



# Neodiptera: New insights into the adult morphology and higher level phylogeny of Diptera (Insecta)

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This paper outlines several aspects of the skeleto-muscular organization of the adult prothorax and cervix pertaining to the ground pattern of Diptera, which in turn leads to the characterization of Neodiptera, a higher level dipterous taxon which includes Brachycera and bibionomorph Nematocera (*sensu* Hennig). The monophyly of Neodiptera is firmly supported by four skeleto-muscular modifications of the pronoto-cervical region. The bibionomorph Nematocera are shown to be paraphyletic in terms of Brachycera. On more preliminary evidence it is argued that the fundamental dichotomy of the extant Diptera lies between a 'polyneurax' clade which includes Trichoceridae, Tipuloidea, Tanyderidae, and Ptychopteridae and an 'oligoneuran' clade which includes all the remaining groups. Preliminary evidence for a sister group relationship between Blephariceroidea and Culicomorpha is also provided. The possible adaptational significance of the cervical specializations in Neodiptera is discussed.

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ADDITIONAL KEY WORDS: — prothorax – cervix – skeleton – musculature – adaptation.

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## INTRODUCTION

The monophyly of Diptera is generally accepted and exceedingly well supported (e.g. Hennig, 1973; Wood & Borkent, 1989), but there is still no consensus as to the

resolution of this major insect order in higher level monophyletic units. Indeed, there are several very species-rich dipterous taxa which represent well corroborated monophyla: Brachycera (e.g. Hennig, 1973; Woodley, 1989; Sinclair, 1992; Sinclair *et al.*, 1994); Cyclorrhapha (e.g. Griffiths, 1972; Hennig, 1973, 1976; McAlpine, 1989, as Muscomorpha); and Schizophora (e.g. Griffiths, 1972; McAlpine, 1989), but these were actually all recognized long before the application of phylogenetics in the classification of Diptera. The monophyly of Eremoneura, a group combining empidoid and cyclorrhaphous Brachycera (Griffiths, 1972; Hennig, 1976; Cumming & Sinclair, 1990; Sinclair, 1992; Wiegmann *et al.*, 1993) has also received substantial support. The monophyly of Culicomorpha (e.g. Hennig, 1973; Wood & Borkent, 1989) has been widely acknowledged, yet it has been suggested only recently (Courtney, 1994; Oosterbroek & Courtney, 1994) that this may require inclusion of the aberrant family Nymphomyiidae.

The purpose of this paper is (1) to establish a new fundamental taxon of Diptera, the Neodiptera, based on several unique specializations in the neck region of the adults and (2) to discuss aspects of the higher level phylogeny of Diptera in the light of this finding. The essentials of the paper, presented orally at the Third International Congress of Dipterology, Guelph, August 1994, were briefly summarized by Michelsen (1994).

Neodiptera represent a very extensive taxon which probably contains more than 75% of all extant species of Diptera. Included are Brachycera plus an assemblage of nematocerous taxa which equals Bibionomorpha *s.l.* (*sensu* Hennig, 1954, 1973): Scatopsoidea, Anisopodidae, Perissomatidae, Axymyiidae, Pachyneuridae, Scarioidea and Bibionoidea. It follows that the only extant dipterous taxa not to be included in Neodiptera are Trichoceridae, Tipuloidea, Tanyderidae, Ptychopteridae, Psychodidae, Blephariceroidea and Culicomorpha (incl. Nymphomyiidae).

The monophyly of Bibionomorpha *s.l.* rests on very tenuous evidence, perhaps only on the reduction of vein C along the posterior margin of the wing and the absence of mandibles and associated muscles in the adults. Evidence presented in the following strongly suggests that Bibionomorpha *s.l.* are paraphyletic in terms of Brachycera. Wood & Borkent (1989) went even further by considering Bibionomorpha *s.l.* as polyphyletic in terms of the remaining nematocerous Diptera. This idea, however, is irreconcilable with the monophyly of Neodiptera.

Hennig (1973) accentuated the paraphyly of Nematocera and the monophyly of Neodiptera in the present sense by suggesting that a sister group relationship might exist between Bibionomorpha *s.l.* and Brachycera. However, the modifications of the mesothoracic laterotergite and postphragma, which he tentatively proposed in support of this idea, remain ambiguous or unsubstantiated (e.g. Griffiths, 1994). Amorim (1992) adopted Hennig's view and added the shortened vein C as a possibly autapomorphy for Bibionomorpha *s.l.* + Brachycera. However, vein C is an ambient vein in virtually all groups of 'lower' Brachycera apart from Stratiomyidae and Xylomyidae. This strongly suggests that the ambient state does belong to the ground pattern of Brachycera. In conclusion, the monophyly of Bibionomorpha *s.l.* + Brachycera (= Neodiptera) has previously not been convincingly demonstrated, or for that sake widely acknowledged.

