Chapter II

Morphology of mayflies

Table 2. Size range in main mayfly taxa

Fore wing length (mm)

Taxon	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	>
† Protephemerida	□	□	□	□	□	□	□	□	■	□	□	□	□	□	□	□	
† Permoplectoptera	□	□	■	■	■	■	■	■	■	■	■	■	■	□			
Prosopistoma/f1=g2	■	■	■	□	□	□	□	□	□	□	□	□	□	□	□	□	
Baetisca/f2=g1	□	□	■	■	■	■	■	□	□	□	□	□	□	□	□	□	
Siphlonurus/fg1	□	□	□	□	■	■	■	■	■	■	□	□	□	□	□	□	
Dipteromimus	□	□	□	□	□	□	■	■	□	□	□	□	□	□	□	□	
Ameletus/fg1	□	□	□	■	■	■	■	■	□	□	□	□	□	□	□	□	
Metretopus/fg1	□	□	□	□	■	■	■	□	□	□	□	□	□	□	□	□	
Acanthametropus/fg1	□	□	□	□	□	■	■	■	■	□	□	□	□	□	□	□	
Ametropus	□	□	□	□	■	■	■	■	■	□	□	□	□	□	□	□	
Tetramerotarsata	■	■	■	■	■	■	□	□	□	□	□	□	□	□	□	□	
Nesameletus/f1=Metamonius/g1	□	□	□	□	□	■	■	■	□	□	□	□	□	□	□	□	
Oniscigaster/fg2	□	□	□	□	□	□	□	■	■	■	□	□	□	□	□	□	
Tasmanophlebia/g1	□	□	□	□	■	■	■	□	□	□	□	□	□	□	□	□	
Ameletopsis/fg1	□	□	□	□	□	□	□	□	■	■	□	□	□	□	□	□	
Rallidens	□	□	□	□	□	■	■	■	□	□	□	□	□	□	□	□	
Coloburiscus/fg1	□	□	□	□	□	■	■	■	■	□	□	□	□	□	□	□	
Isonychia/fg1	□	□	□	■	■	■	■	□	□	□	□	□	□	□	□	□	
Chromarcys	□	□	□	□	□	□	□	■	■	■	■	■	□	□	□	□	
Geminovenata	□	□	□	■	■	■	■	■	■	■	□	□	□	□	□	□	
Heptagennota	□	□	■	■	■	■	■	■	■	□	□	□	□	□	□	□	
Potamanthus/fg1	□	□	□	■	■	■	■	■	■	□	□	□	□	□	□	□	
Euthyplocia/fg1	□	□	■	■	■	■	■	■	■	■	■	■	■	■	■		
Ichthybotus	□	□	□	□	□	□	□	■	■	■	□	□	□	□	□	□	
Ephemera/fg9	□	□	□	■	■	■	■	■	■	■	■	■	■	■	□	□	
Protobehningia	□	□	■	■	□	□	□	□	□	□	□	□	□	□	□	□	
Behningia/fg2	□	□	□	□	□	□	■	■	■	■	■	□	□	□	□	□	
Palingenia/f2=g1	□	□	□	□	□	■	■	■	■	■	■	■	□	□	□	□	
Polymitarcys/f1=Ephoron/g2	□	□	■	■	■	■	■	■	□	□	□	□	□	□	□	□	
Neoephemera/fg1	□	□	■	■	■	■	■	□	□	□	□	□	□	□	□	□	
Caenoptera	■	■	■	■	□	□	□	□	□	□	□	□	□	□	□	□	
Ephemerella/fg2	□	□	■	■	■	■	■	■	□	□	□	□	□	□	□	□	
Vietnamella	□	□	□	□	□	□	□	■	□	□	□	□	□	□	□	□	
Austremerella	□	□	□	□	□	■	□	□	□	□	□	□	□	□	□	□	
Melanemerella/fg1	□	□	■	■	■	■	□	□	□	□	□	□	□	□	□	□	
Teloganodes/fg1	□	■	■	■	■	□	□	□	□	□	□	□	□	□	□	□	
Tricoryptera	■	■	■	■	■	□	□	□	□	□	□	□	□	□	□	□	
Leptophlebia/fg1	■	■	■	■	■	■	□	□	□	□	□	□	□	□	□	□	

Morphological characteristics given below are based mainly on recent representatives, i. e. on Euplectoptera only (see Chapter III); for many derived characters it is unclear if they are autapomorphies of Euplectoptera, or that of Euephemeroptera, or that of Panephemeroptera.

Mayflies are insects of medium size, body length ranges from 2 mm to more than 40 mm (TABLE 2); size is species-specific, being either equal in both sexes, or larger in females; sometimes specimens developed in warmer water are smaller that those developed in colder water.

STAGES OF DEVELOPMENT

The characteristic feature of Pterygota is splitting of postembryogenesis (which, as in all Gnathopoda, consists of several instars separated by moults) to sharply different wingless and winged stages: the wingless stage(s) never have movable wings, while the winged stage(s) have acting wings, modified pterothorax and other features connected with ability to fly. Some authors believe that ancient insects had stages intermediate between wingless and winged ones, with movable but not fully grown wings; however such instars (erroneously called "subimago") have not been found in any living or fossil insects, and probably could not exist (Kluge 2000). Ephemeroptera differ from all other insects by having not one, but two winged stages separated by moult – **subimago** and **imago** (FIG.4). Both subimago and imago have completely developed wings with equal size and venation.

LARVA
(Fig. 3)

In contrast to subimagoes and imagoes, wingless stages of mayflies are always aquatic and obtain

oxygen dissolved in the water. Their tracheostia (i. e. mouths of tracheal system) are closed, and other adaptations for aquatic respiration are present: abdominal tergalii are often used as tracheal gills, and other tracheal gills can appear independently on various parts of the body (see Index of characters [1]). This aquatic wingless stage is called either **larva**, **nymph**, or **naiad**; younger instars (lacking wing buds) can be called larva, and older ones (with wing buds) – nymph or naiad. The youngest instar(s) without tergalii and wing buds can be called **larvula**. Here we use the term **larva** for all wingless instars. Larva has large and often indeterminate number of instars; first instar never has tergalii and wing buds (as in all other insects), and during subsequent moults tergalii and wing buds appear and increase gradually, so that it is difficult to mark boundaries between larvula, larva in strict sense, and nymph.

Initially mayfly larvae have a peculiar swimming **siphlonuroid specialization** (well-expressed in Siphlonurus/fg1): the body is slender, with long abdomen and relatively small thorax; legs are able to be pressed to the body, being stretched posteriorly; abdomen is elongate and able to make undulate dorsoventral swimming movements; caudalii are not long, much shorter than in imago, with primary swimming setae forming a horizontal caudal flipper (see below). Pressing its legs to the body and making undulate movements up and down by its abdomen, the larva can swim rapidly for a short time (FIG.9:A–B). This specialization is initially present at least in Euephemeroptera (larvae of Protephemeroidea are unknown): it is present in Permoplectoptera (FIG.14:C–D), in majority of Mesozoic representatives of Euplectoptera and in many recent mayflies (see Index of characters [1]). In some cases this swimming specialization is secondarily lost: larvae of many mayflies are adapted not for swimming, but for fixing on stones in rapid stream, or for burrowing, or for other modes of life in aquatic environment. But the primary swimming setae are retained in many non-related groups of mayflies (see Index of characters [1.3.66]); sometimes the swimming specialization disappears, but vestigial primary swimming setae are retained. A very constant character of Ephemeroptera is a manner of swimming: mayfly larvae move by their abdomen up-and-down, in contrast to aquatic larvae of Odonata and Plecoptera, which when swimming, always move by their abdomen from side to side. The abdominal movement up-and-down is very effective in the case

when the larva has the siphlonuroid specialization, but it appears to be useless if there is another shape of body and caudalii. In spite of this, such kind of movement is retained even in some mayfly larvae that have completely lost siphlonuroid specialization (FIG.9: C–D, F–H). Only in rare cases have larvae lost ability of the dorsoventral swimming movements (FIG.9:E) (Kluge & al. 1984).

SUBIMAGO AND IMAGO
(Fig. 4)

Both winged stages – subimago and imago, in contrast to larva, are non-feeding, able to fly and inhabit air environment; they sharply differ from larva in structure of head, thorax, legs, abdomen and caudalii, have functional wings and lack tergalii (FIG.4). Transformation from larva to subimago is supplied by great changes comparable with complete metamorphosis, but in contrast to it, is not supplied by immobility: during the whole development before ecdysis the subimaginal leg anlage is located inside the larval leg cuticle in such a manner that subimaginal and larval knee articulations always coincide, and allows active mobility of the leg (FIG.3:A).

Subimago

Subimago has the same shape and size as imago, but differs in cuticle structure and setation; male subimagoes, besides this, have less expressed sexual characters in structure of eyes, fore legs, genitals and caudalii (see below).

Subimaginal cuticle in most part is covered with microtrichia – densely and evenly situated small (about 0.01 mm) immobile crescent-shaped cuticular processes resembling setae; each microtrichion arises from the centre of cuticular area produced by one hypodermal cell. Subimaginal wings are always entirely covered with microtrichia (because of this they look dull); in imago the microtrichia are always absent, and at least the wing membrane is always bare. Possibly, the microtrichia play a positive role, as they keep a layer of air, which protects the wing against getting wet when the insect moults from larva to subimago on water surface or under the water. Besides mayfly subimagoes, similar microtrichia on wings are present in imagoes of many other insects, and allows one to conclude that subimago of mayflies corresponds to imago of Metapterygota.

Subimaginal and imaginal pterothoracic sclerites

usually have different outlines (about differences in mesonotum and mesopleuron sclerites – see below).

Subimaginal cuticle of wing is uniform, thin, elastic, non-sclerotized, equal on veins and on membrane (in contrast to the imaginal one, which is thickened and sclerotized on veins); this allows the insect to take off imaginal wing from the subimaginal cuticle when it moults from subimago to imago. As subimaginal wing veins lack any sclerotization, rigidity of wing necessary for flight is served only by goffered wing form (due to alternating of convex and concave veins – see below) and possibly by hemolymph pressure in veins. Subimago is able to spread wings and fly immediately after escaping from larval exuviae.

In subimago posterior margin of wing always has a row of setae (which are longer than microtrichiae and have different structure), while in imago these setae are nearly always absent, being present only in some specialized groups (see Index of characters [2.2.27]).

When the subimago transforms to imago, its exuviae are taken away as an integral cover (as at other moults), together with covers of wings. Only in some specialized forms that have short-living imago with non-functional legs, the moult to imago is lost, and the subimago becomes a reproductive stage (see Index of characters [2]); in some of these short-living forms males moult in air and throw their exuviae only partly.

Imago

Imaginal organization is adopted to the peculiar mating flight of male: it flies vertically upward, and then passively parachutes down, keeping its wings semi-spread in a V-shape, abdomen turned somewhat upward, and cerci in a V-shape turned to sides and somewhat upward. The male repeats such flying up and down above the same place, sometimes in a swarm with other males of the same species, attracting females. Upon seeing a female coming to the swarm, the male flies to it from beneath, orienting with help of its dorsal eyes (see below). Mating can take place at flight or on ground (FIG.10:G); the male is located under the female by its dorsal side directed upward and holds wing bases of the female by its fore tarsi, arching them dorsally-posteriorly (see below); abdominal apex of the male is curved dorsally-anteriorly, thus gonostyli appear to be directed upward and fix the female's abdominal apex, overlapping it from sides, and the penis

also appears to be directed upward and is inserted into the female genital opening, located between sterna VII and VIII (about genital structure – see below). Such mating flight and manner of copulation are peculiar at least for Euplectoptera, and only in some mayfly taxa are secondarily changed (Brodsky 1973). Possibly, some of peculiarities in structure of pterothorax and wings of mayflies (see below) evolved in connection with the mating behaviour of males, but are present in both sexes.

HEAD

EYES

Facetted **eyes** (**oculi**) and all 3 **ocelli** are always developed in mayfly larvae, imagoes and subimagoes (FIG.3–4) (presence of the facetted eyes and ocelli is an autapomorphy of Euarthropoda, and reduction of ocelli number to three is a peculiarity of Amyocerata). Sexual dimorphism in structure of facetted eyes is initial for Ephemeroptera (at least for Euplectoptera), being expressed in majority of mayflies: eyes of male are enlarged and divided into two portions – dorsal and ventral ones; the ventral portion is more or less similar to the eye of females (FIG.4:B–C). The dorsal portion of the male eye is the largest in imago, can be smaller in subimago, smaller in mature larva and absent in young larva. In the most primitive case (which is characteristic for the majority of mayflies) the division of male eye into two portions is only slightly expressed (FIG.4:B). Evolutionary changing of male eyes took place in two opposite directions, independently several times in each direction: (1) in some cases the dorsal portion of male eye is strongly enlarged, separated from the ventral portion and transformed to **turban eye** (in Turbanoculata and some Leptophlebia/fg1); (2) in other cases the dorsal portion is diminished or disappears at all, thus male eye becomes similar to that of female (see Index of characters [2.1.3]).

ANTENNAE

Antenna of Amyocerata consists of **scapus** (first muscle-bearing segment), **pedicellus** (second, muscle-less, sensory segment) and **flagellum** (third, muscle-less, secondarily segmented part). Structure of mayfly antennae is primitive for Amyocerata: flagellum is bristle-like and consists of indeterminate number of segments, which become

narrower toward apex of flagellum and multiply by division of the proximalmost segment. Larval antennae are well-developed, multisegmented (FIGS 3:A; 76:B), while in imago and subimago flagellum is vestigial, segmentation of flagellum often being indistinct or absent (FIG.4). Reduction of antennae in winged stages is probably an autapomorphy of Euplectoptera: long multisegmented antennae are reported for winged *Protereisma* (Carpenter 1933, 1979).

<center>**MOUTH APPARATUS**
(Fig. 3)</center>

Mouth apparatus is developed in larva, and all features of mouthparts described below relate to larva only. In imago and subimago of Euplectoptera mouth apparatus is always absent; anterior margin of the frons forms a projected lamella – **face fold** (FIG.4:B); this lamella is usually directed ventrally and limits anteriorly a concavity, which corresponds to the area of clypeus and mouth apparatus. Sometimes more or less developed soft non-functional processes arise from this concavity (FIG.50:C); these processes are not vestigial mouthparts of the imago (as some investigators assumed), but are remainders of larval mouthparts that had not disappeared during metamorphosis: their structure repeats that of specialized larval mouthparts of the same specimen. Thus, in phylogenesis these processes originated independently many times, and their presence is not a plesiomorphy. In larva of the last instar, subimaginal mouthpart tissues located under larval cuticle diminish gradually, thus, at moult, only empty cuticle sheds from them (in contrast to tergalii and sometimes paracercus, which cuticle sheds together with remainders of tissues). Absence of mouth apparatus in winged stages is probably an autapomorphy of Euplectoptera, as developed sclerotized mouthparts are reported for *Protereisma* (Carpenter 1979).

Mandibles

The majority of Ephemeroptera have a mandibular structure (FIG.3:F–G) which is probably initial for Mandibulata and occurs in various groups of eucrustaceans. Similarly to Eucrustacea and wingless insects (Entognatha and Triplura), but differing from Metapterygota, the mandibular basis is long, so the **posterior condylus** is far from the biting edge. In Ephemeroptera, besides the posterior one, two

more condyli are present, being situated in one line: a **middle condylus** has a form of concavity on mandible, into which a projection of margin of the head capsule enters (it corresponds to the anterior condylus of Metapterygota); an **anterior condylus** has a form of sclerotized projection of mandible, which enters into concavity on the head capsule margin. Here we shall use the term "**mandible flatness**" for the flatness, in which lie all three mandible condyli and incisor.

In many mayflies the mandible has well-expressed incisor, kinetodontium, prostheca and mola.

Incisor (usually called "apical canine") represents an apical-median process of mandible, usually pointed and dentate; in contrast to kinetodontium, it is never separated from the mandible corpus by a suture.

Kinetodontium (usually called "subapical canine") is the same as lacinia mobilis of eucrustaceans. The term "kinetodontium" proposed by Kukalova-Peck (1991:151) is more convenient for transliteration from Latin to other languages, than the old term "lacinia mobilis". The kinetodontium represents a median process of mandible proximad of the incisor; base of the kinetodontium closely adjoins the incisor base. Like the incisor, the kinetodontium is usually pointed and dentate. In contrast to the incisor, the kinetodontium is often separated from mandible corpus by a suture; sometimes it has mobile articulation with the mandible corpus (FIG.26:C); but in some mayflies, as well as in majority of insects, the kinetodontium is completely fused with the mandible corpus, sometimes it is fused also with the incisor (FIG.29:B). Besides insects, the kinetodontium is present in some Eucrustacea – Peracarida, Thermosbaena/fg1 and Remipedia; probably, it is initial for Mandibulata (Kluge 1999d, 2000). In all cases the kinetodontium never has muscle and is unable to make active movements.

Prostheca is located on median margin of mandible proximad of the kinetodontium; this is an appendage separated by a suture from the mandibular corpus. Usually the prostheca is short and distally divided into a bunch of setiform processes (FIGS 3:F–G; 26:C); sometimes (in many Turbanoculata) prostheca has a form of integral stick with dentate apex (FIG.29:B); sometimes the prostheca is vestigial or lost (FIG.54:E–F) (see Index of characters [1.1.24] and [1.1.25]). Many authors (Snodgrass 1935, and others) erroneously took the prostheca for lacinia

mobilis (i. e. kinetodontium); actually it is probably a result of fusion of group of setae. Because of this error in identification of the kinetodontium in mayflies (and insects in general), there were stated doubts concerning the possibility of comparing mandibles of Hexapoda with mandibles of Eucrustacea, that led to doubts concerning common origin of mandibles and monophyly of Mandibulata.

Mola represents a proximal-median projection of the mandible; distal surface of the mola, faced toward the mola of opposed mandible, has a form of grater with dense dentate ridges stretching perpendicular to the mandible flatness. Probably such mola, as well as the incisor and the kinetodontium, is initial for Mandibulata: it is present in many Eucrustacea and Hexapoda. The overwhelming majority of mayflies have mola well-developed, only in some specialized carnivorous mayflies has the mola lost its grater, become dentate, or is completely lost (see Index of characters [1.1.26]).

Mandibles are asymmetrical. As well as in other Hexapoda (and probably in other Mandibulata in general), in Ephemeroptera the mandible with mola most projected in its distal part, is the left mandible, and the mandible with mola most projected in proximal part, is the right one (FIG.3:F–G). An exception is made only by selected taxa (supra-species taxa, species and infra-species taxa) among Pentamerotarsata, which mandibles look as mirror reflection of the normal ones. In rare cases the asymmetry of mandibles is lost (see Index of characters [1.1.17]).

