heyner (20, 1915) describes the tracheal system of the larvae *Cloeon dipterum, Baetis bi-*

*) the first figure in the bracket denotes the order in which the work is quoted in the bibliography, the second denotes the year in which it was published.

noculatus and *Habrophlebia fusca* and Dürken (15, 1923) the tracheal system of the larva *Ephemerella ignita*. Unfortunately the tracheal system in all these studies is described only in the framework of general anatomy and the authors, who lack data for comparison, miss basic facts. As compared with Palmén they do not bring anything new; Lehmann (25, 1925) collects data about the tracheal system of all orders of insects and on this basis he derives the basic form of the insect tracheal system. With may-flies he basis his deductions on Palmén's work and gives an idealised scheme of the system which however applies to some orders only. Weber (Lehrbuch der Entomologie, 1934) uses his scheme. Neither Imms (Textbook of Entomology 1946) nor Snodgrass (32, 1935) study this problem deeply. Other anatomic work on may-fly larvae is mainly carried out on fixed material and the tracheal system is either completely left out or only its most basic marks are given.

The authors dealing with this are: Vayssière (38, 1881, 39, 1882), Heymons (21, 1896), von Baume (4, 1909), Gross (18, 1923) and again Vayssière (40, 1930, 41, 1937). In the literature dealing with the development and taxonomy of the insect wing we find several references to the tracheal system of the larva wing buds. Adolph (1, 1880) draws the sequence of the tracheae in the wing of a *Baetis*. Comstock-Needham (10, 1899), recognise that in case of may-fly the forewing is tracheated only by one branch from the mesothoracic stigma whereas in other Pterygota by two branches: one from the mesothoracic and the other from the metathoracic spiracle. Šulc (35, 1927) who studies the conditions in the mesothoracic paratergits of the *Cloeon* larva finds in a young larva two tracheal branches which he homologises with two trunks of other Pterygots. The front branch becomes displaced with the older larvae and the rear one takes part in the building of the wing. Ander (2, 1938) opposes this conception and maintains, that one cannot talk here about homology: the two Šulc wing bases at the may-flies are tracheal branches leading from the mesothoracic spiracle. Comstock's wing bases of pterygots are tracheae, each of which leads from a different spiracle: the first from the mesothoracic and the second from the metathoracic.

Palmen (28, 1877) discovered in the head of larvae, subimagi-

nes and imagines in the spot, where four tracheal branches meat a part consisting of concentric chitinous layers covered by a strong matrix. GROSS (19, 1904) called this part the Palmen's organ and gave an exact description of its structure. Wodsedalek (45, 1911) tries to find the significance of this organ, but his findings are not sufficiently convincing. Hsu Yin-Chi (23, 1933) found similar small organs in the two last but one segments of abdomen in the species *Stanonema interpuctata*. Miss Rawlinson (Proc. Zool. Soc. London B, 109, 1939) finds this organ in the one but last segment of the species *Ecdyonurus venosus*.

The morphology of the tracheal gills of the may-fly larves is best dealt with. Their various shape was a good sign for devising and system in this order. Therefore all descriptions and guides give fully their shape and insertion. The microscopic structure of *Caenic macrura* gills was described by Eastham (16, 1936).

In studying the metamorphosis of may-flies it was recognized that in the first stages the tracheal gills do not exist and that they are formed during moulting. The investigators studying this are: Vayssière (39, 1882), Gros (18, 1923), Dürken (15, 1923), Hsu Yin-Chi (31, 1933), Rawlinson.

The tracheal gills of may-flies in the first seven abdominal segments are a singular phenomenon in the animal world and already in the last century they interested comparative morphologists, who tried to solve their origin by their hypotheses. The gills were first of all related to wings. Gegenbauer (1870) is convinced, that both the wings and the gills are of the same origin. Lubbock (1873), Palmen (28, 1887), Brauer (7, 1882), Redtenbacher (1886), Simroth (1891), Voss (1903), Woodworth (46, 1904) are of the same opinion, the last one sees only a small step from the gills of the *Rhithrogena manifesta* larva to the wings. Some of the above named go even further: Palmén believes in a pleural origin of both, Lubbock, Radtenbacher and Simroth in a dorsal origin. Voss (1903) recognizes the untenability of these theories, does not however disprove them but asks for their confirmation by anatomic work. This task is undertaken by Dürken (13, 1907; 14, 1909; 15, 1923). After a careful study of the muscles he comes to the conclusion that the tracheal gills are of a tergit origin, but that their

homology with the wings, which are of the same origin, cannot be proved on the basis of muscles. Parallel with this hypothesis another one is developed, begun by Heymons. This assumes that the tracheal gills are the remains of abdominal extremities. This theory is also supported by Börner (6, 1909), who confirms it on the basis of the tracheal system of Cloeon dipterum. Šulc, on the basis of his studies on the larva of the same species is indifferent to Heymon's hypothesis, because on the basis of the tracheal system one cannot decide either for or against it. Snodgrass (31, 1935) and Weber (Lehrbuch der Ent., 1934) are in favour of Heymon's theory as well as Handlirsch (Die fossilen Insecten, 1908).

Problem.

The topography and anatomy of the tracheal system of may-fly larvae, which has been built hitherto on Palmén's discoveries in 1877 needs not only completing, but also correcting. The results must be compared and weighed as it is required by comparative anatomy, to become the basis for phylogenetical and physiological studies related to the tracheal system. The following study is a contribution to this problem.

II. MATERIAL AND METHODS.

For this study may-fly larvae were used. The term „larva" employed in the sense used by LESTAGE: that is the term larva includes all the last stages between the very young stages („larvula") and the last stage before hatching („nymph"). It is necessary to study the tracheation on fresh material. Only in several cases was material, fixed with Carnoys fixative, used. The larvae of the following species were studied:

*Polymitarcis virgo Oliv., Ephemera danica Müll., Potamanthus luteus L., Oligoneuriella rhenana Imhoff., Epeorus assimilis Eat., Heptagenia flava Rostock., *Heptagenia sulphurea Müll., Heptagenia lateralis Curt., *Ecdyonurus insignis Eat., Ecdyonurus fluminum Pict., Ecdyonurus venosus Fabr., *Ecdyonurus forcipula Koll.-Pict., Rhithrogena semicolorata Curt., Rhithrogena alpestris Eat., Siphlonurus lacustris Eat., Ameletus inopinatus Eat., Baetis inopinatus L., *Baetis gemellus Eat., *Centroptilum luteolum Müll., Cloeon*

dipterum L., Cloeon rufulum Eat., Choroterpes picteti Eat., Leptophlebia marginata L., Paraleptophlebia submarginata Steph., Habrophlebia fusca Curt., Habroleptoides modesta Hagen., Ephemerella ignita Poda., Torleya belgica Lest., Caenis macrura Steph., Caenis horaria L.

Species examinated in the fixed state, are indicated by an asterisk. Most of the larvae were collected in Central and South Bohemia. Some of them came from Slovakia. (*A. inopinatus, R. alpestris.*)

For rapid examination the common method of clearing the body with glycerin was used. Detailed examination was conducted by means of dissection under the binocular microscop at the magnification of 40 and 80 times. For special examination the larvae, after being killed, were left for 1 or 2 hours in water at 30—40 C. The body tissues disintegrated and after the body was opened they went out with the water. The chitinous tracheae were left. WODSEDALEK (45, 1911) used a similar method of examination when studiing Palmen's organ. LEHMANN's (25, 1925) method of tracheal injection by means of paraffin asfalt and TICHOMIROV's (37, 1924) method using Berlin blue, both of which require an air-pump, were not satisfactory. GÄBLER's (17, 1933) method somewhat better but still unsatisfactory results. According to this technic, the larva, deprived of tracheal gills, is placed for about 12 hours in olive oil coloured with Sudan III. This penetrates the tracheae but only the larges ones. Details of the structure of the tracheal system were studied by means of sections.

III. TOPOGRAPHY OF THE TRACHEAL SYSTEM.

List of the tracheae.

Tracheae of the spiracle 1. (mesothorax, prothorax, caput). Tab. 1, 2, 3, 4, 5, 6, 7, 8, 12, 13, 14.

A. Trachea cephalica communis (1)
  1. Trachea cephalica dorsalis (2)
    a) Trachea visceralis stigmatis 1 (3)
      . ramus anterior
      . . ramus medius
      . . . ramus posterior

b) Trachea proparatergalis anterior (4)
. ramus epidermalis et muscularis
. . ramus vasomuscularis
c) Trachea anastomotica transversa dorsalis organi Palmeni (5)
a. Tracheae epistocraniales anteriores et posteriores (6, 7)
d) Tracheae circumcerebralis (8)
. ramus circumlobalis
e) Trachea frontalis (9)
. ramus circumlobalis
f) Trachea lobi optici (10)
g) Trachea cerebralis (11)
h) Trachea antenalis (12)
i) Trachea pharynginalis anterior et posterior (13)
j) Trachea ocelli frontalis (trachea anastomotica) (14)
k) Trachea anastomotica longitudinalis cephalica (15)
. rami clypeales laterales
l) Trachea clypeolabralis (15)
. ramus clypealis
. . ramus labralis

2. Trachea cephalica ventralis (17)
a) Trachea prosubcoxalis (18)
b) Trachea propedialis (19)
a. Trachea procoxalis (20)
c) Trachea neuralis ganglii prothoracalis (21)
a. Tracheae prosternales anteriores et posteriores (22)
d) Trachea prothoracalis muscularis (23)
e) Trachea anastomotica transversa ventralis organi Palmeni (24)
a. Tracheae viscerales anteriores et posteriores (25)
f) Trachea ophthalmica (26)
g) Trachea adductoris mandibulae (27)
h) Trachea abductoris mandibulae (28)
i) Trachea inferrior oesophagi (29)
j) Trachea mandibularis (30)
. ramus internus
. . ramus externus
k) Trachea anastomotica longitudinalis cephalica (15)
l) Trachea neuralis ganglii suboesophagalis (31)

m) Trachea maxilaris (32)
. ramus palpi maxilaris
n) Trachea labialis (33)
. ramus endolobalis
. . ramus exolobalis
. . . ramus palpi labialis
o) Trachea hypopharynginalis (34)

B. Trachea arcus lateralis stigmatis 1 (35)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea ventralis stigmatis 1
b) Trachea neuralis ganglii mesothoracalis (37)
a. Tracheae mesosternales anteriores et posteriores (38)
c) Trachea mesocoxalis (39)

C. Trachea mesopedialis (40)
. rami musculares et epidermales
1. Trachea mesosubcoxalis (41)
2. Trachea mesoparatergalis posterior (42)
a) ramus internus (43)
b) C, Sc, R, Rs, M, Cu, A (44)

D. Trachea mesoparatergalis anterior (45)
. ramus epidermalis
. . ramus muscularis

E. Trachea mesothoracalis muscularis (46)

F. Trachea dorsalis vasomuscularis mesothoracalis (47)

Tracheae of the spiracle 2. (metathorax, prothorax).
Tab.: 6, 7, 8, 12, 13, 14.

A. Trachea arcus lateralis stigmatis 2 (48)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea ventralis stigmatis 2
b) Trachea neuralis ganglii metathoracalis (49)
a. Tracheae metasternales anteriores et posteriores (50)

B. Trachea metapedialis (51)
. ramimusculares et epidermales

1. Trachea metasubcoxalis (52)
2. Trachea metaparatergalis posterior (53)

C. Trachea metaparatergalis anterior (54)

D. Trachea metathoracalis muscularis (55)

E. Trachea dorsalis vasomuscularis metathoracalis (Trachea anastomotica dorsalis stigmatis 2) (56)

F. Trachea visceralis stigmatis 2 (57)
. ramus anterior
. . ramus medius
. . . ramus posterior

G. Trachea gonadarum (58)

Tracheae of the spiracle 3. (segm. abd. I, metathorax). Tab.: 9, 10, 11, 12, 13, 14, 15.

A. Trachea arcus lateralis stigm. 3 (59)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea dorsalis (60)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (61)
c) Trachea neuralis gang. segm. abd. I. ganl. metathoracalis (62)
. rami epidermales et musculares
d) Trachea metacoxalis (63)
e) Trachea pedialis (64)
f) Trachea visceralis (65)
g) Trachea branchialis (66)
. ramus muscularis
. . rami tracheobranchales

Tracheae of the spiracle 4. (segm. abd. II.).
For spiracles 4—10 see tab. at the spiracle 3.

A. Trachea arcus lateralis stigm. 4 (67)
1. Trachea anastomotica longitudinalis stigm. 1—10 (36)
a) Trachea dorsalis (68)
. ramus vasomuscularis
. . rami epidermales et musculares

b) Trachea gonadarum (69)
c) Trachea neuralis gang. segm. abd. II (70)
. rami musculares et epidermales
d) Trachea ventralis (71)
e) Trachea pedialis (72)
f) Trachea visceralis (73)

Tracheae of the spiracle 5. (segm. abd. III, II.)

A. Trachea arcus lateralis stigm. 5 (74)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea dorsalis (75)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (76)
c) Trachea neuralis gangl. segm. abd. III (77)
. rami musculares et epidermales
d) Trachea pedialis (78)
e) Trachea visceralis (79)
f) Trachea anastomotica ventralis (80)
. rami musculares et epidermales
g) Trachea branchialis (81)
. ramus muscularis
. . ramus tracheobranchalis
h) Trachea dorsalis praeposita (82)
i) Trachea ventralis praeposita (83)
j) Trachea gonadarum praeposita (84)

Tracheae of the spiracle 6. (segm. abd. IV, III.)

A. Trachea arcus lateralis stigm. 6 (85)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea dorsalis (86)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (87)
c) Trachea neuralis gangl. segm. abd. IV (88)
. rami musculares et epidermales
d) Trachea pedialis (89)
e) Trachea visceralis (90)

f) Trachea anastomotica ventralis (91)
. rami musculares et epidermales
g) Trachea branchialis (92)
. ramus muscularis
. . rami tracheobranchales
i) Trachea ventralis praeposita (94)
j) Trachea gonadarum praeposita (95)
h) Trachea dorsalis praeposita (93)

Tracheae of the spiracle 7. (segm. abd. V, IV.)

A. Trachea arcus lateralis stigm. 7 (96)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea dorsalis (97)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (98)
c) Trachea neuralis gangl. segm. abd. V (99)
. rami musculares et epidermales
d) Trachea pedialis (100)
e) Trachea visceralis (101)
f) Trachea anastomotica ventralis (102)
. rami musculares et epidermales
g) Trachea branchialis (103)
. ramus muscularis
. . rami tracheobranchales
h) Trachea dorsalis praeposita (104)
i) Trachea ventralis praeposita (105)
j) Trachea gonadarum praeposita (106)

Tracheae of the spiracle 8. (segm. abd. VI, V.)

