

Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics

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Summary. — The features of mayfly pterothorax structure which are necessary for systematics are described. The terms used by different authors are specified and the necessary new terms are given. The correspondence between external structure and musculature is ascertained. Examples of use of the pterothorax structure in mayfly systematics are given.

Résumé. — Les caractères de la structure du ptérothorax des Ephémères nécessaires pour la Systématique sont décrits dans la présente étude. Les termes utilisés par différents auteurs sont rappelés, et de nouveaux termes sont proposés pour les besoins. La correspondance entre la structure externe et la musculature est précisée. Des exemples de l'utilisation de la structure du ptérothorax pour la systématique des Ephémères sont donnés.

Key-words. — Ephemeroptera, pterothorax structure, new terms, terminology, systematics.

In the last century and the beginning of the present one, investigators of Ephemeroptera gave main attention to structure of imagos. At these times, diagnoses of taxa were based on wing venation, legs proportions, number of caudal filaments, form of male eyes, structure of male genitalias, and colour of imagos. Later, it became clear that structures in mayfly nymphs give many important clues: in our days Ephemeropterologists pay principal attention to nymphal characters, and in the modern literature it is accustomed to describe the fine structure of nearly all parts of the nymphal body. As a consequence, the prevalent System of the Order Ephemeroptera has changed and refers mostly to nymphs.

Oppositely the study of imagos remains nearly at the same level as it was last century, with the exception that description of penis structure has become more exact. And we are presently in a situation where some taxa have no diagnoses for imagos; structure of imaginal thorax is still quite poorly used in systematics, although it contains many interesting informations which may be used as very important additions to the nymphal ones for reconstructing the phylogeny and building a system.

There are several papers in which mayfly thorax is described in details, but without comparison between different taxa (KNOX, 1935, MATSUDA, 1956, and others). GRANDI (1947) and BRODSKY (1974) compared musculature, axillar apparatus, and some other details of imaginal thorax of representatives of different mayfly families, but they did not determinate taxonomic status of the most striking structures, and these features

were not used in systematics. Tsui and Peters (TSUI, 1970, TSUI & PETERS, 1972, 1975) described structure of imaginal thorax of several species of Leptophlebiidae and based some phylogenetic ideas on this structure, but their work had no continuation, and later, in many descriptions of new genera and species of Leptophlebiidae, neither Peters nor other authors ever mentioned any features of imaginal thorax. For the first time, imaginal mesothorax structure was used in mayfly taxonomy in the generic revision of Heptageniidae (KLUGE, 1988). Two genera of Leptohyphinae (fam. Tricorythidae) are redescribed on the base of imaginal and subimaginal thorax structure (KLUGE, 1992). In the future, mesothorax structure will also be used in generic description and discussions on phylogeny of Leptophlebiidae, Baetidae, and other families.

MCCAFFERTY (1991) splitted the paraphyletic family Siphonuridae in several smaller families, but did not suggest separate diagnoses of imagos of these new families, all of them having similarity in wing venation and in other traditional imaginal features. Only studying the thorax structure may help to separate imagos of such families, and allow to clear up some questions of higher phylogeny of Ephemeroptera.

As the thorax structure of mayflies was not used formerly in systematics, the necessary terminology is lacking. The names of the thorax parts used in the past are sufficient for morphology but not for systematics. Now comes the time to suggest an adequate terminology convenient for both purposes.

Arbitrary signs used in the fig. 1-21, Table I (left column), and Table II (upper line) :

— **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 ; — **APM** : middle atriculatory process of wing base ; — **APP** : posterior articulatory process of wing base ; — **AxA** : anterior axillary sclerite ; — **AxC** : axillary cord ; — **Ax.Fm** : axillar-furcal muscle ; — **AxM** : middle axillary sclerite ; — **AxP** : posterior axillary sclerite ; **Ax.Pml** : inferior axillar-pleural muscle ; **Ax.PmS** : superior axillar-pleural muscle ; **AxPr** : proximal axillary sclerite ; **BA** : basalaré ; — **BAn** : basanale ; — **BA.Cm** : basalar-coxal muscle ; **BA-Pm** : basalar-pleural muscle ; **BA.SMI** : inferior basalar-sternal muscle ; **BA.SmS** : superior basalar-sternal muscle ; **BA.Trm** : basalar-trochanteral muscle ; **BR** : basiradiale ; **BS** : basisternum ; **BSc** : basisubcostale ; — **CxC** : coxal cavity ; **Cx.Cxm** : coxo-coxal muscle ; — **F** : furca ; — **F.CmA** : anterior furco-coxal muscle ; — **F.CmP** : posterior furco-coxal muscle ; — **F.CmS** : furcal muscle ; — **FS** : furcasternum ; — **FSi** : furcasternal median impression ; — **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 ; — **LS** : lateroscutum ; — **LSs** : lateral scutal suture ; — **MLs** : median longitudinal suture ; — **MNs** : mesonotal suture ; **MPN** : mediopostnotum ; — **MPs** : medioparapsidal suture (or notaulix) ; — **MS** : medioscutum ; — **MTm** : median tergal muscle ; — **PAB:DA** : dorsal arc of prealar bridge ; — **PAB:LA** : lateral arc of prealar bridge ; — **PAB:PA** : posterior arm of prealar bridge ; — **PAB:VA** : ventral arc of prealar bridge ; — **P.Cm** : pleuro-coxal muscle ; — **PCxsA** : anterior paracoxal suture ; — **PCsxP** : posterior paracoxal suture ; — **PhA** : anterior phragma ; — **PhC** : phragmal cavity ; — **PhM** : middle phragma ; **PhP** : posterior phragmal ; — **PhsA** : anterior phragmal suture ; — **PhsP** : posterior phragmal suture ; — **PLS** : prelateposcutum ; — **PLsI** : inferior pleural suture ; — **PLsS** : superior pleural suture ; — **PSA** : postubular sclerite of lateropostnotum ; — **PSL** : parascutellum ; — **PSLccv** : parascutellar lateral concavity ; — **PSLcvx** : parascutellar lateral convexity ; — **PSL.Cm** : parascutello-coxal muscle ; **PSP** : posterior scutal protuberance ; — **P.Trm** : pleuro-trochanteral muscle ; — **PWP** : pleural wing process ; **RSSLs** : recurrent scuto-scutellar suture ; — **SA** : sabalare ; — **SAC** : subalar cavity ; — **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* ; — **SL** : *scutellum* ; — **S.LPNm** : *scuto-lateropostnotal muscle* ; — **SLS** : *sublateroscutum* ; — **SMS** : *submedioscutum* ; — **SPSLs** : *scuto-parascutellar suture* ; — **SrA** : *suralare* ; — **SrA.Pm** : *suralare-pleural muscle* ; — **SSLI** : *scuto-scutellar impression* ; — **S.Trm** : *scuto-trochanteral muscle* ; — **T** : *tegula*.

A. — MUSCULATURE

In the present paper musculature of mayfly pterothorax is described and figured (fig. 5, 6) in order to determinate position of the external structures and to find homology of them. In the areas where large muscles are attached to the body wall, the surface is usually convex : such form prevents from caving in of the body wall during muscular contraction. Between such convexities on the body surface there may be more or less distinct concavities or sutures. Comparison of certain sutures and muscle base position in different insect orders is given by BRODSKY (1991). Besides such sutures which position is determinated by muscle bases, there are also sutures independent from musculature (such as the mesonotal suture — MNs in fig. 2, 12-18).

Musculature of mayfly thorax was described by different authors, who gave different names for the muscles (Table 1). DURKEN (1907), KNOX (1935), and BRODSKY (1970) classified muscles according to their spatial position : dorsal (D), ventral (V), longitudinal (L), dorsoventral (DV), oblique (O) ; some muscles were included into groups of pleural (P) and sternal (S) muscles. In the other classifications (MATSUDA, 1970 ; BRODSKY, 1974) muscles were classified according to their points of attachment : tergal (T), pleural (P), sternal (S), coxal (Cx), and trochanteral (Tr), naming at first the more dorsal attachment. Such classifications are better, because the points of attachment of muscles are more stable than their direction. In all these classifications each group of muscles contains several different muscles, which were marked by arbitrary numbers. Unfortunately the numbers which were given to the same muscle by different authors do not coincide. It is impossible to give an universal numeration of muscles for all insects or even for all Ephemeroptera, because some of them can easily disappear or divide into several independent muscles. So it is more convenient to name muscles without using numbers.

Here all muscles are named according to their points of attachment. As in the Matsuda's and Brodsky's designations, the dorsal points of attachment always come first. Besides the wide term tergum (T) are used terms anteronotum (AN), scutum (S), parascutellum (PSL), suralare (SrA), basalare (BA), axillare (Ax), subalare (SA), and lateropostnotum (LPN) ; besides pleuron (P) is used the term episternum (ES) ; besides sternum (S) is used the term furca (F).