Superlinguae

A pair of well-developed superlinguae is present in nearly all mayflies, except for a few highly specialized carnivorous groups where superlinguae are reduced (see Index of characters [1.1.27]). Superlinguae are a pair of non-segmented appendages belonging to mandibular segment and situated between mandibles and maxillae (FIG.3:A, C) (they are often erroneously regarded as lateral parts of hypopharynx, while hypopharynx belongs to maxillary segment). Probably superlinguae are characteristic for Mandibulata, being known in Eucrustacea under names "paragnatha" or "labium"; among Hexapoda superlinguae are developed, besides Ephemeroptera, only in Entognatha and Microcoryphia (in other Hexapoda they are not described or described erroneously, when lateral parts of hypopharynx are taken for superlinguae). Thus, the presence of superlinguae in Ephemeroptera is a unique plesiomorphy among Pterygota.

Maxillae

Maxilla of Ephemeroptera always has only one biting lobe (FIG.3:B), which is regarded by many authors to be a result of complete fusion of galea and lacinia (which are initially peculiar for Hexapoda); but another assumption is possible, that this lobe is lacinia without galea, while galea is completely lost.

Apex of maxilla bears **maxillary canines** (the term introduced by Kluge 1994c: 35, type of the term is *Habrophlebiodes americana*, designated here) – tooth-like processes, which are not separated from corpus of maxilla. Usually there are 3 maxillary canines (FIG.3:E), and probably this number is initial for Ephemeroptera; sometimes the number of maxillary canines is less than three, or they are lost (see Index of characters [1.1.33]); sometimes maxillary canines have additional denticles.

In various non-related groups of Ephemeroptera the distal margin of the maxilla (laterad of the maxillary canines) bears a regular row of more or less pectinate setae directed distally or ventrally; here this row is called an **apical-ventral row** (see Index of characters [1.1.31]).

The inner (median, or biting) margin of maxilla proximad of the canines, nearly in all Ephemeroptera bears 2 longitudinal rows of setae – the **inner-dorsal** and the **inner-ventral** rows. Setae of these rows can be modified in variable manner; some setae can be thickened, immovable and tooth-like. Modified setae in distal part of the inner-dorsal (but not inner-ventral!) row are named **dentisetae** (the term introduced by Kluge 1994c: 35, type of the term is *Habrophlebiodes americana*, designated here). Number and structure of the dentisetae is constant for large taxa (see Index of characters [1.1.37]–[1.1.40]).

Maxillary palps are 3-segmented (FIG.3:B). The 1st segment contains two muscles – adductor and abductor of 2nd segment; the 2nd segment lacks muscles. Sometimes the 2nd and the 3rd segments are fused together; in this case maxillary palp is 2-segmented, with distal segment representing $2^{nd}+3^{rd}$ segment (see Index of characters [1.1.42]). Only in one taxon – Ameletopsis/fg1 – maxillary palp is secondarily multisegmented (but has no muscles) (FIG.34:D). In some taxa maxillary palp lacks

muscles and can be vestigial up to complete disappearance (see Index of characters [1.1.41]).

The 3-segmented maxillary palp is an apomorphic character (being autapomorphy of Euplectoptera, or Euephemeroptera, or probably Panephemeroptera in general), but not a unique apomorphy of this taxon. Initial for Amyocerata, and probably for Hexapoda in general, is 5-segmented maxillary palp: it is characteristic for Zygentoma, Polyneoptera, Zoraptera and many Oligoneoptera. In many other Amyocerata, as well as in all Entognatha, the number of maxillary palp segments is diminished, more rarely increased.

Labium

Majority of Ephemeroptera have typical for Hexapoda labium structure with division of unpaired portion to **submentum** (sometimes named **postmentum**) and **mentum** (sometimes named **prementum**), bearing paired **glossae**, **paraglossae** and **palps**; in some taxa glossae and/or paraglossae are fused (see Index of characters [1.1.50], [1.1.52]).

Labial palps are 3-segmented (FIG.3:D). The 1st segment contains two muscles – adductor and abductor of 2nd segment; the 2nd segment contains a single muscle – adductor of 3rd segment (sometimes this muscle is absent). Sometimes the 2nd and the 3rd segments are fused together, in this case maxillary palp is 2-segmented, with distal segment representing $2^{nd}+3^{rd}$ segment (see Index of characters [1.1.55]); only in one taxon – Ameletopsis/fg1 – labial palp is secondarily multisegmented (FIG.35:A).

In contrast to maxillary palp (see above), 3-segmented labial palp is a plesiomorphy within Amyocerata and probably within Hexapoda in general: it is characteristic for Microcoryphia, Polyneoptera, Zoraptera, and many Oligoneoptera. In other taxa of Amyocerata, as well as in all Entognatha, number of labial palp segments is diminished, more rarely increased.

THORAX
GENERAL STRUCTURE

Thorax of Ephemeroptera is integral, mobility between three thoracic segments and first abdominal segment is limited or lost because of following modifications:

In larva posterior-lateral angles of pronotum and anterior-lateral angles of mesonotum are brought together (FIG.3P:A) or even fused (FIG.37:A), and articulatory membrane is well-developed only in median part of pronotum-mesonotum joint; because of this, prothorax can make only limited dorso-ventral movements relatively to mesothorax. Imaginal and subimaginal mesonotum strongly differs from larval one, has no anterior-lateral angles and no direct connection with pronotum (FIGS 4–6); however, a nearly immobile connection of prothorax and mesothorax is served by means of prealar bridge (see below).

Both in larva and winged stages sterno-pleural areas of mesothorax and metathorax are connected immobile. Furcasternum of metathorax is completely fused with first abdominal sternite, without any trace of suture between them (while suture between metanotum and first abdominal tergite is retained) (FIGS 4–5; 35:A).

Probably, initially for Pterygota, thoracic segments have following apodemes: paired **furca** (or **sternal apodemes**) in each segment; paired **pleural apodemes** in each segment; **unpaired spina** behind furca in prothorax and mesothorax only. In Ephemeroptera spinae are completely lost. In connection with this, most sternal thoracic muscles are lost, and only muscles inserted on furcae are retained; muscles connecting mesothoracic and metathoracic furcae are also lost. Pleural apodemes and muscles connected with them are also lost on all segments (in larvae of Furcatergaliae propleura are transformed to secondary apodemes, which are not homologous to the pleural apodemes of other Pterygota).

PTEROTHORAX OF IMAGO AND SUBIMAGO
(Figs 5–6)

Structure of mayfly pterothorax is discussed in the separate paper (Kluge 1994a); for all terms that are introduced in that paper and marked there as "new term", the type taxon should be *Siphlonurus aestivalis* (designated here).

Prealar bridge

Prealar bridge of mesothorax (PAB) represents a sclerotized ring, which firmly connects anterior end of mesonotum with anterior end of mesosternum; the stenothoracic spiracle (anterior most spiracle of Hexapoda, initially located on the boundary between prothorax and mesothorax) is located behind the prealar bridge – i. e. in limits of the mesothorax. In this respect the prealar bridge of mayflies differs

from the prealar bridge of some other Pterygota, in which it passes behind the spiracle (the prealar bridge is not present in all Pterygota and probably independently evolved in various groups). The prealar bridge of mayflies consists of the dorsal, lateral, and ventral arcs. The **dorsal arc** (PAB:DA) (term by Kluge 1994a) may contain the anterior and posterior costae separated by a groove – **anterior phragma** (PhA); so the anterior costa of the dorsal arc belongs to acrotergite, and its posterior costa – to notum. The **lateral arc** of prealar bridge (PAB:LA) (term by Kluge 1994a) may also consist of two or three costae separated by grooves. The **ventral arc** (PAB:VA) (term by Kluge 1994a) is known also as **presternite**. From the lateral and dorsal arcs begins a pair of **posterior arms** of prealar bridge (PAB:PA) (term by Kluge 1994a); each of these arms goes posteriorly toward the wing base and joint with a small distinct emargination on the lateral margin of prelateroscutum (PLS – see below). Anteriad of this joint, between the prealar bridge, the posterior arm, and the prelateroscutum, is located a narrow membranous area. Only in Branchitergaliae the posterior arms of prealar bridge are strongly shortened, do not reach the emarginations of prelateroscutum margins, while these emarginations are retained (FIG.45:A, C).

Mesonotum

In anterior part of mesonotum just behind the dorsal arc of prealar bridge there is an unpaired **anteronotal protuberance** (ANp) (term by Kluge 1994a) separated from the remainder part of notum by the **anteronotal transverse impression** (ANi) (see Index of characters [2.2.5] and [2.2.6]).

Along the median line of notum goes the **median** (or **median longitudinal**) **suture** (MLs). It is distinctly developed along the largest part of notum, but disappears in its anterior part (usually near the anteronotal impression) and in its posterior part (usually near the scuto-scutellar impression). Usually the median suture is concave, but in selected Tetramerotarsata it is convex.

Laterad of the median suture there is a pair of **medioparapsidal sutures** (MPs) (term by Kluge 1994a). These narrow concave sutures separate unpaired convex **medioscutum** (MS) (term by Kluge 1994a) (which contains the anterior bases of the pair of largest **median tergal muscles** – MTm) from paired convex **submedioscutum** (SMS) (term by Kluge 1994a) (which contains the dorsal bases of

the pair of large **scuto-episternal muscle** – S.ESm).

Laterad of the medioparapsidal sutures there is a pair of **lateroparapsidal sutures** (LPs) (term by Kluge 1994a) (see Index of characters [2.2.9]). These deep wide strongly sclerotized concave sutures, or furrows, bear mechanical function and at the same time separate the submedioscutum from the paired convex **sublateroscutum** (SLS) (term by Kluge 1994a), which contains the dorsal bases of the **anterior** and **posterior scuto-coxal muscles** (S.CmA and S.CmP) (see Index of characters [2.2.10]). Lateroparapsidal sutures can go exactly between muscle bases or somewhat touch them (FIGS 56:L–M; 63:D–E).

Anteriorly the lateroparapsidal suture turns to **antelateroparapsidal suture** (ALPs) (term by Kluge 1994a), which sets off anteriorly the submedioscutum, separating it from the **anterolateral scutal costa** (ALSC) (term by Kluge 1994a). The anterolateral scutal costa is well developed in all mayflies, separating the dorsal side of notum from the narrow **prelateroscutum** (PLS) (term by Kluge 1994a), which is usually not visible from above. As said earlier, prelateroscutum usually has articulation with the hind end of the posterior arm of prealar bridge. Posteriorly prelateroscutum is connected with suralare (SrA), sublateroscutum (SLS) and lateroscutum (LS), which can be separated by more or less developed sutures or ridges of various forms.

Suralare (SrA) is a portion of scutum which bears the **anterior notal wing process**; it can be separated from the remainder scutum by the **anteronotal scutal suture** (ALSs) (Matsuda 1970: Fig.4).

Lateroscutum (LS) (term by Kluge 1994a) is separated from the sublateroscutum by the **lateroscutal suture** (LSs) (term by Kluge 1994a) (see Index of characters [2.2.12]) and contains in its anterior portion the dorsal base of the **scuto-trochanteral muscle** (S.Trm).

Posteriad of the sublateroscutum is usually present a pair of **posterior scutal protuberances** (PSp) (term by Kluge 1994a) – large convex areas, usually indistinctly outlined, which contain the dorsal bases of large scuto-lateropostnotal muscles (S.LPNm) (see Index of characters [2.2.11]).

Behind the posterior scutal protuberances, is situated the prominent **scutellum** (SL) (term adopted by Audouin 1824), which is separated from the posterior scutal protuberances by a shallow **scuto-scutellar impression** (SSLi). Laterally scutellum is separated from parascutellum (PSL) by an

indistinct invagination, which is called **recurrent scuto-scutellar suture** (RSSLs) (Matsuda 1970).

Parascutellum (PSL) (term used by Crampton 1914) is a large area laterad of scutellum, which bears the **posterior notal wing process** and contains a single small base of the **parascutellar-coxal muscle** (PSL.Cm). Parascutellum is separated from sublateroscutum and lateroscutum by the **scuto-parascutellar suture** (SPSLs). This suture allows to bend the notum when the median tergal muscles contract, that leads to wing depression; it is well developed on mesothorax of all mayflies. Lateral margin of parascutellum bears a sclerotized costa – **parascutellar lateral convexity** (PSLcvx), which is separated from the remainder part of parascutellum by a groove – **parascutellar lateral concavity** (PSLccv).

Behind the notum, winged stages have a sclerotized **postnotum**, which corresponds to an intersegmental articulatory membrane of larva. Postnotum consists of an unpaired infrascutellum, unpaired mediopostnotum and a pair of lateropostnota. The **infrascutellum** (ISL) (term by Kluge 1994a) represents a transverse shelf-like sclerotized convexity located on the deeply concave hind wall of notum under scutellum (FIG.89:A); usually it is separated from mediopostnotum by a transverse membranous suture. Laterally infrascutellum can be produced as a pair of **infrascutellar-postsubalar arms**, which unite it with posterior-dorsal angles of postsubalar sclerites belonging to lateropostnota. Sometimes infrascutellum is reduced (see Index of characters [2.2.13]). The **mediopostnotum** (MPN) lies behind infrascutellum, and continues posteriorly-ventrally as an anterior wall of **middle phragma** – i. e. phragma between mesonotum and metanotum (thus it is also called **phragmanotum**); laterally mediopostnotum is continued as a pair of **lateropostnota** (LPN), uniting there with the infrascutellar-postsubalar arms. About the structure of lateropostnotum see below, in characteristic of mesopleuron.

Besides the sutures whose position is fixed by their mechanical role or by position of muscle bases, there is a suture whose position is not determined by any internal causes – it is the **mesonotal suture** (MNs) (term by Kluge 1994a). In the primitive case the mesonotal suture goes across scutum in its anterior part, behind the anteronotal transverse impression, and laterally connects with the anterior ends of medioparapsidal sutures (FIG.61:A–B). Sometimes the mesonotal suture is stretched backward medially in its point of crossing with the

median suture (FIG.6). In other cases lateral parts of the mesonotal suture are strongly curved and stretched backward (FIG.7:E). Sometimes these lateral portions of mesonotal suture are so strongly shifted backward, that nearly reach the posterior scutal protuberances; in this case it seems that there is not a single suture, but two pairs of longitudinal sutures, the median of which goes parallel to the median suture, and the lateral ones go parallel to the lateroparapsidal sutures close to them (FIG.83:F). Sometimes the mesonotal suture, being strongly curved and stretched backward, is indistinct in imago, and can be seen only in subimago because in front of it is located a pigmented field with microtrichia, and behind it – a light field without microtrichia. Sometimes such mesonotal suture is non-expressed both in imago and subimago. In other cases the mesonotal suture disappears without curvation and stretching backward (see Index of characters [2.2.8]).

In literature when structure of the insect thorax is described, the terms "praescutum", "praescutal suture" and "parapsidal suture" are often used, whose meanings are initially indeterminate (Kluge 1994a). The term **"praescutum"** was introduced by Audouin (1824), and as its type should be regarded the beetle *Dytiscus circumflexus*, because only its structure is illustrated. Originally, on the beetle mesothorax the term "praescutum" was attributed to the anterior phragma, while on the beetle metathorax the same term was attributed to the medioscutum. The term **"parapsides"** (in plural) was introduced by MacLeay (1830) for a pair of lateral lobes of mesonotum in the vesp *Polistes billardieri*; later pair of sutures separating these lobes were called **"parapsidal sutures"**. Among Hymenoptera some species have the parapsidal sutures, some species have notaulici – another pair of sutures, which correspond to the medioparapsidal sutures of mayflies, and some species have both pairs of sutures – the parapsidal sutures and the notaulici (Tulloch 1929). Authorship of the term **"notaulix"** (plural **"notaulici"**) or **"notaulus"** (plural **"notauli"**) is unclear.

Sclerotization of mesonotum is markedly different in subimago and imago. Imaginal mesonotum is nearly evenly sclerotized (if there are colour patterns, they have hypodermal origin); subimaginal mesonotum has distinctly outlined sclerotized pigmented areas and light areas between them. Intensity of pigmentation of these sclerotized areas can strongly vary individually, but their shape allows to

characterize supra-species taxa (see Index of characters [2.2.14]–[2.2.15]). Usually there is an unpaired **anterior pigmented area**, limited from behind by the mesonotal suture, and a paired **lateral pigmented area**. Probably, initially the lateral pigmented area bifurcates backward, forming a **lateroparapsidal stripe,** which stretches along the lateroparapsidal suture, and a **lateral portion,** which occupies antero-lateral part of sublateroscutum and whole lateroscutum (FIG.18:E). Such shape of the lateral pigmented area is peculiar for selected groups both among Tridentiseta (Siphlonurus/fg1, Vetulata, *Siphluriscus*) and Branchitergaliae (*Coloburiscoides*, Heptagennota). In other taxa lateral pigmented area is larger, occupying sublateroscutum and sometimes other areas.

Wing base

Wing base (FIG.6) is connected with lateral margin of notum by two movable sclerites: the **anterior axillary sclerite** (AxA) (term used by Becker 1954: aAx) and **posterior axillary sclerite** (AxP) (term by Kluge 1994a). Both of them are movably connected with the wing base and with notal wing processes: AxA with the anterior notal wing process of suralare, and AxP with the posterior notal wing process of parascutellum. In the FIG.6 wing base is shown stretched with axillary membrane torn, so the both movable sclerites AxA and AxP are visible; on intact wing base one of these axillary sclerites is turned over and appears under the corresponding wing process, while another one is stretched. It allows the wing to move forward (when AxA is turned over) and backward (when AxP is turned over). AxA is flat, not so strongly sclerotized as AxP, its form differs among mayfly taxa. The **proximal axillary sclerite** (AxPr) (term by Kluge 1994a) may be either well-developed (FIG.6), or vestigial, or absent. It is connected with lateroscutum and can not make such movements as AxA and AxP. The **middle axillary sclerite** (AxM) (term by Kluge 1994a) is movably connected with AxA and with the **middle articulatory process** of basal plate (APM) (term by Kluge 1994a). Form of AxM is similar in all mayflies; it has in its posterior part a distinct projection directed medially. The **basal plate of wing** represents a large roundish sclerite convex dorsally and concave ventrally; it consists of immovably fused together **basisubcostale** (BSc), **basiradiale** (BR), the **middle articulatory**

process (APM) and the **posterior articulatory process** (APP).