A. Trachea arcus lateralis stigm. 8 (107)
1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)
a) Trachea dorsalis (108)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (109)
c) Trachea neuralis gangl. segm. abd. VI (110)
. rami musculares et epidermales

d) Trachea pedialis (111)
e) Trachea visceralis (112)
. ramus tubularum Malphigii
f) Trachea anastomotica ventralis (113)
g) Trachea branchialis (114)
. ramus muscularis
. . rami tracheobranchales
h) Trachea dorsalis praeposita (115)
i) Trachea ventralis praeposita (116)

j) Trachea gonadarum praeposita (117)

Tracheae of the spiracle 9. (segm. abd. VII, VI.)

A. Trachea arcus lateralis stigm. 9 (118)

1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)

a) Trachea dorsalis (119)
. ramus vasomuscularis
. . rami epidermales et musculares
b) Trachea gonadarum (120)
c) Trachea neuralis gangl. segm. abd. VII (121)
. rami musculares et epidermales
d) Trachea pedialis (122)
e) Trachea visceralis (123)
. rami tubularum Malphigii
f) Trachea anastomotica ventralis (124)
. rami musculares et epidermales
g) Trachea branchialis (125)
. ramus muscularis
. . rami tracheobranchales
h) Trachea dorsalis praeposita (126)
i) Trachea ventralis praeposita (127)
j) Trachea gonadarum praeposita (128)

Tracheae of the spiracle 10. (segm. abd. IX, X.)

A. Trachea arcus lateralis stigm. 10 (129)

1. Trachea anastomotica longitudinalis lateralis stigm. 1—10 (36)

a) Trachea dorsalis (130)
. ramus vasomuscularis
. . rami musculares et epidermales

b) Trachea neuralis gangl. segm. abd. VIII (131)
c) Trachea pedialis (132)
d) Trachea visceralis (133)
e) Trachea anastomotica ventralis (134)
. rami musculares et epidermales
f) Trachea branchialis (135)
. ramus muscularis
. . rami tracheobranchales
g) Trachea dorsalis praeposita (136)
h) Trachea ventralis praeposita (137)
i) Trachea gonadarum praeposita
j) Trachea anastomotica longitudinalis stigm. 1—10
k) Trachea dorsalis praeposita sgm. abd. VIII (138)
l) Trachea ventralis praeposita sgm. abd. VIII (139)
m) Trachea dorsalis sgm. abd. IX (140)
. ramus vasomuscularis
. . rami epidermales et musculares
n) Trachea visceralis
o) Trachea anastomotica ventralis sgm. abd. IX (141)
p) Trachea ducti seminalis (142)
q) Trachea pedialis (143)
r) Trachea dorsalis praeposita sgm. abd. IX (144)
s) Trachea ventralis praeposita sgm. abd. IX (145)
t) Trachea dorsalis sgm. abd. X (146)
u) Trachea visceralis sgm. abd. X (147)
v) Trachea ventralis sgm. abd. X (148)
x) Trachea cerci medialis (149)
. ramus cerci medialis
. ramus cerci lateralis
y) Trachea cerci lateralis (150)
. ramus cerci lateralis

Description of the tracheae and notes on some of them.

Tracheae of the spiracle 1. — mesothorax, prothorax, caput. — Tab. 1, 2, 3, 4, 5, 6 (1, 2), 7 (1, 2), 8 (1, 2, 5), 12 (1, 2), 13 (1, 2), 14 (1, 2).

A. Tr. cephalica communis (1).

It starts from the first stigma towards the head. It is the common basis to the trunks Tr. cephalica dorsalis and Tr. cephalica ventralis. With the larvae of the crawling type it is

usually short or not discernible at all *(Potamanthus)*. At the flat larves it usually is long. It is of course questionable, whether we can count to it as well the part from the stigma to the place where the tr. anastomotica longatudinalis lateralis stigm. 1—10 joins it or whether this part should be counted to the tr. arcus lateralis stigm. 1. After comparing the situation of various genus, I have come to the first conclusion. At the genus *Oligoneuriella* this trunk leads right to the head, where it branches out. In the prothorax even in the rear part of the head branches lead out from it, which with other genus come already from the dorsal and ventral trunk. Tr. cephalica communis is divided into tr. cephalica ventralis going into the head on its ventral side and into tr. cephalica dorsalis, leading into the head on its dorsal side. Backwards the tr. anastomotica longitudinalis lateralis stigm. 1—10 leads off. (For further details see also the term „tr. cephalica ventralis".)

1. Tr. cephalica dorsalis (2).

With swimming, burrowing and crawling larves it is as strong as the ventral trunk, sometimes even stronger. At flat larves it is weaker. At *Polymitarcis* it forms before entering the head a flat widening and two thinwalled air sacs in the head. Tr. cephalica dorsalis spreads out in the following branches:

a) Tr. visceralis stigm. 1 (3).

Only at the genus *Polymitarcis* and *Oligoneuriella*. At the first it starts right from the beginning of the dorsal part, at the second further to the head from an undivided trunk. It has three branches (ramus anterior, medius, posterior) which may come out from the trunk separately.

b) Tr. proparatergalis anterior (4).

It starts from about the middle of the pronotum. One of the branches feeds the muscles and epidermis (ramus epidermalis et muscularis), the second goes to the middle dorsal line to the dorsal vessel (ramus vasomuscularis). Its branches, which are further divided, start sometimes on their own. It appears at burrowing larves and among the flat ones at Rhithrogena. At the other flat and swimming ones it does not appear. (Opposed to Šulc who draws it at the species Cloeon dipterum.)

c) Tr. anastomotica transversa dorsalis organi Palmeni (5).

A strong transverse anastomosis joining in the Palmen's organ an anastomosis of the same kind of the ventral trunk. It is the first branch of the dorsal trunk after its entrance into the head. Looking at it from the point of view of the development of the tracheal system it is not of course certain, whether we deal here with the transverse anastomosis. It is equally possible, that they are really longitudinal anastomoses, corresponding perhaps to longitudinal anastomoses between the original segments of the head (perhaps even lateral trunks in the head) grown together in the median plane. In any case the link in the Palmen body makes it possible, that this strong anastomosis may function both as transverse and longitudinal ones.

a. Tr. epistocraniales anteriores et posteriores (6).

They lead forward and back from the dorsal anastomosis. From the front ones, the one nearest to the Palmen body and going through the muscles and filling tissues behind the brain or sometimes right up to it, is the strongest developed (7).

The following tr. circumcerebralis and tr. frontalis are really only more strongly specially developed tr. epistocraniales. Tr. epistocraniales posteriores are as far as the strength is concerned strongly developed at the swimming type, where the epicranium is narrow and strongly arched, as far as the number is concerned it is strongly developed at the flat types, where the epicranium is wide, flat and drawn backwards.

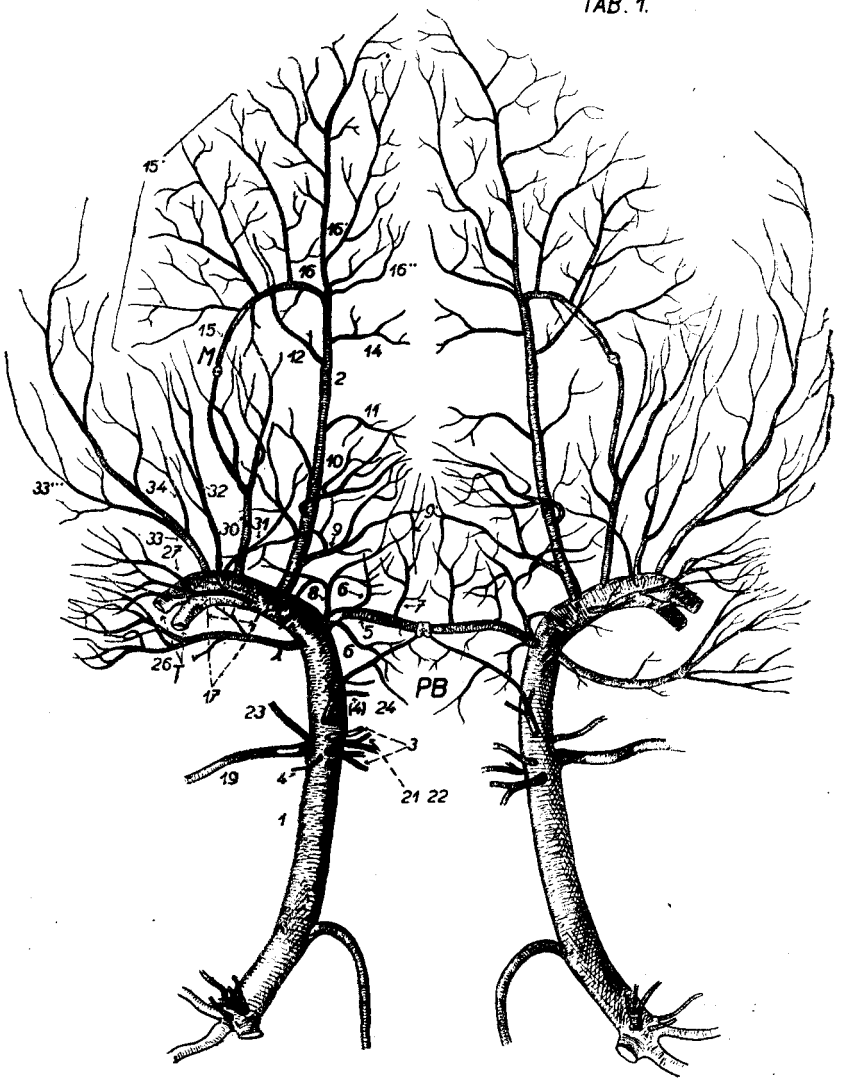
d) Tr. circumcerebralis (8).

It starts either from the foregoing anastomosis or from the place, where this starts from the dorsal trunk. Its fine branches envelop the brain (supraoesophageal gangl.) from the top and the parts without penetrating it deeper. The outer offspring of this branch embraces the lobi optici (r. circumlobalis) jutting out in the same way.

e) Tr. frontalis (9).

Starts out from the anastomosis or from the place of its insertion in the same way as the foregoing. Sometimes it is shifted along the dorsal trunk further to the front. *(Potamanthus, Oligoneuriella).* It branches out mightily, supplies all the tissues (muscles and the filling tissues) in the rear portion of

TAB. 1.



Oligoneuriella rhenana Imhoff. (larva). Tracheation of the head. — M — contact mallet, PB — Palmen's organ, T (correct TG) — places on which the tracheal gills are fixed. Tracheae are numbered according to the list in the chapter III.

the head behind the brain it goes to the epidermis and one of its branches reaches the oesophagus (r. oesophagalis). At flat larves it is usually badly developed and it ranks here with the tracheae epistocraniales. It is particularly strongly developed at the genus *Polymitarcis,* where it reaches right to the front edge of the clypeus and branches out strongly in the whole dorsal part of the head.

f) Tr. lobi optici (10).

With a brush development, at the crawling and burrowing types it has a long trunk, which starts from the insertion point of the anastomosis or only a little further and has a forward direction. At flat and swimming larvae its trunk is short and it starts from the dorsal trunk very much more to the front. Both, the short and the long trunk, branch in the lobus opticus, which they supplie.

g) Tr. cerebralis (11).

It starts from the inner side of the dorsal trunk and branches out like brush. It supplies the brain.

h) Tr. antenalis (12).

From the outside part of the dorsal trunk into the antenae.

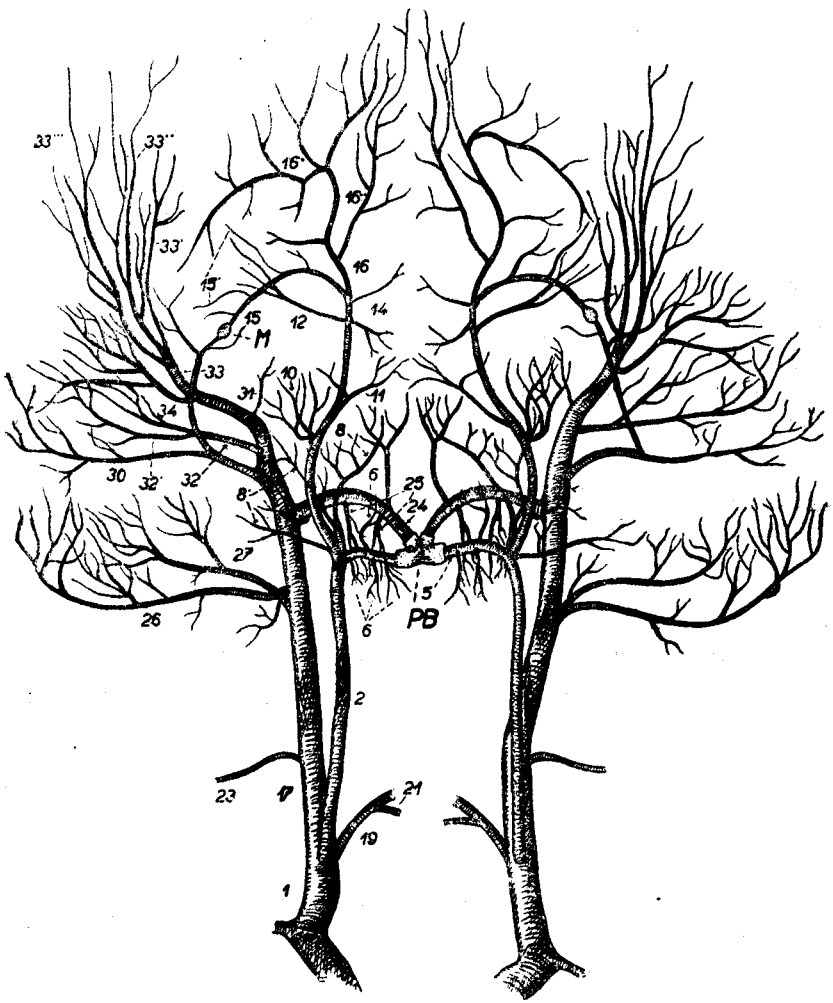
i) Tr. pharynginalis anterior et posterior (13).

Two tracheae starting close to each other on the inside part of the dorsal trunk. They lead to the pharynx and, because in may-fly larvae this is very short, also to the oesophagus. I did not always succeed in finding both.

j) Tr. ocelli frontalis (14).

Only at the species, where the front simple eye is shifted far ahead away from the brain. Otherwise it is tracheated together with the brain. The swimming larvae have the simple eye advanced far ahead. Here then the ocellus is supplied by a special trachea. We can see a very good example of the growth of the single frontal eye at the genus Ephemera. The composit eyes and both rear ocelli are weakly developed bud the front one, shifted forward and protected by the protuberance of the clypeus is developed enormously. It is strongly tracheated and the tracheae form a transverse anastomosis. In the middle of the anastomosis there is a swelling — „the contact mallet" (see chapter IV).