B. — PREALAR BRIDGE OF MESOTHORAX (fig. 1, 2, 6)

Prealar bridge is usually more or less covered by the hind margin of prothorax and not visible, so in order to examine it, it is necessary to detach prothorax, which is connected with metathorax by a thin membrane.

Table I. — Names of muscles of mayfly mesothorax used by different authors.

abbreviations used here (deciphering in the list of arbitrary signs)	Maki, 1938		deciphering of abbreviations here in the text					Matsuda, 1956	Tsui, 1970
	in general for insects	for Ephemeroptera	Matsuda, 1970	Brodsky, 1974	Dürken, 1907 (for <i>Centropitulum luteolum</i>)	Knox, 1935	Brodsky, 1970		
MTm	median dorsal longitud. m.	20	t14	Tm1/3	d1m	DLm1	DLm1/2	30	1
S.LPNm	lateral dorsal muscle	21	t12	Tm2	dm	Dm	ODm	31	4
S.ESm	anterior tergo-sternal m.2	25	t-p5/6	TPm1	dvm1	DVm1	DVm1	43	6
SrA.Pm	ordinary tergo-pleural m.1	29 ?	t-p8 or 10 ?	TPm2	pm9	Pm11	Pm11	45	13
BA.Pm (1)	ordinary tergo-pleural m.2	30	p5 or t-p4 ?	TPm3	-	Pm5	Pm4	42	10
Ax.PmI	pleuro-axillar muscle 1	31	t-p13	TPm4	-	-	-	51	-
Ax.Pms (1)	pleuro-axillar muscle 2	32	t-p14 or 15 ?	TPm5	pm8	Pm6	Pm14	53	22a
AN.Pm	-	-	t-p3	TPm6	pm7	-	-	44	7
S.CmA	tergal promotor of coxa	36	t-cx3	TCxm1	dvm2	DVm2	DVm2	32	11
S.CmP	tergal remotor of coxa 1	39	t-cx7	TCxm2/3	dvm3	DVm3/4	DVm3/4	33/34	19
PSL.Cm	tergal remotor of coxa 2	40	t-cx6	TCxm4	dvm4	DVm5	DVm5	35	21
BA.Cm	-	-	t-cx4	TCxm5	-	Pm4	Pm3	50	18
SA.Cm	coxo-subalar muscle	41	t-cx8	TCxm6/7	pm2	Pm9	Pm9	37	22/23
BA.SmS	sterno-basalar muscle 1	33	p-s12	TSm1	-	Pm1	Pm1	40	8
BA.Sml	sterno-basalar muscle 2	34	p-s12	TSm2	-	Pm2	Pm2	41	9
SA.Sm	sterno-basalar muscle 2	26	t-s5	TSm3	pm6	Pm7	Pm7	38	5
SA.Fm	sterno-subalar muscle 1	27	t-s4	TSm4	pm5	Pm8	Pm8	39	20
Ax.Fm	sterno-axillar muscle	28	t-s3	TSm5	dvm6	Pm10	Pm10	52	17
S.Trm	tergal depressor of troch.	44	t-tr1	TTrm1	-	DVm6	DVm6	48	14
BA.Trm (1)	trochantero-basalar muscle	-	p-tr2	TTrm2	dvm5	Pm3	-	-	-
P.Cm	pleural adductor of coxa	43	p-cx5	-	pm1	Pm12	-	36	-
F.CmS	furco-entopleural muscle	35	s-cx2	-	sm1	-	-	55	-
F.CmP	ord. stern. remotor of coxa	42	s-cx3	-	sm3	-	-	54	26
F.CmA (1)	ord. stern. promotor of coxa	37/38	s-cm5	-	sm3	Sm1	-	56	30
Cx.Cm	-	-	s-cx4 or 8 ?	-	-	-	-	58	-
iFm	longitudinal ventral m.	22	s13	-	v1m (iv1m)	VLm	-	57	3
Fm	posterior ventr. transv. m.	23	s16	-	sm5	Sm2	-	59	29
P.Trm	pleural depressor of troch.	45	p-tr1	-	pm3	Pm13	-	47	16

(1) : not figured

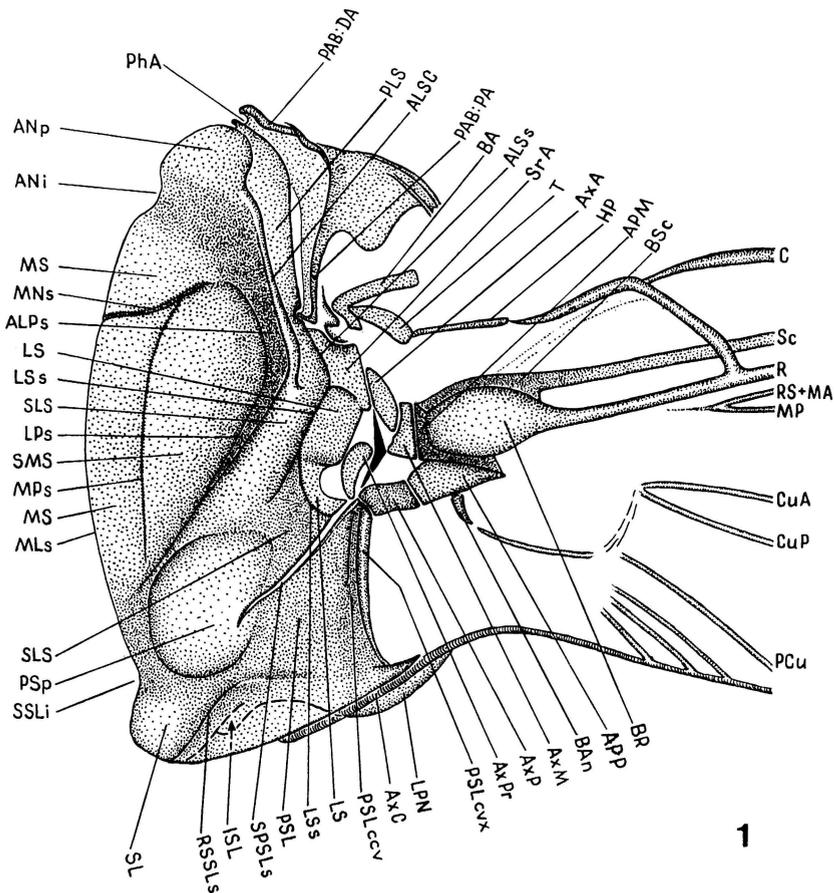


Fig. 1. — Imago of *Siphonurus aestivalis* : right half of mesotergum and wing base smoothed out on slide. Deciphering of abbreviations (except names of veins) in the list of arbitrary signs.

Prealar bridge (PAB) consists of the dorsal, lateral, and ventral arcs. The *dorsal arc* (PAB : DA) (new term) may contain the anterior and posterior costae, which are 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 arcs of prealar bridge* (PAB : LA) (new term) may also consist of two or three costae separated by grooves. The *ventral arc* (PAB : VA) (new term) is known also as *presternum*. Form of these arcs (in the front view, as in fig. 6) and number of their costae (which is better seen in the lateral and dorsal views) is different in different mayflies and may be used as systematics character.

From the lateral and dorsal arcs begins a pair of *posterior arms of prealar bridge* (PAB : PA) (new term) ; these arms go posteriad towards the wing base and joint

with a small distinct emargination on the lateral margin of *prelateroscutum* (PLS). Anteriad to this joint, between the prealar bridge posterior arm and the prelateroscutum there is a narrow membranose area; some authors regard this area to be a prescutal suture, and the posterior arm of prealar bridge to be prescutum (KNOX, 1935, TSUI, 1970, BRODSKY, 1970, 1974, 1991). But the term prescutum is used also in other meanings (see below).

In some groups of mayflies the posterior arms may be reduced. For example in the infraorder Setisura (families Heptageniidae, Isonychiidae, Oligoneuriidae, Arthropleidae, Pseudironidae) they are strongly shortened, do not reach the emarginations of prelateroscutal margins, while these emarginations are distinctly developed; it is a good character of the infraorder.

C. — DORSAL SURFACE OF MESOTERGUM (fig. 1-6, 8, 9, 12-15)

In the anterior part of mesonotum just behind the dorsal arc of prealar bridge there is *anteronotal protuberance* (ANp) (new term) separated from the remainder part of notum by the *anteronotal transverse impression* (ANi) (new term). This impression is more or less developed nearly in all taxa of Ephemeroptera, only in Caenidae it is completely absent. Form of the anteronotal protuberance may be used as systematic feature: for example in the subgenus *Acentrella* (*sensu* NOVIKOVA & KLUGE, 1987) (fam. Baetidae, genus *Baetis* s.l.) it is acute (fig. 3), in contrary to all other Baetidae (fig. 4); it is the best diagnostic imaginal and subimaginal character of this subgenus.

