

# Structure of the coxa and homeosis of legs in Nematocera (Insecta: Diptera)

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## Abstract

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Construction of the middle and hind coxae was investigated in 95 species of 30 nematoceran families. As a rule, the middle coxa contains a separate coxite, the mediocoxite, articulated to the sternal process. In most families, this coxite is movably articulated to the eucoxite and to the distocoxite area; the coxa is radially split twice. Some groups are characterized by a single split.

The coxa in flies is restricted in its rotation owing to a partial junction either between the meron and the pleurite or between the eucoxite and the meropleurite. Hence the coxa is fastened to the thorax not only by two pivots (to the pleural ridge and the sternal process), but at the junction named above. Rotation is impossible without deformations; the role of hinges between coxites is to absorb deformations. This adaptive principle is confirmed by physical modelling.

Middle coxae of limoniid tribes Eriopterini and Molophilini are compact, constructed by the template of hind coxae. On the contrary, hind coxae in all families of Mycetophiloidea and in Psychodidae s.l. are constructed like middle ones, with the separate mediocoxite, centrally suspended at the sternal process. These cases are considered as homeotic mutations, substituting one structure with a no less efficient one.

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## Introduction

The aim of this article is to trace the early phases of partition within the Nematocera and to discuss the biomechanical reasons why a single or double partition was advantageous. Two splits first preadapted the coxa in higher flies for a further split, after which the coxa radially parted into three movable sclerites (coxites) which enabled muscomorph flies to attain a streamlined posture in the flight (Frantsevich and Gladun 2002). Certainly such triple partition could not emerge abruptly; the radial splits probably evolved one by one. These splits may have also contributed to the improvement of flight performance.

## Materials and Methods

The flies were collected from the field or obtained from collections. The methods of preservation, dissection, maceration, and embedding were described in a previous article (Frantsevich and Gladun 2002).

## Results

### *Construction of the middle coxa*

This podomere in flies is usually separated into several sclerites (coxites). Separation is complete in higher flies (Brachycera) where one defines the front sclerite as eucoxite (Ecx), the hind one as distocoxite (Dcx), and the middle one as mediocoxite (Mcx). Even if less distinct, coxites are recognized by their position and landmarks, namely articulations (i.e. the eucoxite – to the pleural ridge and to the trochanter anteriorly, the mediocoxite – to the sternal process, the distocoxite – to the trochanter posteriorly), fields of sensory hairs (i.e. anterior *ac* on the eucoxite, posterior *pc* at the distocoxite), origins of muscles, ridges reinforcing articulations, sutures dividing coxites, etc.

Coxae on the following figures are either depicted as whole mounts or, if they consist of separate sclerites, as flat involutions of the coxa. If, for the sake of brevity, only mediocoxites are depicted in detail, then adjacent sclerites are shown

partly and schematically. In all flat involutions, the medio-coxite is in the middle of the drawing, the eucoxite is from the left, and the area corresponding to the distocoxite is from the right. The articular furcosternal process (Fst) comes to the medio-coxite from above. If omitted, this process is symbolized by an arrow pointing to the articular socket.

The medio-coxite which is the point of interest of this article, is a tiny coxite seen in an intact specimen as an evagination from the narrow posterior side of the coxa above the trochanter. Very small medio-coxites are quite inconspicuous from the lateral view. It is necessary to sprawl middle legs apart in a fresh or alcohol-fixed specimen in order to notice the crescentic or elongated sclerite balancing on the articular furcosternal process. The dorsal rim of the medio-coxite is sclerotized, especially around the socket for articulation with the round-headed furcosternal process. Articular points for the medio-coxite on the eu- and distocoxite are reinforced with ridges. Sclerotized areas are shown on line drawings with denser stipple.

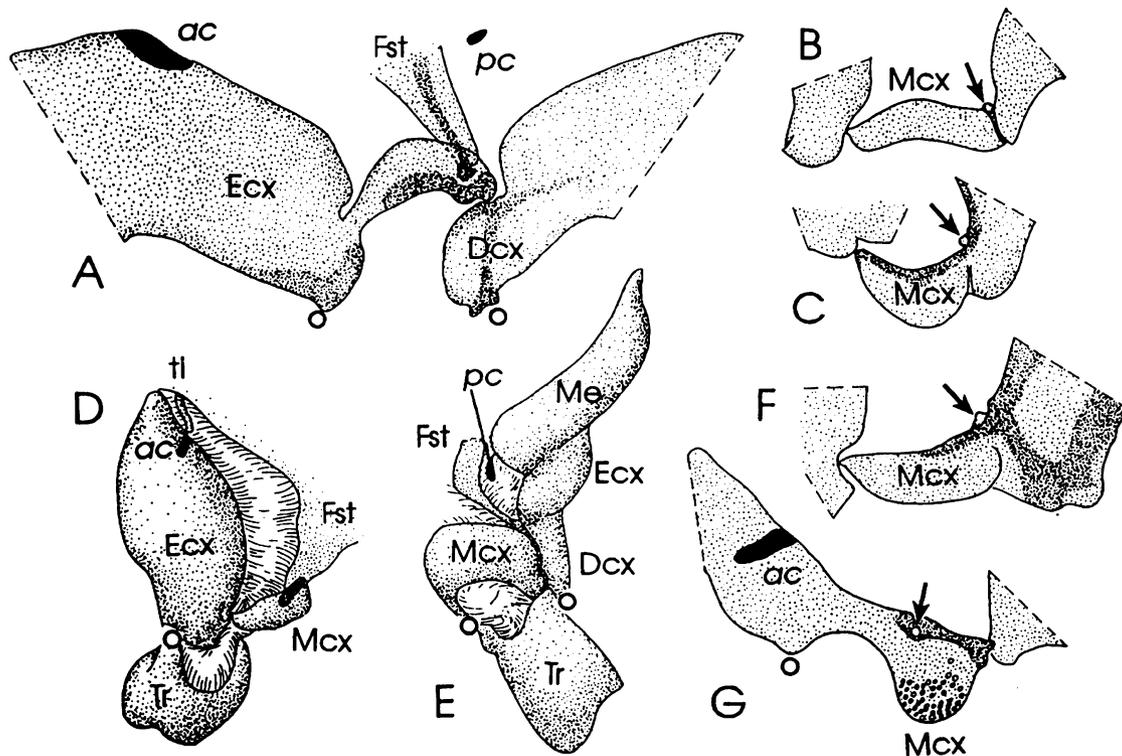
Space above the medio-coxite at both sides of the Fst is covered with the soft articular membrane. Below the medio-coxite, the articular membrane often forms a sac bearing long bristles pointing ventrad.

*Comparative review of structure of the coxa*

Families are listed below in the order proposed by Wood and Borkent (1989). The European tradition ascribes the family status to various subdivisions within tipuloids and mycetophiloids. Generic and specific names are given predominantly by Stackelberg and Narchuk (1969). Totally 95 species of 30 nematoceran families were examined. They are listed in Table 1.

*Tipuloidea.* The middle coxa in a crane-fly, *Tipula*, is stout and rounded (Fig. 1D,E). An observer, looking at the coxa from the side, easily recognizes the anterior part of the coxa, the eucoxite, and above it the convex meron which attaches to the pleurite. The eucoxite articulates with the anterior condyle of the trochanter. The posterior condyle of the trochanter articulates to a triangular plate below the eucoxite. This plate has no definite separation from the eucoxite. We recognize it by certain landmarks as a separate area corresponding to the distocoxite in higher flies.

The postero-medial part of the middle coxa is the crescentic, gibbous, robust sclerite, the medio-coxite (Fig. 1B–F). In the four genera of Tipulidae (s.str.) under study, the medio-coxite

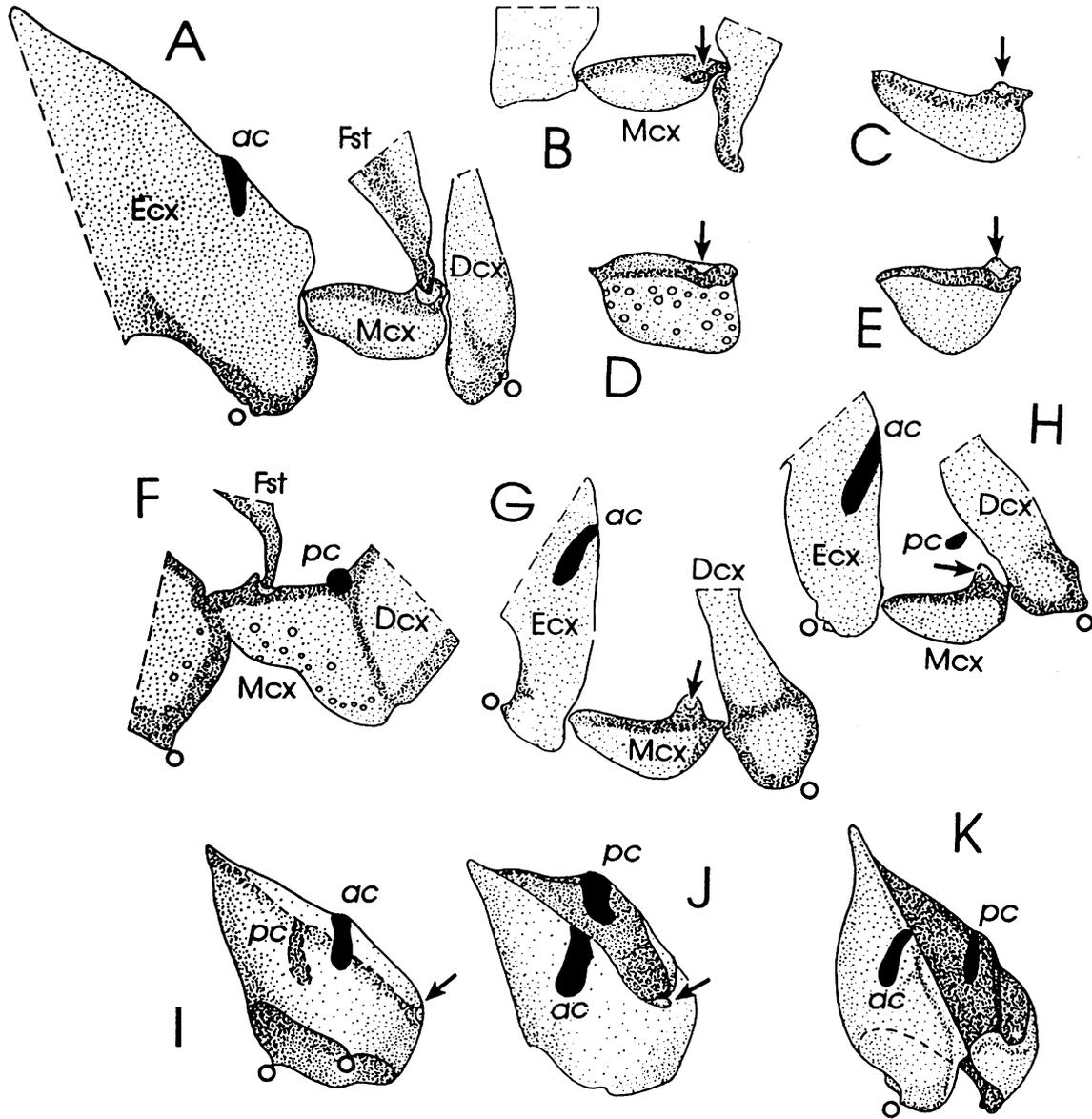


**Fig. 1**—The middle coxa in Tipulomorpha. —A. *Trichocera saltator* (Trichoceridae), flat involution; —B. *Tipula lunata*, medio-coxite, —C. *Ctenophora guttata*, medio-coxite, —D, E. *T. lunata*, whole mount of the right middle coxa, antero-medial (D) and postero-medial view (E); —F. *Tanyptera atrata* (Tipulidae), —G. Blepharoceridae *g.sp.*, medio-coxites. Area of bristles in G is

indicated by the set of small circles. Bold circles indicate coxo-trochanteral articulations, arrows with small circles indicate the coxo-sternal articulation. Abbreviations: ac – anterior sensory field, Dcx – distocoxite, Ecx – eucoxite, Fst – furcosternal process, Mcx – medio-coxite, pc – posterior sensory field, ti – trochantine, Tr – trochanter.