Mesopleuron

Lateral surface of mesothorax has following structure. The most developed suture is a suture composed of the dorsal part of the pleural suture (i.e. **superior pleural suture** – PLsS) and the anterior part of the paracoxal suture (i.e. **anterior paracoxal suture** – PCxA); this combined suture represents a deep wide sclerotized groove running from the **pleural wing process** (PWP) to the episternum; it prevents the pleuron from deformation during contracting of the scuto-episternal muscle (S.ESm). Judging by the form of the anterior paracoxal suture in various mayflies, we can assume that the plesiomorphy is the condition when it is complete, i. e. crosses the whole episternum, completely dividing it to **anepisternum** (AES) and **katepisternum** (KES), turns to its ventral side and reaches the sternite. In some taxa the anterior paracoxal suture is incomplete, i. e. does not turn to the ventral side of episternum and does not divide it completely (see Index of characters [2.2.19]). The remaining parts of the pleural and the paracoxal sutures, i.e. the **inferior pleural suture** (PLsI) and the **posterior paracoxal suture** (PCxsP) are weak and sometimes disappear. In contrast to mayflies, in majority of other Pterygota the mostly developed suture of the pleurite is the whole pleural suture, running from the pleural wing process to the dorsal coxal articulation, and dividing the pleurite into **episternum** and **epimeron** (see Index of characters [2.2.20]). **Subalar sclerite** (SA) is usually large, with its lower portion containing the dorsal base of large **subalar-sternal muscle** (SA.Sm) (see below). The portion of **lateropostnotum** (LPN) situated exactly under the wing base is named **postsubalar sclerite** (PSA) (= posterior subalare: Crampton 1914). Posterior-dorsal angle of the postsubalar sclerite can continue dorsally as an infrascutellar-postsubalar arm (see above). Ventrad of the postsubalar sclerite, along the lateropostnotum in dorsoventral direction usually runs a **lateropostnotal crest** (LPNC) (term by Kluge 1994a). Often outlines of the postsubalar sclerite and the lateropostnotal crest are most distinctly expressed in subimago (see Index of characters [2.2.16]).

Mesosternum

Sternite of mesothorax in Ephemeroptera has an especially strongly developed **furcasternum** (area behind furcal pits); this is connected with the fact that in contrast to Neoptera, it includes bases of large **subalar-sternal muscles** (SA.Sm). The portions of furcasternum, which contain the bases of SA.Sm are strongly convex and are named **furcasternal protuberances** (PSp). The furcasternal protuberances may be brought together (FIG.5:C) or separated by means of **furcasternal longitudinal impression** (FSi). Form of this impression depends upon the position of bases of the subalar-sternal muscles (SA.Sm), while their position depends upon structure of the nerve system. In primitive cases the metathoracic nerve ganglion is located in metathorax, being connected with the mesothoracic ganglion (located in mesothoracic basisternum) by a pair of long slender connectives, which lie at some distance of body wall, thus allowing the bases of SA.Sm to connect medially (FIG.8:B); in this case furcasternal impression is absent (FIG.39:B) or represented by a slender line (FIG.23:E). In some mayfly taxa the metathoracic nerve ganglion is transferred into furcasternum of mesothorax, nearer to the mesothoracic ganglion, and lies between the bases of SA.Sm separating them (Fig.8:D); in this case between the furcasternal protuberances appears a more or less wide furcasternal impression (FIGS 32:D; 34:C). If the metathoracic ganglion is located in the hind part of mesothoracic furcasternum, the furcasternal impression is narrow in its fore part and widened posteriorly (FIG.56:C–D); if the ganglion is transferred into the middle or anterior part of furcasternum, the furcasternal impression becomes wide all over its length (FIG.57:A–B) (see Index of characters [2.2.23]–[2.2.24]). Among Ephemeroptera only in Caenoptera are the subalar-sternal muscles completely lost, but even in this case the furcasternal protuberances are retained, being diminished and widely separated (FIG.87:F).

Metathorax

Metanotum of all Euplectoptera is diminished in connection with anteromotority and diminishing or disappearance of hind wings. Relatively complete development of metathoracic structures is shown in FIG.5. In some mayfly taxa the metathorax is more strongly reduced: pleural wing process and subalar sclerite may disappear; alinotum (scutum + scutellum) becomes shorter while mediopostnotum may become longer, or the whole metathorax becomes shorter. The wing indirect musculature of metathorax may be nearly completely developed (FIG.5:B) or more or less reduced. In metathorax of all Euplectoptera the direct wing depressor – subalar-sternal muscle (SA.Sm) – is lost. In different taxa reduction of hind wings, metathoracic exoskeleton, and metathoracic wing musculature has unequal rate. For example, many Turbanoculata have no vestiges of hind wings or hind wing buds at any stages of development, however their metathorax is rather large and contains very strong wing musculature, which can not function (FIG.8:D); in some other mayflies the hind wings are relatively large, but the metathorax is strongly shortened and its wing musculature is very weak (for example in Posteritorna – FIG.16:H). Most constant metathoracic wing muscles are the median tergal muscle (MTmIII) and scuto-epistenal muscle (S.ESmIII); they undergo reduction only in Caenoptera and Tricorythodes/fg1 (see Index of characters [2.2.26]).

WINGS
(Figs 7–8)

Nearly in all mayflies fore wings are well developed, and length of fore wing is subequal to trunk length (FIG.8:A, C) (because of this, in taxa characteristics fore wing length should be given rather than body length). In contrast to many other insects, in mayflies wing length never exceeds markedly trunk length. The reason is that mayflies have to moult from subimago to imago and shed subimaginal exuviae by abdominal movements. If during the moult imaginal abdominal tip becomes free from subimaginal cuticle earlier than wing tips, the wing tips remain in the subimaginal cuticle forever; such insect can not fly and dies.

Only a few mayfly species are flightless and can have fore wings shorter than trunk (Fig.8:F) (see Index of characters [2]).

In Euplectoptera the hind wings are reduced, their length never exceeds 1/2 of fore wing lengths; in flight they are coupled with fore wings, because the basitornal (hind-proximal) margin of fore wing is bent ventrally, and the costal (fore) margin of hind wing is bent dorsally; in some mayflies the hind wing bears a special **costal process**. In many groups of Euplectoptera independent reduction of hind wings takes place up to their complete disappearance

(see Index of characters [2.2.59]).

Fore wing usually has characteristic triangular form with more or less prominent obtuse hind angle – **tornus**; this angle separates the hind-proximal portion of wing margin, which couples with hind wing, from the rest forewing margin (the same in many other non-related anteromotoric insects which fore wing is able to couple with hind wing).

In entomological literature wing margins are usually called "anterior" (or costal), "outer", and "posterior" ones. Such terminology is not convenient when used for wing buds of Ephemeroptera larva: in this case the margin of wing bud corresponding to outer margin of wing is directed inward, and the margin of wing bud corresponding to posterior margin of wing is directed anteriorly. Below, the following terms are used: **Costal margin** – anterior margin of wing and lateral (or ventral) margin of wing bud, from base to apex. **Basitornal margin** (new term) – hind-proximal margin of fore wing and anterior margin of fore wing bud, from base to tornus. **Tornoapical margin** (new term) – outer (hind-distal) margin of fore wing and median (or dorsal) margin of fore wing bud, from tornus to apex. **Amphitornal margin** (new term) – basitornal and tornoapical margins combined, independently if the tornus is expressed or not.

In winged stages (imago and subimago) at rest the wings are never folded; usually they are raised upwards but some mayflies keep their wings spread laterally.

Larval wing buds

In all Pterygota larval wing buds represent immobile outgrowths of notum margin (i. e. paranota), appear in certain larval instar (but never in the first instar) and subsequently transform to adult wings. In recent mayflies larval wing buds arise from the posterior margin of notum and are directed by their apices posteriorly, by costal margin laterally-ventrally, and by dorsal surface dorsally-laterally (FIG.3:A) – thus, they have the same pose as folded wings of Neoptera, while adult mayfly wings never can strike such an attitude.

Based on wing buds position of recent mayflies and on Handlirsch's reconstruction of Permian *Phtharthus* (in which posteriorly directed wing buds were shown), some authors believed that this was the initial position of wing buds, and even assumed that insect wings evolved from outgrowths of posterior margin of the notum.

Actually the most primitive insects, including Permian mayflies – *Protereisma* – have wing buds arising not from posterior, but from lateral margins of the notum (FIG.14:D). All three specimens, on which the description of *Phtharthus* was based, have no wing buds preserved (FIG.14:C) (that is rather strange, because usually wing buds are well-preserved on fossils, and all three specimens of *Phtharthus* have well-preserved meso- and metanotal relief typical for Pterygota).

Among recent mayflies, in the primitive case wing buds are attached to the body only by their bases (Fig.25:A). Hind wing buds always retain this condition, but fore wing buds can be more strongly fused with mesonotum: in many taxa basitornal margins of fore wing buds are fused with posterior margin of mesonotum; in some taxa tornoapical margins are also partly or completely fused with notum or one with another (see Index of characters [1.2.5]). Even being strongly integrated with notum, the wing bud retains its outline as a relief line on the surface of the notum, and when the subimaginal wing develops, it is crumpled inside this outline; only in Posteritorna are wing buds completely integrated with notal shield (FIG.15).

Wing venation

In the larva wing venation appears at the earliest stages of development of wing buds as a net of lacunas (canals) inside the wing bud. Sometimes certain or all veins are visible as convexities on surface of the wing bud (Fig.3:A). Larval wing bud venation matches imaginal wing venation (FIGS 37:A; 75:A–B); in exceptional cases larval venation can be even more complete than imaginal one [see Geminovenata (3)]. Some authors mix veins and tracheae, which penetrate into some of the veins, which leads to wrong conclusions on vein homology.

Homology and nomenclature of insect wing veins is a subject of long-term discussion. Comstock and Needham (1898–1899 and later publications) proposed a universal usage of insect vein abbreviations C (costa), Sc (subcosta), R (radius), M (media), Cu (cubitus), $1^{st}A$ (first analis), $2^{nd}A$ and $3^{rd}A$; their R divides into R_1 and Rs (radius sector); these names were taken from older literature, where they were differently used for different groups of insects. Recently Comstock's interpretation is most widely accepted for wing venation of many insect groups, but not Ephemeroptera. For Ephemeroptera,

the most generally accepted vein abbreviations are C, Sc, R, MA, MP, CuA, CuP, 1A. The names **MA** (media anterior), **MP** (media posterior), **CuA** (cubitus anterior) and **CuP** (cubitus posterior) were introduced by Martynov (1924), but their recently used interpretation for Ephemeroptera was suggested by Tillyard (1932).

Possibly most of the veins in wings of mayflies and other Palaeoptera are not homologous to any vein in Neoptera: in Palaeoptera each longitudinal vein is either convex or concave, and can not change this feature in course of evolution; in Neoptera a homologous vein in various representatives can be convex, concave or neutral. In order to avoid confusion, probably it would be expedient to use Comstock's vein nomenclature for Neoptera only, designating a stonefly *Nemoura* sp. (Comstock & Needham 1898, p.238, Fig.8) as a type taxon for the vein names C, Sc, R, Rs, M, Cu, 1A, 2A and 3A.

For Ephemeroptera, here are used following names: **C** and **Sc** – both homologous to that of Neoptera; **RA** (term by Kukalova-Peck 1983) – a separate vein homologous to Comstock's R-R$_1$ of Neoptera; **RS** – a separate vein, which homology with Rs of Neoptera is unclear; **MA**, **MP**, **CuA**, **CuP** – four veins, possibly not homologous to branches of M and Cu of Neoptera; **AA** and **AP** (terms by Kukalova-Peck 1983) – two veins corresponding to Tillyard's 1A and 2A, possibly not homologous to 1A and 2A of Neoptera. Tillyard regarded RA (=R$_1$) and RS to be secondarily separated branches of the same vein R, and because of this supplied branches of RS with numbers 2, 3 and 4+5. Here branches of RS are supplied with letters "**a**" (anterior) and "**p**" (posterior) and numbers (see below), to avoid confusion with the Tillyard's numbers (Kluge 2000).

In Ephemeroptera convex and concave veins are alternating forming triads. The **triad** is such a form of branching, when a convex vein is branched to two convex branches with a concave intercalary between them, and a concave vein is branched to two concave branches with a convex intercalary between them (such triads are characteristic for Subulicornes, i. e. Odonata + Ephemeroptera). Veins Sc (concave, as in other Pterygota) and RA (convex, as in other Pterygota) are non-branched, at least on fore wings go parallel to the costal margin (which is armed by the costal vein), reaching the wing apex. On fore wing distal part of the field between C and Sc has membrane slightly thickened and, thus, represents a **pterostigma**. Veins Sc and RA are firmly fused with

a sclerotized plate in wing base; near wing base C, Sc and RA are connected together by a **costal brace** (see Index of characters [2.2.29]). Other veins have soft bases or are secondarily firmly fused with the base of RA. In Euephemeroptera RS and MA are fused in proximal part. Vein RS is concave and is branched forming subordinate triads: its first triad contains concave branches **RSa** and **RSp** and a convex intercalary **iRS**; RSa forms a second triad, which contains concave branches **RSa$_1$** and **RSa$_2$** and a convex intercalary **iRSa**; RSa$_2$ forms a third triad, which contains concave branches **RSa$_2$'** and **RSa$_2$"** and a convex intercalary **iRSa$_2$** [on hind wing only the first of these triads is present – see Euplectoptera (1) below]. Vein MA is convex and forms a single triad with convex branches **MA$_1$** and **MA$_2$** and a concave intercalary **iMA**. Vein MP is concave and forms a triad with concave branches **MP$_1$** and **MP$_2$** and a convex intercalary **iMP**. Vein CuA is convex; in Euplectoptera it is either non-branched or has one or several secondary branches arising posteriorly [see below, Anteritorna (1)]. Vein CuP is concave. Vein AA is convex, vein AP is concave; behind them two or more alternating convex and concave veins can be present. In some triads the intercalary vein incorporates basally with one of branches, thus looking not like intercalary, but like a branch; sometimes, vice versa, a branch becomes free in its basis and looks like intercalary; in rare cases some branches and intercalaries are lost (see Index of characters [2.2.32]–[2.2.54]). Sometimes between the longitudinal veins, their branches and intercalaries, there are present additional intercalary veins (see Index of characters [2.2.55]–[2.2.56]). Usually longitudinal veins are connected by large indeterminate number of cross veins (except for a few extremely specialized groups – see Index of characters [2.2.57]).

LEGS
(Figs 3–4; 10)

While dorsally the coxa is always articulated with katapleurite (as in other Hexapoda), ventral coxal articulation is variable among mayflies: Mesothorax and metathorax always lack trochantines, and coxae are articulated either directly to sternite (mesothorax in FIG.52:B), or to movable paired sclerites articulated with sternite (FIG.35 and metathorax in FIG.52: B); non-functional vestiges of these sclerites can be present on prothorax as well (FIG.35). Prothorax can have a pair of trochantines, which serve ventral

coxal articulations (FIG.35), or trochantines are lost, and coxa have direct articulation with sternite (FIG.70:A–B).

As well as in all other Hexapoda, the leg of Ephemeroptera consists of **coxa**, **trochanter**, **femur**, **tibia** (sometimes called metatibia – see below), **tarsus** (see below) and **pretarsus** (i. e. claw or claws – see below).

Tibia

Probably the **tibia** (or **metatibia**) of Hexapoda is formed as a result of fusion of **patella** and **telotibia** (or tibia itself). In the majority of Hexapoda, including all known primary wingless insects (Entognatha and Triplura), fusion of patella and telotibia is complete, without trace of suture between them. But in Ephemeroptera and Odonata vestigial **patella-tibial suture** is retained. This suture is non-functional, patella and telotibia are connected immobile. Patella-tibial suture is strongly oblique, so patella is very short on its outer side, being several times longer on its inner side. On outer side of leg, the patella-tibial suture always has a form of distinct wide transverse concavity; it can be continued on anterior (dorsal) side and sometimes on other sides – in larva in a form of distinct narrow oblique grove, in subimago and imago in a form of indistinct longitudinal-oblique concavity. Sometimes such oblique grove or concavity is absent (everywhere below, the sentence "patella-tibial suture is absent" means that only the concavity on outer side is present).

Most Euplectoptera have patella-tibial suture on middle and hind legs only, while on fore legs it is absent (FIGS 3–4). In selected taxa patella-tibial suture disappears also on middle and/or hind legs (see Index of characters [1.2.18] and [2.2.82]). Only in two non-related taxa (Tridentiseta-Turbanoculata-Anteropatellata and Bidentiseta-Rhithrogena/fg3) the patella-tibial suture has secondarily restored on larval fore legs. Even in the cases when larval fore tibiae have the same structure as middle and hind tibiae, adults often (but not always) retain distinct vestiges of patella-tibial suture on middle and hind legs only.

Such difference of fore leg from middle and hind leg occurs in all principal phylogenetic branches of Ephemeroptera, being present in majority of species, independently of their leg specialization. In contrast to Ephemeroptera, in Odonata patella-tibial suture is equally developed on all legs. This allows one to conclude that reduction of the patella-tibial suture on

fore legs only is an autapomorphy of Ephemeroptera (either Euplectoptera, or Euephemeroptera, or Panephemeroptera, as structure of extinct Protephemeroidea and Permoplectoptera is unknown).

Tarsus

Tarsi of Ephemeroptera have peculiar structure. Tarsus is immovable or slightly movable: usually tarsi of middle and hind legs lack adductors and abductors (being moved only by adductor of claw) and tarsus of fore leg has a single adductor; sometimes this muscle is also absent. Tarsus has different structure in larva and winged stages. In winged stages (i. e. imago and subimago) the first tarsal segment is usually immobile fused with tibia, while other tarsal segments are joined mobile (FIG.4).

In contrast to winged stages, larval tarsus (including its first segment) is mobile joined with tibia, but all tarsal segments are immobile fused together. Often larval tarsus is non-segmented, without any traces of segmentation; in Siphlonurus/fg1 and some others, slightly visible traces of tarsal segmentation are retained (FIG.3:A); only in Ameletopsis/fg1 are several (but not all) tarsal segments separated by more or less developed articulations (FIG.35:A). Probably non-segmented larval tarsus is an autapomorphy of Euplectoptera, as for the known larva of Permoplectoptera (*americana* [*Kukalova*]) segmented tarsi are described. This apomorphy is not unique, as non-segmented tarsus occurs also in some other Hexapoda.

In Pentamerotarsata and some other mayflies, imaginal and subimaginal tarsus has 1st segment mobile articulated with tibia (see Index of characters [2.2.84]) and externally looks like primitive insect tarsus (probably movable 5-segmented tarsus is initial for Amyocerata). Because of this, one can think that among Ephemeroptera such a completely segmented tarsus should be a plesiomorphy, and fusion of 1st tarsal segment with tibia – an apomorphy; but in this case we would have to assume, that in different phylogenetic branches of Ephemeroptera the same fusion of 1st tarsal segment with tibia took place independently, while in other insects such tendency is not expressed. It is much more probable that the common ancestor of Ephemeroptera had 1st tarsal segment fused with tibia, while in some taxa it became secondarily separated; in all cases tibio-tarsal muscles remain to be reduced. The restoration of the adult tibia-tarsal

joining in some mayflies does not contradict to the principle of irreversibility of evolution, as all mayflies retain mobility of tibia-tarsal joining in larval stage.