TAB. 2.



Eudyonurus venosus Fabr. (larva). Tracheation of the head.
M — contact mallet, PB — Palmen's organ. Tracheae are numbered according to the list in the chapter III.

k) Tr. anastomotica longitudinalis cephalica (15).

It connects the head dorsal trunk (the insertion is a bit forward in front of the insertion of the tr. antenalis) with the ventral head trunk (the insertion is in the branching out of mandibular branches). This longitudinal anastomosis which was not known hitherto, may be important for the study of the development of the tracheal system of the head. We deal here probably with the longitudinal anastomosis between the original head segments. Anastomosis is again swollen in the middle into the contact mallet (see the foregoing trachea and the chapter IV). At crawling and burrowing larvae fine tracheae start from it, particularly in the places under the antena. At flat larvae with a strongly widened clypeus strong branches start from it, which branch out strongly through the clypeus (r. clypeales laterales). The whole anastomosis does not give the impression of a branch, but of a continuation of a trunk. I found this anastomosis at crawling, burrowing and among the flat larvae in the genus *Ecdyonurus, Epeorus* and *Oligoneuriella.* I did not find it at swimming larvae with the hypognathous head, at crawling larvae in the family *Leptophlebiidae* and at flat *Heptagenia* and *Rhithrogena,* although I tried using all the methods which were successful in other cases. It is possible that in the future a similar anastomosis will be found also at these genus, but in any case it would be very fine and it would separate these genus from those with an anastomosis developed strongly.

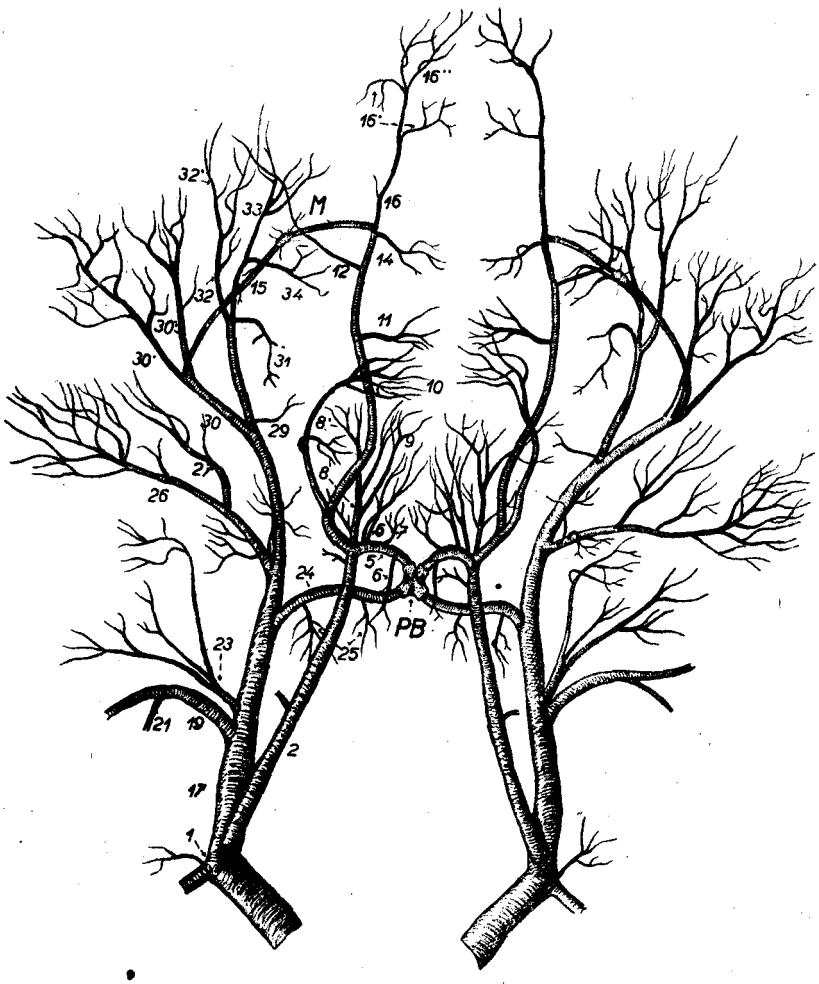
l) Tr. clypeolabralis (16).

It starts in the direction of the continuation of the dorsal trunk from the place where the tr. anastomotica longitudinalis cephalica branches off. It divides in the clypeus (ramus clypealis). Its inner branch goes into the labrum (ramus labralis).

2. Tr. cephalica ventralis (17).

Wherever the tr. cephalica communis is developed, this is its direct continuation. At the genus, where the dorsal trunk as compared with the ventral is weak, its origin is problematic. The dorsal trunk here appears as a typical branch of the basic ventral trunk. In that case of course the tr. cephalica communis is only the beginning sector of the tr. cephalica

TAB. 3.



Potamanthus luteus L. (larva). Tracheation of the head.
M — contact mallet, PB — Palmen's organ. Tracheae are numbered according to the list in the chapter III.

ventralis. However even in these cases I note in the illustrations the term. tr. cephalica communis, although I am aware that this here is a purely mechanical term. At the species *Oligoneuriella,* according this mechanical scheme, is the tr. cephalica ventralis only a short piece of branch, leading from the point of insertion of the branch into the labium. In reality the whole tr. cephalica communis, which is not separated from it in any way, is its integral part. At the genus *Polymitarcis* the ventral trunks, on the same way as the dorsal ones, widen out into two thinwalled air sacs.

Tr. cephalica ventralis has in the prothorax still the following branches.

a) Tr. prosubcoxalis (18).

It starts before the branch leading into the leg, sometimes directly from it, sometimes further back right at the beginning of the ventral trunk of the spiracle. It supplies the subcoxa of the front leg. It is very developed at the burrowing type and very little developed or missing altogether at the swimming or flat type. It cannot here be recognized from the prosternal tracheae, which reach into the flat subcoxa.

b) Tr. propedialis (19).

It starts about in the middle of the thorax. It forms a vertical arch leading into the front leg, where it divides into short rami musculares et epidermales. At flat larvae with flat and wide legs, in the femur parallel to the main trachea there is another bigger one branching out in the same way.

a) Tr. procoxalis (20).

It separates from the tr. propedialis and branches out in the coxa. Very strong again at the burrowing type, visible at crawling type.

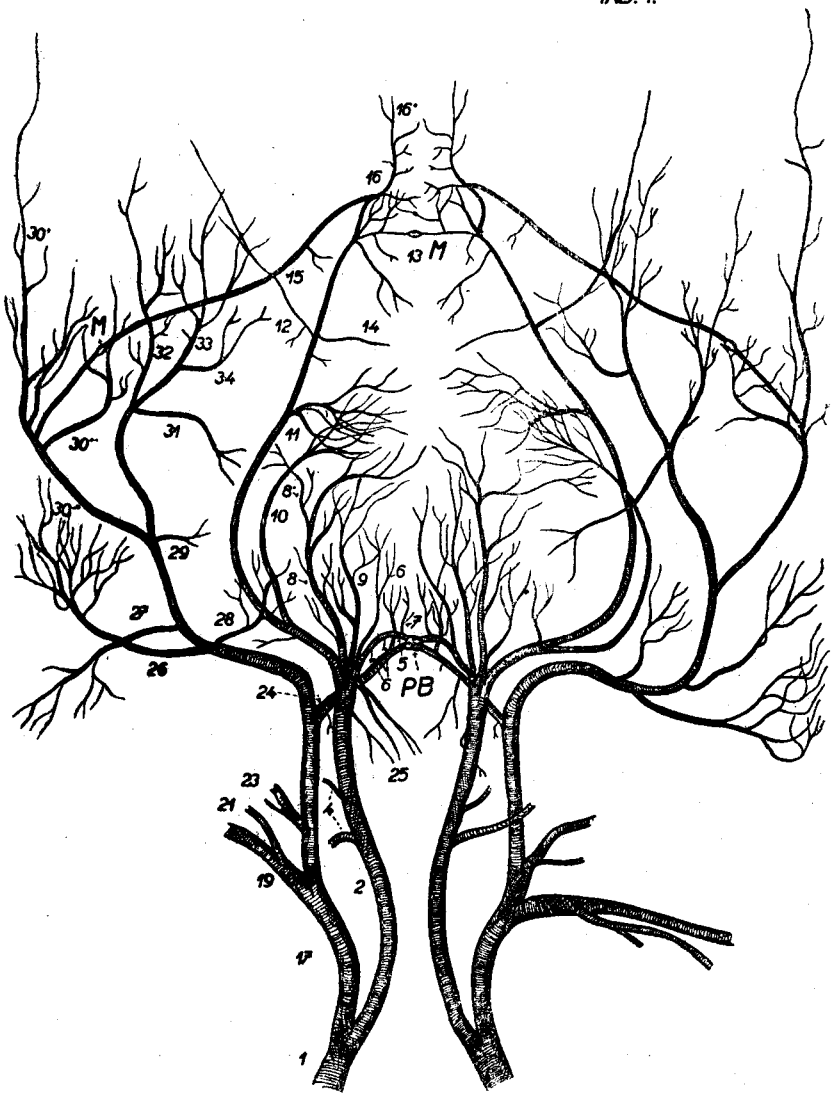
c) Tr. neuralis ganglii prothoracalis (21).

It supplies the prothoracic ganglium. It starts from the arc of the propedial trachea. Only at the *Oligoneuriella* it joins the trunk separately on the other side than the above mentioned trachea.

a) Tr. prosternales anteriores et posteriores (22).

They start from the foregoing tr. neuralis ganglii prothoracalis forward and backward and they branch out in the wide

TAB. 4.



Ephemera danica Müll. (larva). Tracheation of the head.
M — contact mallet, PB — Palmen's organ. Tracheae are numbered according to the list in the chapter III.

prosternum, supplying here the muscles and epidermis. Sometimes *(Oligoneuriella)* they start from the trunk independently on both sides near the tr. neuralis.

d) Tr. prothoracalis muscularis (23).

It starts from the ventral trunk somewhat forward behind the propleuralis. It points forward and branches out in the muscles. At the genus which do not have tr. proparatergalis anterior (see above number 4) — *Ecdyonurus, Heptagenia, Epeorus* and swimming larvae — its branches turn also to the dorsal side and substitute this missing one.

e) Tr. anastomotica transversa ventralis organi Palméni (24).

Ventralis means, that it starts from the ventral trunk, its correct name should really be: Tr. anastomotica transversa dorsalis tr. cephalicae ventralis organi Palméni. After the entrance of the ventral trunk into the head its first branch. In the middle it joins in the Palmen's organ the transverse anastomosis of the dorsal trunk. Looking from above this anastomosis is always further back, than the anastomosis of the dorsal trunk. At flat larvae it is the other way round (see tab. 1—5). At Oligoneuriella this commissure is very weak.

a) Tr. viscerales anteriores et posteriores (25).

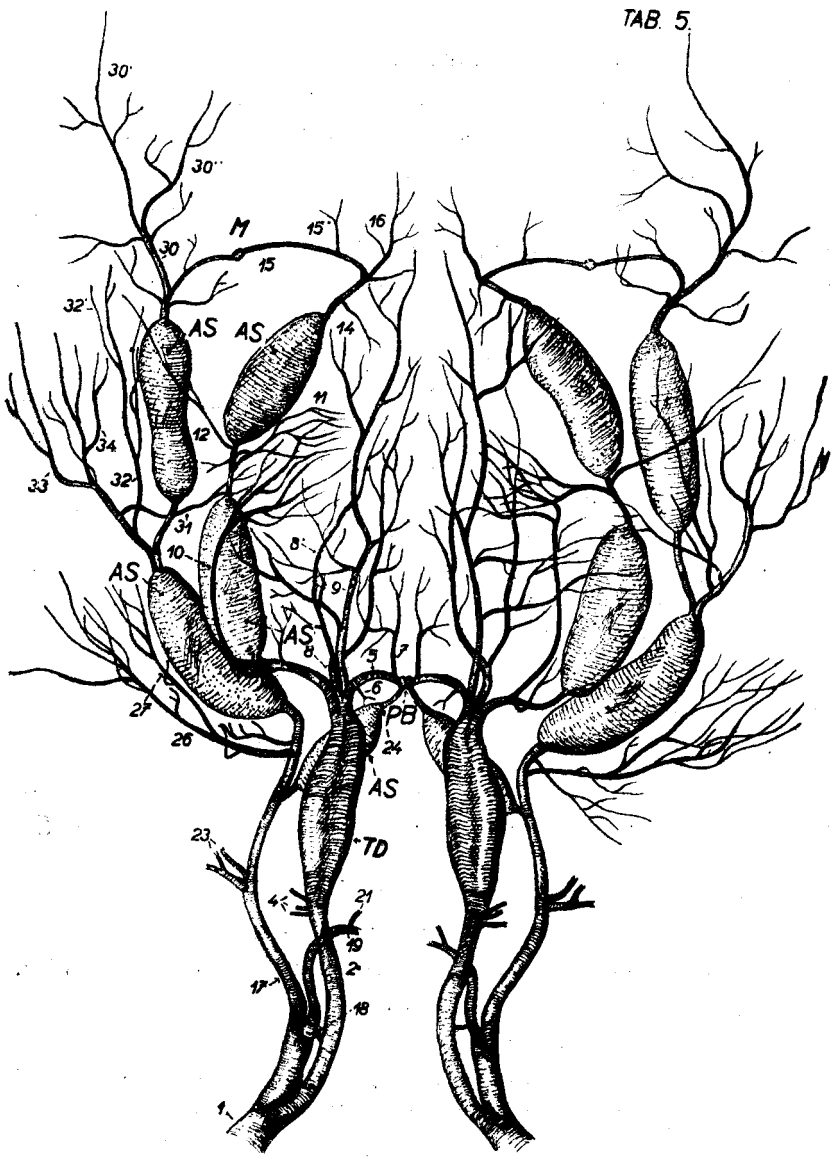
They start from the foregoing anastomosis of the ventral trunk, backwards they join the mid-intestine, downward and forward the oesophagus. A special position among them is given at flat larves to the trachea nearest to the Palmen's organ and pointing forward. It branches out and its branches supply the muscles and partly also the oesophagus. It probably takes even here the function of the epicranial tracheae of the upper anastomosis, which being somewhat further back cannot supply this region.

f) Tr. ophthalmica (26).

It starts from the ventral trunk immediately behind the anastomosis, but mostly in front of it, immediately behind the entrance of the ventral trunk into the head. It branches and supplies the composit eye. Its magnitude is governed by the size of this eye.

g) Tr. adductoris mandibulae (27).

It starts from the ventral trunk very near to the foregoing



Polymitarcis virgo Oliv. (larva). Tracheation of the head.