**Table 1** List of examined species. Species in round brackets were observed intact and superficially for the shape of the mediocoxite

Superfamily	Family	Examined species
Tipuloidea	Tipulidae	<i>Tipula lunata</i> Linnaeus 1758, <i>T. luteipennis</i> Meigen 1830, <i>Nephrotoma maculata</i> Meigen 1804, <i>N. crocata</i> Linnaeus 1758, <i>N. pratensis</i> Linnaeus 1758; <i>Ctenophora guttata</i> Meigen 1818, <i>Tanyptera atrata</i> Linnaeus 1758 ( <i>Pedicia littoralis</i> Meigen 1804, <i>Dicranota bimaculata</i> Schummel 1829)
	Limoniidae – Pediciinae	<i>Helius longirostris</i> Meigen 1818 (Elephantomyini) <i>Paradelphomyia senillis</i> Haliday 1833 (Paradelphomyini) <i>Epiphragma ocellare</i> Linnaeus 1761 (Epiphragmini) <i>Phylidorea ferruginea</i> Meigen 1818, <i>Pilaria discicollis</i> Meigen 1818, <i>Pseudolimnophila lucorum</i> Meigen 1818, <i>Eloeophila marmorata</i> Meigen 1818, <i>Neolimnomyia nemoralis</i> Meigen 1818 (Limnophilini) <i>Hexatoma chirothecata</i> Scopoli 1763 (Hexatomi)
	Limoniidae – Hexatominae	<i>Niphadobata lutescens</i> Lundstrom 1907 (Cladurini) <i>Erioptera divisa</i> Walker 1848, <i>E. lutea</i> Meigen 1804 (Eriopterini) <i>Eriocnopa trivialis</i> Meigen 1818, <i>Molophilus griseus</i> Meigen 1804, <i>M. ochraceus</i> Meigen 1818, <i>M. medius</i> Meijere 1918, <i>M. pleuralis</i> Meijere 1920, <i>Ilisia punctigera</i> Laskschewitz 1940, <i>Ormosia lineata</i> Meigen 1804, <i>Cheilotrichia cinerascens</i> Meigen 1804 (Molophilini) <i>Dicranoptycha fuscescens</i> Schummel, <i>Idiocera pulchripennis</i> Loew 1856, <i>Gonomyia simplex</i> Tonnoir 1920, <i>Gnophomyia lugubris</i> Zetterstedt 1838 (Gonomyini)
	Limoniidae – Eriopterinae	<i>Antocha vitripennis</i> Meigen 1830 (Antochini) <i>Limonia nubeculosa</i> Meigen 1804, <i>Limonia tripunctata</i> Fabricius 1781, <i>Metalimnobi quadrimaculata</i> Linnaeus 1761, <i>Dicranomyia modesta</i> Meigen 1818, <i>D. tristis</i> Schummel (1829), <i>D. chorea</i> Meigen 1818 (Limoniini)
	Trichoceridae	<i>Trichocera saltator</i> Harris 1776, <i>T. hiemalis</i> De Geer 1776, <i>Nothotrichocera cingulata</i> Alexander 1926, <i>Paracladura lobifera</i> Alexander 1922, <i>P. maori</i> Alexander 1921 ( <i>Blepharocera fasciata</i> Westwood 1842), <i>Blepharocera</i> sp.
Blepharocero-morpha	Blepharoceridae	<i>Protaxyomyia melanoptera</i> Mamajev et Krivosheina 1966
Axymyioidea	Axymyidae	<i>Biblio marci</i> Linnaeus 1758, <i>B. pomonae</i> Fabricius 1775, <i>B. lanigerus</i> Meigen 1818, <i>Dilophusfebrilis</i> Linnaeus 1758
Bibionoidea	Bibionidae	<i>Penthetria motschulskii</i> Gimmerthal 1845 ( <i>P. japonica</i> Wiedemann 1830) ( <i>Hesperinus rohdendorfi</i> Krivosheina et Mamajev 1967)
Mycetophiloidea	Penthertriidae	<i>Asioditomyia japonica</i> Sasakawa 1963
	Hesperinidae	<i>Diadocidia valida</i> Mik 1874
	Ditomyiidae	<i>Keroplatus tipuloides</i> Bosc 1792
	Diadocidiinae	<i>Macrocera stigmoides</i> Edwards 1925
	Keroplastidae	<i>Brachypeza armata</i> Winnertz 1863, <i>Syntemna setigera</i> Lundstrom 1914
	Macroceridae	<i>Bolitophila rectangulata</i> Lundstrom 1913
	Mycetophilidae	<i>Sciara thomae</i> Linnaeus 1767
	Bolitophilidae	<i>Tetraxyphus ater</i> Meigen 1804
	Sciariidae	Cecidomyiinae spp.
	Cecidomyiidae – Lestremyiinae	
Psychodoidea	Cecidomyiidae – Cecidomyiinae	<i>Pericoma nubila</i> Meigen 1830, <i>P. fuliginosa</i> Meigen 1851, <i>Telmatoscopus</i> sp.
	Psychodidae	<i>Phlebotomus mongolensis</i> Sinton 1928, <i>Ph. grimmi</i> Porschinsky 1876, <i>Sergentomyia dentata</i> Sinton 1933
	Phlebotomidae	( <i>Hyperoscelis veteriosa</i> Mamajev et Krivosheina 1969)
	Hyperoscelidae	<i>Sylvicola zetterstedti</i> Edwards 1923, <i>S. punctata</i> Fabricius 1787
	Anisopodidae	<i>Mycetobia pallipes</i> Meigen 1818, <i>Trichomycetobia notabilis</i> Mamajev 1968
	Mycetobiidae	<i>Swammerdamella</i> sp.
	Scatopsidae	
Ptychopteroidea	Ptychopteridae	<i>Ptychoptera contaminata</i> Linnaeus 1758, <i>P. lacustris</i> Meigen 1830, <i>P. minuta</i> Tonnoir 1919
Culicoidea	Dixidae	<i>Dixella aestivalis</i> Meigen 1818
	Chaoboridae	<i>Chaoborus flavicans</i> Meigen 1818
	Culicidae	<i>Aedes cinereus</i> Meigen 1818, <i>A. excrucians</i> Walker 1856, <i>A. communis</i> De Geer 1776, <i>A. behningi</i> Martini 1926, <i>A. cantans</i> Meigen 1818, <i>Anopheles maculipennis</i> Meigen 1818 ( <i>Thaumalea</i> spp.)
Chironomoidea	Thaumaleidae	<i>Odagmia ornata</i> Meigen 1818, <i>Cnephia</i> sp.
	Simuliidae	<i>Atrichopogon minutus</i> Meigen 1830, <i>Mallochochelea inermis</i> Kieffer 1909, <i>Culicoides chiopterus</i> Meigen 1830, <i>Neurohelea luteitarsis</i> Meigen 1838
	Ceratopogonidae	<i>Chironomus plumosus</i> Linnaeus 1758
	Chironomidae	



**Fig. 2**—The middle coxa in Limoniidae. —**A.** *Helius longirostris* (Hexatominae, Elephantomyiini), flat involution of the middle coxa, —**B.** *Paradelphomyia senilis* (Hexatominae, Delphomyiini), —**C.** *Eloeophila marmorata* (Hexatominae, Limnophilini), —**D.** *Epiphragma ocellare* (Hexatominae, Epiphragmini), —**E.** *Neolimnomyia nemoralis* (Hexatominae, Limnophilini),

—**F.** *Niphadobata lutescens* (Eriopterinae, Cladurini), middle mediocoxites; —**G.** *Dicranomyia modesta* (Limoniinae, Limoniini), —**H.** *Limonia tripuctata* (Limoniinae, Limoniini), partial flat involutions of the middle coxa; —**I.** *Erioptera luteum* (Eriopterinae, Eriopterini), —**J.** *Molophilus pleuralis*, —**K.** *Ormosia lineata* (Eriopterinae, Molophilini), whole mounts of the middle coxa.

was always hinged to the eucoxite at a point. The anterior corner angle created by the attachment between the eu- and the mediocoxite was acute (Fig. 3A). On the contrary, the posterior border of the mediocoxite is broad and fuses with the distocoxite area down a deeply invaginated suture; the superior end of this suture bears a socket for the Fst. Thus the sternal articulation of the mediocoxite is of a marginal type.

The hind coxa of a crane-fly looks like a skewed truncated cone, with its broad face articulated to the pleurite and the

narrow face articulated to the Fst. No separate sclerites could be discerned in the hind coxa.

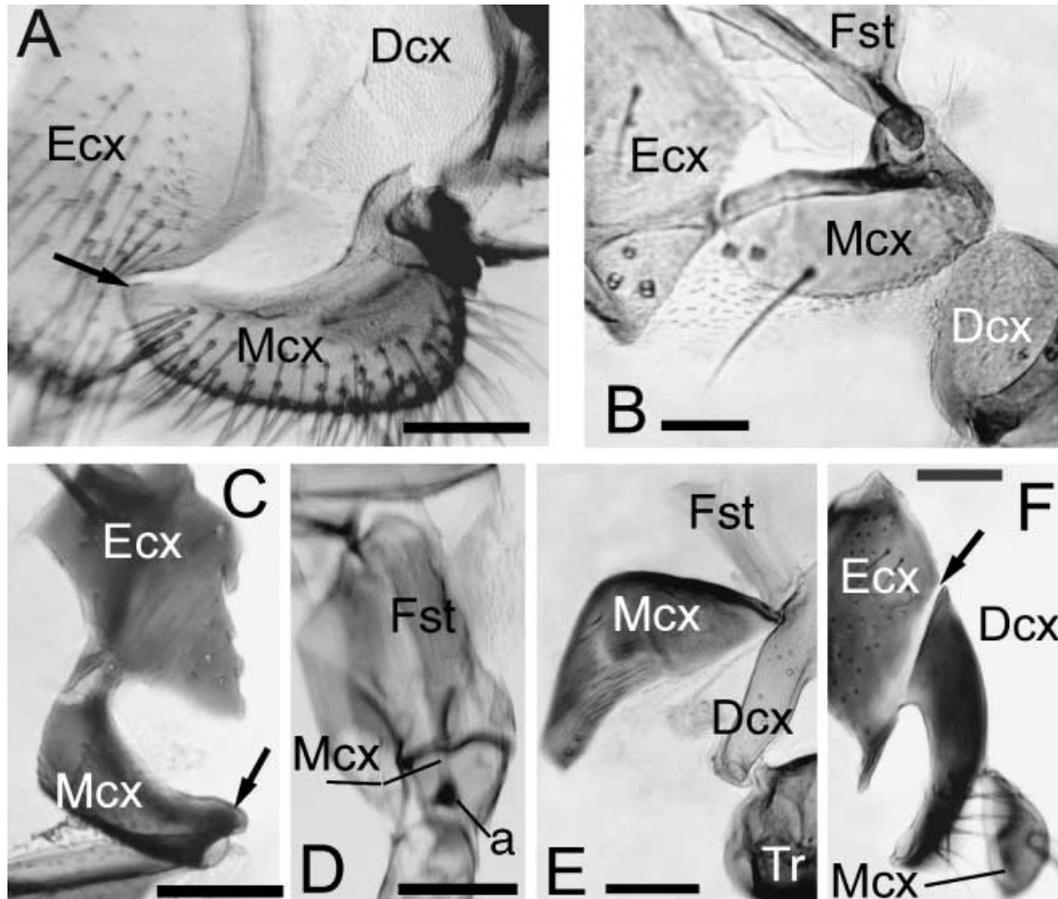
Crane-flies of the family Limoniidae (*sensu* Savchenko 1986) are very heterogeneous with respect to the construction of their middle coxae (Fig. 2). The mediocoxite in species of the subfamily Pediciinae (*Pedicia littoralis*, *Dicranota bimaculata*) is connected to the eucoxite by a narrow bridge; the articulation to the distocoxite area is at a point. Representatives of subfamilies Hexatominae and Limoniinae possess