Along the median line of notum goes the *median* (or *median longitudinal*) *suture* (MLs). It is distinctly developed in 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 the subgenus *Centropilum* s.str. (genus *Cloeon*) and the genus *Baetopus* of the fam. Baetidae this suture is convex, it allows to distinguish winged insects of these taxa from other Baetidae (KLUGE & NOVIKOVA, 1992: fig. 8, 11). All Caenidae have in the anterior part of the median suture a short broadening — the median notal membrane (PROVONSHA, 1990: fig. 57, mnm), which is a unique diagnostic character of the family.

Laterad from the median suture there is a pair of *medioparapsidal sutures* (MPs). These narrow concave sutures separate the convex *medioscutum* (MS) (new term) (which contains the anterior bases of the largest *median tergal muscles* — MTm) from the convex *submedioscutum* (SMS) (new term) (which contains the dorsal bases of the large *scuto-episternal muscle*, S.ESm). Medioparapsidal sutures of mayflies are also known under the names “first parapsidal sutures” (BRODSKY, 1970), “parapsidal sutures” (BRODSKY, 1974, 1991), “inner parapsidal sutures” (TSUI, 1970), and “anterior parapsidal sutures” (PROVONSHA, 1990: fig. 57, aps). They correspond to *notaulici* of Hymenoptera (TULLOCH, 1929). Position of the medioparapsidal sutures is constant, but their depth may be different. They may be distinct on all their length and reach the median suture turning medially in their hind parts. Or they may disappear in their hind parts not reaching the median suture (fig. 1). It may be a useful generic sign of some genera of Leptophlebiidae.

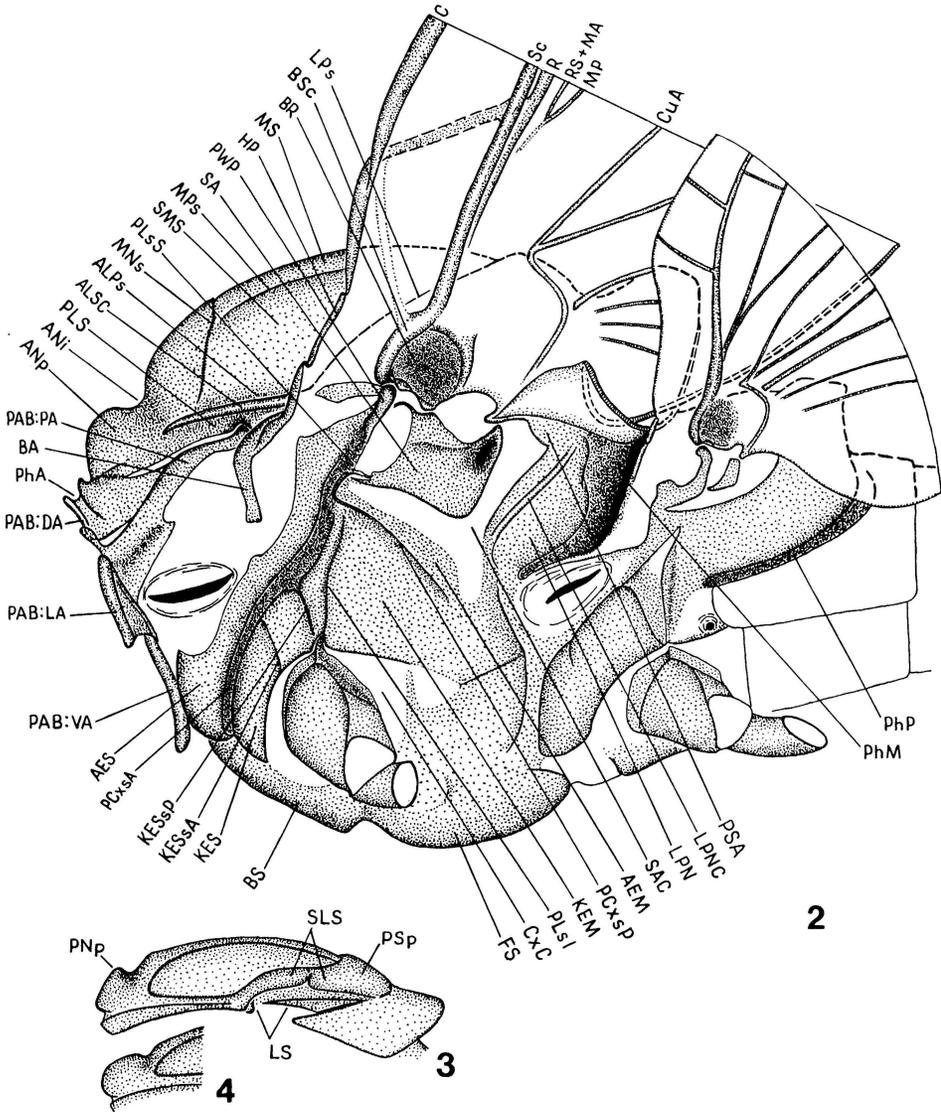


Fig. 2-4. — Lateral view of pterothorax of mayfly imagos. — 2, *Siphonurus aestivalis*; — 3, mesonotum of *Baetis (Acentrella) lapponicus*; — 4, anterior part of notum of *B. (Baetiella) muchei*. Deciphering of abbreviations (except names of veins) in the list of arbitrary signs.

Laterad from the medioparapsidal sutures there is a pair of *lateroparapsidal sutures* (LPs), also known as “second parapsidal sutures” (BRODSKY, 1970), “outer parapsidal sutures” (TSUI, 1970), and “posterior parapsidal sutures” (PROVONSHA, 1990 : fig. 57, pps). These deep wide strongly sclerotized concave sutures, or furrows, bear mechanical function and at the same time separate the convex *sublateroscutum* (SLS) (new term) (which contains the dorsal bases of the *anterior* and *posterior scuto-coxal muscles*, S.CmA, S.CmP) from the submedioscutum. Lateroparapsidal sutures can go exactly between muscle bases or somewhat turn them (KLUGE, 1988 : fig. 88-91). Form of the lateroparapsidal sutures is a good diagnostic feature, which allows to distinguish tribes of the family Heptageniidae (KLUGE, 1988, and some other taxa, fig. 12-18).

Anteriorly the lateroparapsidal suture turns into the *antelateroparapsidal suture* (ALPs) (new term), which sets off anteriorly the submedioscutum, separating it from the *anterolateral scutal costa* (ALSC) (new term). Some authors regard the antelateroparapsidal suture to be a part of lateroparapsidal suture (KNOX, 1935, BRODSKY, 1970, 1974, 1971), other regard it to be prescutal suture (PROVONSHA, 1990).

The *anterolateral scutal costa* (ALSC) is well developed in all groups of Ephemeroptera, separating the dorsal side of notum from the narrow *prelateroscutum* (PLS) (new term), 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 may be separated by more or less developed sutures or costae of various forms.

Suralare (SrA) is a portion of scutum which bears the *anterior notal wing process* and is separated from the remainder scutum by the *anterolateral scutal suture* (ALSS) (MATSUDA, 1970 : fig. 4). The anterolateral scutal suture of mayflies was also named “notal furrow” (TSUI, 1970, NF).

Structure of *sublateroscutum* may be different. In Baetidae it is divided by incomplete transverse suture into two parts : the anterior one, which does not bear muscle bases, and the posterior one, which is fused with the *posterior scutal protuberance* and contains the bases of the anterior and posterior scuto-coxal muscles (fig. 3).

Lateroscutum (LS) (new term) is separated from the sublateroscutum by the *lateroscutal suture* (LSs) (new term) and contains in its anterior portion the dorsal base of the *scuto-trochanteral muscle* (S.Trm). BRODSKY (1974, 1991) regards this suture to be the anterolateral scutal suture. But it is not so, because in this case lateroscutum must be regarded to be suralare, but suralare of Neoptera does not contain the bases of scuto-trochanteral muscles (BRODSKY, 1991 : fig. 3, 4, 6-8).

Medioposteriorly from the sublateroscutum is situated a pair of *posterior scutal protuberances* (PSP) (new term) — large convex areas, usually indistinctly outlined, which contain the dorsal bases of large *scuto-lateropostnotal muscles* (S.LPNm). Usually there is no distinct suture between sublateroscutum and the posterior scutal protuberance, but in Caenidae and some groups of Tricorythidae there is a distinct secondary *transverse interscutal suture* (PROVONSHA, 1990 : fig. 57 tis, KLUGE, 1992), which separates the dorsal bases of the scuto-coxal and the scuto-lateropostnotal muscles.

Behind the posterior scutal protuberances is situated the prominent *scutellum* (SL). Opposite to some of Neoptera, Ephemeroptera have no distinct scuto-scutellar suture ; it allowed MATSUDA (1970) to write about united *scutoscutellum* of mayflies. Instead of the scuto-scutellar suture mayflies have *scuto-scutellar impression* (SSLi) — the concave area surrounded by scutellum, posterior scutal protuberances, and medio-scutum. Laterally scutellum is separated from *parascutellum* by the indistinct invagination which is called *recurrent scuto-scutellar suture* (RSSLs) (MATSUDA, 1970).