M — contact mallet, PB — Palmen's organ, TD — tracheal widening, AS — air sacs. Tracheae are numbered according to the list in the chapter III.

trachea. It has very frequently a common trunk with it. It supplies the adductor mandibulae, fixed at the back under the head.

h) Tr. abductoris mandibulae (28).

It supplies the abductor mandibulae but is usually badly visible. It starts near the two above described tracheae.

i) Tr. inferior oesophagi (29).

A weakly branched out trachea starting from places, where the trachea leading to the mandibula separates from the ventral trunk. It joins the bottom and lateral side of the oesophagus.

j) Tr. mandibularis (30).

It supplies the mandibula, in which it splits fundamentally into two branches-ramus externus et internus. The first leads into its external toothed part, which particulary at the burrowing larvae is usually drawn out into a long tooth, which projects a long way over the head, the second goes into the chewing part. Both these parts branch out further, particularly strongly there, where the mandibules are prominent among other mouth organs.

k) Tr. anastomotica longitudinalis cephalica (15).
(see no. 15.)

l) Tr. neuralis ganglii suboesophagalis (31).

It starts at the bend of the ventral trunk before the trachea enters the mandibula. It finishes in the suboeosophagal ganglium.

m) Tr. maxilaris (32).

It starts from the arc, by means of which the ventral trunk enters the labium. Inside the maxilla it sends out a branch into the palpus maxilaris.

n) Tr. labialis (33).

It enters the labium and forms the end of the ventral trunk. It is particularly strongly developed at flat larvae with a prominent labrum. It separates in the submentum and sends mighty branches into the inner and outer lobe and into the palpus.

o) Tr. hypopharynginalis (34).

It branches away from the trachea leading into the la-

bium. It goes into the body of the hypopharynx and by a short branch also into its lobe. These lobes are sometimes supplied by a separate branch directly from the maxils.

[p) Tr. branchialis cephalica.]

Only as the species *Oligoneuriella*. Analogically we can call in this way the end of the ventral trunk leading to the tracheal gills which at this species are on the head under the maxils. The gills are brushes from fibres into which this trachea branches out with rami branchiales.

B. Tr. arcus lateralis stigmatis 1 (35).

It joins the place of the future stigma with the trunk. It is a closed trachea without lumen, only a sort of badly visible band. Before moulting the matrix separates from it and forms with the new intima, which is produced around the old intima, a normal trachea with a lumen. The old band intima, which remains inside, is fixed to the exuvium; it draws out during moulting from the body the old intima of the body tracheae through the pipe, formed by the new widened trachea. After moulting, this pipe is drawn together and the spiracle grows into an invisible band. During the last larva stages the first and second stigma in the thorax do not grow together, but are only tightly closed. During these later moulting the trachea arcus lateralis of the first two spiracles does not close any more after moulting. At burrowing and crawling larvae there is a knot at the end of the band, from which all the branches start: into the head, the lateral trunk and branches into the muscles. The same is the case with flat and swimming larvae, only the lateral trunk and the branch leading in the head do not start directly from the knot, but are connected by a longer joining piece (see Tab. 8, fig. 1, 2). We may also consider this joining piece as a part of trachea arcus lateralis stigm. 1, which remains open. We may rather consider it as a part of the branch into the head along which the point of insertion of the lateral trunk was shifted from the original position — i. e. from the knot. The same case even more complicated is at *Oligoneuriella* (see also tracheae 1 and 17).

1. Tr. anastomotica lateralis stigm. 1—10 (36).

The lateral trunk is characteristic for mayflies. It goes

from the first to the last spiracle. It is the strongest trachea in the body of the larva. It passes the thorax either in a straight line or in a regular slightly bent arc (flat larvae) or it forms a sharp bend *(Potamanthus, Leptophlebiidae)*, or it forms special morphological shapes, which I shall deal with in the next chapter. In the abdomen it forms waves and in the eighth abdomen segment it splits into two branches. At the first stigma, as we have already pointed out, it starts directly from the knot at the end of the trachea arcus lateralis stigm. 1, or its insertion is shifted along tr. cephalica communis or ventralis forward. Tr. anastomotica lateralis stigm. 1—10 is connected with the second stigma by a link — tr. arcus lateralis stigm. 2. With the other abdominal spiracles it is connected by a firm band without lumen, which basically really is a closed trachea which opens only during the moulting of the tracheae. ŠULC homologizes this trunk with the dorsal trunk of the Thysanoptera. I do not agree with this wiew, because both organs are basically different. Let us compare the tracheal system on the schematic illustrations of the cross-section of may-flies with ŠULC's diagram showing the conditions at the Lepisma. (Tab. 15, figs. 2, 3.) From this we see that the title is correct in the case of Thysanura, because there lead dorsal, visceral and ventral branches from each stigma. The dorsal branches form anastomosis and therefore a regular dorsal trunk. In case of may-flies it is different. Here all the branches start from the lateral trunk, which is connected with the spiracle normally by a closed band. If we consider, that dorsal as well as visceral and ventral branches start from the lateral trunk, we see that a point of wiew

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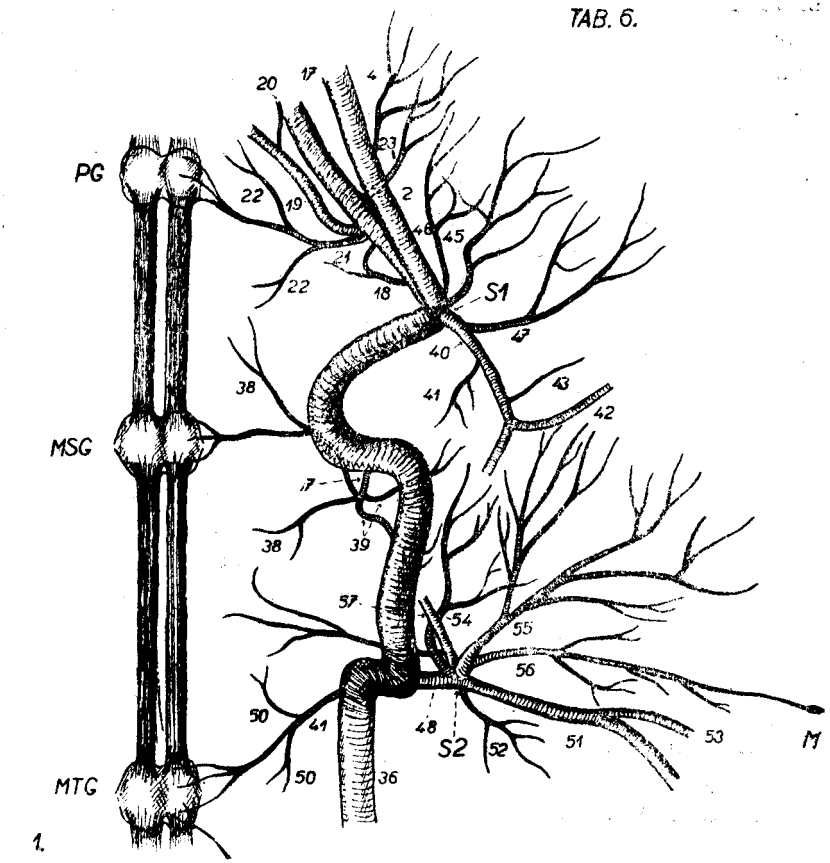
Fig. 1. Potamanthus luteus L. Tracheation of the thorax.
MSG — mesothoracic ganglium, MTG — metathoracic ganglium, PG — prothoracic ganglium, M — contact mallet, S 1 — spiracle 1, S 2 — spiracle 2.

Fig. 2. Potamanthus luteus L. Tracheation of bud of the forewing.
A — analis, CU_1 — cubitus 1, CU_2 — cubitus 2, M — media, R — radius, RS — sector radii, SC — subcosta.

Fig. 3. Potamanthus luteus L. Tracheation of bud of the hindwing.
A — analis, Cu — cubitus, M — media, R — radius, RS — sector radii, SC — subcosta.

Fig. 4. Potamanthus luteus L. Tracheation of the leg.
Tracheae are numbered according to the list in the chapter III.

TAB. 6.


PG
MSG
MTG
S1
S2
M
20
17
4
23
2
22
19
46
45
21
22
18
47
40
38
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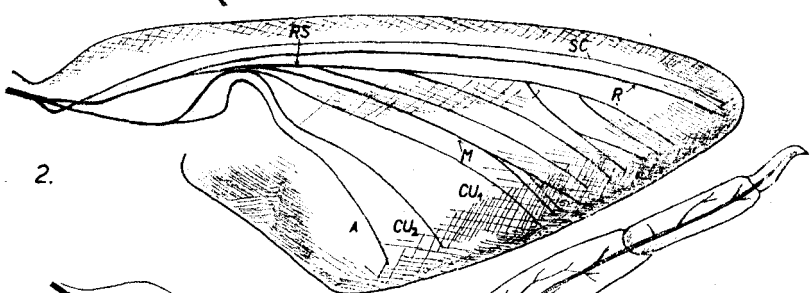
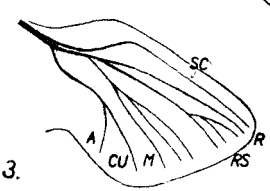
36

1.


RS
SC
R
M
CU1
A
CU2

2.


SC
A
CU
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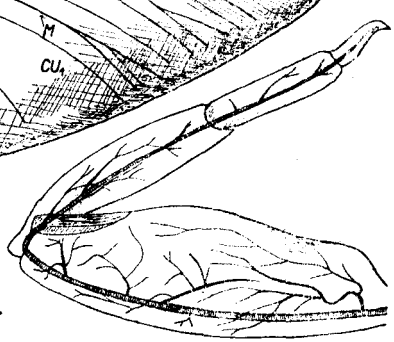
RS

3.



4.

regarding this trunk as a dorsal one is absurd. It is not possible that from the dorsal trunk, which originated by anastomosis of dorsal tracheae, there should start visceral or even ventral tracheae. Therefore I am suggesting a new name for this trunk: (tr. anastomotica longitudinalis lateralis) instead of dorsalis as given by ŠULC. This name has already been, used by some authors for similar organs in phylogenetically more developed insects. From the knowledge, gained in the study of the moulting of tracheal trunks and from some other facts I came to the conclusions, that the lateral trunk is not an ordinary anastomosis, but a quite special organ, superior to anastomoses and other tracheation.

a) Tr. ventralis stigm. 1.

It is a questionable trachea, therefore I am quoting it but not giving it a number. I found it at some specimens of *Potamanthus*, where it started near the knot at the first spiracle and tracheated the mesosternum. Its function is the same as that of tracheae leading from the main trachea going into the nerve ganglium. It probably is identical with them, only sometimes its point of insertion is shifted to the main trunk, as it by the way happens with other tracheae too.

b) Tr. neuralis ganglii mesothoracalis (37).

As can be seen from the diagram it starts from the trunk probably somewhere half way between the 1st and 2nd spiracle. At the *Oligoneuriella* it starts already from the narrow

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Fig. 1. Oligoneuriella rhenana Imhoff. (larva). Tracheation of the thorax. B — bubble-like widening in the mesothorax on the lateral trunk of larva of Oligoneuriella rhenana, MSG — mesothoracic ganglium, PTG — metathoracic ganglium, PG — prothoracic ganglium.

Fig. 2. Polymitarcis virgo Oliv. (larva). Tracheation of the thorax. B — U-like widening in the mesothorax on the lateral trunk of larva of Polymitarcis virgo, MSG — mesothoracic ganglium, MTG — metathoracic ganglium, PG — prothoracic ganglium, S 1 — spiracle 1, S 2 — spiracle 2.

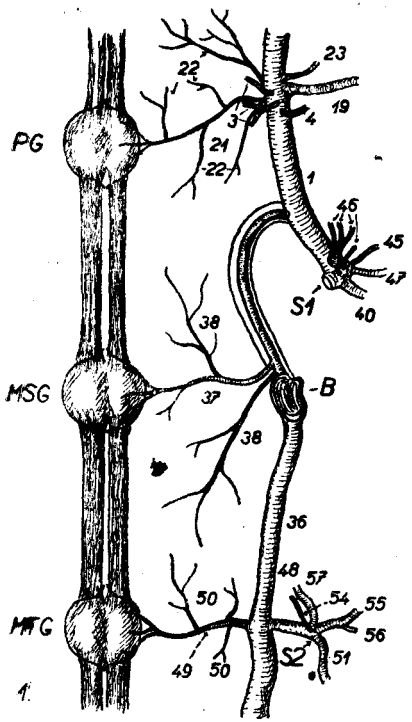
Fig. 3. Potamanthus luteus L. (larva). Palmen's organ. L — layers.

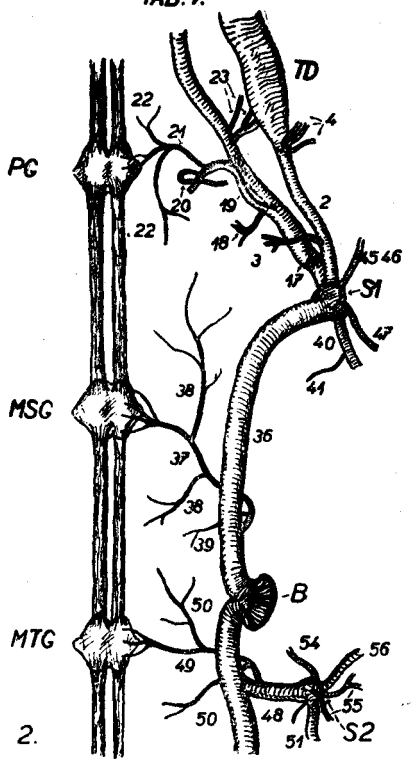
Fig. 4. Potamanthus luteus L. (larva). Contact mallet with layers in the shape of triaangles (see chapter IV). L — layers.

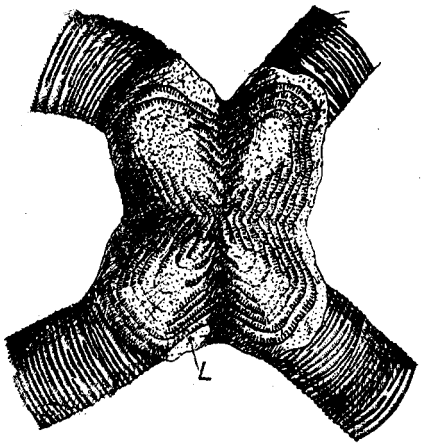
Fig. 5. Heptagenia flava Rostock. (larva). Contact mallet with layers in the shape of triangles (see chapter IV). L — layers.

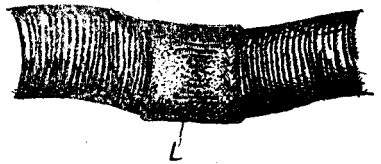
Tracheae are numbered according to the list in the chapter III.