the mediocoxite obviously separated both from the eucoxite and the distocoxite area (tribes Elephantomyiini, Delphomyiini, Limnophilini, Epiphragmini, Limoniini, Fig. 2A–E,G,H). The coxo-sternal articulation in the limoniids named above is situated on a short process protruding inwards from the posterior corner of the mediocoxite or close to it. Most interesting are the middle coxae within the subfamily Eriopterinae. The coxa in the aberrant, wingless *Niphadobata lutescens* (Cladurini) is compact, the area corresponding to the mediocoxite a triangular shape, completely fused with the distocoxite area and the eucoxite; the last junction is strangulated compared to the former one (Fig. 2F). Articulation with the Fst is amidst the superior border of the mediocoxite.

The coxa in species from Eriopterini and many species from Molophilini is compact, without any trace of division into separate sclerites (Figs 2I,J and 6D). Despite the similarity of the coxo-thoracic suspension in the middle and hind legs, these legs slightly differ in proportions of the podomers

and details of chaetotaxy. Flies of the last two tribes are distinguished by the broad meron built in the pleurite, the wide divergence of the sternal processes, and the enlargement of the sternal area. Middle legs are set distantly from each other and from the hind pair (Edwards 1921 in Savchenko 1982). No junction with the meron hinders excursions of the coxa. The strange exceptions among Molophilini were *Ormosia lineata* and *Cheilotrichia cinerascens*: the wall of the middle coxa was interrupted with a point junction between the areas corresponding to the eu- and mediocoxites (Fig. 2K). Such a single split of the middle coxa was not observed by us in any other fly. On the contrary, crane-flies of Eriopterinae-Gonomyini have their mediocoxites well-separated, alike to members of Hexatominiae and Limoniinae (Fig. 3B). Hind coxae in all limoniids studied by us were compact.

The middle coxa in winter flies Trichoceridae (Figs. 1A and 6A) possesses the same gibbous mediocoxite like most crane-flies, but junctions with the front and hind faces of the



**Fig. 3**—The mediocoxite and adjacent sclerites in the middle coxa. —A. *Ctenophora guttata* (Tipulidae), an arrow indicates a hinge between the eu- and mediocoxite; —B. *Dicronoptycha fuscescens* (Limoniidae); —C. *Bibio lanigerus* (Bibionidae), an arrow indicates the socket for the furcosternal process;

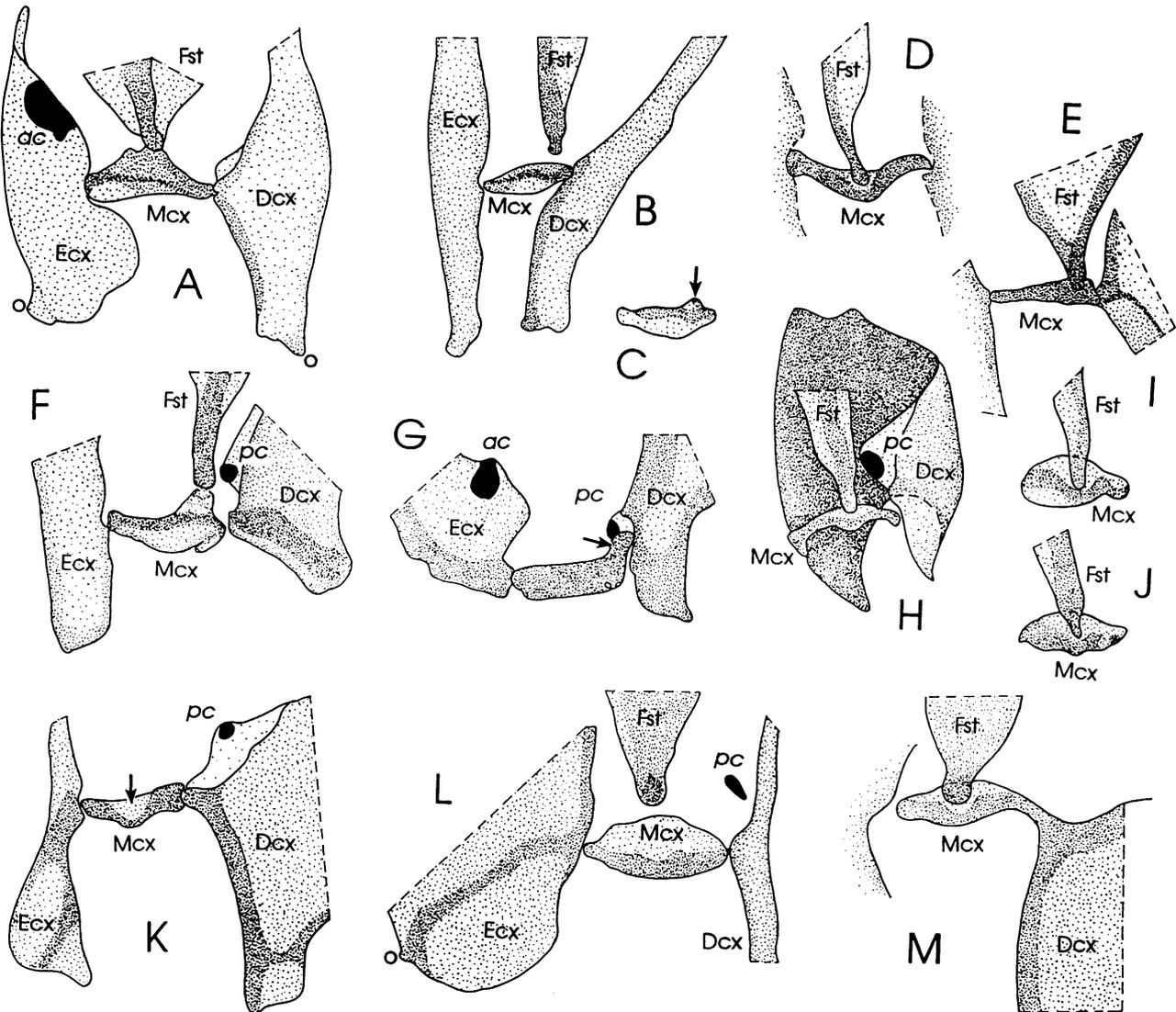
—D. *Swammerdamella* sp. (Scatopsidae), a- apodema of the depressor muscles; —E. *Aedes cantans* (Culicidae); —F. *Odagmia variegata* (Simuliidae), an arrow indicates the junction between the eu- and distocoxite. Scale bars 500  $\mu$ m in A, 100  $\mu$ m in B, C, E, F, 50  $\mu$ m in D.

coxa resemble the limoniids, not the tipulids. The sternal articulation is of marginal type. Strangely enough, the hind coxa in five trichocerid species representing three subfamilies (Krzeminska 1992) is not compact, but cut radially, with a point contact joining edges of disruption (Figs 8E and 9A).

*Blepharoceromorpha*. Construction of the middle leg mediocoxite in blepharocerids is remarkable in several aspects: (i) it is connected with the eucoxa by a broad bridge and separated from the distocoxite area to which it is hinged with its acute posterior corner; (ii) the pivot for the Fst is amidst

the dorsal rim of the mediocoxite (i.e. centrally suspended); and (iii) the mediocoxite is elongated ventrad and armoured with large number of strong bristles (Fig. 1G). The elongated shape was unique among flies.

*Axymyioidea*. The coxa in intact axymyids is inconspicuous because of the dense hairs around it. The flat involution of the middle coxa reconstructed from the micropreparation is depicted in Fig. 4(A). The mediocoxite is coarse, strongly sclerotized, and separated both from the eu- and distocoxite. The furcosternal process attaches centrally to the stout



**Fig. 4**—Mediocoxites in Axymyiomorpha, Ptychopteromorpha, Bibionomorpha, and Psychodomorpha. —**A**. *Protaxymyia melanoptera* (Axymyidae), flat involution of the middle coxa; —**B**. *Trichomyctobia notabilis*, —**C**. *Mycetobia pallipes* (Mycetobiidae), —**D**. *Ptychoptera lacustris* (Ptychopteridae), —**E**. *Sylvicola zetterstedti* (Anisopodidae), —**F**. *Dilophus febrilis*

(Bibionidae), —**G**. *Pentethrea motschulskii* (Pentethriidae), middle mediocoxites; —**H**. *Swammerdamella* sp. (Scatopsidae), whole mount of the middle coxa; —**I**, **J**. *Phlebotomus mongolicus* (Phlebotomidae), middle (**I**) and hind mediocoxite (**J**); —**K**. *Pericoma nubilis*, middle mediocoxite, —**L**, **M**. *Telmatoscopus* sp. (Psychodidae), middle (**L**) and hind mediocoxite (**M**).

inward process of the mediocoxite. Such a robust process was not observed in any other fly.

**Bibionoidea.** The mediocoxite in three species of March flies *Biblio* (Bibionidae) is in the shape of a flat arched ribbon in the horizontal plane, fused with the eucoxite and divided from the distocoxite area by a crist. The mobility of these junctions is dubious. The inward process for articulation with the sternum is short, situated marginally at the posterior end of the coxite. This process and fusion with the eucoxite is seen on the micrograph Fig. 3(C). On the other hand, in *Dilophus febrilis* from the same family, the mediocoxite is well separated from other coxites; its articular process is

marginal (Fig. 4F); the shape of this coxite resembles the mediocoxite in a representative of the related family Pentethriidae (Fig. 4G) or in limoniins described above. *Hesperinus* (Hesperinidae) was inspected only superficially; the mediocoxite was similar to that in *Dilophus*. The hind coxa in bibionoids is compact, broad at its mesal sector.