Usually winged stages of Ephemeroptera have 5 tarsal segments (including the first segment fused with tibia), but sometimes number of tarsal segments is less than five (see Index of characters [2.2.78] and [2.2.83]). 5-segmented tarsus is probably plesiomorphic within Amyocerata (and possibly within Hexapoda in general), as 5-segmented tarsi occur in many groups of Amyocerata, and number of tarsal segments never increases five.

Pretarsus

Pretarsus of Ephemeroptera has peculiar structure and differs in different stages. As well as in majority of Pterygota and in some other insects, in winged stages of Ephemeroptera pretarsus consists of two claws articulated with a single unguitractor. In majority of mayflies one of these claws (the **anterior** one, if the leg is directed laterally with its knee articulation directed dorsally) is blunt, while another claw (the **posterior** one) has form typical for a claw – pointed, curved and sclerotized. Everywhere below this claw structure is called **ephemeropteroid claws**. Such structure is probably an autapomorphy of Euplectoptera, or Euephemeroptera, or Panephemeroptera; this apomorphy is unique, being never found in other insects. In selected taxa of Euplectoptera both claws are similar – pointed, curved and sclerotized (see Index of characters [2.2.85]). Some authors regarded this structure of pretarsus to be plesiomorphic, because it is the same as in the outer-group – many non-ephemeropterous Hexapoda; but this assumption requires that ephemeropteroid claws appeared independently many times among Ephemeroptera, but never appeared in other insect groups. Much more reliable is the assumption that ephemeropteroid claws appeared once, being an autapomorphy of Ephemeroptera, but all Ephemeroptera retain genetic potentiality to form ancestral pointed claws, and this potentiality is realised independently in some taxa of Ephemeroptera.

In contrast to the winged stages, in larvae of all Euplectoptera the pretarsus consists of a single claw; only on the fore leg of Metretopus/fg1 is the claw bifurcate (Fig.22:C), but this bifurcation probably is not connected with double claws of adults. Probably the single claw is an autapomorphy of Euplectop-

tera, as for the known larva of Permoplectoptera (*americana* [*Kukalova*]) double claws are described. This apomorphy is not unique, as a single claw occurs in some other insect groups. Some authors believe that the single claw of Ephemeroptera larvae is a plesiomorphic condition, because in many arthropods only a single unpaired claw is present – in Eucrustacea, Diplopoda, Chilopoda, Ellipura and marine Pseudognatha. At the same time, paired claws are secondarily substituted by unpaired claw in larvae of many Oligoneoptera and some other insects. In Ephemeroptera this character also can be a secondary one.

Fore leg of male

Fore leg of the male imago is specialized for grasping female at copulation. It is elongate, usually tibia and tarsal segments are especially long. Articulation of tibia and tarsus has such a construction, which allows to turn the tarsus around at 180^0 (FIG.10:A–F); thanks to this, the tarsus can be arched upward to hold the female wing base at copulation (FIG.10:G). Claws of male imaginal fore legs can have the same structure as claws of other legs; but in some mayflies they have another structure, being blunt (this character appears independently several times – see Index of characters [2.2.77]).

ABDOMEN

GENERAL STRUCTURE

In all stages the abdomen consists of ten segments – condition initial for Hexapoda. Many authors assume that the abdomen of Hexapoda, and particularly that of Ephemeroptera, consists of 11 or 12 segments, regarding some structures at the end of abdomen to be vestiges of segments XI and XII; however, such assumptions are not proved (see below).

In the winged staged each of segments I–IX has tergite and sternite distinctly separated by soft pleura. In the larva the sutures between tergite, pleura and sternite are lost, so borders of these parts of segment can be found only by tracing how inside them the corresponding parts of the subimago develop. Posterolateral angles of abdominal segments are usually stretched forming paired flat denticles or spines; in the primitive case (characteristic for majority of mayflies) such posterolateral

spines are larger in larva and smaller in adults, and are the largest on segment IX, being progressively smaller on previous segments; sometimes they are modified or lost.

Abdominal tergites and sternites of the imago and subimago are weakly sclerotized and lack setation (in subimago they are covered by microtrichia – see above). In the larva the abdominal cuticle has the same degree of sclerotization as that on its head and thorax, varying from moderate in the majority of mayflies, to rather hard in some taxa, and often bears peculiar setation. The posterior margin of the larval tergite (and sometimes sternite) is often armed with a regular row of small flat denticles (possibly modified setae), which project posteriorly as a continuation of the tergite surface and overlap the intersegmental membrane; in many cases these denticles are vestigial or absent (for some of them – see Index of Characters [1.3.5]).

TERGALII
(Fig. 13)

In the larva abdominal segments bear paired movable joined appendages – **tergalii** (singular – **tergalius**). In previous publications this term was used either as feminine – "tergaliae" in plural and "tergalia" in singular (Kluge 1989a: 49; 1996: 73), or as neuter – "tergalia" in plural (Kluge 1989a: 77). In order to avoid confusion between plural and singular, gender of the Latin term is now changed to masculine (Tiunova & Kluge & Ishiwata 2003), while in Russian it remains to be feminine ("тергалия" in singular, "тергалии" in plural). Type of the term is *Siphlonurus lacustris* (FIG.13:A, reproduced from Kluge 1989a: Fig.4; designated here). Tergalii are often called "tracheal gills"; the term "tergalii" is attributed to a set of homologous organs, while the "tracheal gills" are analogous organs of various origin (Kluge 1989a, 1996a, 2000). A tergalius may or may not serve as a gill, and a gill may or may not be a tergalius; sometimes the tergalius bears a special gill (FIG.36:B), sometimes gills are present on other body parts (see Index of characters [1], [1.3.25] and [1.3.30-32]).

In winged stages tergalii are absent, so here all characters connected with tergalii structure are attributed to larvae only (see Index of characters [1.3.19]–[1.3.59]). In the larva of 1st instar tergalii are never present, they appear after one of next moults. Tergalii of young larva can strongly differ in their structure and number from tergalii of mature

larva; so here in descriptions of taxa all characters connected with tergalii are attributed only to mature larva (several last instars) and would be wrong if apply them to young larvae.

In Euplectoptera seven pairs of tergalii can be present on abdominal segments I–VII. In some euplectopteran taxa number of tergalii pairs is less, as the tergalii are retained only on some of these segments (see Index of characters [1.3.19]–[1.3.20]); only in abnormal specimens tergalii can be present on abdominal segment VIII. In extinct Permoplectoptera nine pairs of tergalii were present on abdominal segments I–IX. Here certain pairs of tergalii are indicated by Roman numerals corresponding to abdominal segments; for example, "tergalius III" means tergalius of third abdominal segment, independently of the presence or absence of tergalii on the two first abdominal segments.

Tergalii are joined at the sides of the posterior margin of the tergite, nearly always on the dorsal side of the body; only in rare cases are their bases translocated together with the lateral margin of tergite to the ventral side; in some specialized mayflies the bases of some tergalii are shifted to the anterior part of the tergite (see Index of characters [1.3.22]).

Tergalius always has mobile articulation with the body, being articulated to it by narrow base and moved by special tergalial muscles located inside the segment (inside the tergalius itself muscles are absent). Tergalial muscles are the most lateral group of muscles of the segment; they are more lateral than dorsoventral muscles and run from the basis of tergalius obliquely anteriorly-ventrally, to the ventral wall of the segment – sternopleuron. In some cases each tergalius has only one tergalial muscle (FIG.13:C), in other cases a bunch of 2-4 parallel muscles which can work as antagonists arises from the basis of each tergalius. In larvae of many mayflies tergalii are able to make fast rhythmic fluctuations and are used by the larva to create a water current around its body. Such an ability to create a water current is very important for respiration of larvae inhabiting stagnant waters, but has no practical significance for rheophilous (lentic) larvae inhabiting fast streams. In some rheophilous mayfly larvae tergalii have the same mobility, in others they are able only to slow movements, and can not create a water current. Mobility of tergalii is an important systematic character of some taxa (see Index of characters [1.3.30]).

As a whole, the character of musculature and the

places of attachment of tergalii on the abdomen in mayfly larvae correspond to musculature and places of attachment of wings on mesothorax and metathorax of adult Pterygota (Kluge 1989a), so the tergalii are most probably the serial homologues of wings. The bunch of tergalial muscles probably corresponds to a complicatedly differentiated complex of wing muscles of direct action running from the basalar, subalar and axillary sclerites to the pleurite, sternite and furca (sternal apodeme). Some researchers stated the alternate point of view – that these appendages on the abdomen of mayfly larvae are homologous not to the wings, but to the limbs, thus the places of their attachment were considered to be located not on the tergite, but on the sternopleurite. It is quite difficult to compare a segment of abdomen with a segment of thorax, because of the great difference in their structure, but it is possible to compare structure of different abdominal segments and to trace development of a segment from larva to imago (FIG.13:A–B). Such comparison shows that styliger and gonostyli of male (being homologous to coxites and styli, that is, limb derivatives) have another, more ventral, position on a segment than tergalii do; that is, tergalii can not be homologous to limbs. With the idea about homology of tergalii and wings some theories about origin of wings and phylogeny of Pterygota are connected. Some authors, naming tergalii "tracheal gills", compare them with tracheal gills of other insects, in particular, with paired abdominal gills of some Odonata, Plecoptera, Megaloptera and some other insects. However tergalii essentially differ from these gills, as they are articulated to the tergite, and the muscles, which move them, run not dorsally, but ventrally to the sternum. Though it is supposed that tergalii have a very ancient origin, their homologues in other groups of insects are not found. Ideas about the phylogeny of Ephemeroptera strongly depend upon point of view on tergalii origin (if they are homologous to wings or to legs), as in these cases the initial plan of tergalii structure is assumed differently.

Tergalial form and structure are diverse. Usually the tergalius is lamellate, its dorsal surface is directed dorsally or anteriorly, and its ventral surface is directed ventrally or posteriorly. One of margins (from tergalius base to its apex) is named here **costal margin;** this is the margin which can be directed anteriorly or ventrally (if tergalius apex is directed laterally) or laterally (if tergalius apex is directed posteriorly). The opposite of it is an **anal margin –**

this is the margin, which can be directed posteriorly or dorsally (if tergalius apex is directed laterally) or medially (if tergalius apex is directed posteriorly). As a rule, the tergalius has two sclerotized ribs – a **costal rib** (running from tergalius basis by its costal margin or at some distance from it) and an **anal rib** (running from tergalius basis by the anal margin, or at some distance from it) (FIG.13:C–G); sometimes these ribs are vestigial or lost (see Index of characters [1.3.27] and [1.3.28]). Inside tergalius, more or less advanced tracheae pass. In difference from wings, in which tracheae pass inside sclerotized veins, in tergalius tracheae always pass irrespectively of sclerotized ribs, so tergalii have no true veins.

Basing on a wrong reconstruction of the Permian *Phtharthus*, where ventral stylus-like abdominal appendages were shown (Handlirsch 1904a, 1906–1908, 1925), some authors believed that ventral attachment (occurring in recent Behningia/fg2 as well) and slender shape (characteristic for recent Pinnatitergaliae in general) were initial features of the mayfly abdominal appendages, which they regarded to be limb derivatives. This led to the assumption of a very ancient origin of the Pinnatitergaliae. Actually abdominal appendages of *Phtharthus* have posterior-lateral-dorsal attachment typical for mayfly tergalii, and probably lamellate shape (FIG.14:C), as well as tergalii of another Permian mayfly – *Protereisma* (FIG.14:D), that is most probably the initial tergalial structure.

Functions of tergalii are various. In some mayflies they create a water current necessary for respiration. In many cases tergalii are used as tracheal gills (as far as they increase the body surface and this facilitates respiration). Tergalii can execute a role of organs of attachment (overlapping one another by their edges and forming one large sucker in larvae of some Holarctic Radulapalpata and Australian Atalophlebia/fg1 – see Index of characters [1.3.31]). Sometimes tergalii are transformed into protective gill opercula (see Index of characters [1.3.32]). In Coloburiscus/fg1 tergalii, being sclerotized and covered by large spine-like setae, probably, execute a protective role. In a many cases tergalii lack any function, but nevertheless are retained together with the tergalial musculature.

GENITALS
(Figs 11, 18:A–D)

In the female imago, the sexual aperture opens between abdominal sternites VII and VIII. Usually

on this place no external morphological structures are present (FIG.18:A–B); the sternite VII can be produced posteriorly, forming a **pregenital plate**; in rare cases (in some Leptophlebia/fg1) the pregenital plate forms a tubular process – an unpaired secondary ovipositor. If pregenital plate is present, it is expressed only in imago and subimago, but not in larva. Mayflies have no any vestiges of the primary ovipositor (inherent in many other Amyocerata).

Abdominal sternum IX is produced posteriorly in the form of a plate. In the female this is a simple plate called **postgenital**, or **preanal** plate (see Index of characters [2.3.6]). In the male this plate, named **styliger** (see Index of characters [2.3.7]), bears a pair of mobile appendages – **gonostyli**, or **forceps** (see Index of characters [2.3.8]–[2.3.14]). Gonostyli are used by the male imago at copulation for holding female abdomen (FIG.10:G–H). Gonostylus is a derivative of the abdominal stylus – such styli are developed on abdominal segments I–IX (or at least some of them) in Triplura, on abdominal segments I–VII (or some of them) in Diplura, and only on abdominal segment IX of males and/or females in some Pterygota. In all insects which have abdominal styli or their derivatives the stylus is non-segmented; in some Diplura and Triplura the stylus bears an apical pointed appendage – tarsellus (only in some palaeontological publications segmented styli are described for extinct insects, but these descriptions are quite doubtful, not being supported by fossils). Gonostylus of Ephemeroptera looks segmented, but its segments are secondary ones, they have no active mobility and no muscles or apodemes inside. Gonostylus is moved only by a muscle located in the styliger and attached to its first segment. A lateral paired portion of styliger, which contains the muscle of gonostylus, is named here a **pedestal of gonostylus**; in some mayflies the styliger is strongly reduced, but its gonostyli pedestals are prominent, segment-like, thus sometimes they are erroneously taken for proximal segments of gonostyli. Gonostylus usually consists of the following 4 secondary segments: a short thick 1st (proximal) segment is immobile connected with a long 2nd segment, further follow two passively-mobile articulated **distal** segments – 3rd and 4th ones. In some mayfly taxa the number of gonostylus segments is reduced, in more rare cases it is increased (see Index of characters [2.3.10]–[2.3.14]). Inner surface of the gonostylus often bears numerous mechanoreceptorial globular papillae representing modified setae (Gaino & Rebora 2002).

The projection of abdominal sternum IX (the subanal plate of female and the styliger with gonostyli of male) is better developed in the imago, and usually is present not only in imago and subimago, but in the larva as well (in contrast to the subanal plate of female). Larval gonostyli are small and have no more than one distal segment, from which the both subimaginal distal segments are developed; often larval gonostyli are non-segmented, sometimes reduced or fused with styliger. In the majority of mayflies structure of abdominal sternum IX allows to distinguish male and female larvae; only in Turbanoculata larval gonostyli are reduced, and in Caenoptera larval gonostyli are completely fused with styliger, thus in these two taxa sexual dimorphism in larval abdominal sternum IX is not expressed (see Index of characters [1.3.60]).

In the male imago, from a membrane between styliger base and paraproct bases (i. e. from the boundary of segments IX and X), a **penis** arises. Cuticle laterad of penis base is sclerotized in such a manner that forms a pair of curved sclerotized **penial arms.** Each penial arm has a lateral-ventral angle articulated with a peculiar small proximal-dorsal projection of styliger, and a lateral-dorsal end articulated with posterior margin of tergite IX somewhat mediad of its lateral-posterior corner. Styliger is able to bent ventrally by contraction of longitudinal sternal muscles. At rest, the articulation of lateral styliger margin with immobile lateral margin of sternite is located somewhat distad of the articulation of styliger with penial arm; thanks to this, when styliger bents ventrally, penis is protracted posteriorly and dorsally (FIG.11). The penial arms are well developed in the overwhelming majority of mayflies, with exception for a few taxa (see Index of characters [2.3.17]).

Penis is usually paired (in contrast to majority of other insects); its left and right lobes can be either completely separated, or more or less fused together. Paired seminal ducts usually open on penis by a pair of gonopores, rarely by an unpaired gonopore (particularly, in *fragilis* [*Ametropus*]); seminal ducts can be paired all aver their length (FIG.23:G) or are fused in penial base (FIG.93:C) (see below).

Form and structure of the penis are extremely diverse, it can have complex musculature and movable spines – **titillators** (see Index of characters [2.3.15]–[2.3.17]).

Subimaginal and larval penis (FIG.18:D) never has sclerotized arms and can have other differences if compared with the imaginal one – its structure can

be more simple, rarely more complex than in imago; in a few taxa larval penis is lost (see Index of characters [1.3.60]).

ABDOMINAL SEGMENT X AND CAUDALII
(FIG.12)

The last, tenth abdominal segment has a well-developed tergite, whose lateral-anterior angles are produced ventrally more strongly than that of preceding tergites, but do not meet on the ventral side (in contrast to Microcoryphia, Odonata, some Plecoptera and some other insects). Tenth tergite is well-outlined both in adults and larvae (in contrast to preceding tergites, which are not laterally outlined in larva); its posterior margin is produced posteriorly as a flap above bases of caudalii.

Ventral wall of the tenth segment is formed by a pair of **paraprocts**. In the larva paraprocts have a form of distinct sclerites (see Index of characters [1.3.62]), while in the imago they are usually soft and indistinct. As the tenth tergite is interrupted ventrally, paraprocts are directly articulated to sternum IX.

Posterior wall of the tenth segment is formed by a **tricaudale** (new term) – integral sclerotized formation consisting of a **basitricaudale** (new term) – transverse sclerite of body wall, and **caudalii** (new term) – three processes arising from the basitricaudale in caudal direction. Formerly caudalii of mayflies were called "caudal filaments", as they often have a thread-like form, especially in adults. Lateral paired caudalii are **cerci**, and median unpaired caudalius is **paracercus**. Between lateral margin of basitricaudale, lateral-posterior margin of paraproct and lateral-posterior margin of tergite, body wall is formed by a paired sclerite – **cercotractor** (new term). Type taxon of the new terms tricaudale, caudalius, basicaudale and cercotractor is *aestivalis* [*Siphlurus*] in FIG.12:A–E. Usually the cercotractor has triangular shape, is movably connected with tergite, movably articulated with lateral base of cercus and fused with paraproct (FIG.12:A–F); but in some taxa the cercotractor has another shape, can be separated from paraproct (FIG.12:G) and/or fused with cercus (see Index of characters [1.3.62] and [2.3.18]). Basitricaudale has a pair of deep dorsoventral grooves, which serve its flexibility and divide it into three portions each bearing one caudalius; **direct caudalial muscles** stretch from tergite to these grooves and serve as adductors of cerci. Probably no primary direct

abductors of cerci are present in insects. Abduction is served by **tergo-cercotractoral muscles** (Figs.12: A–E); in the cases when cercotractors are fused with cercal bases, the tergo-cercotractoral muscles look as direct cercal abductors (FIG.12:G). Each caudalius has a **basi-basal muscle,** which connects dorsal and ventral edges of its base. Such basi-basal muscles are well developed in all mayflies, being retained even in vestigial paracercus of that mayflies, which look as two-tailed. Besides Ephemeroptera, basi-basal muscles are developed in Triplura (both in Zygentoma and Microcoryphia), but lost in Metapterygota.