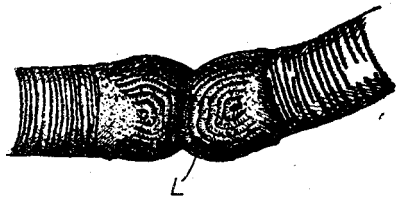
TAB. 7.











link behind the „buble". With flat and swimming larvae its point of insertion is shifted considerably forward. It supplies the mesothoracic ganglium.

a) Tr. mesosternales anteriores et posteriores (38).

They start from the last trachea (37), go forward and back and supply the muscles and the epidermis of the mesosternum. Sometimes (Oligoneuriella) they have a common trunk and start separately.

c) Tr. mesocoxalis (39).

This trachea usually starts from the tr. neuralis ganglii mesothoracalis (37) and only rarely has its own insertion on the trunk. It goes into the middle leg and into the coxa, which it tracheates. Sometimes it reaches even further into the leg. It can be best seen at burrowing larvae, but it is also developed at the crawling type. The swimming and flat larvae, whose legs are not subjected to such strain and have not so well developed coxas, do not have it at all or if they have it, it does not reach the coxa but gives an impression of one of the mesosternal tracheas. (See the foregoing paragraph.)

C. Tr. mesopedialis (40).

A strong trachea which separates at all genus from the knot at the first spiracle, goes backward where it turns in a vertical arc into the leg. There it branches in all directions into the muscles and epidermis (r. musculares et epiderma-

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Fig. 1. Ecdyonurus venosus Fabr. (larva). Tracheation of the thorax. MSG — mesothoracic ganglium, PG — prothoracic ganglium, S 1 — spiracle 1, S 2 — spiracle 2 (closed spiracles of the future imago).

Fig. 2. Heptagenia flava Rostock. (larva). Tracheation of dorsal side of the thorax.

MS — mesothorax, MT — metathorax, PT — prothorax.

Fig. 3. Baetis binoculatus L. (larva). Tracheation of sternits of the abdominal segments.

N — ventral nerve-cord, S 3 — spiracle 3, S 4 — spiracle 4, TG — places, on which the tracheal gills are fixed, I-II — abdominal segments I-II.

Fig. 4. Ephemerella ignita Poda (larva). Tracheation of abdominal segment IV and V (without visceral and gonadal branches).

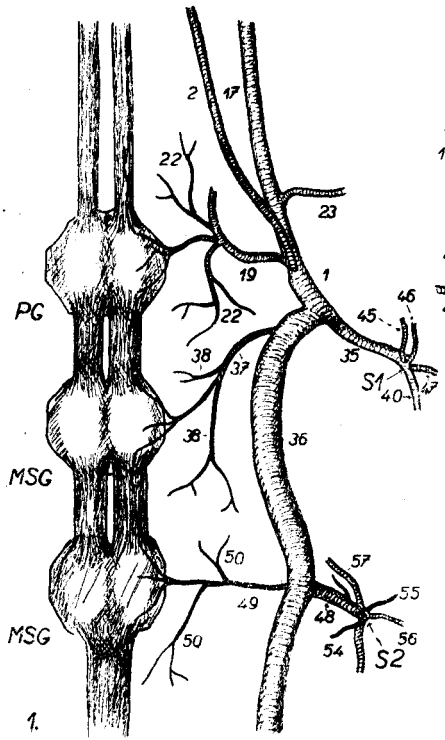
N — ventral nerve-cord, S 6 — spiracle 6, S 7 — spiracle 7, TG — places on which the tracheal gills are fixed, IV-V — abdominal segments IV-V.

Fig. 5. Potamanthus luteus L. (larva). Tracheation of dorsal side of the thorax.

MS — mesothorax, MT — metathorax, PG — prothorax, M — contact mallet.

Tracheae are numbered according to the list in the chapter III.

TAB. 8.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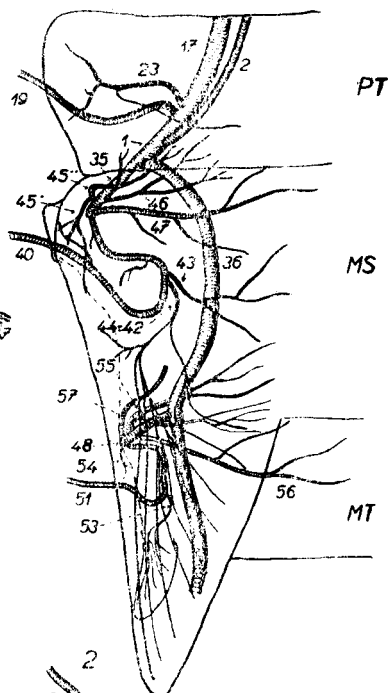
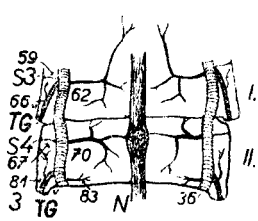
MSG
S1
S2
1.


PT
MS
MT
2


S3
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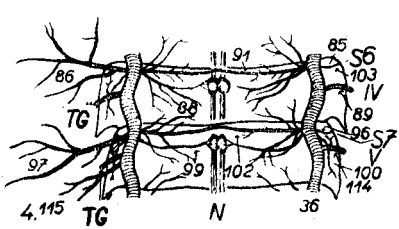
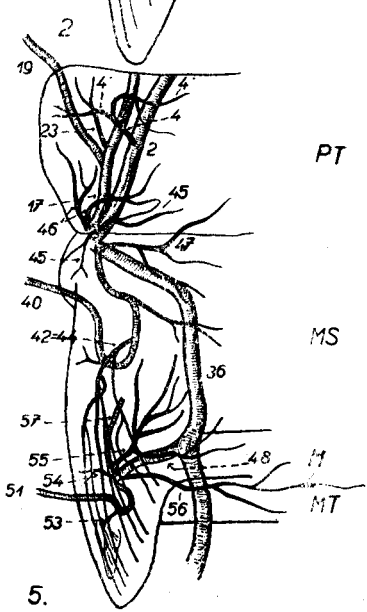
TG
N
I.
II.
3


S6
IV
S7
V
TG
N
4.115


PT
MS
MT
5.

les). In flat larvae with a broad femur a comparatively strong branch splits off there and carries on parallel with it.

1. Tr. mesosubcoxalis (41).

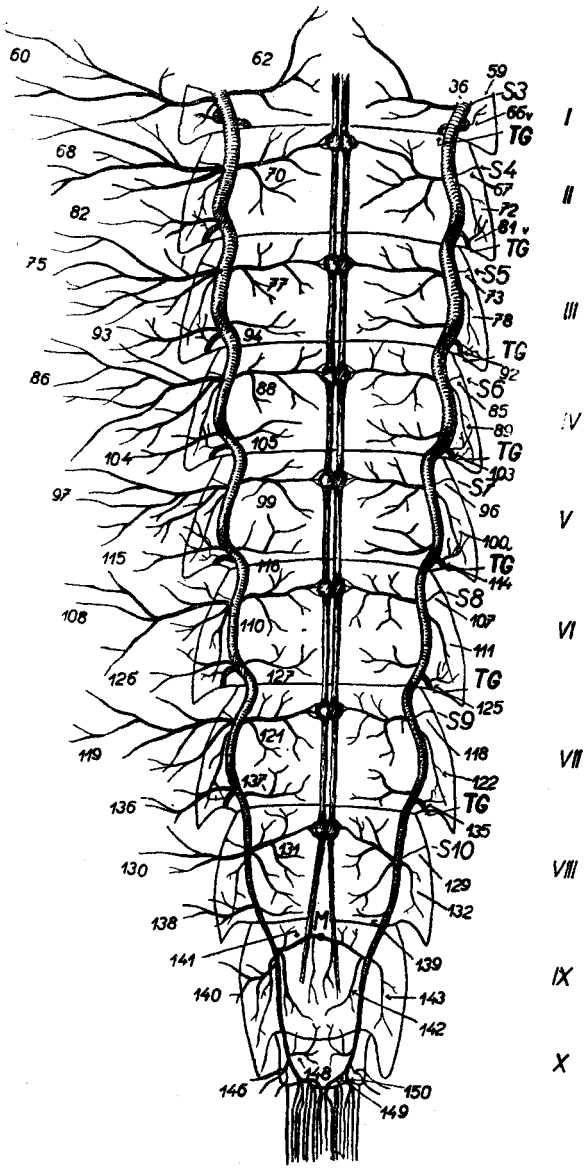
It starts from the beginning of the last trachea (40) and supplies the subcoxa.

2. Tr. mesoparatergalis posterior (42) — (43, 44).

A strong trachea which goes from the trachea leading into the middle leg in its vertical bend. Soon after the branching out a trachea supplying the dorsal part of the mesothorax and reaching right to the dorsal line (r. internus) branches off. The main branch goes into the wing bud, forming here two veins — the later venation of the wing. By detailed study I found on the *Potamanthus* buds that there originate first of all three branches corresponding to Sc, Rs, and Cu. From those then there start transverse veins which turn longitudinally, come together and form further veins. The Costa originates very much later. All veins then in the case of may-flies start from one trunk. It is an example of the original tracheation of a wing.

D. Tr. mesoparatergalis anterior (45).

It starts from the knot of the first stigma and reaches with its muscular branch (r. muscularis) into the prothorax, where it supplies the muscles, particularly in burrowing and crawling larvae. Some of the muscular branches and in particular the epidermal branch (r. epidermalis) remain in the mesothorax, where they spread under the front part of the mesoparatergit. ŠULC found in a young larva of the genus *Cloeon* that this branch originally reaches into the wing bud when this is being formed, and is squeezed out of it during the later growth. Only the tr. mesoparatergalis posterior takes then part in the building of the wing. As in phylogenetical more advanced insects the wing is tracheated by two branches, ŠULC assumes, that it is a proof, that this has been the case also originally with may-flies and that only secondarily the front tr. mesoparatergalis was displaced and only the rear one took part in the building of the wing. Although this wiew is well worked out, we cannot agree with it, because the tr. mesoparatergalis anterior and posterior cannot be homological with two trunks, which form the venation in phylogenetical more



Oligoneuriella rhenana Imhoff. (larva). Tracheation of the abdomen (without visceral and thoracic branches).

S3-S10 — future spiracles of the imago, TG — places on which the tracheal gills are fixed, I-X — abdominal segments I-X.

Tracheae are numbered according to the list in the chapter III.

developed insects. Here one trunk comes from the mesothoracic and one from the metathoracic spiracle. In case of mayflies both tracheae, which we are discussing, are only branches of a trachea starting from the mesothoracic spiracle only.

E. Tr. mesothoracalis muscularis (46).

It starts again from the knot at the first spiracle, branches out strongly and sometimes its branches are inserted separately *(Oligoneuriella)*. It reaches the prothorax and supplies the muscles.

F. Tr. dorsalis vasomuscularis mesothoracalis (47).

A very strong branch starting again from the knot at the first spiracle. Sometimes its point of insertion is shifted beyond the strong trachea leading into the leg. It branches out, but the main straight branch goes to the dorsal line where it adjoins the dorsal vessel.

Tracheae of the spiracle 2. — metathorax, mesothorax. — Tab. 6 (1, 3, 4), 7 (1, 2), 8 (1, 2, 5), 12 (1, 2), 13 (1, 2), 14 (1, 2).

A. Tr. arcus lateralis stigmatis 2 (48).

This is a short normally closed trachea on whose end there is a knot from which there lead all the important tracheae. The lateral trunk does not lead into the knot and it is connected with it by means of a strong link which we may also regard as part of the tr. arcus lateralis stigm. 2.

1. Tr. anastomotica longitudinalis lateralis stigm. 2 (36).

See the same number at spiracle 1.

a) Tr. ventralis stigm. 2.

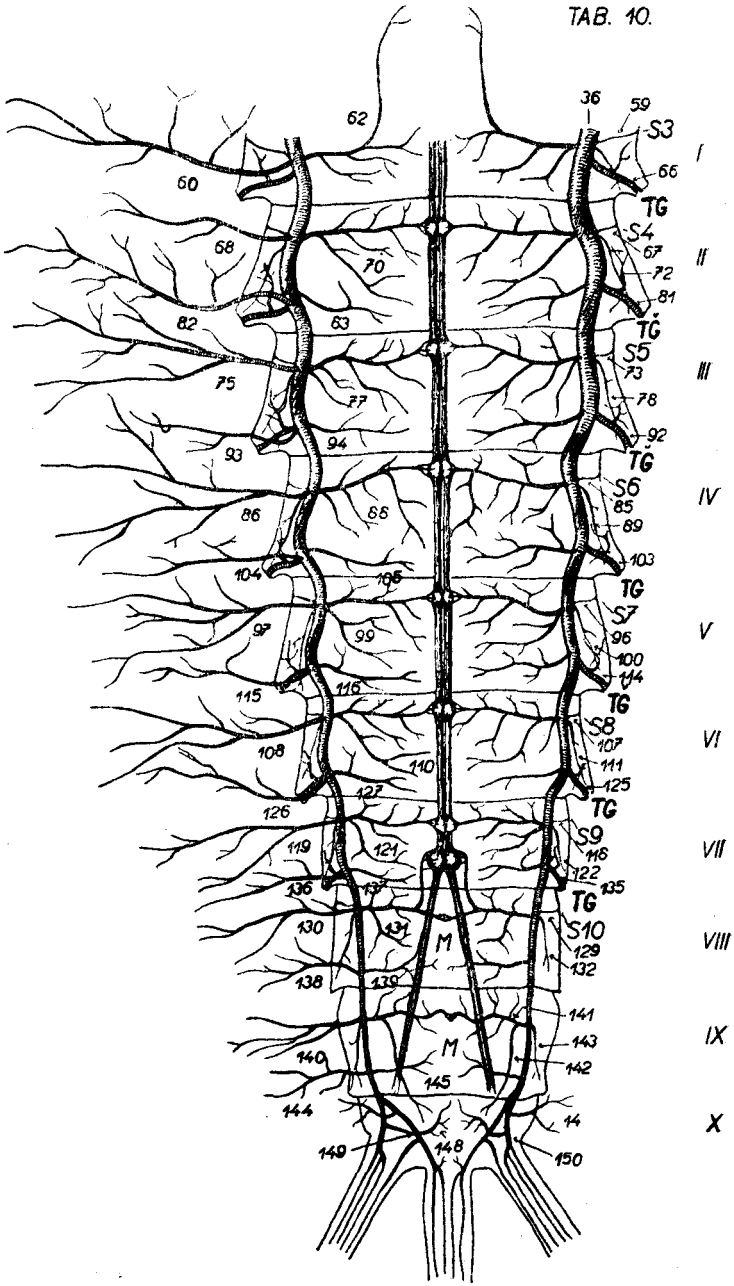
See the same trachea at spiracle 1. The conditions are similar.

b) Tr. neuralis ganglii metathoracalis (49).