**Mycetophiloidea.** Numerous families of fungus gnats composing this suprafamily (Ditomyidae, Diadocidiinae, Keroplataidae, Macroceridae, Mycetophilidae, Bolitophilidae, Sciaridae, Cecidomyiidae) comprise a homogenous group with respect to construction of their coxa (Fig. 5). The middle coxa is long. The mediocoxite is always a small separate

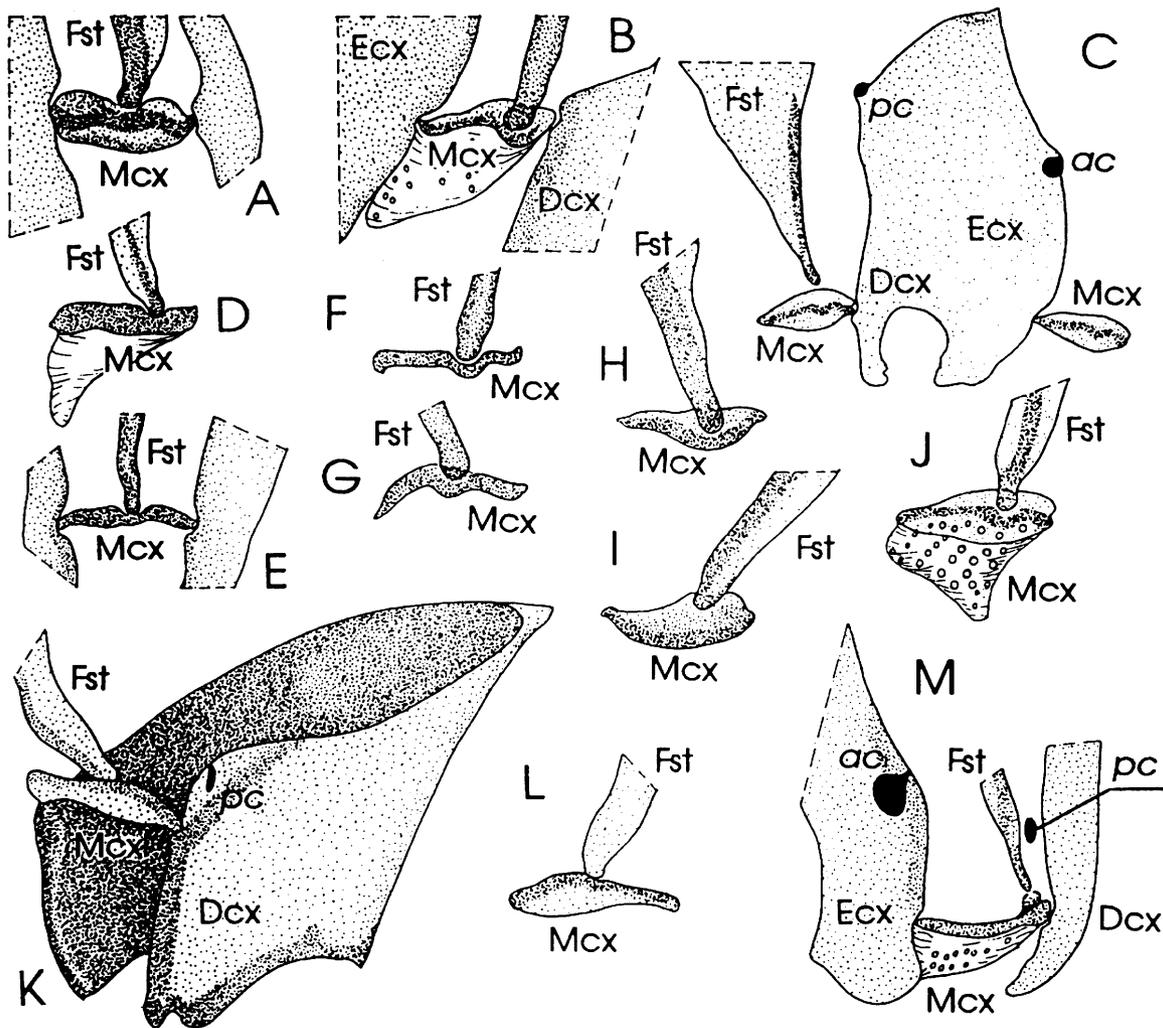


Fig. 5—Middle and hind coxae in Mycetophiloidea.

—A. *Asioditomyia japonica* (Ditomyidae), —B. *Keroplatus tipuloides* (Keroplataidae), middle mediocoxites; —C. *Sciaria thomae* (Sciaridae), flat involution of the coxa; —D. *Bolitophila rectangularata* (Bolitophilidae), —E. *Diadocidia valida* (Diadocidiidae), —F. *Macrocera stigmoides* (Macroceridae), middle mediocoxites;

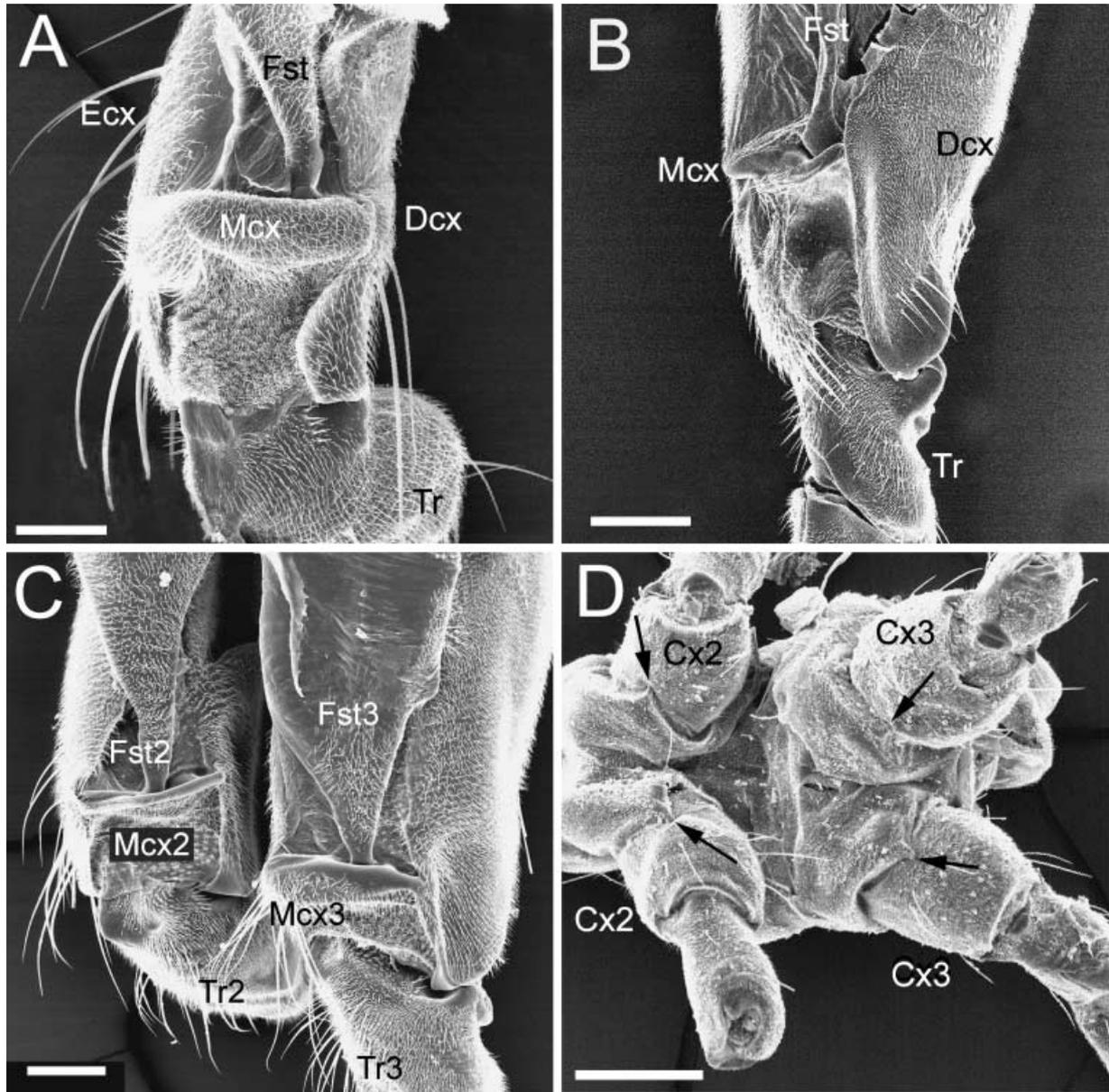
—G. same species, hind mediocoxite; —H. *Brachypeza armata*, —I. *Syntenna setigera* (Mycetophilidae), middle mediocoxites; —J. *Sc. thomae*, hind mediocoxite; —K. *Tetraxypus ater* (Cecidomyiidae-Lestremyinae), whole mount of the middle coxa; —L. same species, hind mediocoxite; —M. Cecidomyiinae g.sp., middle mediocoxite.

sclerite. Typically it looks like a flattened crescent or shuttle with a soft sack of desclerotized membrane below. This sack is partly or completely covered with bristles. Sometimes the mediocoxite is seen as a narrow sclerotized arm.

Articulations of the mediocoxite to the eucoxite area anteriorly and to the distocoxite area posteriorly are point hinges and presumably mobile ones. In most taxa, the socket for the coxo-sternal articulation is of central location, only in *Keroplatus* and the cecidomyin gnat (not identified) was the sternal suspension nearly of the marginal type (Figs 5B and 6B).