Parascutellum (PSL) (term used by CRAMPTON, 1914) is a large area laterad from scutellum, which bears the *posterior notal wing process* and contains a single small base of the *parascutellar-coxal muscle* (PSL.Cm). Some authors regard this area to be a part of scutellum (KNOX, 1935, GRANDI, 1947, TSUI, 1970, BRODSKY, 1991), according to another version it is a part of scutum (MATSUDA, 1970). Parascutellum is separated from sublateroscutum and lateroscutum by the *scuto-parascutellar suture* (SPSLs) (new term). This suture is developed in different orders of insects, it was called by A. K. Brodsky “oblique suture” (BRODSKY, 1991 : OS), but this term seems to be not quite good because it looks like epithet. Some authors call this suture “scuto-scutellar suture” (KNOX, 1935, MATSUDA, 1956, TSUI, 1970), but it does not correspond to the typical scuto-scutellar suture of Neoptera (MATSUDA, 1970 : fig. 3 ; BRODSKY, 1991 : fig. 1). MATSUDA (1970 : fig. 42) called it “posterolateral scutal suture”, but actually this suture is not homologous to the posterolateral scutal suture of Neoptera, because the base of the parascutello-coxal muscle (t-cx in MATSUDA, 1970 and BRODSKY, 1991) is situated posteriad to it (fig. 5) (BRODSKY, 1991 : fig. 2a), while in Neoptera the base of this muscle is situated anteriad to the true posterolateral scutal suture (BRODSKY, 1991 : fig. 1, 3, 4, 6-8). The scuto-parascutellar suture has very important mechanical function : it allows to bend the notum when the median tergal muscles contract, that leads to wing depression ; so this suture is well developed on mesonotum of all mayflies.

Lateral margin of parascutellum bears a sclerotized costa — *parascutellar lateral convexity* (PSLcvx) (new term) which is separated from the remainder part of parascutellum by a groove — *parascutellar lateral concavity* (PSLccv) (new term). It is possible that the parascutellar lateral concavity is homologous to the posterolateral scutal suture of Neoptera.

The hind wall of notum is deeply concave, in this concavity under scutellum is situated transverse shelf-like convexity — *infrascutellum* (ISL) (new term) (fig. 5, 8, 9). In Caenidae and Tricorythidae, in contrary to other Ephemeroptera, scutellum is strongly modified and infrascutellum is absent (KLUGE, in press).

The area between infrascutellum and the middle phragma is called *mediopostnotum* (MPN) (fig. 5, 8, 9), on the lateral sides of the body it continues as *lateropostnotum* (LPN) (see below). Length of mediopostnotum is different in different families of Ephemeroptera.

Besides the sutures which position is fixed by their mechanical role or by position of the muscle bases, there is a suture which position is not dependent of any internal causes — it is the *mesonotal suture* (MNs) (new term), named also “transverse suture” (KLUGE, 1988 : TS) and “additional suture” (TSHERNOVA *et al.*, 1986). In the primitive case the mesonotal suture goes across scutum in its anterior part, behind the anterotal

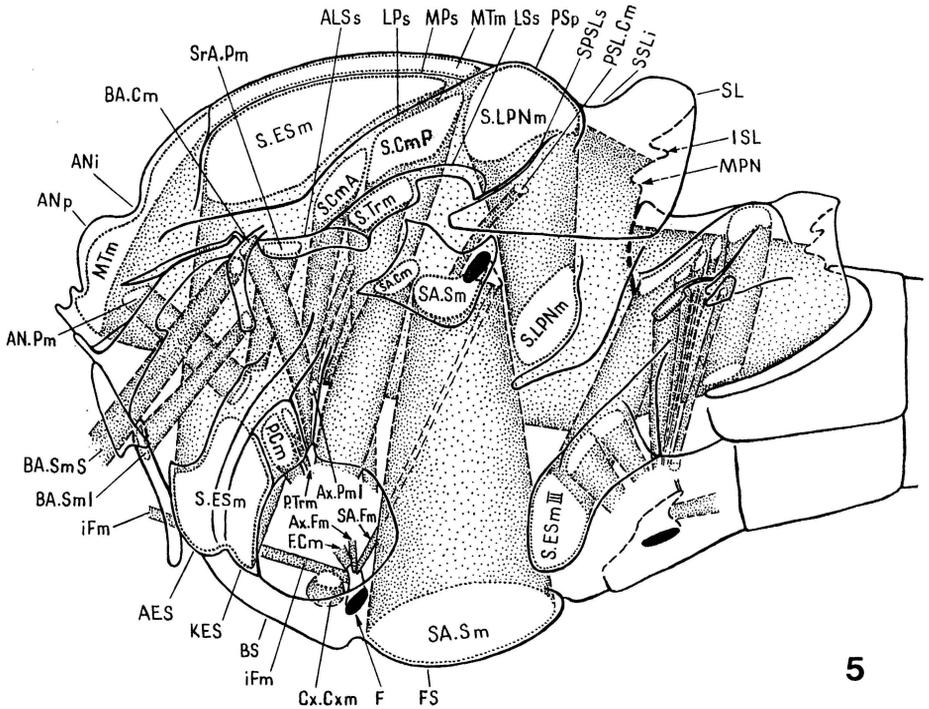


Fig. 5. — *Siphonurus aestivalis*: musculature of pterothorax (compare with fig. 2). Muscle bases are outlined by dotted lines. Deciphering of abbreviations in the list of arbitrary signs.

transverse impression, and laterally connects with the anterior ends of medioparapsidal sutures. In the genera *Siphonurus*, *Ameletus*, and *Cretoneta* (mesozoic genus) of Siphonuridae s.l. the mesonotal suture is removed backward in the point of crossing with the median suture (fig. 12, 13). In the genus *Parameletus*, which is closely related to *Siphonurus*, it crosses the median suture perpendicular to it. In the families Ephemeridae and Potamanthidae the mesonotal suture is strongly curved and removed backward in its lateral parts. In *Eatonica* (fam. Ephemeridae) and in all Neophemeridae the lateral parts of mesonotal suture are so strongly removed backward, that they nearly reach the posterior scutal protuberances and it seems that there is not a single mesonotal suture, but two pairs of longitudinal sutures: the median one goes parallel to the median suture, and the lateral one goes parallel to the lateroparapsidal suture close to it (as in Leptophlebiidae, fig. 17). In our key of the families of mayflies (Tshernova *et al.*, 1986) the median portion of mesonotal suture of Neophemeridae is called "additional suture" and its presence is used to separate Neophemeridae from Palaearctic representatives of Ephemeridae and Potamanthidae. In Leptophlebiidae (fig. 17) the form of mesonotal suture is similar to those of Neophemeridae, but the suture becomes indistinct: in imago it is not visible, and only in subimago it is visible

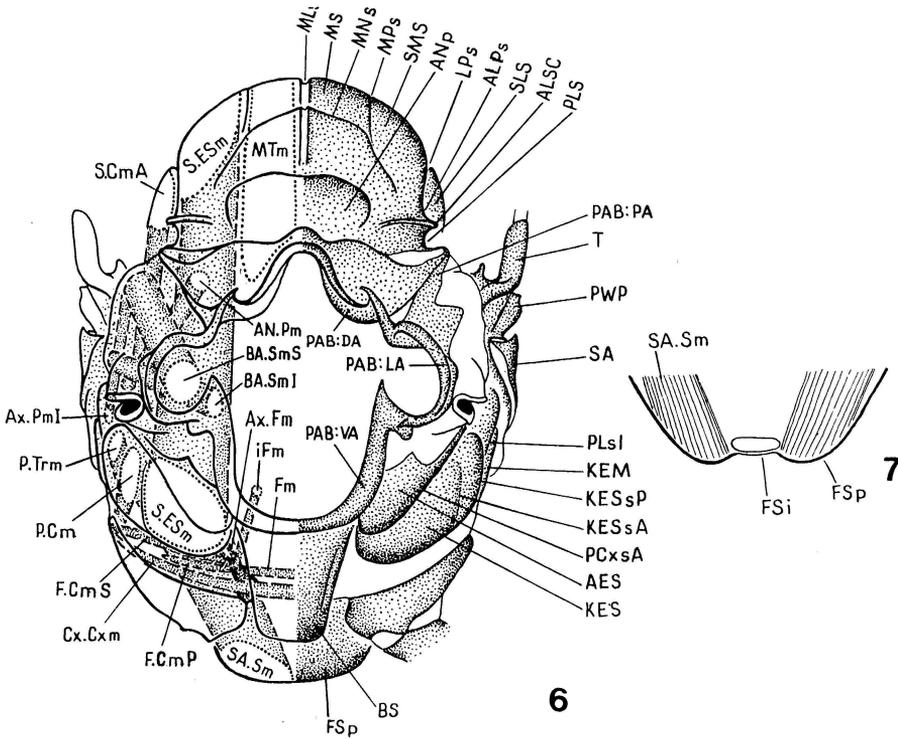


Fig. 6-7. — Frontal view of mesothorax of mayfly imagoes. — 6, *Siphonurus aestivalis* (in the left musculature is shown and muscle bases are outlined by dotted line ; — 7, *Baetis vernus* : transverse section through mesothoracic furcasternum (between subalar-sternal muscles metathoracic nerve ganglion is visible). Deciphering of abbreviations in the list of arbitrary signs.