Some authors (Snodgrass 1935, et al.) erroneously regard paraprocts to be coxites of abdominal segment XI, cerci to be leg derivatives of abdominal segment XI (i. e. appendages of paraprocts), and the paracercus to be a dorsal appendage of another origin. This assumption is based on examination of Microcoryphia and some other insects with specialized abdomen, where abdominal tergite X forms an integral ring, separating paraprocts from sternum IX (so the ring formed by tergite X is taken for a fusion of tergite X and sternite X). Such homologization contradicts to muscles arrangement, as no special sternal muscles are attached to the "sternite X" (which is actually a ventral part of the tergite X). Abdominal structure of Ephemeroptera (as well as that of Zygentoma and some other insects) is more primitive, so the sternite X (pair of paraprocts) is situated here not behind, but ventrad of the tergite X and just behind the sternum IX. In all Amyocerata the cerci and paracercus are in the equal manner articulated with abdominal tergite X and all muscles going from their bases are attached to the tergite X only. Most probably, cerci and paracercus are organs of the same origin, being dorso-posterior appendages of tergite X (Kluge 1999d, 2000). In contrast to leg derivatives, the caudalii never have primary segmentation, never have muscles or apodemes inside.

In Ephemeroptera caudalii have such a kind of secondary segmentation, which is most primitive among Amyocerata, being the same as in all Triplura: the number of segments is large and indeterminate; at each moult it increases thanks to division of proximal segments half-and-half; each caudalius is thickest in its base, and becomes thinner toward apex (i. e. has a bristle-like shape); proximalmost segments are shortest and indistinctly divided one from another, and in distal part segments become longer and distinctly separated. This structure and kind of growth resembles that of the

antennal flagellum of primitive representatives of Amyocerata, including Triplura and Ephemeroptera (but not of antenna as a whole, which have besides the flagellum, also scapus and pedicellus).

Besides Ephemeroptera, cerci are retained in many other Pterygota, but the paracercus is lost in all Matapterygota (in some Plecoptera and some other Metapterygota presence of paracercus was erroneously stated in literature). In Ephemeroptera cerci are always developed, and the paracercus can be as long as cerci or even somewhat longer, or it is more or less reduced, up to a non-segmented vestige (see Index of characters [1.3.64] and [2.3.20]). In many mayflies the paracercus is reduced only in winged stages, being developed in the larva; in this case, when subimaginal tissues are developed under larval cuticle, hypodermal paracercus narrows and breaks near base, thus subimaginal vestige of paracercus develops only from the basal part of larval paracercus, and at moult larval cuticle shads together with remainder of hypoderm of most part of paracercus (in contrast to mouthparts – see above). Sometimes the paracercus is reduced in larva of first instar, being developed in mature larva; sometimes it is developed in larva of first instar, being reduced in mature larva and winged stages; sometimes it is reduced in all stages.

In male imagoes nearly of all Ephemeroptera caudalii are longer than the body (see Index of characters [2.3.18]) and are used in the mating flight: most mayflies have in their mating flight a stage of parachuting, when the insect passively moves down with its wings are V-like elevated upwards, and its cerci are widely divergent. In male subimagoes caudalii are not so long as in the imago. In female imagoes caudalii are less long, little longer than the body or shorter than it.

Larval caudalii often have denticles on posterior margins of segments, similar to denticles on posterior margins of abdominal tergites (see above).

In larvae of the primitive siphlonuroid type (see above), caudalii have a peculiar structure (FIG.28: A): they are not long (much shorter than in imago, shorter than the body); paracercus is subequal to cerci; cerci have oblique margins of segments, so each segment on lateral (outer) side is situated more distally, than on median (inner) side; **primary swimming setae** are present – these are setae arranged in four regular rows – one row on median (inner) side of each cercus and a pair of rows on lateral sides of paracercus. Such structure of caudalii allows larva to swim, moving by its abdomen up-

and-down (FIG.9:A–B). In various mayfly taxa this primary siphlonuroid specialization is secondarily lost or changed to other specialization. Sometimes on lateral (outer) sides of cerci **secondary swimming setae** can be developed, they differ in structure from the primary swimming setae (see Index of characters [1.3.67]). Sometimes primary swimming setae are reduced (see Index of characters [1.3.66]) or substituted by secondary swimming setae, which have the same structure on both lateral and median sides of cerci and lateral sides of paracercus. Margins of segments of cerci can be not oblique, paracercus can be more or less shortened, and cerci elongate, being more similar to cerci of winged stages; such modification is especially usual for rheophilous larvae, which lost ability to active swimming.

Based on a wrong reconstruction of Permian *Phtharthus*, where cerci were shown as fringed by setae on both sides (Handlirsch 1904a, 1906–1908, 1925), some authors believed that such setation (occurring in recent Pinnatitergaliae as well) was initial for mayflies. Actually caudalii of *Phtharthus* have typical siphlonuroid setation with cerci bearing setae on median sides only (FIG.14:C), as well as that of another Permian mayfly – *Protereisma* (FIG. 14:D). The same siphlonuroid setation is most common for Mesozoic and Recent mayflies (see Index of characters [1.3.66]), which leads to the assumption of its primary nature.

INTERNAL ANATOMY

ALIMENTARY CANAL AND MALPIGHIAN TUBES

The alimentary canal is functional in larvae and non-functional in subimagoes and imagoes; it is straight and simple; the stomodaeum is slightly separated or non-separated from the mesenteron, thin-walled and lacking sclerotized formations (characteristic for ectodermal proventriculus of many other insects); the proctodaeum is more differentiated (Needham et al. 1935: Pl.6), varying among mayfly taxa (Landa & Soldán 1985: Figs 44-59).

Malpighian tubes are numerous (from several dozens to several thousand) and have unique structure: each tube consists of a distal portion usually coiled spirally or S-like, and of a very thin duct arising from the inner end of the spiral (Needham & al. 1935:Pl.7:5–10). Ducts of Malpighian tubes fall either directly into the intestine, or into special projections of the intestine – **trunks of Malpighian**

tubes (Landa 1969b:Fig.12; Kluge 1993a:Figs 1–19; 1998:Figs 32–34). The trunks of Malpighian tubes occur in many (but not all) mayfly taxa and have various number, length and arrangement, can be simple or branched; most of the trunks are directed anteriorly. Number, arrangement and branching of the trunks were regarded to be characters of high level taxa (Landa 1969b, Landa & Soldán 1985), but actually the number of trunks and their branches is under great individual variability; it can differ in specimens of the same species and in left and right halves of the same specimen (Kluge 1993a:Figs 1–19). Most constant are longest trunks, while short trunks and short branches can easily appear and disappear, varying individually (Kluge 1993a, 1998). In many taxa examined (Posteritorna, Isonychia/fg2, Fimbriatotergaliae) there are 2 longest lateral trunks directed anteriorly; sometimes anterior end of each trunk bears a peculiar straight Malpighian tube partly fused with its duct (Kluge 1998: Figs 32–34); an identical pair of peculiar Malpighian tubes directed anteriorly occur also in some mayflies, which have no trunks – Turbanoculata (Landa 1968:Fig.12BR) and some Ephemerella/fg1. So, the lateral paired position of Malpighian tubes is usual for many non-related groups of Ephemeroptera. Some other mayflies, particularly Radulapalpata, instead of one pair, have 2 equal pairs of longest trunks directed anteriorly (Kluge 1993a: Figs 1–19).

TRACHEAL SYSTEM

Mayflies have all 10 pairs of **tracheostia** (mouths of tracheal system) that are initial for Amyocerata: 2 intersegmental thoracic pairs – **stenothoracic** (between prothorax and mesothorax) and **cryptothoracic** (between mesothorax and metathorax), and 8 segmental abdominal pairs – one pair on each abdominal segment I–VIII (Kluge 2000). All tracheostia are lateral, each abdominal tracheostium is located at the anterior part of its segment (FIG.13). In subimago and imago the both pairs of thoracic tracheostia have a form of widely opened spiracles lacking closing apparatus, and the abdominal tracheostia are either closed or have a form of small spiracles (FIG.4). In the larva all tracheostia are closed, but at each moult serve for escaping of old tracheal intima thorough them.

The tracheal system of mayflies is described and figured in detail by Landa (1948). Tracheae originating from different tracheostia are connected by a single pair of thick lateral **longitudinal trunks** (the same in many other insects). Left and right trunks are connected one with another only by **transverse anastomoses,** which have no passage for the air: each transverse anastomose is formed by a pair of tracheal branches meeting medially and fused by their apical cuticular thickenings. One of such transverse anastomoses, named **Palmen's body**, is located in the head dorsad of oesophagus and is formed by fusion of apices of two pairs of tracheae meeting at one point; some other transverse anastomoses can be present in the head, thorax and abdomen. Abdominal anastomoses, if present, are located ventrad of the intestine close to the nerve cord, no more than one anastomose per a segment. They can be present in abdominal segments VIII and/or IX only, or in other abdominal segments as well. Arrangement of transverse abdominal anastomoses was regarded as an important character of high rank taxa (Landa 1968b; Landa & Soldán 1985; McCafferty 1991a); however, the number of anastomoses varies individually. During ontogenesis, new anastomoses are added, thus their number is less in the young larva and more in the mature one.

Arrangement of visceral tracheae was regarded as another character of high rank taxa (Landa 1968b; Landa & Soldán 1985). Sometimes tracheae penetrating into the same internal organs or muscles originate from different tracheostia; this can vary individually or in the left and right sides of the same individual. Taking into account that examination of thin tracheae is rather difficult and needs special methods, characters connected with the tracheal system are hardly usable in taxonomy.

Thoracic and abdominal tracheae arising from different pairs of tracheostia are connected by the single pair of lateral trunks only, and have no other longitudinal anastomoses; particularly, in contrast to Metapterygota, there are no loops connecting stenothoracic and cryptothoracic tracheostia and giving rise to mesothoracic leg and wing tracheae, and no loops connecting cryptothoracic and first abdominal tracheostia and giving rise to metathoracic leg and wing tracheae. Instead of this, each leg and each wing is supplied by a single trachea; mesothoracic leg and wing get trachea from stenothoracic tracheostium, and metathoracic leg and wing get trachea from cryptothoracic tracheostium only.

The single trachea coming into the wing divides into several branches, which penetrate through the wing base either passing as a single bunch anteriad of the basal wing plate, or a branch going to MP and CuA passes separately from others posteriad of the

basal plate, and then unites with others just before the place where tracheae diverge penetrating into RA, RS+MA and MP. Among the taxa examined, only Campsurus/fg1 have unusual separate entering of the trachea into CuA (see Index of characters [2.2.50] and FIGS 79–80).

NERVE SYSTEM

As in other Hexapoda, the central nerve system of Ephemeroptera initially consists of a supraoesophageal synganglion (fused preoral brain and tritocerebrum), suboesophageal ganglion (fused ganglia of mandibular, maxillary and labial segments), 3 thoracic ganglia and 8 abdominal ganglia (last of which is probably a synganglion of abdominal segments VIII–X). This or that thoracic or abdominal ganglion can be shifted anteriorly, and is sometimes fused with ganglion of the preceding segment. Thus, the 1st abdominal ganglion is often fused with the metathoracic ganglion, and the last two abdominal ganglia can be fused together; nerve connectives can be fused together partly or completely (Landa & Soldán 1985:Figs 1–4). Position of the metathoracic ganglion in adults is well-indicated externally, thanks to the structure of the mesothoracic furcasternal protuberances (see paragraph "Mesosternum" and Index of characters [2.2.23]). Location of abdominal ganglia in this or that abdominal segment is not well-fixed, as abdominal segments are able to protract backward and retract into preceding ones.

REPRODUCTIVE SYSTEM

It is usual to regard that mayfly gonads and gonoducts are paired all over their length and always open by paired gonopores. Actually, this is true for a part of mayflies only (FIGS 23:G; 59:B). In males of various non-related mayflies, left and right seminal ducts are fused one with another inside the penial base, and in the distal part of the penis diverge again, thus open by a pair of gonopores (FIG.93:C); rarely there is an unpaired gonopore. In females, left and right oviducts often unite to form a short unpaired genital chamber opened by an unpaired gonopore; in Siphlonurus/fg1 this chamber is sclerotized (FIG.18:A–C), in other mayflies membranous.

Some authors regarded the paired gonopore of mayflies to be a plesiomorphy unique among insects. This opinion is based only on a general idea about the primary nature of paired organs and secondary nature of unpaired ones, being not supported by comparison of this structure in concrete insect groups. Most probably, Hexapoda initially have an unpaired gonopore, which is present in all Entognatha, Triplura and majority of Pterygota. Paired gonopore of male mayflies can be a new formation connected with the peculiar genital structure (see above and FIG.11): As the penis is constantly articulated with a ninth abdominal tergite by a pair of penial arms, its movement should be limited by rotation around a single transverse axis; more composite movements can be made only if left and right halves of the penis are movably connected one with another; this becomes possible only if gonoducts are paired all along their length. As well as other insects, mayflies have great specific diversity in genital structure and manner of genital movement (that probably serves species reproductive isolation). Due to this, most mayfly species have paired gonoducts, and only a few species have a penis with limited mobility and unpaired gonopore. Other insects are able to combine diversity in penis structure with an unpaired gonopore, because they have no such penial arms.

Mayfly ovaria have a large indeterminate number of ovarioles (approximately from 100 to 500 in different species). Formerly it was regarded that the ovaria of mayflies have the primitive panoistic type, i. e. lack trophocytes (Soldán 1979c); however, detailed examination of a few species indicated that mayfly ovarioles belong to the meroistic telotrophic type, with linear clusters of trophocites concentrated in the apical zone of each ovariole. (Gottanka & Buning 1993). In the end of development, the trophocytes degenerate, the oocytes lost connection with them, and all ovarioles with oviduct fuse to a common sack containing numerous eggs.

Testes have a large indeterminate number of testacular follicles, each falling directly to a seminal duct.

Shape and position of ovaria and testes somewhat differs among mayfly taxa (Landa & Soldán 1985:Figs 18–20).
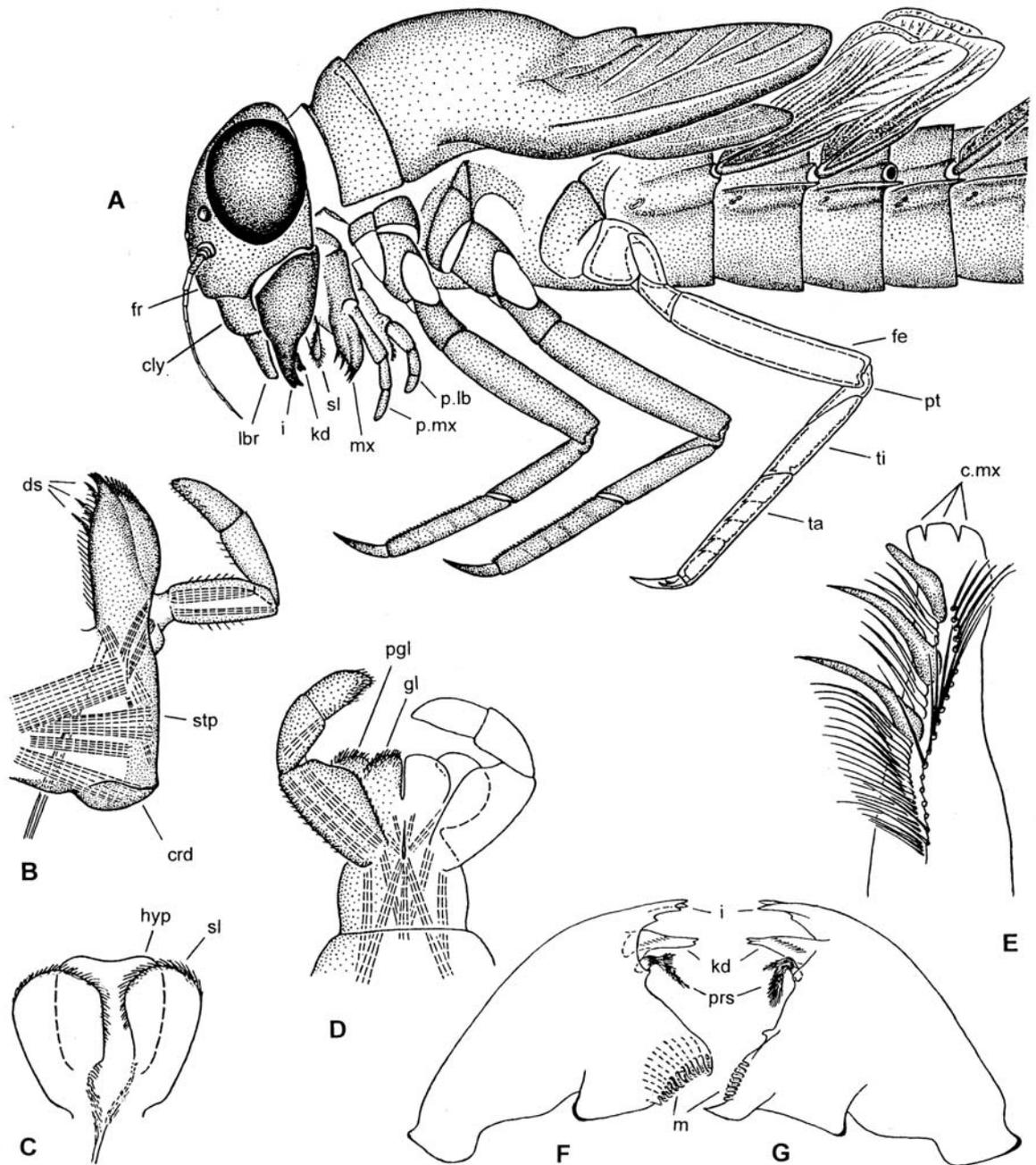
Figure 3. Larva of Siphlonurus/fg4 *aestivalis* [*Siphlurus*].
A – Anterior half of male larva of last instar, lateral view (tergalius III removed; subimaginal hind leg shown by interrupted line); **B** – left maxilla, ventral view (muscles shown by interrupted lines); **C** – hypopharynx and superlinguae, dorsal view; **D** – labium, ventral view (muscles shown by interrupted lines); **E** – apex of left maxilla, median view (dentisetae shown by dots); **F** – left mandible; **G** – right mandible. (A, B, E–G – from Kluge 1997 and 2000).