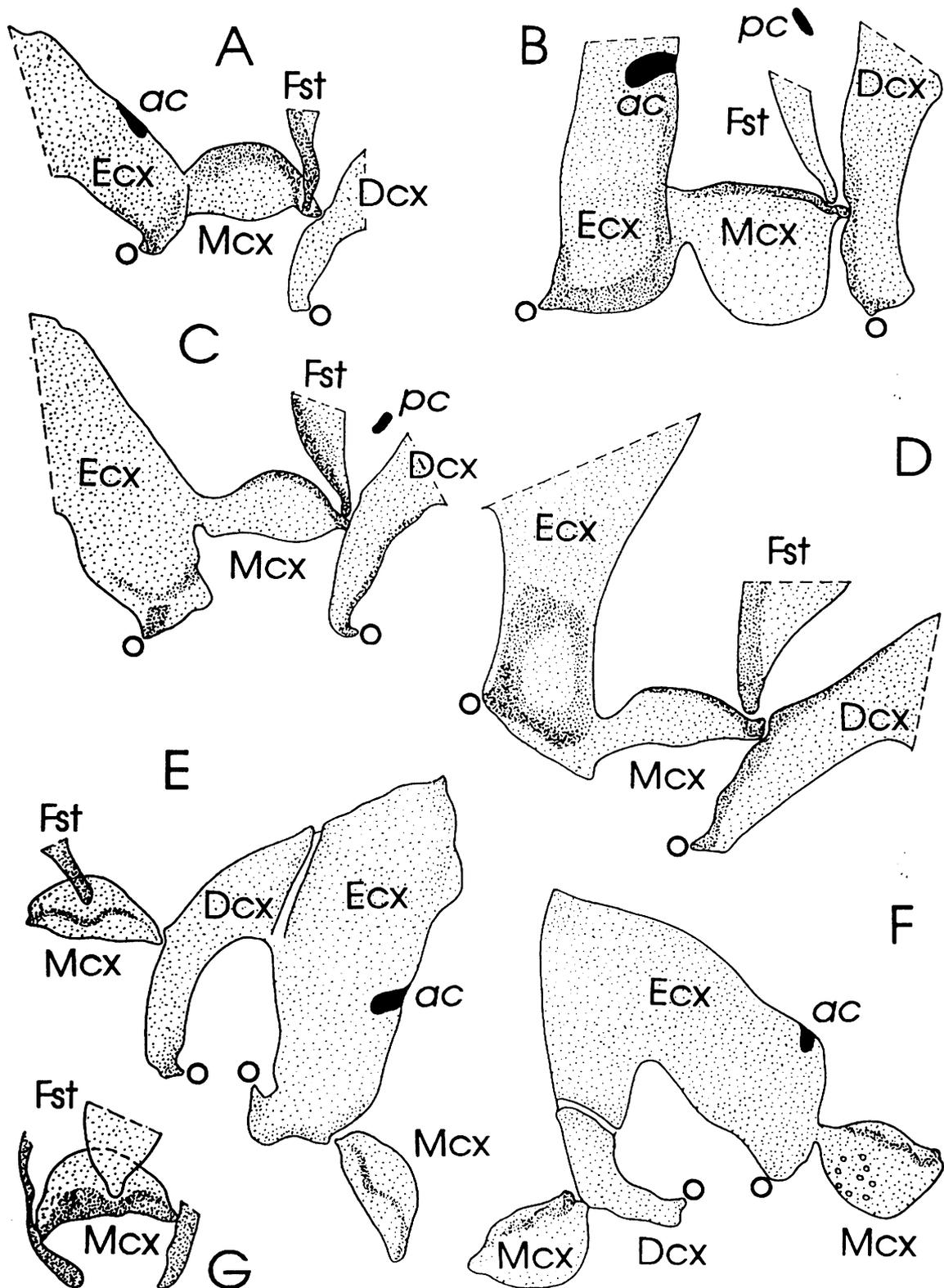
The most remarkable character common to all mycetophiloids is that the hind coxa possesses the small separate mediocoxite, similar to the middle coxa (Figs 5G,J,L and 6C). Podomers of the middle and hind legs slightly differ in proportions and details of chaetotaxy.

*Psychodoidea*. Unlike the previous suprafamily, the present one includes families with distinct constructions of their middle and hind coxae. The anisopodids *Sylvicola* spp. possess in their middle legs the fairly separated narrow mediocoxites



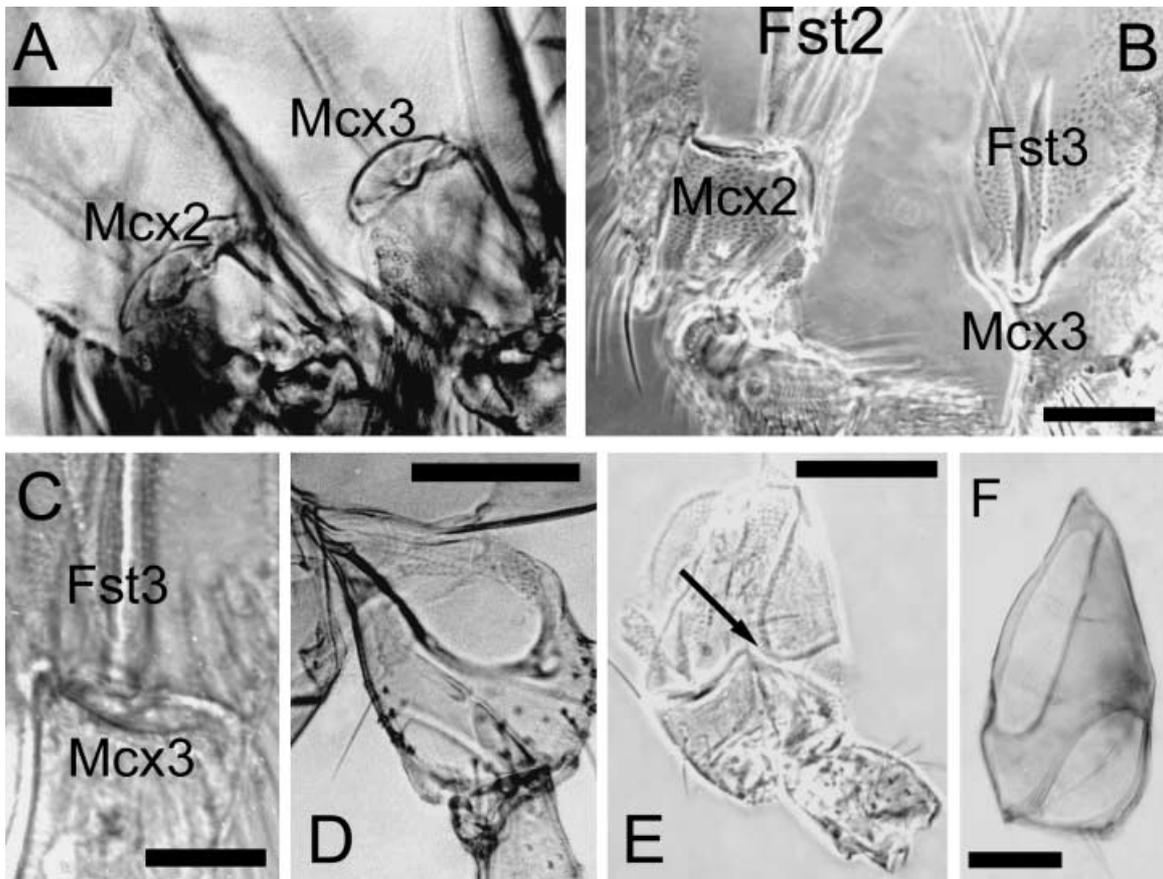
**Fig. 6**—Sternal articulations of the middle and hind coxae. —A. *Trichocera hiemalis* (Trichoceridae), middle coxa; —B. *Keroplatus tipuloides* (Keroplataidae), middle coxa; —C. *Sciaria*

*thomae* (Sciaridae) and —D. *Molophilus griseus* (Limoniidae), middle and hind coxae. Scale bars 50 µm in A, 100 µm in C, 200 µm in B and D.



**Fig. 7**—The middle coxa in Culicoidea and Chironomoidea. —A. *Dixa aestivalis* (Dixidae), —B. *Chaoborus flavicans* (Chaoboridae), —C. *Aedes behningi* (Culicidae), —D. *Chironomus plumosus* (Chironomidae), —E. *Odagmia ornata*

(Simuliidae), —F. *Mallochochelea inermis* (Ceratopogonidae), partial or complete flat involutions of the middle coxa; —G. *Atrichopogon minutus* (Ceratopogonidae), middle mediocoxite.



**Fig. 8**—Middle and hind coxae in nematocerans. —**A.** *Sergentomyia dentata* (Phlebotomidae), —**B.** *Mycetobia pallida* (Mycetobiidae) middle and hind coxae; —**C.** *Diadocidia valida* (Diadocidiidae), mediocoxite in hind coxa; —**D.** *Molophilus griseus* (Limoniidae),

compact middle coxa; —**E.** *Paracladura maori* (Trichoceridae), hind coxa, an arrow indicates the split of the coxa; —**F.** *Chironomus plumosus* (Chironomidae), compact hind coxa. Scale bars 50  $\mu\text{m}$  in A, 100  $\mu\text{m}$  in B–E, 200  $\mu\text{m}$  in F.

with marginal suspension (Fig. 4E). Similar coxites were revealed in *Mycetobia pallipes* (Fig. 4C) and in *Hyperoscelis veternosa* (the last species was inspected only superficially). Central suspension was also found in a scatopsid *Swammerdamella* sp. (Figs 3D and 4H). Hind coxae in the insects mentioned above were of compact construction, with the narrow mesal sector; the dorsal rim under the coxo-sternal articulation was sclerotized; the cuticle below it was transparent in small insects but was evidently fused with the rest of the sclerotized coxal ring (Fig. 8B).

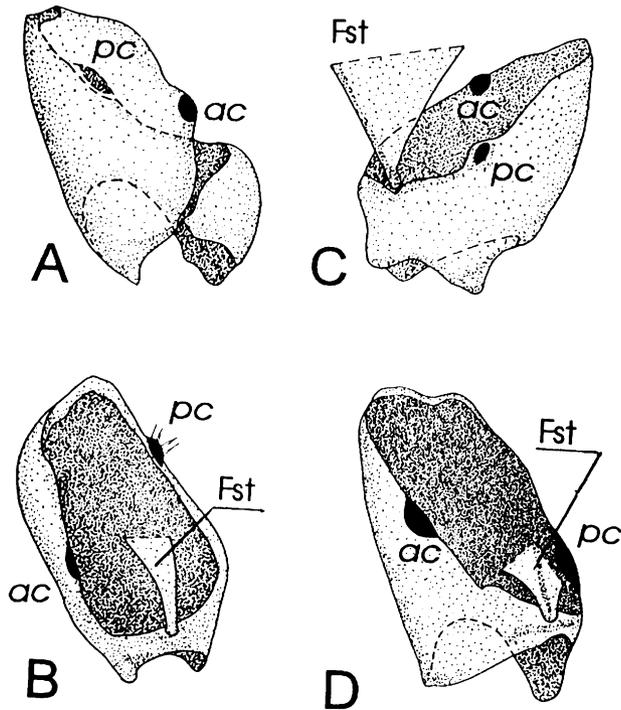
We pay attention to the hind coxa, because in the next two families, moth flies Psychodidae and Phlebotomidae, both middle and hind coxae are equipped with the fairly separated, crescentic flat mediocoxites, suspended centrally (Figs 4I–L and 8A). However, in a moth fly *Telmatoscopus* sp. we have not found distinct separation of the mediocoxite in the hind leg from the distocoxite area (Fig. 4M).

*Ptychopteroidea.* We have dissected several *Ptychoptera* species. The mediocoxite in the middle leg is a narrow separate

sclerite with central suspension to the furcosternal process (Fig. 4D), while the hind coxa is compact, narrow in the mesal sector (Fig. 9D).

*Culicoidea.* The mediocoxite in the middle leg of representatives of Dixidae, Chaoboridae, and Culicidae is large and flat. It is separated from the distocoxal area, but fused with the eucoxite (Figs 3E and 7A–C). The posterior corner of the mediocoxite has no inward process and the socket for the coxo-sternal articulation is situated marginally. The hind coxa is robust and compact (Fig. 9C).

*Chironomoidea.* The mediocoxite in the middle leg in the midge *Chironomus* is evidently similar to the type of the previous group (Fig. 7D). On the contrary, this sclerite in simuliids and ceratopogonids is crescentic, centrally suspended and fairly well separated from the rest of the coxa (Fig. 7E–G). The distocoxite is separated from the eucoxite by a long desclerotized suture (Fig. 3F). It is unclear whether this suture can be a hinge for rotation of the distocoxite relative



**Fig. 9**—Whole mounts of the hind coxa. —**A.** *Trichocera saltator* (Trichoceridae), —**B.** *Epiphragma ocellare* (Limoniidae), —**C.** *Aedes behningi* (Culicidae), —**D.** *Ptychoptera contaminata* (Ptychopteridae).

to the eucoxite. The mediocoxite in *Thaumalea* spp. (inspected only superficially) was narrow, marginally suspended and probably separated from the rest of the coxa. The hind coxa in the flies of this suprafamily was always compact (Fig. 8F).