It starts from the trunk opposite to the place, where this is connected by a link with the second spiracle, sometimes *(Polymitarcis)* it still starts directly from this link. It supplies the metathoracic ganglium.

a) Tr. metasternales anteriores et posteriores (50).

They supply the metasternum. Conditions similar to number 38.



Heptagenia flava Rostock. (larva). Tracheation of the abdomen. (without visceral and thoracis branches).

M — contact mallet, S 3-10 — spiracles 3-10, TG — places on which tracheal gills are fixed, I-X — abdominal segments I-X.

Tracheae are numbered according to the list in the chapter III.

B. Tr. metapedialis (51).

It starts from the knot of the second spiracle and after a vertical arc it enters the rear leg. Otherwise conditions are the same as at number 40.

1. Tr. metasubcoxalis (52).

It branches off at the beginning of the tr. metapedialis and supplies the subcoxa under same conditions as in spiracle 1.

2. Tr. metaparatergalis posterior (53).

It leads from the leg trachea into the hind wing. See similar trachea number 42 from the mesothorax.

C. Tr. metaparatergalis anterior (54).

See similar trachea number 45 in the mesothorax.

D. Tr. metathoracalis muscularis (55).

Particularly strongly developed, because it supplies the strong muscles of the future wings. It widens particularly before the subimago moulting.

E. Tr. dorsalis vasomuscularis metathoracalis (56).

Similar to the trachea number 45. At burrowing larvae of the *Potamanthus, Ephemera* and *Polymitarcis* type, the branches going against each other touch in the dorsal line and form the contact mallet. In this way the tr. anastomotica dorsalis stigm. 2 (Tab. 8, fig. 5) originate.

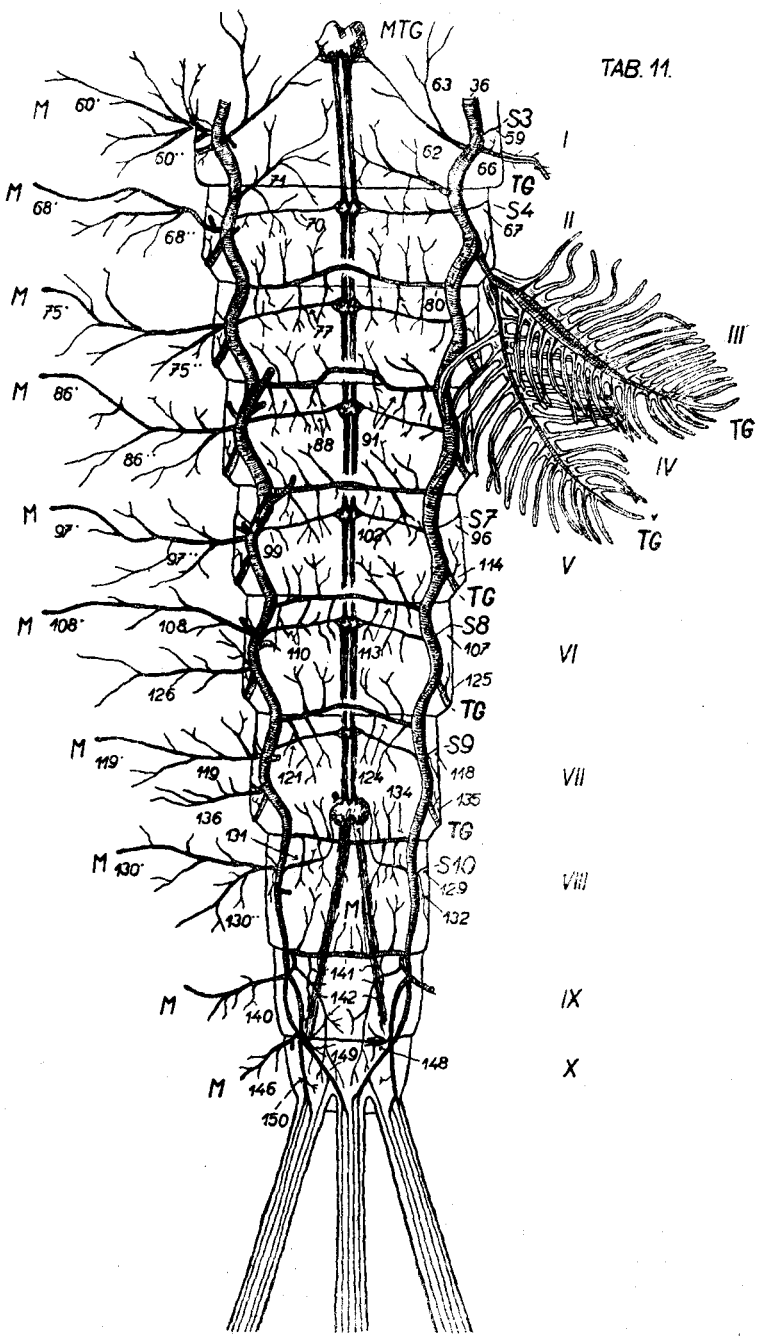
F. Tr. visceralis stigm. 2 (57).

A strong trachea clinging to the digestion tract. It has three branches (R. anterior, medius, posterior). It does not exist at the larva of the *Polymitarcis virgo* type and at the larvae of the genus *Caenis*. Mostly it leads only forward, at the species of the *Ephemerella* and *Torleya* genus it reaches far into the abdomen.

G. Tr. gonadarum (58).

It exist at the *Baetis* genus only and is quite strongly developed there. At this phylogenetically young and specialized genus the gonads reach far into the thorax and are here supplied by this trachea.

Potamanthus luteus L. (larva). Tracheation of the abdomen (without visceral and thoracic branches).
MTG — metathoracic ganglium, M — contact mallet, S 3-10 — spiracles 3-10, TG — places, on which tracheal gills are fixed, I-X — abdominal segments I-X.
Tracheae are numbered according to the list in the chapter III.


TAB. 11.
MTG
M
60'
50''
63
36
S3
59
I
62
66
TG
71
S4
67
II
68'
68''
70
M
75'
80
77
III
75''
M
86'
TG
88
91
86''
IV
M
97'
S7
96
TG
99
102
97''
114
V
TG
M
108'
108
S8
110
113
107
VI
126
125
TG
M
119'
S9
119
121
124
118
VII
134
135
136
TG
131
M
130'
S10
129
VIII
130''
M
132
141
M
142
IX
140
149
148
X
M
146
150

Tracheae of the spiracle 3. — abdominal segment I, metathorax. — Tab. 9, 10, 11, 12 (1, 2), 13 (1, 2), 14 (1, 2).

A. Tr. arcus lateralis stigm. 3 (59).

All the links of future spiracles with the tracheal trunk are at all the abdominal segments (where of course they are, t. i. I.—VIII.) quite equal. In principle they agree with those, which we have described at the spiracles 1 and 2. They differ only in that, that not all the body tracheas start from the knot former at their end, but from the lateral trunk, from which the link starts. After the moulting the spiracles always grow together and the links are drawn together into bands. Not even during the last moultings of the larvae do they remain open as it is the case with both thoracic spiracles and links.

1. Tr. anastomotica longitudinalis lateralis stigm. 1—10 (36).

See the same number at stigm. 1. All the body tracheae in abdominal segments start from two insertion rings. The first main insertion band is in the place, where tr. arcus lateralis joins the trunk. The second one is in the rear portion of the segment, its branches are weaker but the same as in the first ring. It is in the place where the strong trachea branchialis starts from the trunk. The tracheae of this second ring belong as far as the development is concerned always to the spiracle of the following segment, as can be ascertained from the moulting of the tracheae.

a) Tr. dorsalis (60).

It starts from the first insertion band and goes along the dorsal side to the middle dorsal line. It branches out in the epidermis of the dorsal parts of the segments and probably

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Fig. 1. Oligoneuriella rhenana Imhoff. (larva). Tracheation of the alimentary canal and of the gonads.

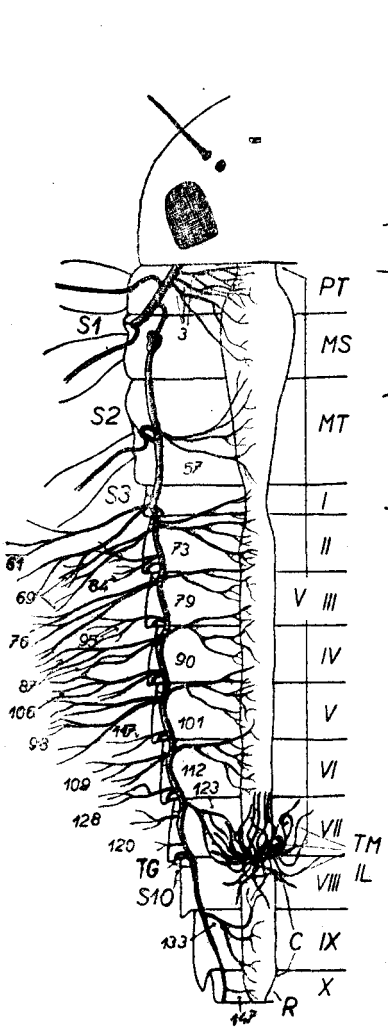
C — colon, TM — Malpighian tubes, MS — mesothorax, MT — metathorax, PT — prothorax, IL — ileum, R — rectum, V — mid-intestin, S 1-10 — future spiracle of the imago, TG — places, on which tracheal gills are fixed, I-X — abdominal segments I-X.

Fig. 2. Ecdyonurus venosus Fabr. (larva). Tracheation of the alimentary canal and of the gonads.

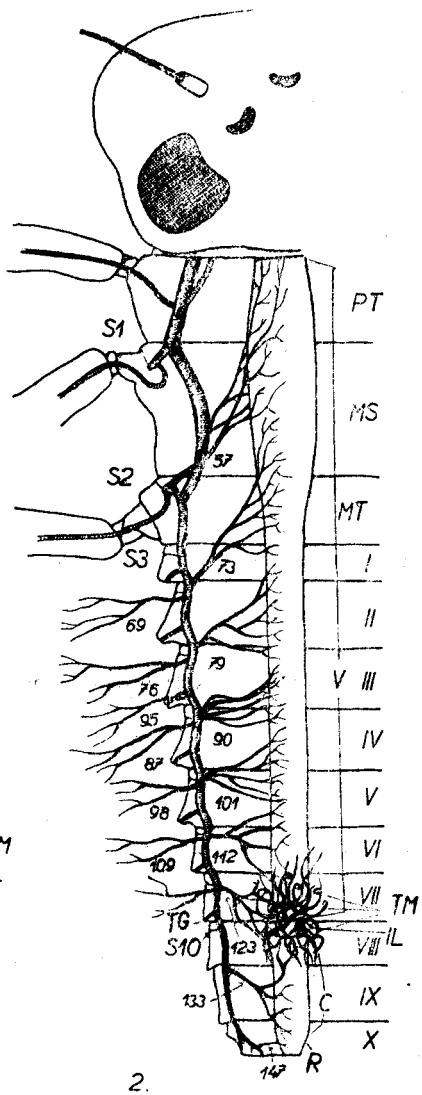
C — colon, IL — ileum, TM — Malpighian tubes, MS — mesothorax, MT — metathorax, PT — prothorax, R — rectum, V — mid-intestin, S 1-10 — future spiracle of the imago, I-X — abdominal segments I-X.

Tracheae are numbered according to the list in the chapter III.

TAB. 12.


PT
MS
MT
I
II
V III
IV
V
VI
VII
VIII
C IX
X
TM
IL
S1
S2
S3
TG
S10
R
3
57
73
79
90
101
112
123
133
147
61
69
76
87
98
106
109
120
128

1.


PT
MS
MT
I
II
V III
IV
V
VI
VII
VIII
C IX
X
TM
IL
S1
S2
S3
TG
S10
R
57
73
79
90
101
112
123
133
147
69
76
87
95
98
109

2.

has an important significance at skin respiration. At larvae of the *Potamanthus, Ephemera* and *Polymitarcis* type, two of the against each other leading branches join in the dorsal line and form the contact mallet.

b) Tr. gonadarum (61).

It supplies at all the genus and species the organs of distribution. It is particularly strongly developed at the genus *Caenis.* Here namely, the same as in the case of *Baetis,* the internal genitalia reach far into the thorax right to the occipital opening. Tr. gonadarum from the mesothorax, the same as in *Baetis,* does not exist here, and therefore, this trachea from the third spiracle is strongly developed and passes through the whole thorax.

c) Tr. neuralis gangl. segm. abd. I (62).

It starts from the first insertion ring and leads forward into the metathoracic ganglium. It is the best proof, that the original ganglium of the first abdominal segment joined during the phylogenetical development the metathoracic ganglium. It sends out forward and back into the muscles and epidermis branched out branches. (Rami musculares et epidermales.)

d) Tr. metacoxalis (63).

It is a very interesting trachea, because it leads away from the foregoing trachea and goes into the coxa of the last leg in the metathorax.

e) Tr. pedialis (64).

A very weak trachea starting on the underside of the first ring. It leads back and is particularly developed at those species whose segments are broad and drawn out in the rear into a tooth. It is not sure, whether this small trachea is homological with similar tracheas of the thorax, but I am using this name, as this has already been used by ŠULC.

f) Tr. visceralis (65).

Only at the larvae of the *Baetis* and *Cloeon* genus.

g) Tr. branchialis (66).

A strong trachea connecting the trunk with the tracheal gills. Still in the body it sends out a branch into the muscle moving tracheal gills. (r. muscularis). In the tracheal gills it

branches out both in the filaments as well in the lamellae (r. tracheobranchales). In the first abdominal segment the interesting point about the trachea is, that it moults through the stigma of the same segment. This is not the case at all the others; there all these tracheae are moulted through the following spiracles.

Tracheae of the spiracle 4. — segment abdom. II.

c) Tr. neuralis gangl. segm. abd. 2 (70).

It supplies the ganglium of this segment. If it is shifted into the first segment, it reaches out beyond it. This is the case with all abdominal segments, where the ganglia are shifted. The tracheae follow them from the places at those segments where they have been originally, even over three segments. (See the genus *Caenis*, tab. 15, fig. 1.)

d) Tr. ventralis (71).

At the genus without ventral anastomoses branches, starting from the foregoing trachea supply the sterna of the segments. At the genus with commissures there exists moreover in this segment the tr. ventralis, which is in the place, where on the other segments there are anastomoses.

f) Tr. visceralis (73).

Does not exist at burrowing and crawling larvae.

For other tracheae see stigm. 3.

Tracheae of the spiracle 5. — segment abd. III, II.

e) Tr. visceralis (79).