Abbreviations: **c.mx** – maxillary canines; **cly** – clypeus; **crd** – cardo; **ds** – dentisetae; **fe** – femur; **fr** – frons; **gl** – glossa; **hyp** – hypopharynx, **i** – incisor; **kd** – kinetodontium; **lbr** – labrum; **m** – mola; **mx** – maxilla; **pgl** – paraglossa; **p.lb** – labial palp; **p.mx** – maxillary palp; **prs** – prostheca; **pt** – patella, **sl** – superlingua; **stp** – stipes; **ta** – tarsus; **ti** – telotibia.
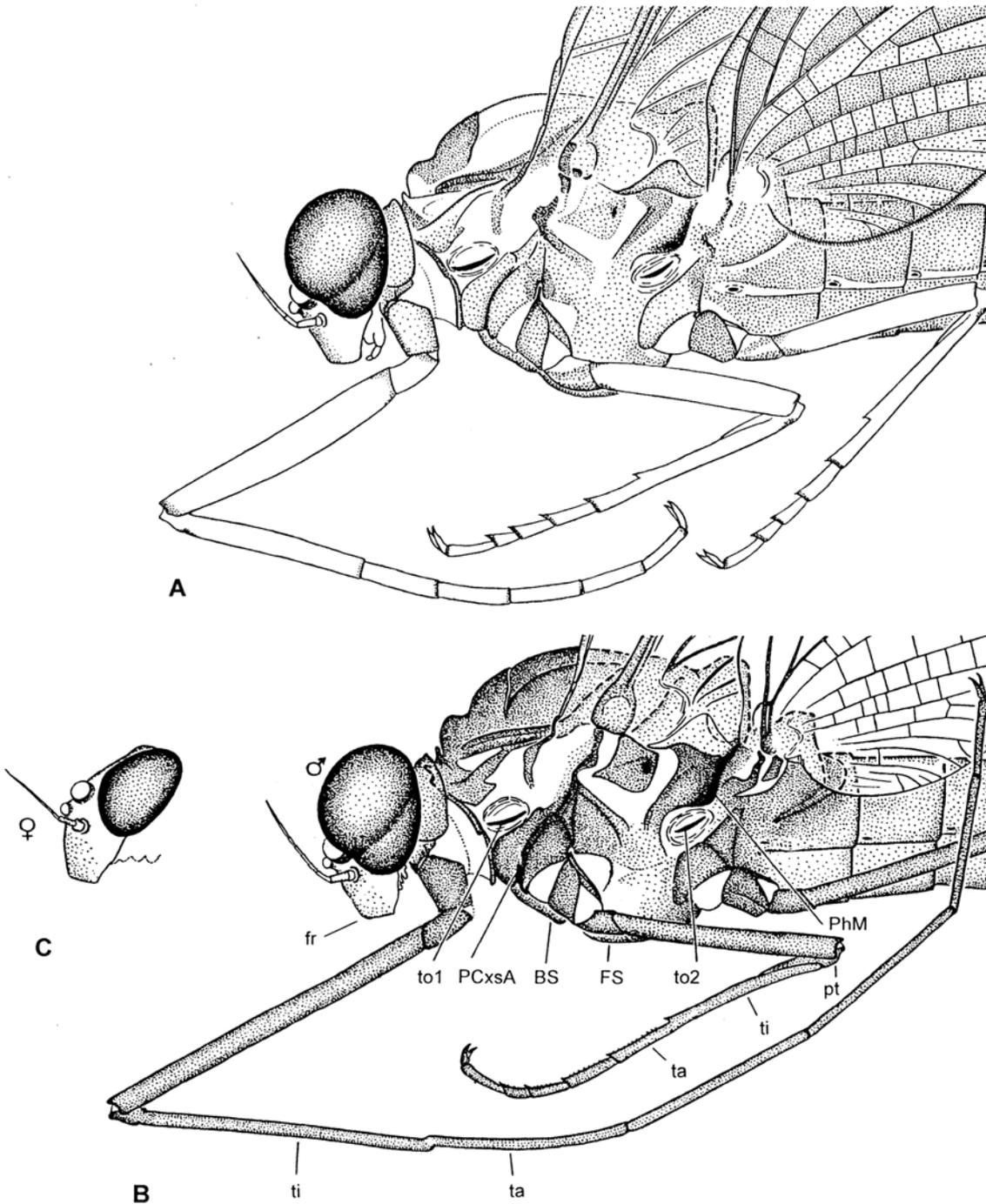
Figure 4. Winged stages of Siphlonurus/fg4 *aestivalis* [*Siphlurus*].
A – male subimago, head and thorax, lateral view; **B** – male imago, the same; **C** – female imago, head, lateral view. (B, C – from Kluge 2000)

Abbreviations: **BS** – basisternum of mesothorax; **fr** – face fold (frons); **FS** – furcasternum of mesothorax; **PCxsA** – anterior paracoxal suture of mesothorax; **PhM** – middle phragma; **pt** – patella; **ta** – tarsus; **ti** – telotibia; **to1** – stenothoracic tracheostium (first thoracic spiracle); **to2** – cryptothoracic tracheostium (second thoracic spiracle).
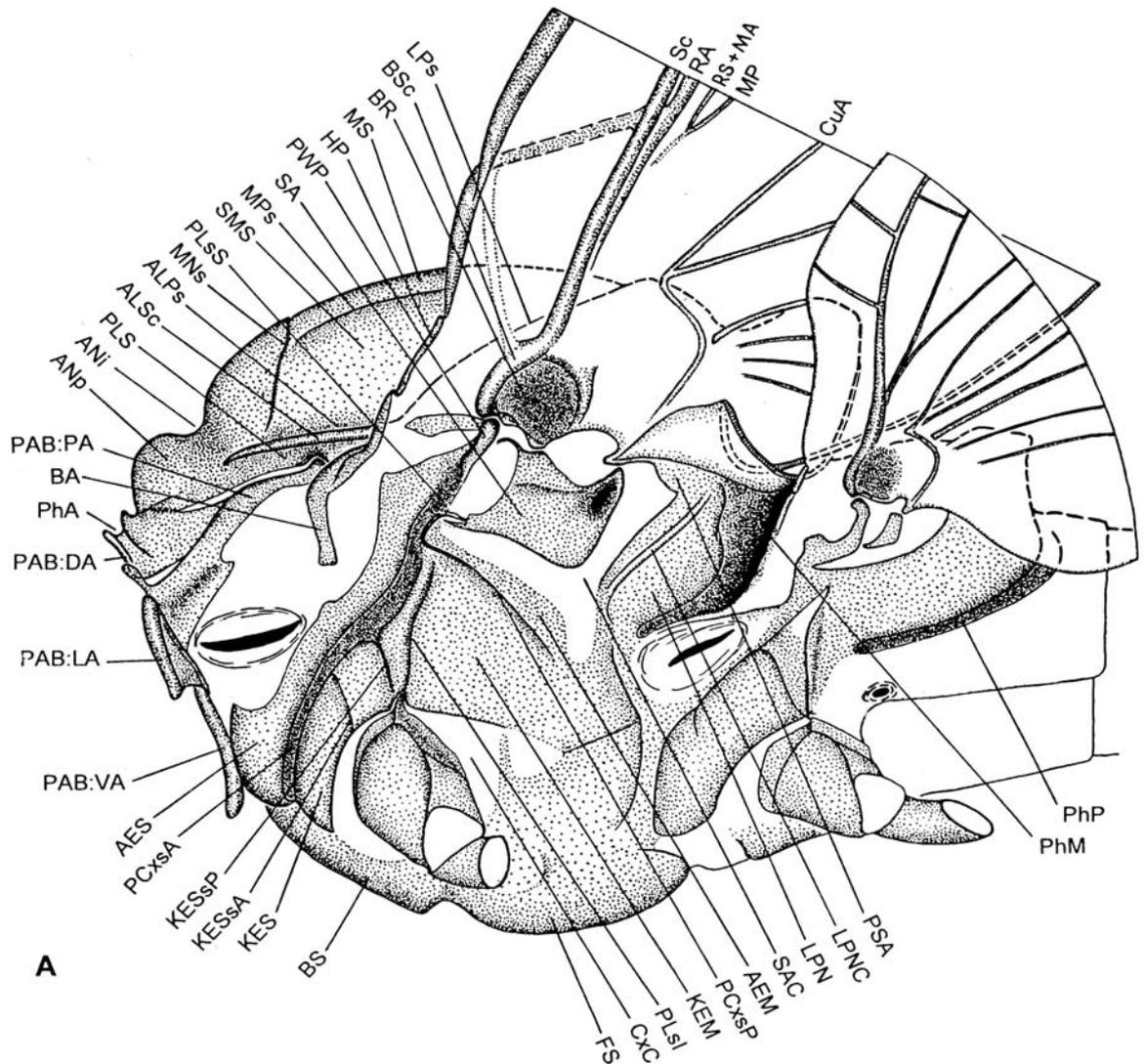
Figure 5. Pterothorax of Siphlonurus/fg4 *aestivalis* [*Siphlurus*].
A–C – imaginal pterothorax: **A–B** – lateral view; **C** – anterior view (muscles shown by interrupted lines and dotted, muscle bases outlined by dotted lines); **D** – subimaginal exuviae of left mesopleuron. (From Kluge 1994a).

Abbreviations: **AEM** – anepimeron; **AES** – anepisternum; **ALPs** – antelateroparapsidal suture; **ALSc** – anterolateral scutal costa; **ALSs** – anterolateral scutal suture; **ANi** – anteronotal transverse impression; **ANp** – anteronotal protuberance; **AN.Pm** – anteronoto-pleural muscle; **Ax.Fm** – axillar-furcal muscle; **Ax.PmI** – inferior axillar-pleural muscle; **BA** – basalare; **BA.Cm** – basalar-coxal muscle; **BA.SmI** – inferior basalar-sternal muscle; **BA.SmS** – superior basalar-sternal muscle; **BR** – basiradiale; **BS** – basisternum; **BSc** – basisubcostale; **CxC** – coxal conjunctiva; **Cx.Cxm** – coxo-coxal muscle; **F** – furca; **F.Cm** – furca-coxal muscle; **F.CmP** – posterior furca-coxal muscle; **F.CmS** – superior furca-coxal muscle; **Fm** – furcal muscle; **FS** – furcasternum; **FSp** – furcasternal protuberance; **HP** – humeral plate; **iFm** – intersegmental furcal muscle; **ISL** – infrascutellum; **KEM** – katepimeron; **KES** – katepisternum; **KESsA** – anterior katepisternal suture; **KESsP** – posterior katepisternal suture; **LPN** – lateropostnotum; **LPNC** – lateropostnotal crest; **LPs** – lateroparapsidal suture; **LSs** – lateral scutal suture; **MLs** – median longitudinal suture; **MNs** – mesonotal suture; **MPN** – mediopostnotum; **MPs** – medioparapsidal suture (notaulix); **MS** – medioscutum; **MTm** – median tergal muscle; **PAB:DA** – dorsal arc of prealar bridge; **PAB:LA** – lateral arc of prealar bridge; **PAB:PA** – posterior arc of prealar bridge; **PAB:VA** – ventral arc of prealar bridge; **P.Cm** – pleuro-coxal muscle; **PCxsA** – anterior paracoxal suture; **PCxsP** – posterior paracoxal suture; **PhA** – anterior phragma; **PhM** – middle phragma; **PhP** – posterior phragma; **PLS** – prelateroscutum; **PLsI** – inferior pleural suture; **PLsS** – superior pleural suture; **PSA** – postsubalar sclerite of lateropostnotum; **PSL.Cm** – parascutellar-coxal muscle; **PSp** – posterior scutal protuberance; **P.Trm** – pleuro-trochanteral muscle; **PWP** – pleural wing process; **SA** – subalare; **SAC** – subalar conjunctiva; **SA.Cm** – subalar-coxal muscle; **SA.Fm** – subalar-furcal muscle; **SA.Sm** – subalar-sternal muscle; **S.CmA** – anterior scuto-coxal muscle (tergal promotor of coxa); **S.CmP** – posterior scuto-coxal muscle (tergal remotor of coxa); **S.ESm** – scuto-episternal muscle of mesothorax; **S.ESm3** – scuto-episternal muscle of metathorax; **SL** – scutellum; **S.LPNm** – scuto-lateropostnotal muscle; **SLS** – sublateroscutum; **SMS** – submedioscutum; **S.PSLs** – scuto-parascutellar suture; **S.Trm** – scuto-trochanteral muscle; **SrA.Pm** – suralare-pleural muscle; **S.SLi** – scuto-scutellar impression; **Teg** – tegula.
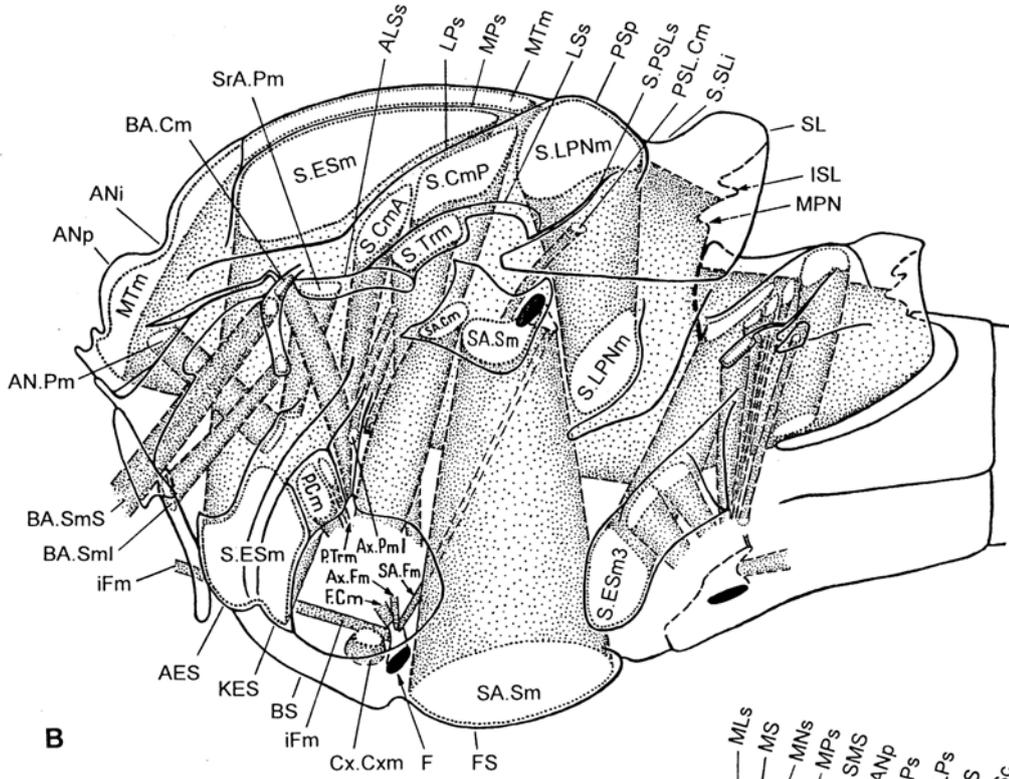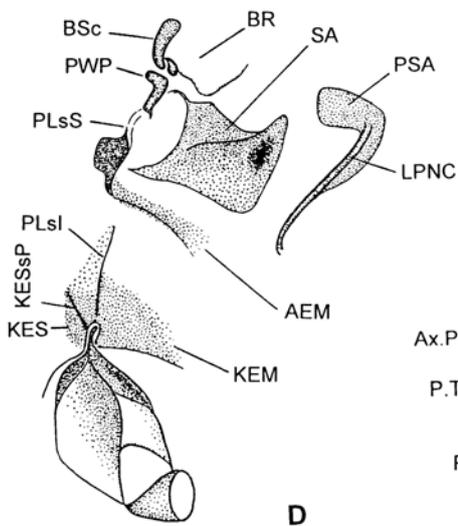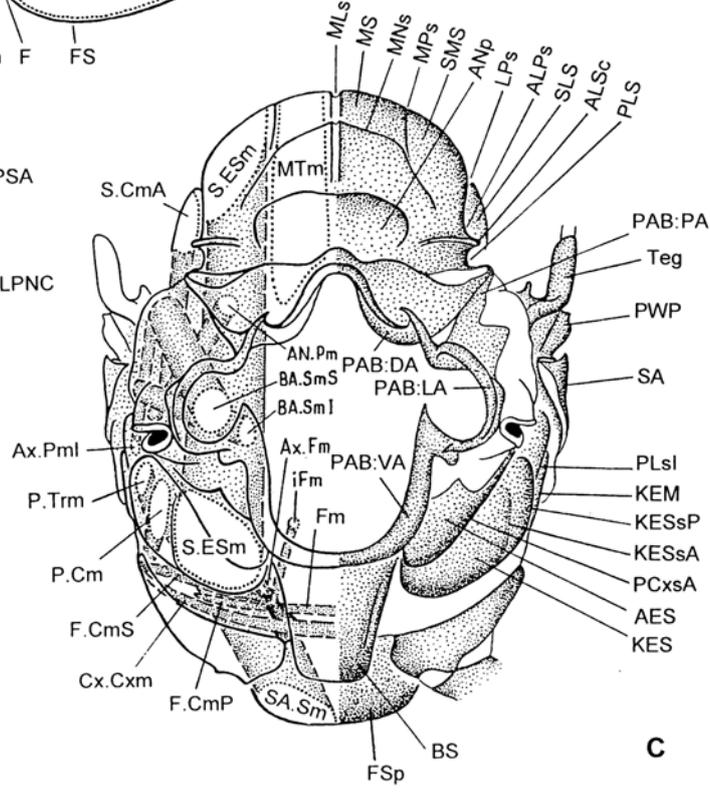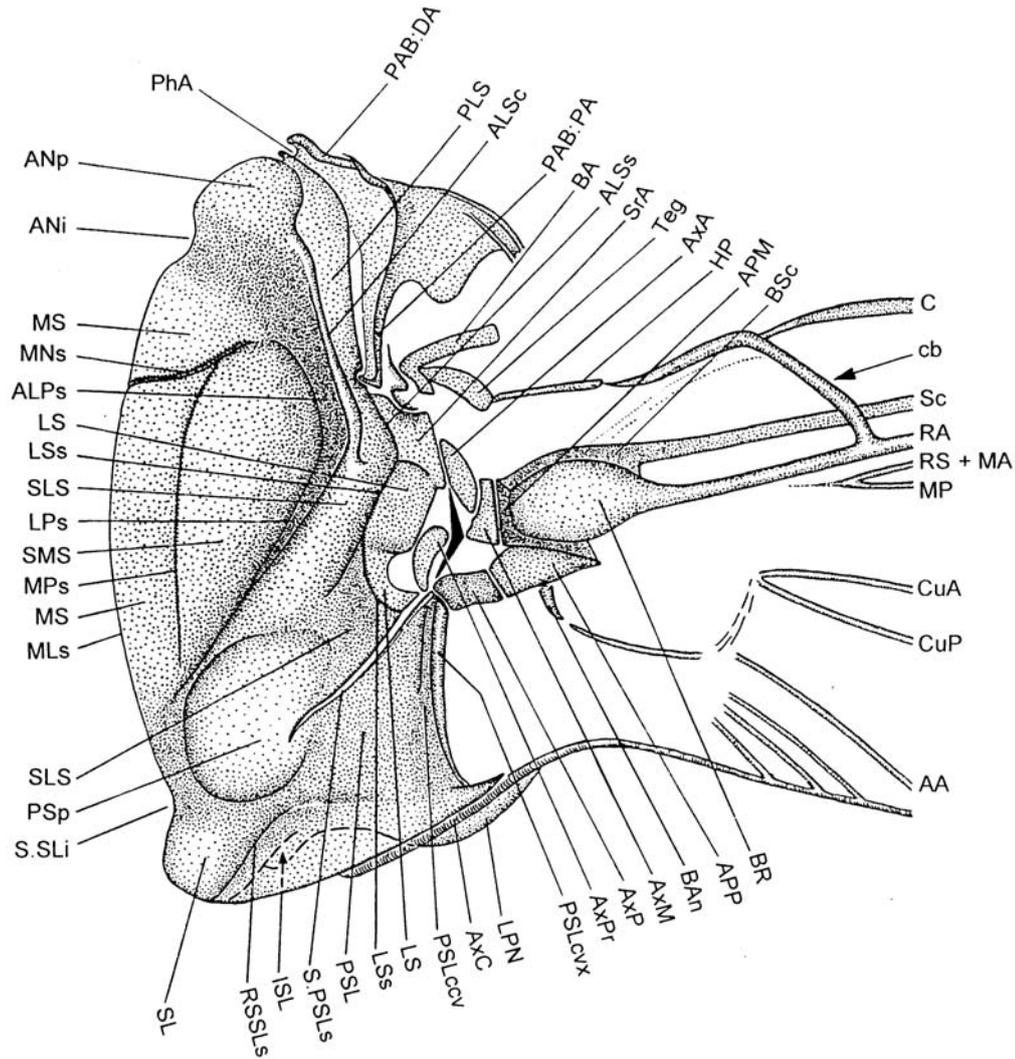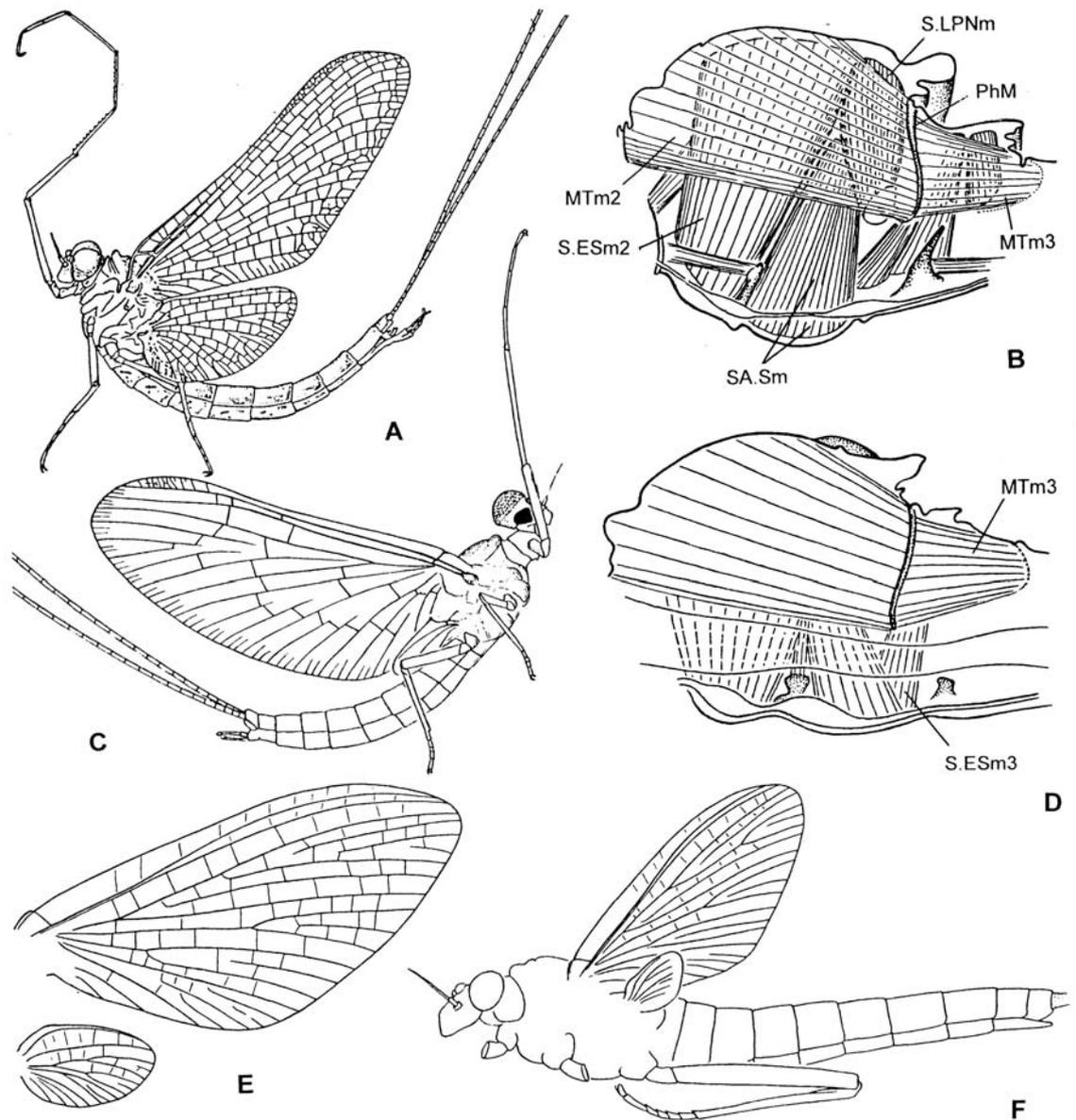
Figure 6. Right half of imaginal mesonotum and forewing base of Siphlonurus/fg4 *aestivalis* [*Siphlurus*], smoothed on slide (membrane between axillary sclerites broken, the break shown by black) (from Kluge 1994a).