The distribution of the characteristics mentioned in this chapter is summarized in Table 2.

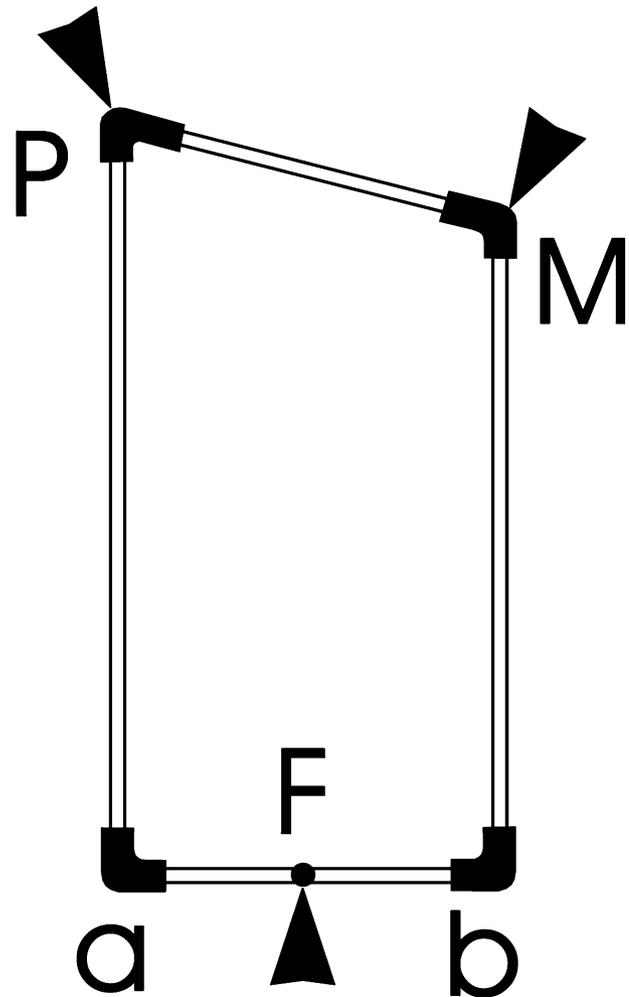
#### *Leg position in flight*

Line drawings of some representative nematocerans in tethered flight against an airstream were prepared from photographs. They are depicted on Fig. 12. These insects hold their legs straddled. The same posture in male *Bibio marci* was described earlier by Zeil (1983).

## Discussion

### *The prototype of the dipteran middle coxa*

The ancestral state of the integument of the coxa was without doubt a compact ring without radial splits, which is typical for legs of insects other than flies, and for the front and hind legs of flies (Fig. 13F). In the scorpion fly *Panorpa* (Mecoptera), the longitudinal suture divides the anterior part of the coxa from the meron, similarly in the middle and hind legs (Fig. 13A). This partition is retained in some lower Diptera



**Fig. 10**—A flexible frame modelling a multisclerite coxa. Straight segments are of glass rods, pieces of rubber tubes connecting segments are painted black. Arrowheads indicate points of elastic suspension by rubber loops, representing the coxo-pleural articulation at P, articulation to the meron at M, coxo-sternal articulation at F; a, b – articulations of the mediocoxite to the eucoxal and distocoxal areas of the coxa, respectively. Protraction force is applied to the segment Pa, retraction to Mb.

with the separated meron. After inclusion of the meron into the pleurite in some Nematocera and all higher Diptera (Crampton 1925), this partition is recognized as a fold between the thorax and the coxa. The anterior part of the middle or hind coxa in *Panorpa* has no radial splits.

We could not investigate representatives of Tanyderidae, Deuterophlebiidae, and Nymphomyidae. Besides them, we can state that, probably, none of the recent nematoceran groups retained a primary, compact middle coxa. It is difficult to suppose that some tribes among Limoniidae-Eriopterinae (Molophilini, Eriopterini) represent the ancestral state and do not display some secondary change.

**Table 2** Features of the middle and hind coxae in Nematocera

Family	Split of the middle coxa	Articulation to the sternum	Other characteristics
Tipulidae	Ecx//Mcx	marginal	
Limoniidae – Pediciinae	Mcx//Dcx	marginal	
Limoniidae – Hexatominae and Limoniinae	Ecx//Mcx//Dcx	marginal	
Limoniidae – Eriopterini, Molophilini	compact or splitted once	at the compact coxa	middle coxae compact as hind ones
Limoniidae – Gonomyini	Ecx//Mcx//Dcx	marginal	
Trichoceridae	Mcx//Dcx	marginal	hind coxae splitted once
Blepharoceridae	Mcx//Dcx	central	Mcx elongated
Axymyidae	Ecx//Mcx//Dcx	central	Mcx robust, strongly sclerotized
Bibionidae	Mcx//Dcx or Ecx//Mcx//Dcx	marginal	
Penthertriidae	Ecx//Mcx//Dcx	marginal	
Hesperinidae	Ecx//Mcx//Dcx	marginal	
Ditomyidae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Diadocidiinae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Keroplastidae	Ecx//Mcx//Dcx	marginal	hind coxa by the type of middle one
Macroceridae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Mycetophilidae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Bolitophilidae	Ecx//Mcx//Dcx	at posterior 1/3	hind coxa by the type of middle one
Sciaridae	Ecx//Mcx//Dcx	at posterior 1/3	hind coxa by the type of middle one
Cecidomyiidae – Lestremyinae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Cecidomyiidae – Cecidomyiinae	Ecx//Mcx//Dcx	marginal	hind coxa by the type of middle one
Psychodidae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Phlebotomidae	Ecx//Mcx//Dcx	central	hind coxa by the type of middle one
Hyperoscelidae	Ecx//Mcx//Dcx	marginal	
Anisopodidae	Ecx//Mcx//Dcx	marginal	
Mycetobiidae	Ecx//Mcx//Dcx	marginal	
Scatopsidae	Ecx//Mcx//Dcx	central	
Ptychopteridae	Ecx//Mcx//Dcx	central	
Dixidae	Mcx//Dcx	marginal	
Chaoboridae	Mcx//Dcx	marginal	
Culicidae	Mcx//Dcx	marginal	
Thaumaleidae	Ecx//Mcx//Dcx	marginal	
Simuliidae	Ecx//Mcx//Dcx	central	Dcx separated from Ecx by a suture
Ceratopogonidae	Ecx//Mcx//Dcx	central	Dcx separated from Ecx by a suture
Chironomidae	Mcx//Dcx	marginal	

We may only speculate on the possible shape of the compact prototype just before partition. The area of the mediocoxite lies between (i) the ridge connecting articulations with the furcosternal process and the posterior condyle on the trochanter; and (ii) the origin of the muscle, the anterior coxal depressor of the trochanter. This area is marked as well by origins of posterior muscles: the depressor and elevator of the trochanter. In a scorpion fly *Panorpa* (Mecoptera), this area is flattened.

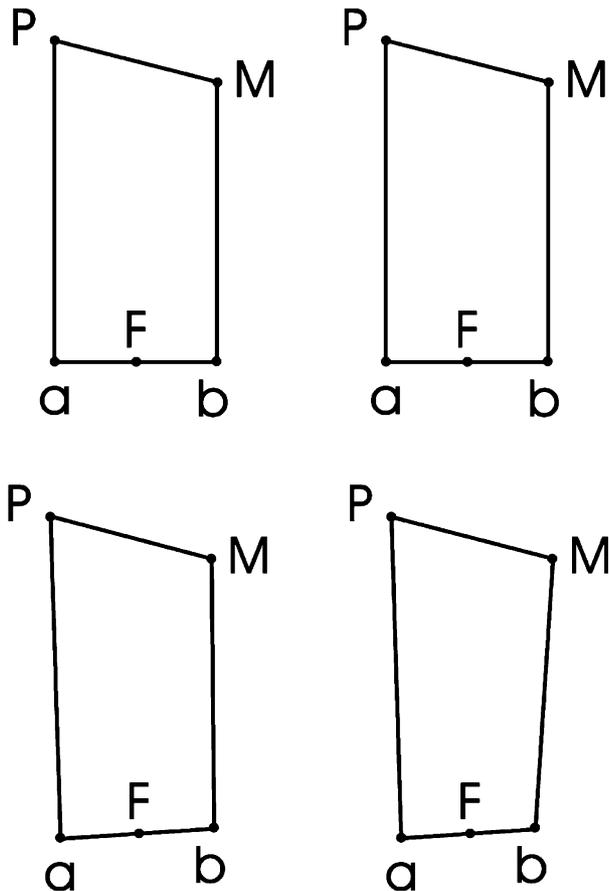
Steps to isolation of the mediocoxite were (i) protrusion of the wall of the mediocoxite area, the vault shape of the wall provided some additional firmness (Fig. 13B); (ii) invagination of the mentioned ridge, which displaced the coxo-sternal articulation inward and directed the subcoxal axis of rotation amidst two coxo-trochanteral articulations; and (iii) strangulation of the wall of the coxa between the medio- and eucoxite areas, providing local flexibility. After these transformations, the mediocoxite acquired its crescentic shape. Further

reinforcement of the coxo-sternal articulation was achieved by sclerotization of the dorsal rim of the mediocoxite.

The middle coxa of most nematocerans inspected by us has the separate mediocoxite, movably articulated to the rest of the coxa at two narrow, practically point hinges. In particular cases explained below the mediocoxite has a bridge-like junction either with the anterior area of the coxa (the eucoxite) or with the posterior area corresponding to the distocoxite in brachycerans. Hence the middle coxa has split radially twice or at least once (Fig. 13C,D). Is this split of any adaptive value and does it have any biomechanical function?