Does not exist at the genus *Potamanthus, Ephemera, Polymitarcis, Caenis, Ephemerella, Torleya.*

f) Tr. dorsalis praeposita (82).

It starts from the second insertion ring. It supplies the same as a similar trachea from the first ring the dorsal side of the segment, but it never forms commissures.

i) Tr. ventralis praeposita (83).

A small trachea starting from the second ring and branching out in the sternum.

j) Tr. gonadarum praeposita (84).

It also starts from the second ring and has the same task

as the similar trachea from the first ring. Not all the tracheae of the second ring are always developed and their presence varies even at different specimens of the same species. They are best developed usually at flat larvae.

For other tracheae see spiracles 1, 2, 3, 4.

Tracheae of the spiracle 6. — segment abd. IV, III.

Tr. visceralis (90).

Strongly developed particularly at the larvae *Potamanthus. Ephemera, Polymitarcis,* where they reach along the digestive tube right to the head.

For other tracheae see spiracle 5.

Tracheae of the spiracle 7. — segment abd. V, IV.

See tracheae spiracle 5.

Tracheae of the spiracle 8. — segment abd. VI, V.

e) Tr. visceralis (112).

This branch sends branches already back to the Malpighian tubules (r. tubularum Malpighii). At the genus *Caenis,* where the Malpighian tubules reach far forward, they are of course supplied also by branches from the visceral tracheae of the foregoing segments.

For other tracheae see spiracle 5.

Tracheae of the spiracle 9. — segment abdominal VII, VI.

e) Tr. visceralis (123).

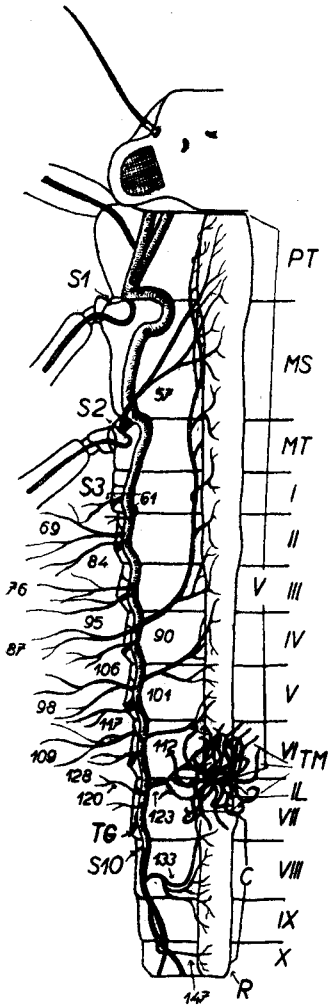
Most of their branches go into the Malpighian tubules (r. tubularum Malpighii).

For other tracheae see spiracle 5.

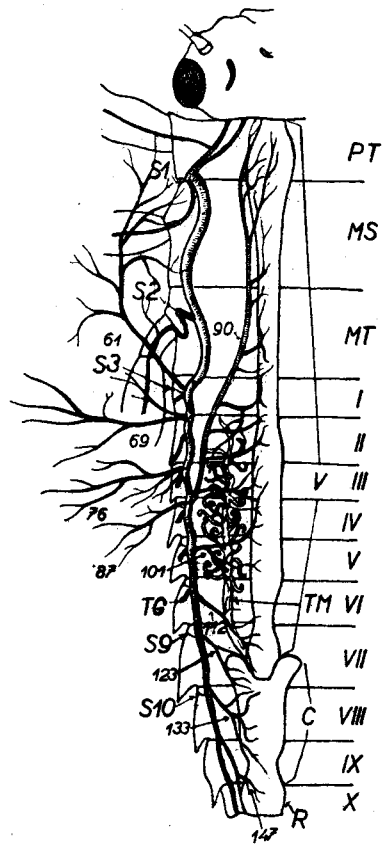
Tracheae of the spiracle 10. — segment abdominal VIII, VII, IX, X.

e) Tr. anastomotica ventralis (134).

It exists at burrowing and crawling larvae. At larvae without commissures it grows only at *Heptagenia* and then only in their later larve stages. The tracheae in the abd. segm. VIII, IX start from two insertion rings the same as the



1.



2.

Fig. 1. Potamanthus luteus L. (larva). Tracheation of the alimentary canal and of the gonads.

C — colon, TM — Malpighian tubes, MS — mesothorax, MT — metathorax, PT — prothorax, R — rectum, S1-10 — future spiracles of the imago, TG — places, on which the tracheal gills are fixed, I-X — abdominal segments I-X, V — mid-intestine, IL — ileum.

Fig. 2. Caenis horaria L. (larva). Tracheation of the alimentary canal and of the gonads.

C — colon, TM — Malpighian tubes, MS — mesothorax, MT — metathorax, PT — prothorax, V — mid-intestine, S1-10 — future spiracles of the imago, TG — places, on which the tracheal gills are fixed, I-X — abdominal segments I-X.

Tracheae are numbered according to the list in the chapter III.

tracheae of the other segments, although there are no spiracles (in segm. IX, X) and no tracheal gills (in segm. VIII,, IX). The regular distribution of the tracheae and of their insertion rings proves, that the stigmas and tracheal gills have been also here sometime ago. The tracheae numbers 138, 139, 140, 133, 141, 143, 144, 145, 146, 147, 148 correspond to similar tracheae of other abdominal segments, which have both the spiracles and the tracheal gills. We shall quote only the more important ones and special ones.

n) Tr. visceralis (133).

It starts always from the trunk on the boundary between segments VIII an IX from the places, where there has been the original spiracle 11, which has disappeared already nowadays. It is a trachea surrounding with its branches the colon of intestine. Perhaps it is important for intestine respiration. At the genus, where the tracheation shows signs of irregularity *(Potamanthus, Ephemera)* the point of insertion of this branch is sometimes shifted right to the position of the first ring of the spiracle 10.

o) Tr. anastomotica ventralis sgm. abd. IX (141).

It exist at swimming and flat larvae where it originates till during the larva development. Further we find it at the larvae of the genus *Potamanthus, Ephemera* and *Polymitarcis.*

p) Tr. ducti seminalis (142).

Only at males. It separates from the last ventral anastomosis or starts directly from the trunk. It supplies the testis and the genital duct.

u) Tr. visceralis sgm. abd. X. (147).

Fig. 1. Polymitarcis virgo Oliv. (larva). Tracheation of the alimentary canal and of the gonads.

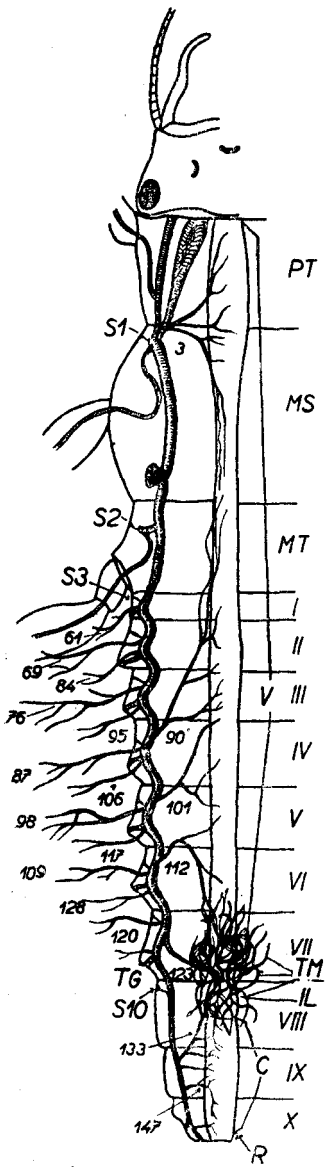
C — colon, IL — ileum, TM— Malpighian tubes, MS — mesothorax, MT — metathorax, PT — Prothorax, R — rectum, V — mid-intestine, S1-10 — future spiracles of the imago, TG — places, on which the tracheal gills are fixed, I-X — abdominal segments I-X.

Fig. 2. Ephemera danica Müll. (larva). Tracheation of the alimentary canal and of the gonads.

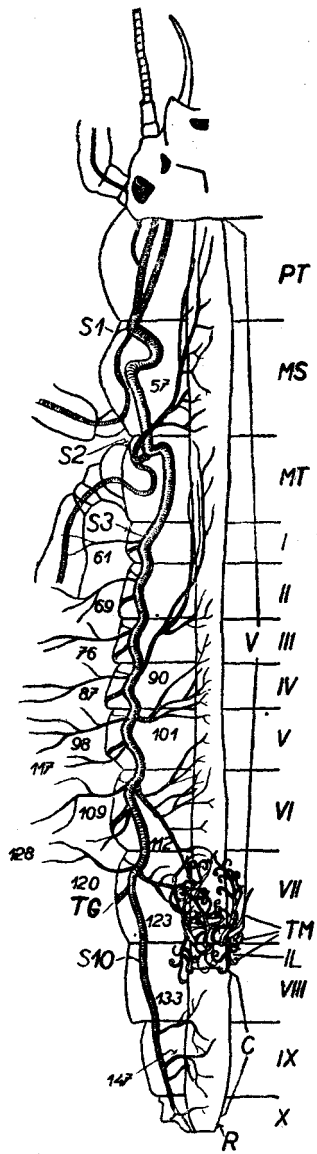
C — colon, IL — ileum, TM — Malpighian tubes, MS — mesothorax, MT — metathorax, PT — prothorax, R — rectum, V — mid-intestine, S1-10 — future spiracle of the imago, TG — places, on which the tracheal gills are fixed, I-X — abdominal segments I-X.

Tracheae are numbered according to the list in the chapter III.

TAB. 14.


PT
S1
3
MS
S2
MT
S3
I
61
II
69
84
V
III
76
95
90
IV
87
106
101
98
V
117
109
112
VI
128
120
VII
TM
TG
123
IL
S10
VIII
133
C
IX
147
X
R

1.


PT
S1
MS
57
S2
MT
S3
I
61
II
69
V
III
76
90
87
IV
98
101
V
117
109
VI
128
112
120
VII
TG
123
TM
S10
IL
VIII
133
C
IX
147
X
R

2.

It goes into the rectum either directly from the trunk, or even from the branch leading into the medial caudal filament.

x) Tr. cerci medialis (149).

The main trunk is divided sometimes already on the border of segm. VIII, IX. The trachea leading into the medial filament sends out a branch into the lateral cercus. It branches out further in the medial filament.

y) Tr. cerci lateralis (150).

It goes into the lateral cercus where it branches out into three branches.

Summary of the basic signs of the tracheal system.

Head.

Two head trunks — the dorsal and the ventral one — lead into the head. Immediately after their entrance both send out a strong transverse anastomosis. The anastomoses join in the Palmen's organ. From the dorsal anastomosis there start forwards and back branches supplying muscles, the filling tissues behind the brain and the epidermis of the epicranium. The trunk itself continues and soon there starts a trachea strongly branched at the end going into the eye brain-lobes. In the place, where the forward going dorsal trunk passes the brain it sends into it the brain trachea. Before this, two little branches going into the pharynx and oesophagus start out. The terminal branch of the dorsal trunk branches out in the clypeus and a offspring of this branch reaches into the labrum. In the place where the above mentioned branch leading into the pharynx starts, the trunk bends downward and forms an anastomosis with a simple branch leading from the mandible. This anastomosis may be for comparative anatomy and the head development very important, because it probably is the anastomosis between the original head segments. The ventral head trunk sends out after coming through the occipital opening a strong trachea into the lower part of the strong mandibular muscle branches off. (tr. abductoris mandibulae). This branch also starts often separately. From the anastomosis leading from the ventral branch into the Palmen's organ there starts small branches, which join the front part of the mid-intestine. The trunk continues and through

a small branch it supplies the oesophagus and through a larger one the suboesophageal ganglium. The main part of the trunk branches out in the mandible and goes on into the maxil, hypopharynx and labium. From the mandibles there starts a trachea forming a longitudinal anastomosis with the dorsal trunk which we have mentioned already. In the middle

TAB. 15.

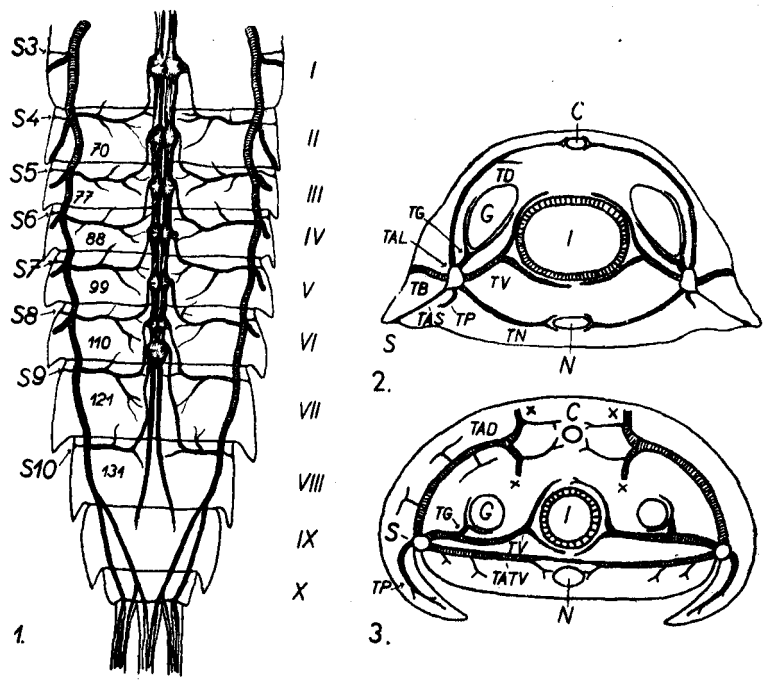


Fig. 1. Caenis horaria L. (larva). Ventral nerve-cord in the abdomen and its tracheation.

S 3-10 — future spiracles of the imago, I-X — abdominal segments I-X.

Fig. 2. Heptagenia flava Rostock. (larva). Scheme of the tracheation of abdominal segments on cross-section.

C — dorsal vessel, G — gonads, I — alimentary canal, N — ventral nerve-cord, S — closed spiracles of the future imago, TAL — tr. anastomotica longitudinalis lateralis stigm. 1-10, TAS — tr. arcus stigmatis, TB — tr. branchialis, TD — tr. dorsalis, TG — tr. gonadarum, TN — tr. neuralis, TP — tr. pedialis, TV — tr. visceralis.

Fig. 3. Lepisma saccharina L. (larva). Tracheation of the first abdominal segment on cross-section (after Šulc).

S — spiracle, TAD — tr. arcus dorsalis, TATRV — tr. anastomotica transversa ventralis, TP — tr. paratergalis, TV — tr. visceralis, x (cross) — tr. anastomotica longitudinalis dorsalis.

Tracheae are numbered according to the list in the chapter III.

where the against each other going tracheae join, there is the contact mallet.