Abbreviations: **ALPs** – antelateroparapsidal suture; **ALSc** – anterolateral scutal costa; **ALSs** – anterolateral scutal suture; **ANi** – anteronotal transverse impression; **ANp** – anteronotal protuberance; **APM** – middle articulatory process of wing base; **APP** – posterior articulatory process of wing base; **AxA** – anterior axillary sclerite; **AxC** – axillary cord; **AxM** – middle axillary sclerite; **AxP** – posterior axillary sclerite; **AxPr** – proximal axillary sclerite; **BA** – basalare; **BAn** – basanale; **BSc** – basisubcostale; **BR** – basiradiale; **cb** – costal brace; **HP** – humeral plate; **ISL** – infrascutellum; **LPN** – lateropostnotum; **LPs** – lateroparapsidal suture; **LS** – lateroscutum; **LSs** – lateral scutal suture; **MLs** – median longitudinal suture; **MNs** – mesonotal suture; **MS** – medioscutum; **MPs** – medioparapsidal suture (notaulix); **PAB:DA** – dorsal arc of prealar bridge; **PAB:PA** – posterior arc of prealar bridge; **PhA** – anterior phragma; **PLS** – prelateroscutum; **PSL** – parascutellum; **PSLccv** – parascutellar lateral concavity; **PSLcvx** – parascutellar lateral convexity; **PSp** – posterior scutal protuberance; **RSSLs** – recurrent scuto-scutellar suture; **SL** – scutellum; **SLS** – sublateroscutum; **SMS** – submedioscutum; **S.PSLs** – scuto-parascutellar suture; **SrA** – suralare; **S.SLi** – scuto-scutellar impression; **Teg** – tegula.

Figure 7. Wings.
A – Scheme of wing base and venation of Ephemeroptera (compare with D); **B** – scheme of triad branching of veins; **C–D** – right fore and hind wings of Siphlonurus/fg4 *aestivalis* [*Siphlurus*]; **E** – scheme of wing base and venation of Neoptera (compare with A) (B and C – from Kluge 2000).

Abbreviations: **cb** – costal brace; **pts** – pterostigma.

Figure 8. Reduction of wings and pterothorax among mayflies.
A–B – Siphlonurus/fg3 spp., mayflies with most usual plesiomorphic proportions: **A** – general view; **B** – median section of pterothorax. **C–D** – Turbanoculata, mayflies with reduced hind wings: **C** – *vernus* Curtis 1834 [*Baetis*], mayfly with vestigial hind wings; **D** – median section of pterothorax of Cloeon/fg* *diptera* [*Ephemera*], mayfly without hind wings. **E–F** – individual variability of wing size in an undescribed short-winged species of Rhithrogena/fg2 from Chukotka (River Amguema 12 km below meteorological station, 1 IX 1976, leg. E. Makarchenko). (A – from Tshernova 1964, B – from Kluge 2000, C – from Kluge 1997d).

Abbreviations: **MTm2** – median tergal muscle of mesothorax; **MTm3** – median tergal muscle of metathorax; **PhM** – middle phragma; **SA.Sm** – subalar-sternal muscle; **S.ESm2** – scuto-episternal muscle of mesothorax; **S.ESm3** – scuto-episternal muscle of metathorax; **S.LPNm** – scuto-lateropostnotal muscle.
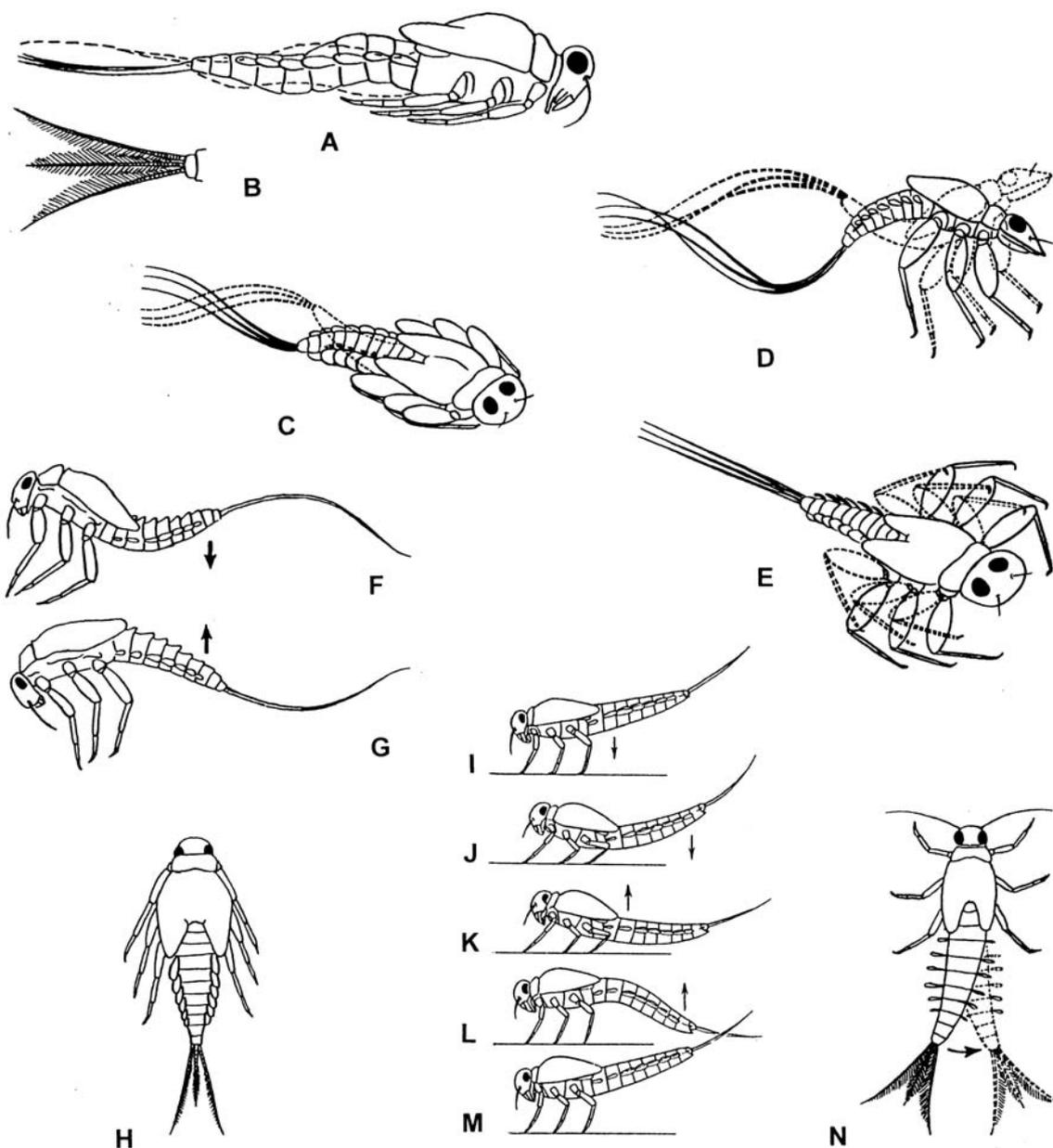
Figure 9. Movements of larvae.
A–B – Siphlonurus/fg1 (larva with primary siphlonuroid swimming specialization): **A** – lateral view of swimming larva; **B** – dorsal view of its caudalii. **C–E** – swimming larvae of various Radulapalpata (rheophilous taxon, in which swimming siphlonuroid specialization is partly or completely lost): **C** – Rhithrogena/fg3 (leg pose differs from siphlonuroid); **D** – Heptagenia/f6=g5 (legs free); **E** – Ecdyonurus/fg1 (swims by legs rather than by abdomen). **F–H** – rheophilous representatives of Turbanoculata: **F–G** – Baetiella/g1 *tuberculatum* Kazlauskas 1963 [*Pseudocloeon (Baetiella)*]; **H** – Acentrella/g1 *gnom* Kluge 1983 [*Pseudocloeon*]. **I–N** – Respiratory movements: **I–M** – respiratory movements of Ameletus/fg1 representing modified primary siphlonuroid swimming movements; **N** – special respiratory movements of Baetis/fg* different from its swimming movements. (F–N – from Kluge & Nivikova & Brodsky 1984).
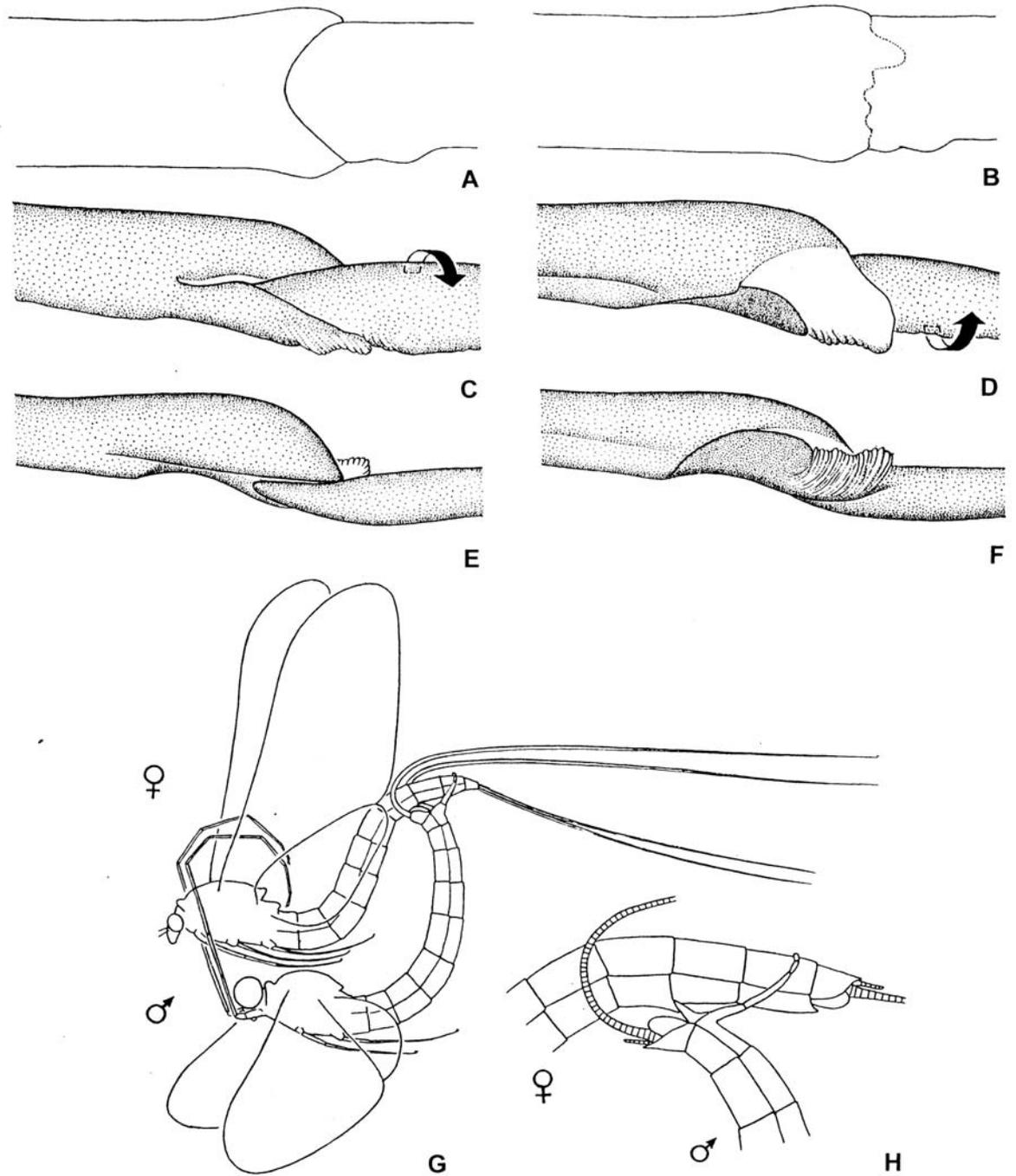
Figure 10. Copulation.
A–F – Tibia-tarsal articulation of male fore leg of Metretopus/fg* *borealis* [*Heptagenia*] (each leg lies with knee articulation directed up and tarsus directed to the right); left figures (**A**, **C**, **E**) – left leg in median view; right figures (**B**, **D**, **F**) – right leg in lateral view: **A–B** – subimago; **C–D** – imago with normal position of tarsus (arrow shows future rotation which leads to position on Figs E and F); **E–F** – imago with tarsus turned around at 180˚. **G–H** – Pose of copulation of Parameletus/fg2 *chelifer* [*Parameletus*] (from Kluge 2000 based on Brinck 1957).
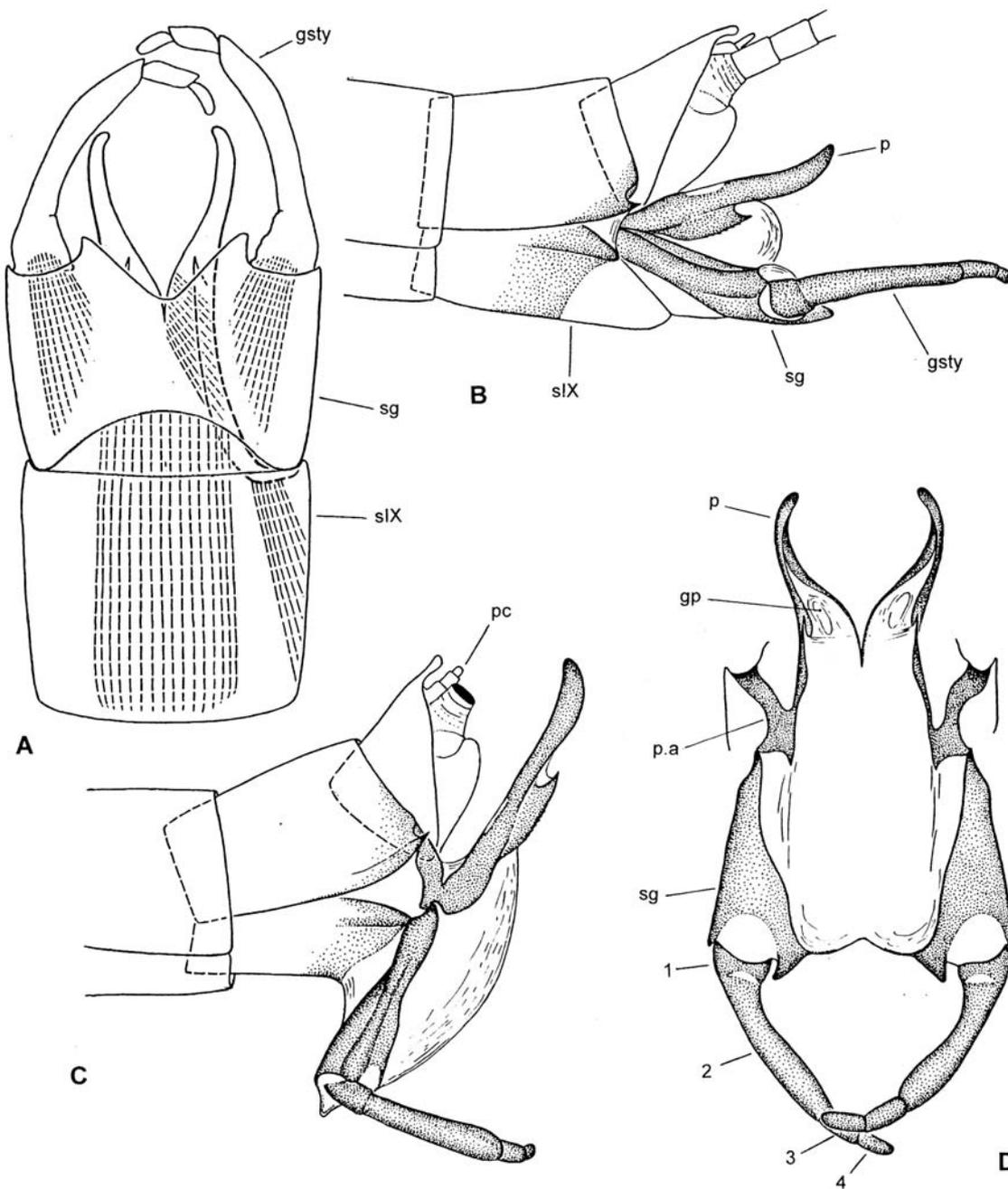
Figure 11. Genitals of male imago of Ameletus/fg2 *camtschaticus* [*Ameletus*].
A – Abdominal sternum IX with styliger, gonostyli and penis, ventral view (muscles of styliger and right half of penis are shown by interrupted lines). **B** – Apex of abdomen, lateral view. **C** – Apex of abdomen with genitals in excited condition, lateral view (left cercus removed). **D** – the same, posterior view.