#### *Deformation and split of the coxa*

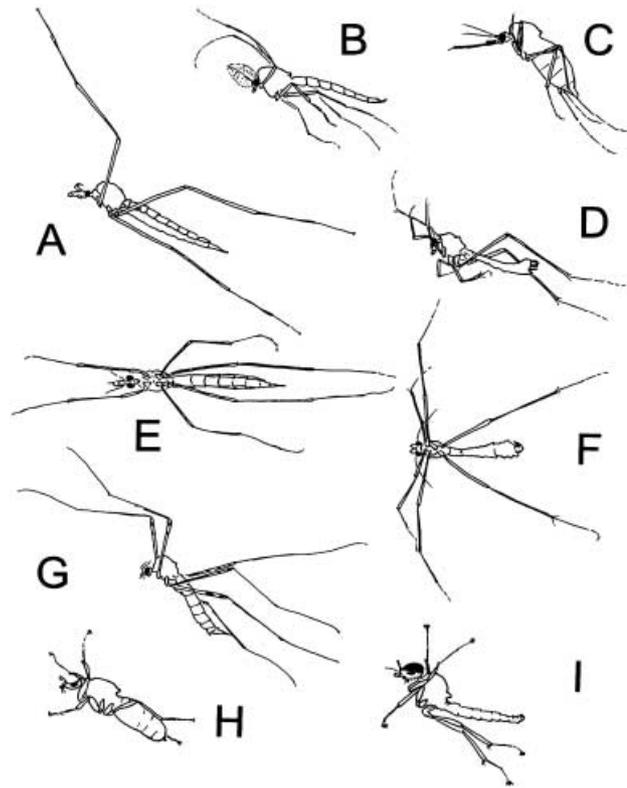
In a previous article (Frantsevich and Gladun 2002), we have suggested that after partial or complete junction of the meron with the mesopleurite in Diptera (Crampton 1925), the middle coxa was fixed to the thorax not only at the inferior end



**Fig. 11**—Stereopairs of conformations of the model frame. Top pair – flat conformation without any force applied. Bottom pair – distorted conformation upon retraction. Note noncomplanarity of parts Pma and Mba in B. The segment PM is fixed in space.

of the pleural ridge and at the furcosternal process, but along the expanded junction with the pleurite. Rotation of the coxa about the subcoxal axis defined by the former and second points is impossible without deformation because of the presence of the third fixed point or zone. Facts of deformation were confirmed by observations on the scorpion fly *Panorpa* and the crane fly *Tipula* (Frantsevich 2002). They are briefly reviewed below.

The middle coxa of the scorpion fly *Panorpa* (Mecoptera) possesses three coxo-thoracic articulations: to the pleurite, via the trochantine and at the furcosternal process. The feeble and flexible trochantine gives no support to the coxa, and the last has apparently only two pivots and might rotate about the axis connecting these pivots. However, the situation is more complicated: the coxo-pleural articulation is not of the condylar type. The junction with the pleurite runs for some distance along the dorsal side of the meron. The ability of the meron to rotate is thus severely restricted. And, indeed, during protraction-retraction, the front part of the middle coxa rotates about 70–100°, while the meron

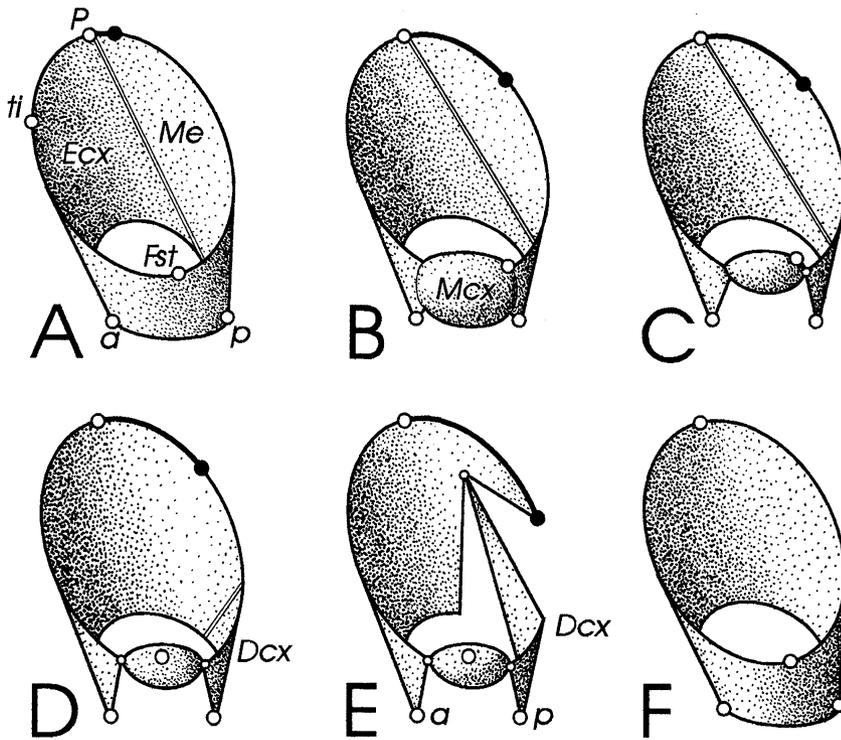


**Fig. 12**—Flight postures in Nematocerans. —A, E. *Tipula lunata*, —B. *Chironomus plumosus*, —C. *Aedes communis*, —D, F. *Ptychoptera contaminata*, —G. *Limonia nubeculosa*, —H, I. *Bibio marci*.

performs quite another motion – abduction-adduction of about only 10–12°. The deep fold between the meron and the front part of the coxa opens, or closes like a book. The tracing of transverse cross-sections of the coxa in its protracted and retracted conformation revealed alteration in the shape of a transection, i.e. deformation of the coxa.

The middle coxa of *Tipula* has a single radial split at the hinge between the eu- and mediocoxites. The junction between the meron and the coxa is more extended and less mobile than in the scorpion fly. Mickoleit (1962) noted that the front part of the coxa and the meron perform different movements during protraction-retraction. In addition, we have demonstrated that the mediocoxite rotated with respect to the eucoxite about approximately 1 radian. This motion might have been accompanied with deformation in the medio-posterior part of the coxa, not traced because of lack of reliable position landmarks.

Deformation is inevitable if the rotating body is fastened at three fixed points. This hypothesis was tested with the aid of a simple model prepared from hard glass rods and pieces of a rubber pipe. The model presented on Fig. 10 is a trapezium-like frame of four rods connected with short pieces of the pipe. The connections are flexible. Four rods represent four sclerites: the eucoxite (between points P, a), the mediocoxite



**Fig. 13**—Types of coxal splitting in Mecoptera and Diptera. View from the medial side. —**A.** compact coxa with the meron (e.g. middle and hind coxae in *Panorpa*); —**B.** swelling of the mediocoxite area in the narrow part of the coxa (hypothetical); —**C.** one-sided separation of the mediocoxite (e.g. Trichoceride, Culicoidea); —**D.** double-sided separation of the mediocoxite and separation of the distocoxite area, shift of the sternal articulation to the central position in the mediocoxite (e.g. Simuliidae, Asilidae; both middle and hind legs in Mycetophiloidea and Psychodoidea, except of separation of the distocoxite area); —**E.** separation of the mobile distocoxite (e.g. Tabanoidea, Cyclorrhapha); —**F.** return to the compact coxa (e.g. hind legs in most of flies, both middle and hindlegs in Eriopterini, Molophilini, Acroceridae). Circles mark articulation points, small circles – intracoxal joints; double lines mark sutures; black circle symbolizes second point of fixation of the coxa to the epimeron or meropleurite. Abbreviations: a – anterior coxo-trochanteral joint, Dcx – distocoxite, Ecx – eucoxite, Fst – articulation to the furcosternal process, Mcx – mediocoxite, Me – meron, P – articulation to the pleural ridge, p – posterior coxo-trochanteral joint, ti – articulation via the trochantine.

(ab), the meron (PM), and the distocoxite area (Mb). The frame is suspended inside a stage by rubber loops at three points: P is the coxo-pleural articulation, M is the mero-pleural one and F, amidst the mediocoxite, is the coxo-sternal articulation. Now let force to be applied to the segment Pa (protraction) or to Mb (retraction) perpendicularly to the plane of the frame. If the loop at M is set loose, the frame rotates as a solid body. But if M is elastically fixed as well, then the frame becomes distorted about the diagonal Ma.

Measurements on a model and further 3D computer modelling showed that despite considerable flexion by 30° about the named diagonal, other elements of the model suffered only small distortions: angles between segments altered by 2–3°, and diagonals Ma and Pb changed their length by 1–2%. Flat and distorted configurations of the frame are illustrated on stereopairs, Fig. 11. Movable articulations between coxites absorb deformations exerted by rotation of the ‘wrongly’ mounted coxa. As a result, sclerotized areas supporting muscles do not suffer deformation.

The model illustrates the advantage of the central coxo-sternal suspension at the mid-point F comparing to marginal suspension at b: radii of a capstan in the case of central suspension are equal, and moments of protractor and retractor muscles are fairly balanced. This balance is advantageous in the situation when the coxa is operated only by a feeble pair of muscles: the sternal protractor and retractor, the situation inherent in Brachycera (Wisser and Nachtigall 1984). *Panorpa*, representing the ancestral stem for dipterans, enjoys a

rich set of subcoxal muscles: the coxo-basalar and sternal protractors, tergo-coxal, coxo-subalar and two sternal retractors or adductors (Hasken 1939). The powerful tergo-coxal retractor in nematocerans switches to its alternative function of wing elevation as the second dorso-ventral muscle; the coxo-basalar protractor is lost. Retention of the powerful coxo-subalar adductor in nematocerans (Smart 1957) probably permits retraction of the coxa despite the short capstan arm even in the case of the marginal suspension, but the general tendency in the evolution of the mediocoxite is the displacement of the coxo-sternal suspension to the middle of the mediocoxite. This tendency might be illustrated by the suprafamily Mycetophiloidea with various grades of suspension sites, from almost marginal in *Keroplatus* (Fig. 5B) or in a cecidomyin (Fig. 5M) to fairly central in *Diadocidia* (Fig. 5E) via intermediate positions in other midges.

*Number of splits*

Now we trace the site of the first split at some basal level of fly evolution.

Many families of Nematocera possess the well-separated mediocoxite with movable articulations to the eucoxite and the distocoxite area, i.e. the coxa is split twice in representatives of suprafamilies Axymyioidea, Mycetophiloidea, Psychodoidea, Ptychopteroidea and in representatives of some families among Tipuloidea (limoniids Hexatomiinae, Limoniinae, Gonomyini in Eriopterinae), Bibionoidea

(Pentethriidae, Hesperinidae, *Dilophus* in Bibionidae), Chironomoidea (Simuliidae, Ceratopogonidae, probably Thaumaleidae).

We regard a single radial partition of the coxa as a more primitive state, preceding the double partition. Possible sites of the single partition are ahead or behind the crescentic mediocoxite area. The first case is implemented in tipulids s.str.; the second one in trichocerids and limoniids Pediciinae (Tipuloidea), blepharocerids (Blepharoceraomorpha), *Biblio* in Bibionidae (Bibionoidea), and representatives of three families of Culicoidea, *Chironomus* in Chironomoidea.

Thus, some groups of Nematocera are heterogenous with respect to the grade of separation of the mediocoxite. The fact implies, in our opinion, on convergent, parallel origin of separation in different branches of Nematocera, due to adaptive biomechanical value of the movable mediocoxite.

The appearance of the third split between the eucoxite and distocoxite in the form of a desclerotized straight suture in the black-flies (Simuliidae, Fig. 13D) and biting midges (Ceratopogonidae) is peculiar. This feature is combined with the centrally suspended mediocoxite and the coxa separated from the pleurite. Superficial similarity of their middle coxae to that of asiloids and empedoids indicates, once more, the convergent origin of a successful biomechanical solution.

Intracoxal mobility appeared after the third split and separation of the movable distocoxite at the level of Tabanoidea in the lineage of higher flies (Fig. 13E). This split enabled flies to attain the streamlined leg position in flight, the ability lacking in nematocerans (Fig. 12).

#### Taxonomic considerations

We avoid reconciliation of the existing phyletic system of flies, basing on a new set of characters of highly adaptive values (e.g. neural or biomechanical). Nevertheless, we intend to indicate some features in the construction of the coxae which do not fit well to recent views on the lineage of flies.