owing to pigmentation, sclerotization, and setation of subimaginal cuticle. Subimaginal cuticle of Leptophlebiinae and *Choroterpes* (fam. Leptophlebiidae) before the mesonotal suture is covered with microtrichiae and completely or partly pigmented, while the colourless area between mesonotal and median sutures lacks microtrichiae (just the same in Ephemeridae, Potamanthidae, and Neoephemeridae). In the Leptophlebiid genus *Hagenulus* s.l. position of the mesonotal suture becomes indistinct, because in subimago microtrichiae cover not only the area before it, but also the median area between mesonotal and median sutures. In another Leptophlebiid genus — *Farrodes* — subimaginal notal cuticle have no pigmented areas, so all tracks of the mesonotal suture completely disappear. In Palingeniinae, Polymitarcyidae, and Behnigiidae mesonotal suture is also absent, and it is possible that it disappeared by the same way as in certain Leptophlebiidae.

In another way mesonotal suture disappeared in the lineage *Bleptus-Epeorus* (fam. Heptageniidae) and its absence is the good diagnostic character of these genera

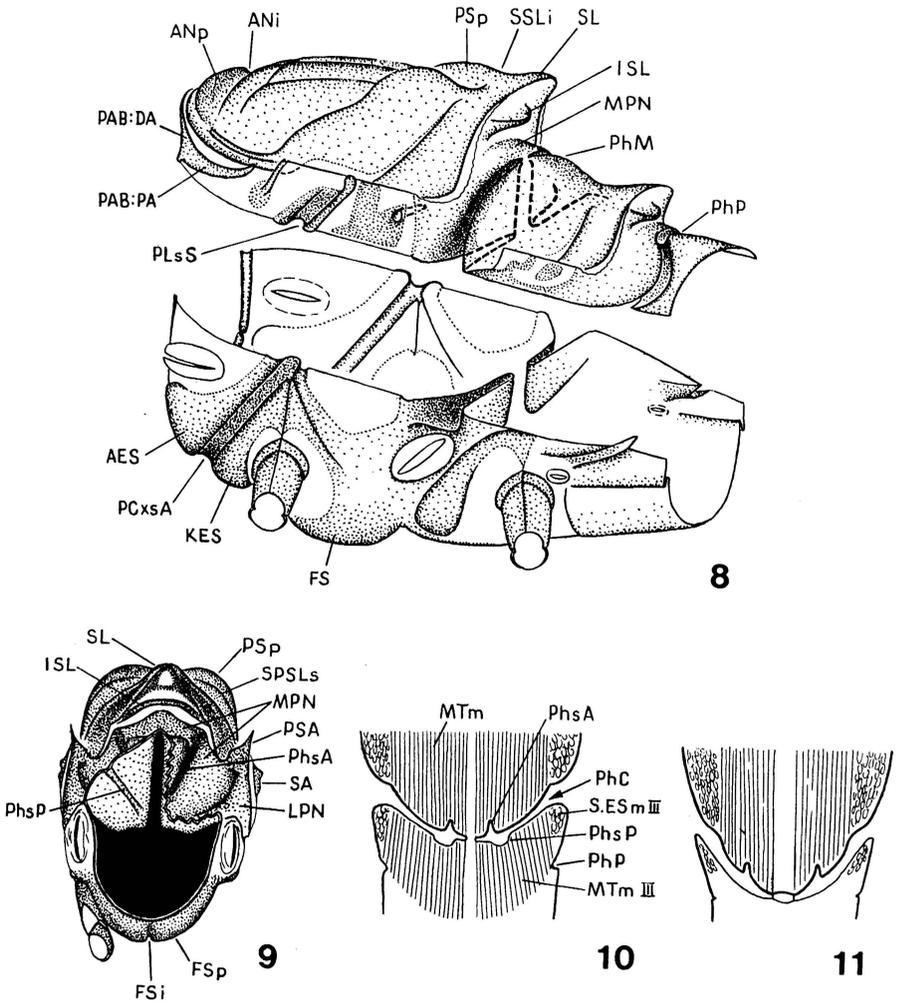


Fig. 8-11. — Structure of mayfly phragmae. — 8, scheme of mayfly pterothorax dissected horizontally; — 9, *Ephemera vulgata*: mesothorax in back view (in the right half the posterior wall of phragma is turned away); — 10, the same, middle phragma in horizontal section; — 11, male of *Caenis macrura*, middle phragma in horizontal section. Deciphering of abbreviations in the list of arbitrary signs.

(KLUGE, 1988). Mesonotal suture is completely absent also in the families Baetidae and Caenidae; its absence is used as a generic feature of *Tricorythodes* (KLUGE, in press).

Here are not used the terms “prescutum”, “prescutal suture”, and “parapsidal suture”, although these terms are employed in literature. Under the term “parapsidal sutures” (or “parapsidal furrows”) different authors understand different sutures. As it was shown by TULLOCH (1929) and accepted by SNODGRASS (1935), in its primary

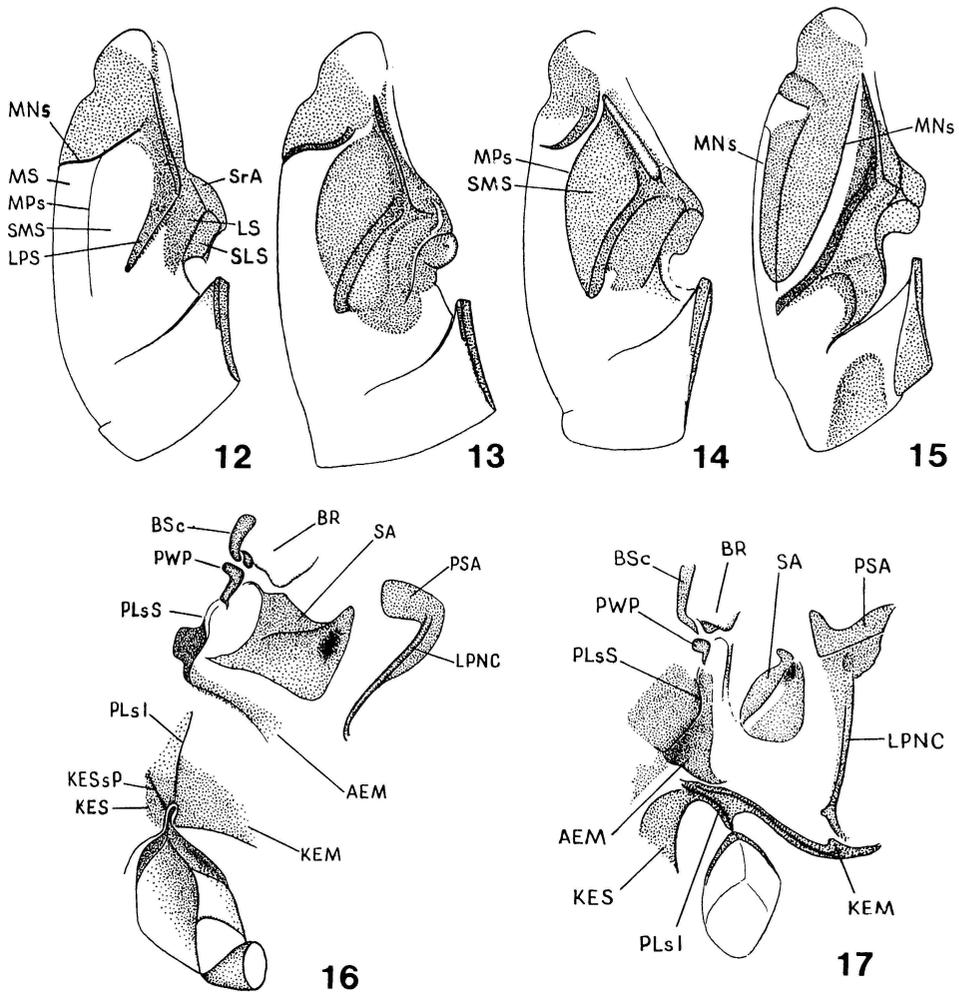


Fig. 12-17. — Details of mayfly subimaginal skin. — 12-15, skin of right half of mesonotum (axillary sclerites and prealar bridge are not shown); — 16-17, skin of mesothoracic left lateral wall (fig. 16 on the same scale as figs 2 and 5); — 12, 16, *Siphonurus aestivalis*; — 13, *Ameletus montanus*; — 14, *Isonychia ignota*; — 15, *Leptophlebia (Paraleptophlebia) lunata*; — 17, *Baetis vernus*. Deciphering of abbreviations in the list of arbitrary signs.