The differences in the tracheation of the head of various genus are obvious from the foregoing description of the tracheae and from tables 1—5. Burrowing larvae and among the crawling ones *Potamanthus* have in principle a tracheation as described above. The ventral branch finishes really in the strong mandible and only a secondary branch leads into the labium, maxil, and hypopharynx. Ephemera has the front simple eye strongly shifted forward and therefore it is supplied by separat branches of the dorsal trunk. The branches touch behind it in the middle and form thus the contact mallet in the head. In the head of *Polymitarcis* there are 10 thinwalled air sacs. Swimming larvae and larvae of the *Leptophlebiidae* family do not have a longitudinal anastomosis in the head. The tracheation of the swimming ones is adapted to the hypognathous head. The branches starting from the anastomosis, which goes back towards the Palmen's organ, are particularly prominent. They supply the arched epicranium. Flat larvae with a strongly developed clypeum have many veins starting from the longitudinal anastomosis and branching out here. Among the mouth-parts the labium is prominent and therefore the main branch of the ventral trunk leads into it, whereas only an offspring goes into the mandible. At *Oligoneuriella,* shown on tab. 1, the conditions are complicated by the fact that the larva of this genus has tracheal gills on its head.

Thorax.

On the thorax there exist two future spiracles of the imagoes which are closed at the larva stage. Tracheal gills do not exist here (at least not at our genus) and air for the thorax is supplied by tracheal gills from the abdomen. (At *Oligoneuriella* the prothorax is supplied by tracheal gills on the head.) The tracheas are concentrated round both spiracles (in the mesothorax and metathorax), connected by a strong lateral trunk. From the knot of the first spiracle, as it already has been mentioned, there start two head trunks: the ventral and the dorsal one. Both branch out for the supply of the prothorax. From the lower one there starts a strong trachea leading into the front leg. At flat and cylindrical larvae there do not

start any branches from the dorsal trunk. The muscular and the mesoparatergal branches start directly from the knot and lead forward into the prothorax; these supply the muscles and epidermis. A branch turning into the middle leg leads backward. A branch going into the wing bud leads out of it. It branches out there and forms the venation of the future wing. The Ephemera wing is tracheated only by this one trachea from the first stigma, whereas the wing of other phylogenetical more developed insects is tracheated by two tracheae: one from the first and one from the second spiracle. The prothoracic ganglium is tracheated by a trachea from the lower head trunk and into the mesothoracic ganglium there leads a trachea from the lateral trunk about half way between the first and second spiracle. The nerve tracheae send out branches supplying the thoracic sternum. The conditions at the second spiracle in the mesothorax are similar to those at the first one. The alimentary canal is tracheated by a strong branch from the metathorax. Only at *Oligoneuriella* and *Polymitarcis* there is still another branch leading from the dorsal head trunk in the prothorax. The branch in the mesothorax at the genus *Polymitarcis* and *Caenis* is missing.

Abdomen.

Two strong lateral trunks pass through the whole abdomen. In segments I—VIII they are connected by narrow bands — closed tracheae — with the places of the future spiracles of the imagines. The tracheal system is moulting through these spiracles. The tracheal gills exist on segments I—VII, at the genus *Caenis* I—VI, at *Ephemerella* and *Torleya* on segments II—VI. The tracheae always start from insertion rings on lateral trunks. The main one is at the place, where the already mentioned band joins the trunk. From the trunk there start the dorsal branch, the ventral branch finishing in the ganglium, the visceral branch and the branch leading into the gonads. In the second ring, which is in the place where the trachea branchialis starts, these branches are repeated in a smaller scale or they may be missing altogether. The ventral commissures are the basic sign through which the tracheation of various genus differs. These exist at larvae of the genus *Potamanthus* in segments III—IX, at larvae of the

family *Leptophlebiidae* and at the genus *Ephemerella* and *Torleya* in segments III—VIII. At flat and swimming larvae the commissure is only in the ninth segment, at *Heptagenia* also in the eighth segment. The gonads are tracheated regularly from each segment, only at the genus *Baetis* there leads into them another trachea from the mesothorax. The alimentary canal is at swimming larvae supplied from all abdominal segments. This is also the case with flat larvae with the exception of a branche from the first segment. At the larvae of the family *Leptophlebiidae* the branches from segments I and II are missing. At the genus *Caenis, Ephemerella, Torleya, Potamanthus, Ephemera* and *Polymitarcis* is in abdomen the first visceral branch in the segment IV. At the genus *Caenis, Potamanthus* and *Ephemera* goes this along the alimentary canal right to the head.

The tracheal gills are well described and illustrated in various studies. Therefore they are not described here.

IV. THE STRUCTURE OF THE TRACHEAL SYSTEM.

The structure of the tracheae of may-fly larves is quite equal to the structure in other insects. The matrix, which is in action for the whole time of the larval development, stands out after borax-carmine or Ehrlich staining. Its cells are hexagonal with large nucleus. In the intima there predominantes exocuticula forming tenidium. On lateral trunks, where the intima tears during moulting, the tenidium is interrupted and the intima forms here a narrow white band without texture. Otherwise the tenidium is uninterrupted.

Widenings of the Tracheae. Tab. 7, figs 1, 2.

On the lateral trunk of the larva of the species *Oligoneuriella rhenana* there is a bubble-like widening in the mesothorax. (Tab. 7, fig. 1.) It forms the end of the wide lateral trunk going from the abdomen. From there on the trunk carries on only by a narrow band again to a wide trunk in the prothorax. At present it seems that this widening has no significance for the function of the tracheae and for the life of the larva in general. It is however very interesting and important from the point of wiew of comparative anatomy of the tracheal system. Its wall is not thinned so that we are not

dealing here with an air sac. The tenidium, equally strong as in the other parts of the trunk, passes without a change in direction only at side turned toward the nervous ganglium. On the outer side its fibres turn longitudinally. By comparison with other places where strong tracheae join the trunk, we see that the tenidium is also here formed in exactly same way. The bubble is during moulting drawn out through the second stigma. Its position and the texture of the tenidium corresponds, comparing it with conditions in abdomen, exactly to the fact, that some time ago (in a phylogenetical development) a strong trachea branchialis started here, leading to the tracheal gils, which were also here in the mesothorax. If we consider that *Oligoneuriella rhenana* is a relict, whose anatomic conditions are substantially original, this explanations becomes acceptable. Anyhow the larva of closely related species *Isonychia ignota* has still now tracheal gills even on the prothorax.

About in the same place the species *Polymitarcis* has a similar outward pointing widening. The widening gives the impression of a bend of the trunk into the shape U, whose arms got near to each other. The tenidium goes regularly transversely and we cannot fix from its course the position of the joint of a possible original trachea. But even so we can judge from this, that there has been a change in the trunk in this place. The larva with commissures in the abdomen, particularly *Ephemera* and *Potamanthus* have the trunk in the mesothorax bent in a loop. Other genus have it straight. *Polymitarcis virgo* has still another widening on the trachea cephalica dorsalis. This widening is flat, because the trachea is enlarged in one direction only, whereas in the perpendicular direction it remains equally wide. Again it is not an air sac, because the thick walls do not differ in any way from the walls of the rest of the trunk. Its significance will probably by the same, as that of air sacs in the head of this larva.

Air-Sacs, Tab. 5.

At the larva of the species *Polymitarcis virgo* I found 10 big air sacs in the head. It is the first case, when these have been found at may-flies at all. They do not exist in any others species which I dissected not even to the closely re-

lated *Ephemera*. On each side of the head there are two sacs on the dorsal trunk and two on the ventral trunk. Further the link of the lower branch with the Palmen's organ is widened into a sacs. The sacs have thin walls. They are compressible and can be blown up by air. The nucleus of the matrix can be well stained. A fine but visible tenidium passes through the sacs and is drawn out during moulting. The sacs on the link with the Palmen's organ are closed to the alimentary canal. Because there are none of the several tracheae, which start at other species from this link and which supply the alimentary canal, it seems that the tracheation is somehow done directly by the thinwalled air sacs. Perhaps also from the other sacs oxygen may penetrate into the neighbouring muscles. Otherwise I do not know for certain the purpose of the air sacs. The biology of the *Polymitarcis* larvae is not fully known. I studied their way of life on the river Berounka at Srbsko, but not in special relation to the air sacs about which I did not known then. The larva has strong forward projecting mandibles and a big strongly chitinous head. Perhaps the air sacs serve for its lightening. Lastly they may play a certain part during the subimago moulting, which takes place in this case on the water surface. The air accumulated in them and the bubble in the alimentary canal bring the larva easily to the water surface. On the other hand it remains of course a fact, that the genus *Ephemera*, which also has a big head with proturbing mandibles and which also flies out from the water surface does not have similar sacs. The air sacs of the species *Polymitarcis virgo* deserve for their importance the attention in the future.

Commissures and Contact Mallets.

May-flies have two kinds of anastomoses: transverse and longitudinal; the slanting ones are missing. The longitudinal anastomosis is formed by a strong lateral trunk, which is analogical with similar ones in more advanced insects. Apart from this, there are however further anastomoses, which have not mostly been known so far. They are listed in chapter III. There are two longitudinal at some species in the head, two transverse ones go in all species to the Palmen's organ, there are other transverse ones in the abdomen of many species

(see chapter III and tables). If we clear the anastomoses from the abdomen of the *Potamanthus luteus* larva, we see that they are really unpassable and that in the center there are fine layers, filling two triangles put on top of each other as a sand-glass (Tab. 7, fig. 4). The matrix is in this part thickened and on the anastomosis there is visible a wide band. We can understand the origin of layers best by remembering the forming of the anastomoses and their growth in the width during the moulting of the tracheation. From both lateral trunks there grow against each other tracheae, which join and grow together in the middle. This place is covered by a stronger matrix. During moulting there remains in the middle the intima always in a wider and wider band unmoulted and so during further and further moulting these triangles or as we call them the contact mallets are formed. The contact mallet in the shape of triangles, one of which is shown on tab. 7, fig. 4, we can find on the commissures of *Potamanthus, Ephemera* and *Polymitarcis.* They are formed then, when two trachea are going against each other already in the embryonal time or still when the larva is young and the tracheae are narrow. We have a very good example of the forming of contact mallets at the genus *Ecdyonurus* and mainly at the genus *Heptagenia.* As one can see from tab. 10, *Heptagenia* has a commissure in 9th and 8th abdominal segment. The commissure in the segment VIII is being formed much later, sometimes in the one but last larval stage. I several times watched how the tracheae, which have on their ends a considerably widened mallet grow against each other. Finally the mallets touch and the matrix grows round them. A shape with layers is being formed, but of a somewhat different kind than the shape of triangles (Tab. 7, fig. 5). Of this kind are the contact mallets in the ninth segment of flat and swimming larvae and the mallets on the longitudinal anastomoses in the head. At the genus *Habroleptoides, Habrophlebia, Leptophlebia, Paraleptophlebia* the joints originate also later and the matrix, which has grown together then still flaps away so that it forms a sphere of a two- or four times the diameter of the anastomosis. Of the same kind is the anastomosis behind the front simple eye at the genus *Ephemera* (Tab. 4). From all the contact mallets which are described

in chapter III only the mallets on the two bud last segments of the genus *Stanonema* were described (HSU YIN-CHI, 1933, 23) and the mallet in the ninth segment of the species *Ecdyonurus venosus* (RAWLINSON, 1939) was mentioned.

Palmen's Organ.

Palmen found in his original description of the tracheal system of may-flies that in the head, where four tracheae — two transverse anastomoses — touch, there is an organ composed of concentric layers. GROSS (19, 1904) studied it thoroughly and called it the Palmen's organ. WODSEDALEK (45, 1911) completed his results by a series of experiments and he proves that the Palmen body is a static organ because after its explantation the larves lose the sense of their position. (He experiments with the species *Heptagena interpunctata.*) Let us look now more closely at the organ. Its position on the tracheae is clear from tab. 1, 2, 3, 4, 5. It lies behind the brain closely above the oesophagus. From tab. 7, fig. 3 we can see, that this build is quite identifical with contact mallets and complicated only by that, that it originates on the growth of four tracheae. We do not now yet the exact significance of this organ. Of course, the fact, that we succeded in finding identifical organs — contact mallets — in various places in the body, about which Palmen himself and the other workers in this field did not known, throws new light on this problem and may bring its solution closer.

Let us now state the basic facts which are known about the Palmen's organ:

1. The Palmen's organ and contact mallets are on all commissures. Apart from the lateral trunk, there does not exist in the may-fly body a single commissure without contact mallet. These are not formed after the origin of the anastomosis but they are already on the ends of tracheae growing against each other *(Heptagenia).*
2. The layers which remain after moulting are not only mere remains of the intima. They are darker and much stronger than the intima itself. They are formed by the matrix which is in the places of the organ developed far mighter than on the tracheae themselves.
3. Under the organ it goes back from the brain a nerve.

(See also GROSS nec WODSEDALEK.) During careful preparation I found definitely that this nerve does not reach into the organ. This fact was also confirmed by special staining. WODSEDALEK explanted this organ and comes to the view that it has a static significance.

4. Palmen mentions in a small note that he found a similar organ at Myriapoda. As far as I know from the literature, his remark has been forgotten.

5. Contact mallets which are formed only during the larval stage (in the head and abdomen of some genus) are in the place of a very complicated tracheation.

6. Up to this time, similar organs are not known at any other insect.

Contact mallets and the Palmen's organ are formed by the original growth of anastomoses which is still taking place in may-flies in this way. No commissure nor the narrow commissures on the dorsal side are without mallets. Only the lateral trunk, which has a completely special position forms an exception. It is possible, that all mallets have some special significance. Perhaps they may help during moulting. In any case these organs will probably influence only directly the tracheal system. The finding of contact mallets on all anastomoses, the same as the fundamentally equal Palmen's organ, in spite of WODSEDALEK's experiments, is in contrast with the fact that they might be organs having another significance outside the tracheal system itself.

At the end, I should like to take this oportunity to thank to my teacher Prof. Dr. JULIUS KOMÁREK. Already when the universities were closed he devoted much of his time to me and after the war, he enabled me my studies and gave me all the help in scientific work.

SUMMARY.

1. On the basis of 21 genus a detailed topography of the tracheal system of may-fly larves has been worked out. Most of the results are quite new, some of them are of a fundamental importance. It was found that the tracheation of various genus or groups of genus is different. The tracheae were described and drawn.

2. At the genus *Oligoneuriella* a widening was found on the lateral trunk in the mesothorax which was recognized as the remained of the original tr. branchialis and the conclusion was drawn, the tracheal gills were originally also in the mesothorax.

3. In the head of the larve *Polymitarcis* virgo ten air-sacks were found which have not hitherto been known at may-flies.

4. Contact mallets were found in various places and it was proved that they are identical with Palmen's organ. This threw some new light on the old problem of Palmen's organ.

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