Tipuloidea with the composition listed in Table 1 are a monophyletic group, in the opinion of many dipterologists (reviewed by Oosterbroek and Courtney 1995), except Wood and Borkent (1989). Subdivisions of this clade obtain various ranks, from subfamilies (–inae) to infraorders (–omorpha), which depends on philosophical position and taste of any author; but commonly Trichoceridae and Tipulidae s.l. are regarded as sister groups, while Tipulidae s.l. include the ancient family Limoniidae and two younger ones, Tipulidae s.str. and Cylindrotomidae.

This natural group illustrates various ways and grades of split, as if ‘testing’ various solutions for better fitness. The winter flies Trichoceridae manifest construction of the middle coxa closer to limoniids than to Tipulidae s.str. Hind coxae of trichocerids have the single radial split, the unique feature among flies. Middle coxae of Tipulidae and Limoniidae (including Pediciinae) are of different construction. Sary (1992) put his Pediciidae closer to Tipulidae than to

Limoniidae. Limoniidae and Tipulidae have different cytological characters (White 1949). The state within the Eriopterinae will be discussed below.

Among flies where the middle coxa is split once, one finds Blepharoceridae, Culicoidea, Chironomidae and even *Biblio* with the Trichoceridae-Limoniidae style of split, but not Tipulidae themselves. With respect to leg construction, Trichoceridae and Limoniidae might be closer to the common stem of recent Diptera, than Tipulidae s.str.

On the other hand, the middle coxa of midges, Chironomidae, does not resemble those in the black flies, Simuliidae and the biting midges, Ceratopogonidae, where the most remarkable feature is the separation of the distocoxite. Biting midges are closer to midges and further from black flies in all recent propositions (Rohdendorf 1964; Hennig 1973; Wood and Borkent 1989; Oosterbroek and Courtney 1995). However, Crampton (1925) emphasized the resemblance between Simuliidae and Ceratopogonidae.

Mycetophiloidae comprise a compact group with respect to construction of their middle coxa and, moreover, to repetition of this construction in their hind coxae. This strange feature is shared, quite unexpectedly, with Psychodidae and Phlebotomidae. The position of the Psychodidae in the system of Diptera was always uncertain: they were related to Ptychopteridae (Hennig 1973; Rohdendorf 1964), Culicomorpha (Hackman and Väisänen 1982), Blepharoceridae + Culicomorpha (Courtney 1991; Michelsen 1996), Ptychopteromorpha and Culicomorpha (Sinclair 1992), Tanyderomorpha (Stark *et al.* 1999; Krzeminski and Evenhuis 2000), Anisopodidae + Scatopsidae and Trichoceridae (Wood and Borkent 1989), Anisopodidae and Tipulomorpha (Oosterbroek and Courtney 1995), derived as a separate lineage to all non-Tipuloid flies (Crampton 1925) or left in uncertain state (Friedrich and Tautz 1997). The morphological peculiarity quoted above certainly divides Psychodidae (including Phlebotomidae) from Scatopsidae, Anisopodidae, and Mycetobiidae.

We suppose that the noted similarity between psychodids and mycetophiloids, as well as the construction of the middle coxa by the type of the coxa of the hind leg in some Eriopterinae and Acroceridae are cases of homeosis and probably of homeotic mutations which might have occurred independently in different clades.

#### Leg homeosis as a taxonomic character

Pterothoracic segments of a scorpion fly (Mecoptera) are homonomous, with similar wings and legs. Differentiation of pterothoracic segments, wings and halteres in Diptera was accompanied by profound differentiation of the legs. The middle and hind legs in *Drosophila*, as well as in other flies, differ not only in proportions and subtle details of chaetotaxy (Rozowski and Akam 2002; Stern 2003), but in fundamental mechanics of leg suspension to the thorax, intracoxal motility, and multisclerite construction of the middle coxa. The

last feature, multisclerite construction, is observed almost in all lower Diptera in a primitive form of the once- or twice-split coxa and probably has appeared at early stages of the evolution of the order. In turn, hind legs, also in most of flies, underwent their way to a simplified, compact and versatile structure with a pair of condylar articulations with the metathorax.

Thus we discern two designs which specify and identify middle and hind legs in flies. Astonishingly, there exist some well-separated taxa (from suprafamilies to tribes) in which middle and hind legs are both constructed either by the middle leg plan or by the hind leg plan. No intermediate stages in the related taxa of the same rank were observed. This exchange of leg plans is a manifestation of homeosis, expression of the complex of morphological characters, typical for one position in the series of segments, at another position in the same series (see definition in Jacobs 1990).

The most striking homeotic mutation, found in *Drosophila*, was *bithorax* which led to an abnormal fly with the third thoracic segment built like the second one, with wings or vestigial wings instead of halteres (Goldschmidt 1952; Lewis 1998). This great structural modification emerged in a saltational way. The wild type allele of the mentioned mutant gene is the *Ultrabithorax* (*Ubx*) which controls normal development of the third thoracic segment.

*Ubx* is representative of the important set of homeotic genes (*Hox*) that control body demarcation down the antero-posterior axis in Bilateria and specify segment identity in arthropods. *Hox* genes are an important intermediate link between the superior demarcators of the body and local gene flows which build certain morphological structures (Budd 1999). *Hox* genes are active during the whole period of individual development. They are differently expressed down the antero-posterior body axis and change their activity in time. The specific ratio between activities of different *Hox* genes determines the segment identity. In particular, *Ubx* completely represses leg formation in the first abdominal segment, supports normal leg formation in the metathorax during the whole time of development, and is shortly expressed only at the early stage of embryogenesis in the mesothorax (Castelli-Gair 1998).

Activity of the homeotic genes is finely regulated. Over 98% of the nucleotide chain of the *Ubx* gene consists of many (dozens) modules with individual affinity to various regulating proteins which repress or release synthetic activity of the same structural part of the chain, rest 1.4% (Akam 1998). Their effect depends on the cell identity and cell location (Castelli-Gair 1998; Stern 2003).

*Hox* genes may have contributed to the formation of high rank taxa. They control tagmatization in arthropods by different ways in myriapods, crustaceans, chelicerates, and insects (Averof and Akam 1995; Popadic *et al.* 1998). In insects, they were responsible as well for the repression of development of wing-like appendages on any trunk segment except of two thoracic ones and thus participated in formation of recent Pterygota (Carroll 1995; Carroll *et al.* 1995;

Stark *et al.* 1999). They control diversification of mouthparts, maxillipeds, legs and prolegs, wings and halteres and contribute to diversification at the ordinal level in crustaceans, centipedes, and insects (Whiting and Wheeler 1994; Averof and Patel 1997; Popadic *et al.* 1998).

The obvious importance of *Hox* genes for individual development and the general character of their mutational effects gave rise to the hypothesis of their selector function, channeling development down one of several alternative routes. However, dramatical phenotypical effects without clear adaptive value create doubts over the creative role of saltational homeotic mutations in evolution. For example, a crippled *bithorax* fly has no chance to survive in the natural environment. Its second wing pair is devoid of appropriate muscles, because the ectodermal and mesodermal tissues are controlled by *Hox* genes in different ways (Roy *et al.* 1997). Even though mobile, the second wing pair would not fit to the existing flight motor selected for aerodynamics produced by a single wing pair (Budd 1999).

Recent careful reviews propose the inverse order of evolutionary events: firstly many mutations with small effects at the local level have been selected, and then the general control over the set of local morphogenetic mechanisms has been taken over by the homeotic gene by means of mutations in regulating modules (Akam 1998; Budd 1999). But where is a quantitative margin between 'small' and 'large' mutations? Stark *et al.* (1999) demonstrated striking phenotypical parallelisms between local mutations of wing venation in *Drosophila* with known differences in venation between various fly taxa.

We found out that the *Drosophila* mutant *bithorax* (provided by R. Strauss) had the wild-type middle legs in its third thoracic segment (Frantsevich and Gladun 2002; Fig. 8F). The middle-leg plan is readily recognized by the multisclerite construction of the middle coxa and presence of the midcoxal prong in addition to known shape differences and disposition of bristles (Rozowski and Akam 2002; Stern 2003). Hence, leg identity in the metathorax is also under control by the *Ubx* gene.

Is it possible that the *bithorax* type of the third leg pair in Mycetophiloidea and Psychodidae (incl. Phlebotomidae) was a result of saltational mutation at the *Hox* level or any intermediate stage instead of selection of many small mutations shaping the leg? It is worth mentioning that extreme development of the metathorax in moth flies, relatively the broadest one among nematocerans (the feature resembling the *bithorax Drosophila*) has been noted long ago (Young 1921; Crampton 1925). A rather broad metanotum was depicted in the mycetophiloid *Sciaria ochrolabis* (Young 1921; Fig. 13). We see no biomechanical reason for an allometric change in the notal region when shaping legs in particular. However, these '*bithorax*' families of flies possess normal halteres in their metathorax.

Another homeotic mutation in *Drosophila* leads to the development of a haltere at the place of the wing (*contrabithorax*).

We see its analogue in the compact coxa present in the middle leg (by the plan of the hind leg, Fig. 13F) in Limoniidae-Eriopterini and Molophilini. Similar homeosis has been reported by us for *Acrocer* (Frantsevich and Gladun 2002) and confirmed for other genera, representing three subfamilies of Acroceridae (provided by E. Narchuk). Even the orientation of the leg mounting into the thorax is the same in the middle and hind legs: the coxo-trochanteral axes orientate both leg pairs backward, while in other Brachycera this axis in the middle leg is directed so that the middle leg is orientated forward. Again, quoted ‘*contrabithorax*’ taxa possess normal wings on the mesothorax.

Certainly, documented homeotic pattern does not prove homeotic mutation (Budd 1999). It is a good model for further genetic and immunological study. However, we suppose that homeotic leg exchange in the lineage some taxa might be a real saltational mutation. It has not been eliminated by selection because it substituted one structure with another efficient one. Such a mutation might appear elsewhere and does not bear witness in favour of common lineage of fungus gnats with moth flies or, even more unlikely, of eriopterine crane-flies with nemestrinoid acrocerids.

Homeosis as a saltational change of the body plan is not a rare event in nature. Since the discovery of the first *bithorax* mutant in 1915, many alleles of the *bithorax* complex and other *Hox* genes were observed or obtained in laboratory populations of *Drosophila melanogaster* (Lewis 1998). Usually, they would be eliminated in natural populations. But the age of the ‘homeotic’ fly taxa has to be taken into account.

The Limoniids were reported from the Upper Triassic period, while the Eriopterinae were first found to have been present only in the Cretaceous period. The moth flies Psychodidae are known from the Lower Jurassic age, the Acroceridae from the Upper Jurassic period, the complex of Mycetophyloid families – from the Lower Cretaceous (Krzeminski and Evenhuis 2000) age. However, Kovalev (1983) noted the presence of Mycetophyloids in the Lower or Middle Jurassic period. Anyhow, the time span of appearance of the mentioned taxa lasted about 100 MA, starting 200 MA ago. We assume that the emergence of a ‘hopeful monster’ on the way of separation from certain taxa is really a rare event, occurring once per 25 MA. Nothing strange, that middle and hind legs differ in ‘homeotic’ taxa, not only due to the positioning effect of gene expression. These taxa had at least 100 MA to adjust their structures for better performance.

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