meaning this term was used for the paired sutures in the hind part of scutum of wasps and some other Hymenoptera. These true parapsidal sutures of wasps go through the dorsal bases of the scuto-episternal muscles, so they do not correspond to any sutures of Ephemeroptera. In Ephemeroptera the area corresponding to the location of parapsidal sutures is submedioscutum, it is surrounded by three sutures, which I suggest to name medioparapsidal, lateroparapsidal, and antelateroparapsidal ones

(see above). Some authors understand under the term “parapsidal sutures” the medio-parapsidal sutures of Ephemeroptera and sutures of other insects (notaulici of Hymenoptera) homologous to them. According to some authors (WEBER, 1933 and others) the area limited posteriorly by the “parapsidal sutures” (actually : notaulici) is called “prescutum” so these sutures may be also called “prescutal sutures”. But if used for Ephemeroptera in a such sense, the “prescutum” should be a large median area including the anteronotal protuberance and the whole medioscutum ; in fact nobody named it “prescutum” in this group. For Diptera, the term “prescutum” designates often the mere wide area corresponding to the mesoscutum + submesoscutum of Ephemeroptera. Applied to Ephemeroptera, the term “prescutum” was used for the anteronotal protuberance (WEBER, 1933 : fig. 181a) or for the lateral area, which includes neither the anteronotal protuberance nor medioscutum. From the incorrect figures by MATSUDA (1956 : Plate 2 A,B ; 1970 : fig. 42 A-C) it is unclear which of the lateral sutures (anterolateral parapsidal suture, or groove between the anterolateral scutal crest and prelateroscutum, or membrane between prelateroscutum and the posterior arm of prealar bridge) is called “prescutal suture”. KNOX (1935), GRANDI (1947), TSUI (1970), and BRODSKY (1970, 1974, 1991) used the term “prescutum” for the posterior arms of the prealar bridge.

As there is no definition of the term “prescutum” and as it is used for quite different areas of notum, it is better not to use this term at all, as well as the term “parapsidal sutures”.

D. — DORSAL WING ARTICULATION (fig. 1)

Wing base is connected with the lateral margin of notum by two movable sclerites : the *anterior axillary sclerite* (AxA) (term used by BECKER, 1954 : aAx) and the *posterior axillary sclerite* (AxP) (new term). Both of them are movably connected with the wing base and with notal wing processes : AxA with the anterior notal wing processes of suralare, and AxP with the posterior notal wing process of parascutellum. In the fig. 1 wing base is shown stretched with axillary membrane teared, 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 in different taxa. For example, in all Ephemereinae AxA has form similar to capital letter gamma.

The *proximal axillary sclerite* (AxPr) (new term) may be well developed (fig. 1), or rudimentary, or absent. It is connected with lateroscutum and cannot make such movements as AxA and AxP. The *middle axillary sclerite* (AxM) (new term) is movably connected with AxA and with the *middle articulatory process of wing base* (APM) (new term). Form of AxM is similar in different mayflies ; it has in its posterior part a distinct projection directed medially.

The basal plate of wing consists of immovably fused together *basisubcostale* (BSc), *basiradiale* (BR), the *middle articulatory process* (APM) and the *posterior articulatory process* (APP) (new term).

The new terms for sclerites of mayfly wing base are used here because there is no agreement on homologization of these sclerites with axillary sclerites of Neoptera. SNODGRASS (1935) wrote about axillary sclerites of Ephemeroptera without homologizing them with the first to fourth axillary sclerites of Neoptera. Opinion of other authors is shown in Table II.

Table II. — Different opinions on homology of axillary sclerites of Ephemeroptera and Neoptera.

Names of sclerites of Ephemeroptera used here (deciphering in the list of arbitrary signs)	AxA	AxM	AxPr	AxP	APM	APP
Knox, 1935	ANP	Ax	—	PNP	—	—
Grandi, 1947	Ax1	Ax2	«scler. semilunare»	—	Ax3	—
Bekker, 1966 (1954)	AxA	Ax1	—	Ax3	Ax2	—
Matsuda, 1956, 1970	Ax1	Ax2	Ax3	PNP	—	—
Brodsky, 1970	ANP	Ax1	—	PNP	Ax2	Ax3
Brodsky, 1974	Ax1	Ax2	MNP	PNP	—	Ax3

Ax1, Ax2, Ax3 — first, second, and third axillary sclerites of Neoptera ;

ANP, MNP, and PNP — anterior, middle, and posterior notal wing processes. Abbreviations used by these authors in some cases are not the same.

E. — LATERAL SURFACE OF MESOTHORAX (fig. 2, 5)

In majority of winged insects the mostly developed suture of the pleuron is the pleural suture, which runs from the pleural wing process to the coxartus, and prevents the pleuron from deformation during contraction of dorso-ventral muscles. In Ephemeroptera this suture is functionally substituted by a combined suture, which consists of the dorsal part of the pleural suture — *superior pleural suture* (PLsS) and the anterior part of the paracoxal suture — *anterior paracoxal suture* (PCxsA). This combined suture is wide, deep, and strongly sclerotized, it runs from the *pleural wing process* (PWP) to episternum and prevents the pleuron from deformation during contraction of the *scuto-episternal muscle* (S.ESm). The remainder parts of the pleural and paracoxal sutures, i.e. the *inferior pleural suture* (PLsI) and the *posterior paracoxal suture* (PCxsP) are weak and in some taxa disappear.

Katepisternum (KES) (the area surrounded by the anterior paracoxal suture, the inferior pleural suture, and the coxal cavity) is subdivided by the *anterior katepisternal suture* (KESsA) (new term) and the *posterior katepisternal suture* (KESsP) (new term) in portions containing different muscle bases. The portion below KESsA contains the base of *scuto-episternal muscle* (S.ESm) ; the portion between KESsA and KESsP contains bases of the *pleuro-coxal* and *pleuro-trochanteral muscles* (PCxm, PTrm) ; the portion between KESsP and the *inferior pleural suture* (PLsI) contains the ventral part of the *basalar-coxal muscle* (BA.Cxm) and the base of the *axillar-pleural muscle* (Ax.Pm).

Form of the anterior paracoxal suture, anepisternum, and katepisternum may be successfully used in diagnoses of families (KLUGE, 1988), as these structures are distinct, sclerotized, relief and well visible from lateral and ventral sides. Form and position of other sutures named above may also be used in systematics.

Behind the pleural wing process, under the wing base lies the *subalar sclerite* (SA). Its lower portion bears the base of large *subalar-sternal muscle* (SA.Sm) and is well sclerotized and distinct, while the upper portion may be slightly sclerotized, translucent, and indistinct. In the hind part of the subalar sclerite there is a well developed apodeme, to which is attached thin *subalar-furcal muscle* (SA.Fm) and is partly attached SA.Sm. In Caenidae, SA.Sm have disappeared, so the subalar sclerite is rudimentary, but its apodeme is still developed and bears only the base of SA.Fm. The membranose area around the subalar sclerite may be called *subalar cavity* (SAC) (new term), it is situated between *anepimeron* (AEM) and *lateropostnotum* (LPN); in some cases the form of the subalar cavity may be used in systematics.

Lateropostnotum (LPN) (which is also called "pleurotergite" or "pleurophragmite" (CRAMPTON, 1914) is a lateral prolongation of mediopostnotum, which ventrally reaches the hind spiracle. In its lower portion lateropostnotum is more or less convex, as it contains the ventral base of the *scuto-lateropostnotal muscle* (S.LPNm), strongly developed in all mayflies. The portion of lateropostnotum situated exactly under the wing base may be called *postsubalar sclerite* (PSA) (= posterior subalare : CRAMPTON, 1914). Below the postsubalar sclerite in the dorsoventral direction runs more or less developed a *lateropostnotal crest* (LPNC) (new term), which in some taxa may be indistinct. In Caenidae and some of Tricorythidae lateropostnotum is very large, reaches the coxal cavity and furcasternum (it connects with extremely strong development of S.LPNm); in Tricorythidae the form of the secondary ridges and sutures on lateropostnotum is used as important generic character (KLUGE, 1992).

F. — MESOSTERNUM (fig. 2, 5-9)

Form and proportions of sternum may be successfully used as diagnostic character of some mayfly taxa, but it is necessary to remember that sternum of females is usually wider than that of males.

Mesosternum consists of two well developed portions : *basisternum* (BS) (anteriorad from the pair of furcal pits, which lies between the coxal cavities) and *furcasternum* (FS) (posteriorad from the furcal pits).

Basisternum does not contain any muscle bases, inside it is situated large mesothoracic nerve ganglion. Form of basisternum may be different, for example in *Leptophlebia* s.l. (incl. *Paraleptophlebia*) it has a distinct longitudinal carina; it allows to distinguish this genus from other genera of Leptophlebiidae (TSUI, 1970, TSUI & PETERS, 1972).