Abbreviations: **1**, **2**, **3**, **4** – segments of gonostylus; **gp** – gonopore; **gsty** – gonostylus; **p** – penis; **p.a** – penial arm; **pc** – paracercus; **sIX** – abdominal sternite IX; **sg** – styliger.
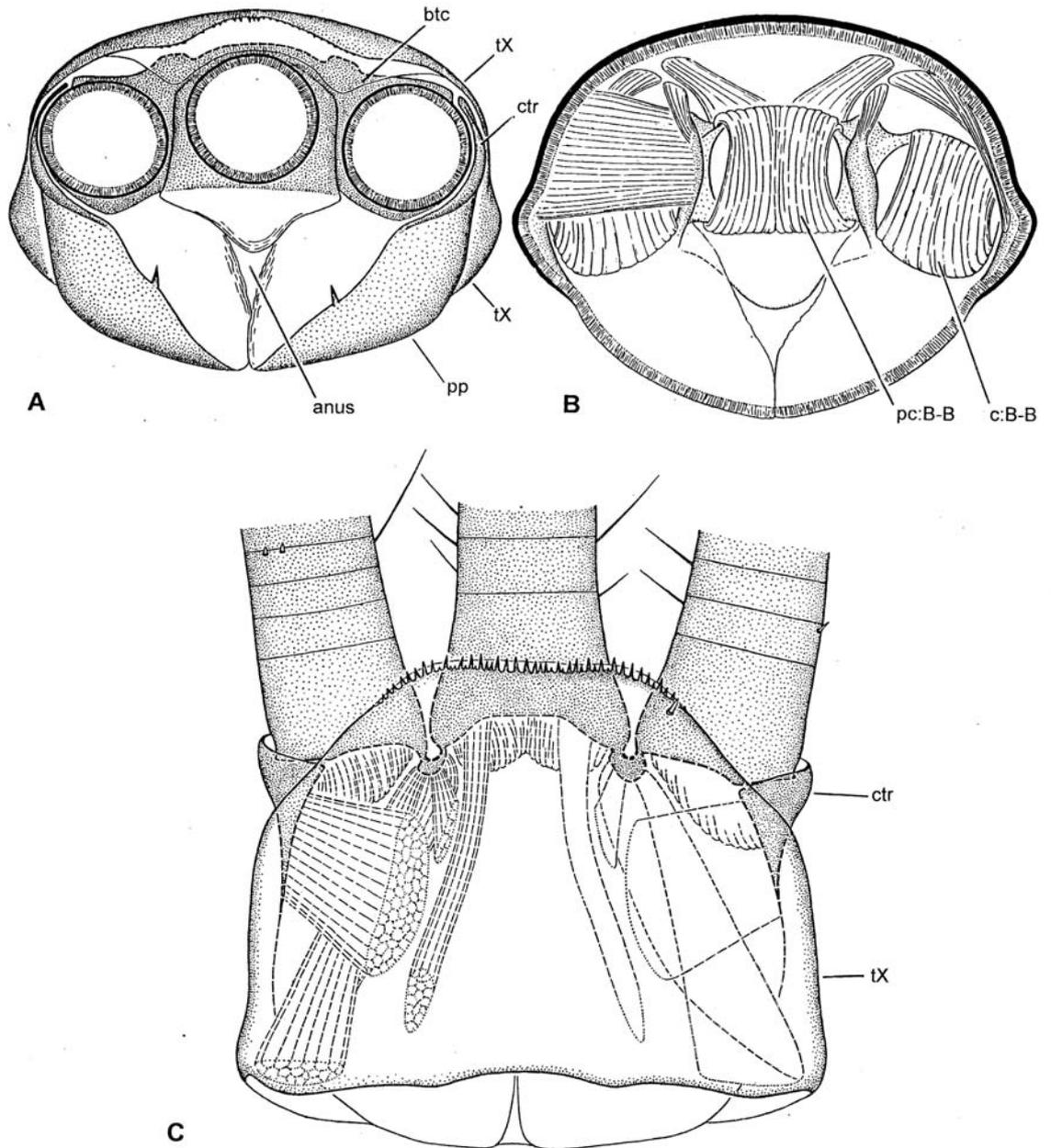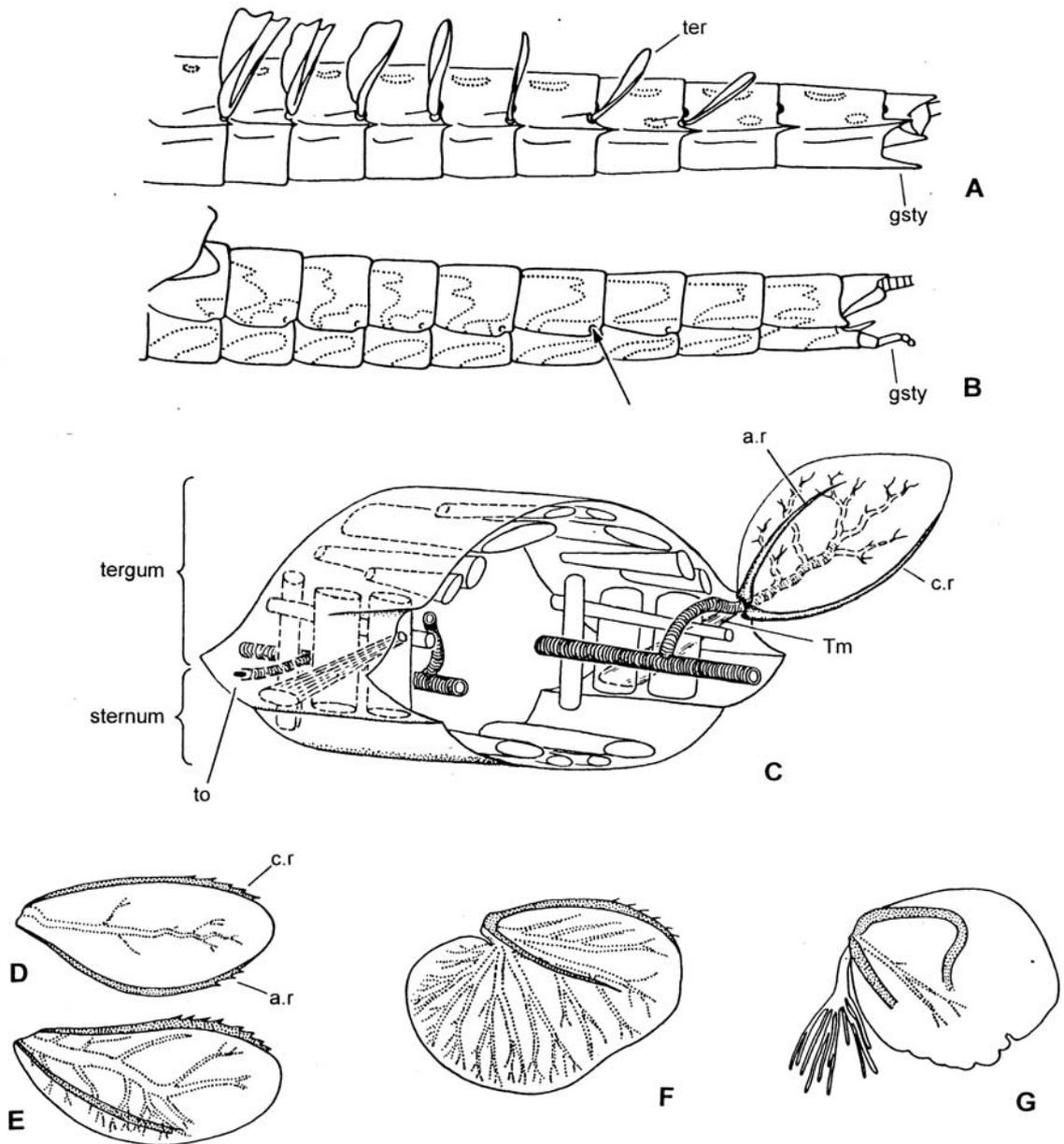
Figure 12. Larval 10th abdominal segment.
A–E – Siphlonurus/fg4 *aestivalis* [*Siphlurus*] (intestine and all muscles connecting intestine with body wall are removed): **A** – posterior view (cerci and paracercus removed, instead them three round sections are shown); **B** – anterior view, from inside; **C** – dorsal view (hidden sclerites shown by interrupted lines and dotted, muscles shown by interrupted lines, their dorsal bases – by dotted polygons); **D** – longitudinal section; **E** – lateral view (muscles shown by interrupted lines). **F** – scheme of structure usual for Ephemeroptera (corresponds to A–E); **G** – scheme of sctructutru peculiar for Geminovenata, Fossoriae and Caenotergaliae.

Abbreviations: **btc** – basitricaudale; **c** – cercus; **c:B-B** – basi-basal muscle of cercus; **ctr** – cercotractor; **pc** – paracercus; **pc:B-B** – basi-basal muscle of paracercus; **pp** – paraproct; **tX** – abdominal tergite X.

D

pc:B-B   c:B-B   pp

E

ctr   pp

F

ctr

G

btc

pc

c

tX   ctr   pp
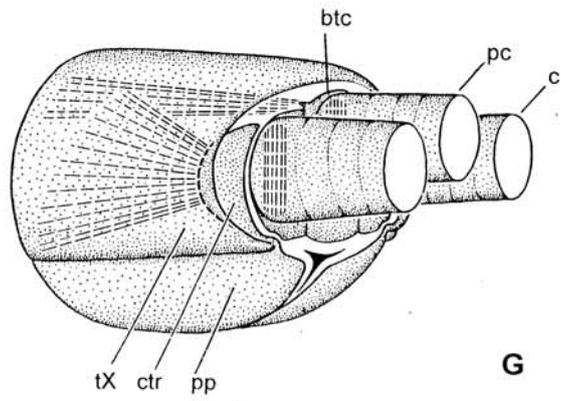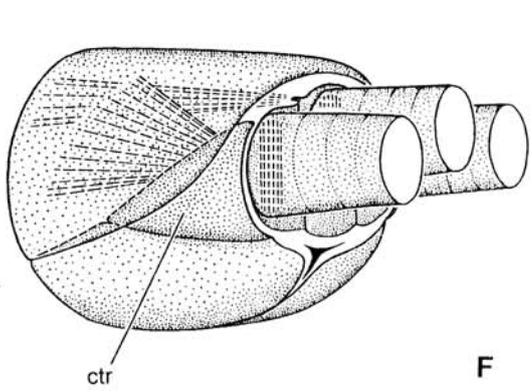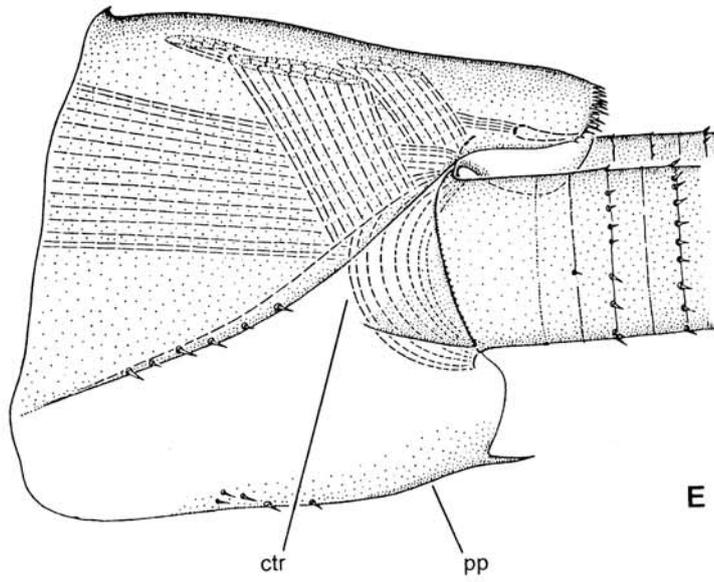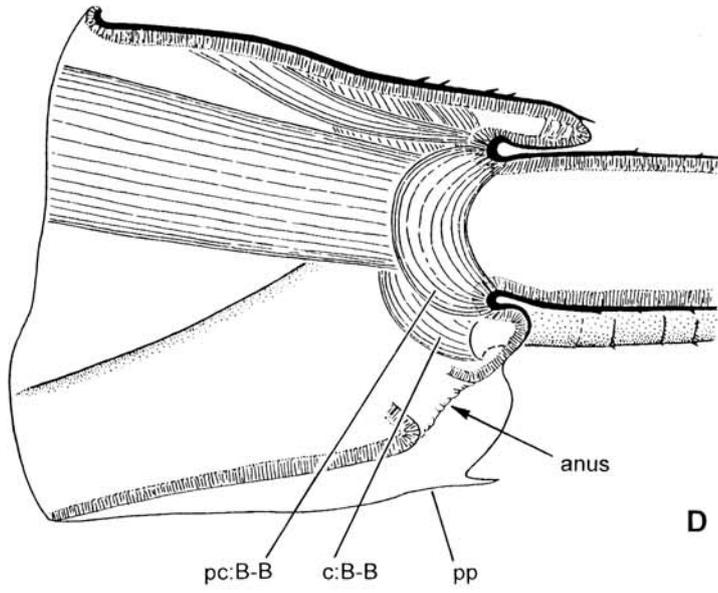
Figure 13. Tergalii.
A–B – Abdomen of male Siphlonurus/fg4 *lacustris* [*Siphlonurus*] (boundaries of pigmented spots shown by dotted lines): **A** – larva; **B** – imago (arrow shows trace of tergalia attachment). **C** – Scheme of musculature of larval abdominal segment (tergalial muscle shown by longitudinal striation, tracheal trunks – by transverse striation). **D–G** – position of ribs and tracheae in tergalii of various mayflies (ribs shown by integral lines and dotted, tracheae shown by dotted lines): **D** – *procerus* [*Ameletus*]; **E** – *montanus* [*Ameletus*]; **F** – *immanis* [*Siphlonurus*]; **G** – *eugeniae* [*Rhithrogena*]. (A–B, D–F – from Kluge 1989a; C – from Kluge 2000).

Abbreviations: **a.r** – anal rib; **c.r** – costal rib; **gsty** – gonostyli buds of larva and gonostyli of imago; **ter** – tergalius; **Tm** – tergalial muscle; **to** – tracheostium.