Mesothoracic furcasternum of Ephemeroptera is more developed than in other Pterygota, because it contains the ventral bases of large *subalar-sternal muscles* (SA.Sm) — the direct wing depressors, which are absent in Neoptera. The portions of basisternum which contain the bases of SA.Sm are strongly convex and may be called *furcasternal protuberances* (FSp). Furcasternal protuberances may be brought

together (fig. 6) or separated by the *furcasternal longitudinal impression* (FSi). Form of this impression may be successfully used as systematic feature ; it depends upon the position of the bases of SA.Sm, while their position depends upon structure of the nerve system. In primitive cases (Siphonuridae, Isonychiidae, Oligoneuriidae, Ephemeroida and some other taxa) the metathoracic nerve ganglion is situated in metathorax and is connected with the mesothoracic ganglion (which is situated in mesothoracic basisternum) by a pair of long slender connectives which lies at some distance from the body wall and allows the bases of SA.Sm to lie close together. In this case furcasternal impression is absent (fig. 6) or developed as a slender line. In progressive cases (Baetidae, Heptageniidae, Leptophlebiidae, Ephemerellidae, Tricorythidae, Neophemeridae) the metathoracic nerve ganglion transfers into furcasternum of mesothorax, nearer to the mesothoracic ganglion. Metathoracic ganglion lies close to the body wall, and the bases of SA.Sm in this place are turned backward, so between the furcasternal protuberances appears a more or less wide furcasternal impression (fig. 7). If the metathoracic ganglion is situated in the hind part of mesothoracic furcasternum, the furcasternal impression is narrow in its fore part and is widened posteriorly ; if the ganglion turns into the middle or fore part of furcasternum, the furcasternal impression becomes wide in all its length, parallel-sided (KLUGE, 1988 : fig. 74-79). This character was used as generic in Heptageniidae (KLUGE, 1988, TSHERNOVA *et al.*, 1986). In Caenidae the subalar-sternal muscles are completely reduced, but the furcasternal protuberances are preserved, being very small and very widely separated.

Thus the form of furcasternal impression gives convenient diagnostic features for some taxa and at the same time allows to clear up the direction of evolution in different lineages.

G. — PHRAGMAE (fig. 2, 5, 8-11)

The *anterior phragma* (PhA) (between pro- and mesotergum) in Ephemeroptera is nearly reduced, and the most part of the anterior base of the *median tergal muscle* (MTm) attaches not to it, but to the dorsal surface of notum.

The *middle phragma* (PhM) (between meso- and metatergum) is very large. It consists of a pair of large lateral folds, which anterior and posterior walls do not remain contiguous or fuse (in contrary to Neoptera), so between anterior and posterior walls there is a space, the *phragmal cavity* (PhC). On the median line of the body, the phragmal fold is shallow or absent, so the left and right halves of phragma are divided by a chink up to the dorsal body surface. The middle phragma may be nearly flat or curved, with convex posterior surface and concave anterior surface, deeply jutting out into the metathorax (fig. 10, 11). The walls of phragma may bear sutures : a pair of *anterior phragmal sutures* (PhsA) (new term) on the anterior wall of phragma (convex towards the mesothorax and concave towards the phragmal cavity) and a pair of *posterior phragmal sutures* (PhsP) (new term) on the posterior wall of phragma (convex towards the metathorax and concave towards the phragmal cavity). Males of Caenidae have left and right halves of phragma fused medially by secondary anterior and posterior walls, so besides the two phragmal cavities appears an additional closed cavity between them (fig. 11) ; it is the unique discriminating character of this family.

Structure of the middle phragma may give some important characters of higher taxa, but is difficult to examine, because it may be observed only after breaking the specimen.

The *posterior phragma* (PhP) (between metatergum and the first abdominal tergum) has another structure, it is a curved canal, mostly deep on the dorsal side.

H. — MESOTHORACIC CUTICLE OF SUBIMAGO (fig. 12-17)

In the modern literature subimago is usually considered as under-developed imago, but actually subimagos have some features, which are absent in imaginal and nymphal stages, and examination of subimaginal characters may be very useful, especially in phylogenetic study.

In order to examine subimaginal cuticle it is convenient to use a cast skin and make a slide; instead may be used a skin detached from the body of a subimago ready to molt. For preparing the slide, one must detach both halves of notum together with the dorsal cuticle of proximal part of the fore wing, detach abdomen from the thorax, and detach legs. Cuticle of notum is smoothed out on the slide as shown in fig. 1. Cuticle of the ventral and lateral parts of mesothorax, together with metathorax, prothorax, and head, is also smoothed out. It is useful also to dissect the cuticle of abdomen along its pleura of one side and smooth out it on the same slide. As in canadian balsam some details of the surface structure are poorly visible, it is better not to flood cuticle in balsam, but to keep it dry, covered by a thin glass stuck in the corners by balsam. On such slide, patterns seem to be quite different in transmitted and in opaque light.

While cuticle of mayfly imagos nearly lack setae, subimaginal cuticle is covered by microtrichiae — dense minute setae about 0,01 mm length (their size does not depend upon size of the insect). On the wings of subimago microtrichiae cover the whole surface, making subimaginal wings mat. On the body of subimago such microtrichiae cover only certain areas, which position and form may be used as systematic characters for certain families and genera.

Relief of thorax of subimago and imago is nearly the same, but areas of sclerotization in subimago are not the same as in imago.

Mesonotum of imago is nearly evenly sclerotized (if there are colour patterns, they usually have hypodermal origin); mesonotum of subimago has distinct sclerotized pigmented areas and light areas between them (fig. 12-15). Intensity of pigmentation of these sclerotized areas may be under great species or individual variability, but their form, very constant in the large taxa, allows to characterize families, tribes, and genera. For example mesonotal subimaginal sclerotization allows to distinguish Siphonuridae-like taxa. In all examined *Siphonurus* and *Parameletus* (Siphonuridae s. str.) sclerotization behind the mesonotal suture occupies short lateroparapsidal suture, antelateroparapsidal suture, and small part of sublateroscutum (fig. 12). In all examined species of *Ameletus* (Ameletidae or Siphonuridae s.l.) sclerotization occupies all submedioscutum and large part of sublateroscutum; behind lateroparapsidal suture there is an area with particular surface structure, which form remains constant for the genus (fig. 13). In all examined *Isonychia* (which belongs to Isonychiidae — Siphonuridae-like representative of Setisura) sclerotization also occupies all submedioscutum and

a part of sublateroscutum, with specific emargination behind the end of the latero-parapsidal suture (fig. 15). As stated above, areas of sclerotization and microtrichiae allow to determinate position of the mesonotal suture, which has important meaning for systematics. Sclerotization areas of mesonotum allow to distinguish tribes of the family Heptageniidae, certain taxa of Baetidae, Leptophlebiidae.

Sclerotization of subimaginal lateral surface of thorax also differs from that of imago (fig. 16, compare with fig. 2). Instead integral pleural sclerite which is developed in imago, subimago has three independent sclerites : *pleural wing process* (PWP) ; the *superior pleural sclerite* (above the paracoxal suture, includes PLsS and AEM) ; and the *inferior pleural sclerite* (below the paracoxal suture, includes PLsI, KEM, and KES). These three sclerites are separated by areas with thin membranose cuticle. Form of these sclerites is particular for certain taxa (fig. 17).

Subimaginal sclerotization of lateropostnotum occupies the *postsubalar sclerite* (PSA) and the *lateropostnotal crest* (LPNC), forming an axe-like figure. In some cases its form may be used as important systematic sign. In some taxa subimaginal sclerite of katepimeron (KEM) is joined or fused with sclerite of lateropostnotal crest (LPNC), forming a rigid frame (fig. 17).

Sclerotized areas on sternum of subimago usually are not so distinct, as on tergum and pleuron, but sometimes they are distinct and also may be used in systematics.

In some taxa, Caenidae, Tricorythidae, and mayflies with functional legs of imago (Palingeniinae, Polynitarciidae, Behningiidae, Oligoneuriidae, Prosopistomatidae) subimaginal cuticle lack distinct sclerotized areas, at least on lateral surface.

I. — METATHORAX

In the Order Ephemeroptera, reduction of metathorax and hind wings takes place. Relatively complete development of metathoracic structures is found in Siphonuridae (fig. 2, 5). In some mayfly taxa metathorax is more strongly reduced : pleural wing process and subalar sclerite disappear ; alinotum (scutum + scutellum) becomes shorter, while mediopostnotum may become longer, or the whole metathorax becomes shorter ; other structures connected with flight more or less completely reduce. Degree of reduction of some metanotal structures is used in diagnoses of certain genera of Baetidae (EDMUNDS *et al.*, 1976 : p. 100, fig. 258-264).

The wing indirect musculature of metathorax may be nearly completely developed (fig. 5) or more or less reduced. In all recent mayflies the direct wing depressor — subalar-sternal muscle (SA.Sm) of metathorax is absent.

Speed of reduction of hind wings, exoskeleton of metathorax, and its wing musculature may be different. For example *Cloeon dipterum* (the species which have not any rudiments of hind wings or their wing pads in any stage of development) has very strong hind wing musculature, while some mayflies with well developed hind wings (for example Baetiscidae) have metathorax much smaller and hind wing musculature much weaker.

Among the mostly constant metathorax wing muscles are the median tergal muscle (MTmIII) and scuto-episternal muscle (S.ESmIII), they undergo reduction only in Caenidae and Tricorythidae. Presence or absence of these muscles allows to distinguish

genera of Leptohiphinae (Tricorythidae) (KLUGE, 1992). Development of S.ESmIII is connected with external structure of metathoracic episternum, which bears the ventral base of this muscle; so the external structure of metathoracic episternum may be used as generic character of these genera.

In majority of mayflies metathoracic lateral surface of subimago has distinct sclerotized areas, which are not the same as in imago, form of subimagonal lateral sclerites may be used in systematics.

REFERENCES

- BEKKER E. G., 1954. — Origine and development of Insect wings. II. Structure, mechanism and origine of the fly apparatus of Ephemeroptera. *Vest. Mosc. Inst.*, **5** [In Russian].
- BRODSKIY A. K., 1970. — Organization of the flight system of the mayfly. *Ephemera vulgata* L. (Ephemeroptera). *Entomo. Obozr.* **49** (2) : 307-315. [In Russian].
- 1974. — Evolution of the wing apparatus in the Ephemeroptera. *Entomo. Obozr.* **53** (2) : 291-303.
- 1991. — Structure functioning and evolution of tergum in alate insects. I. Generalized scheme of structure. *Entomo. Obozr.* **70** (2) : 297-315. [In Russian].
- DÜRKEN B., 1907. — Die Tracheenkiemenmuskulatur der Ephemeriden unter Berücksichtigung der Morphologie des Insectenflügels. *Zeitschr. Wiss. Zool., Leipzig*, Bd. **87** : 435-550.
- EDMUNDS G. F., JENSEN Jr., S. L. & BERNER L., 1976. — *The mayflies of North and Central America*. Univ. Minnesota Press, Minneapolis.
- GRANDI M., 1947. — Contributi allo studio degli "Efemeroidei" Italiani. VIII. Gli scleriti ascellari (pseudopteralia) degli Efemeroidei, loro morfologia e miologia comparate. *Boll. dell. Inst. Ent. Univ. di Bologna*, v. **16** : 85-114.
- KLUGE N. Ju., 1989. — About the homology of tracheal gills and paranotal structures of the larvae of the mayfly and winged insects, and their relationships with systematic and phylogeny of the suborder (Ephemeroptera). Lectures in Memoriam of N. A. Kholodkovskogo, 1988, p. 48-77.
- 1992. — Redescription of *Leptohyphes eximius* Eaton and diagnoses of the genera *Leptohyphes* and *Tricorythodes* based on the structure of pterothorax (Ephemeroptera : Tricorythidae, Leptohiphinae). *Opuscula Zool. Fluminensia*, **98** : 1-16.
- KLUGE N. Ju. & NOVIKOVA E. A., 1992. — Revision of the palaeartic genera and subgenera of the subfamily Cloeoninae (Ephemeroptera, Baetidae) with the description of new species for the URRS. *Entomol. Obozr.*, **71** (1) : 38-55 [In Russian].
- KNOX V., 1935. — XI. The body-wall of the thorax. XII. The musculature of the thorax. In : Needham, J. G., J. R. Traver, Yin-Chi Hsu. *The biology of mayflies, with a systematic account North American species*. N.Y., Comstock Publ., 16, 769 pp. : 135-178.
- MAKI T., 1938. — Studies of the thoracic musculature of insects. *Mem. Fac. Sci. Agric. Taihoku imp. Univ.*, **24** : 1-343, 17 pl.
- MATSUDA R., 1956. — Morphology of the thoracic exoskeleton and musculature of a mayfly *Siphonurus columbianus* McDunnough (Siphonuridae, Ephemeroptera), a contribution to the subcoxal theory of the insect thorax. *Kansas Entomol. Soc.*, **29** (3) : 92-113.
- 1970. — Morphology and evolution of the insect thorax. *Mem. Ent. Soc. Canada*, No. **76**, Ottawa, 431 pp.
- MCCAFFERTY W. P., 1991. — Toward a phylogenetic classification of the Ephemeroptera (Insecta) : a commentary on systematics. *Ann. Entomol. Soc. Amer.*, **84** (4) : 343-360.

- NOVIKOVA E. A. & KLUGE N. Ju., 1987. — Systematics of the genus *Baetis* (Ephemeroptera, Baetidae) with description of a new genus from middle Asia. *Vestn. Zool.*, **4** : 8-19 [In Russian].
- PROVONSHA A. V., 1990. — A revision of the genus *Caenis* in North America (Ephemeroptera, Caenidae). *Trans. Amer. Entomol. Soc.*, **116** (4) : 801-884.
- SNOODGRASS R. E., 1935. — *Principles of Insect Morphology*. N.Y.
- CHERNOVA O. A., KLUGG N. Y., SINICHENKOVA N. D. & BELOV V. V., 1986. — *Ephemeroptera*, **1** : 99-142, illustr. In : LER P. A. (Ed.) [*Identification of insects of the Far East of the USSR in 6 volumes. Volume 1. Apteriygota and Palaeoptera with incomplete metamorphosis*]. Nauka, Leningrad. 1986 : 1-452 [In Russian].
- TSUI P. T. P., 1970. — *The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera)*. A thesis for the degree of Master of Sci., FLA State Univ.
- TSUI P. T. P. & PETERS W. L., 1972. — The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). *J. Zool., London*, **168** (3) : 309-367.
- 1975. — The comparative morphology and phylogeny of certain Gondwanian Leptophlebiidae based on the thorax, tentorium, and abdominal terga (Ephemeroptera). *Trans. Amer. Entomol. Soc.*, **101** (4) : 505-595.
- TULLOCH G. S., 1929. — The proper use of the terms parapsides and parapsidal furrows. *Psyche*, **36** : 376-382.
- WEBER H., 1933. — *Lehrbuch der Entomologie*. Jena, Gustav Fisher, 726 pp.

ANALYSES D'OUVRAGES

BITSCH J. & LECLERCQ J. — *Hyménoptères Sphecidae d'Europe occidentale. Volume 1*. Paris, Fédération française des Sociétés de Sciences naturelles, 1993, Faune de France : 79, broché, 325 pages, 59 planches, 98 cartes.

Les Hyménoptères aculéates, en tant que composants majeurs des biocénoses, bénéficient d'un regain d'attention en Europe occidentale et centrale, comme dans beaucoup d'autres régions développées du monde. En France l'intérêt pour ce groupe est manifeste, mais les outils d'identification fiables font souvent défaut. Or le temps n'est plus aux études de biomasse associant un bocuf charolais, une demi-douzaine d'oiseaux, et quelques millions d'invertébrés d'identité incertaine. La biologie et l'écologie exigent des identifications précises. La publication du premier volume d'une faune des Sphecidae d'Europe occidentale est donc particulièrement opportune.

Ce premier volume consacre plus de 60 pages à l'avant-propos et aux généralités sur les Sphecidae, environ 230 pages à la sous-famille des Crabroninae, et près de 30 pages à une bibliographie tant générale que spécifique. Les généralités méritent d'être lues par tous les hyménoptéristes car elles comportent une mise à jour de la terminologie morphologique dont on peut espérer qu'elle sera unanimement adoptée ; elles contiennent aussi une clé des familles d'aculéates présentes en Europe, des cladogrammes commentés de ces familles et des tribus de Sphecidae, et enfin une clé des genres de Sphecidae d'Europe.

La section consacrée à la sous-famille des Crabroninae contient, pour chacun des genres connus d'Europe, une clé des espèces observées à l'ouest de l'Oural (sauf pour les *Lindenius*), et des rubriques résumant, pour chacune des espèces présentes en France, les données bibliographiques, morphologiques, écologiques et biogéographiques essentielles, la distribution en France (avec le département comme unité géographique de base) et toutes les synonymies rencontrées dans les publications. Les espèces mentionnées dans les clés, mais non présentes en France, sont traitées de façon beaucoup plus concise. Deux annexes résument les changements nomenclatoriaux introduits et la liste des fleurs butinées. Les clés de détermination ont été rédigées afin de tenir compte de la variabilité intraspécifique, parfois fort importante. Les dessins au trait sont d'une excellente qualité. L'index, très complet, permet de trouver rapidement les paragraphes ou rubriques traitant d'un genre, ou d'une espèce.

La bibliographie est particulièrement soignée, couvrant toutes les données pertinentes publiées avant 1993 et même, dans certains cas, en 1993. Un effort particulier a été fait, dans le cas des espèces à distribution paléarctique ou holarctique, pour exploiter les données biologiques recueillies sur la totalité de l'aire de distribution.