#### METHODS AND MATERIAL

The data presented here in support of the monophyly of Neodiptera were

TABLE 1. Overview of terminology for selected set of primary muscles associated with the prothorax and cervix of adult Antliophora

Present		Matsuda, 1970
M.1	episterno (I)-dorsocervicalis	<i>op-p 1, 2</i>
M.2	laterocervico-postoccipitalis	<i>op-cv 1, 2, 3</i>
M.3	antecosta (II)-laterocervicalis	<i>t-s(cv) 9</i>
M.4	noto (I)-laterocervicalis	<i>t-cv 1, 2, 3</i>
M.5	dorsocervico-laterocervicalis	<i>t-cv 1, 2, 3</i>
M.6	furcasterno (I)-laterocervicalis	<i>cv-s 1</i>
M.7	coxo (I)-laterocervicalis cruciatus	<i>cv-cx1(X)</i>
M.8	sterno (I)-praesternalis	<i>s?</i>
M.9	noto (I)-pleuralis (I) medialis	<i>t-p?</i>
M.10	noto (I)-pleuralis (I) lateralis	<i>t-p?</i>
M.11	episterno (I)-coxalis (I)	<i>p-cx 4, 5</i>

extracted from an ongoing, large-scale comparative study of the head, cervix and prothorax of adult Diptera with special emphasis on skeleto-muscular anatomy. Specimens used for examination of musculature were fixed in Pampel's fluid (cf. Oldroyd, 1958) and then transferred to 70% ethyl alcohol. A smaller amount of material was fixed in alcohol only. The relevant body parts were isolated by transverse cuts, then further partitioned along a sagittal or horizontal plane. Orange G diluted in alcohol was used for differential staining of muscles. Specimens were dissected under glycerol and examined using a Leitz Greenough stereomicroscope with up to 100 × magnification. Drawings were made using an ocular grid.

A list of the specimens examined for the present study is given in Appendix 1. Tables 1 and 2 review terminology and homology of muscles discussed in the text.

TABLE 2. Homologous muscles described by various authors in adult Mecoptera (Hasken, 1939 *Panorpa*; Mickoleit, 1968: *Bittacus*, *Harporbittacus*) and Diptera (Mickoleit, 1962: *Tipula*; Bonhag 1949: *Tabanus*; Ulrich, 1971, 1984: Empidoidea; Valdez & Prado, 1990: *Ceratitis*)

Present Nos.	Hasken 1939	1968	Mickoleit 1962	Bonhag 1949	Ulrich 1971, 1984	Valdez & Prado 1990
M.1	0 ism <sub>1</sub>	11	3	4	—	32
M.2	0 dvm <sub>1,2</sub>	3	2	3	4	31
M.3	0 ism <sub>3</sub>	—	—	—	—	—
M.4	0 ism <sub>2</sub>	1	—	8	5	38
M.4ac	—	—	—	9	7	40
M.5	—	2	—	—	—	—
M.6	0 ism <sub>4</sub>	4	5	6, 7	9	41
M.7	0 ism <sub>5</sub>	—	—	—	—	—
M.8	—	—	17	—	10	44
M.9	I pm <sub>4</sub>	12	16	—	—	—
M.10	I pm <sub>3</sub>	13	—	—	—	—
M.10ac	—	—	—	5	6	39
M.11	I pm <sub>1</sub>	14	9	16	14	79
M.11ac	—	—	—	17	11	42, 43

## RESULTS

*Some fundamentals of the prothorax and cervix of adult Diptera*

This section provides some necessary background for the proper assessment of the skeleto-muscular features constitutive for Neodiptera. It details a selection of morphological traits pertaining to the prothorax and cervix of adult Diptera.

*The pronoto-propleural consolidation*

In Mecoptera (Fig. 1), as in the ground pattern of Endopterygota, the pronotum laterally overhangs the propleuron and is completely separated from the latter by a zone of membranous cuticle, the noto-pleural cleft. Further, the posterolateral angle of the pronotum extends posteriorly and articulates with episternum II beneath the anterior spiracle. A transnotal suture, which divides the pronotum in anterior and posterior parts, is also developed. This suture arches backward laterally and ends at the apex of the posterolateral pronotal angle. Both the subspiracular articulation and the transnotal suture are traits which should possibly be considered plesiomorphic for Antliophora (Mecoptera + Siphonaptera + Diptera), because an identical configuration is found among tenthredinids and other 'lower' Hymenoptera (unpubl.obs.). Accordingly, I challenge Schlein's (1980) assertion that the subspiracular articulation is synapomorphic for Mecoptera and Siphonaptera.

The prothorax of Diptera (Fig. 4) also shows a strong development of the transnotal suture, but otherwise exhibits a suite of unique specializations of which the following are of present concern: (1) abandonment of the subspiracular articulation between pronotum and mesopleuron; (2) more or less extensive fusion of pronotum and propleuron. The noto-pleural fusion has been accomplished by perfect adjustment of the transnotal and pleural sutures (these may only be distinguished by meeting at a more or less discrete angle) accompanied by extensive fusion of the internal crests arising from these sutures. At the level of the transnotal suture the pronotum extends laterally to the top of the fusion point between the profurcasternal arm and the propleural apophysis.

In consequence of the noto-pleural consolidation, the noto-pleural cleft of Diptera is incomplete, at the best maintained between the anterior notum I and episternum I. This consolidation has also been accompanied by innovations in the locomotory musculature of the fore leg: Pleural abductor of coxa I (Fig. 22: M. 11) and pleural depressor of trochanter I have both gained increased length and strength by moving their origins dorsally, onto the lateral extension of the pronotum.

*The propleura*

Episternum I is in the ground pattern of Endopterygota divided by a paracoxal suture or cleft (Matsuda, 1970) in a dorsal anepisternum and ventral katepisternum. It is the katepisternum which supports the trochantin, a precoxal sclerite articulated at the anterior margin of coxa I. The trochantinal articulation is not retained in any Antliophora. Also, there is no obvious division of the propleural episternum in an- and katepisternal parts. An unmusculated sclerite which in Mecoptera (incl. Nannochoristidae) lies isolated in the soft cuticle in front of coxa I may represent trochantin I (Figs 1, 3). Siphonaptera and all nematoceros Diptera apparently lack this structure, which suggests that the 'trochantin' of some eremoneuran Brachycera, cf. Speight (1969, 1987) and Ulrich (1984), is a secondary development.

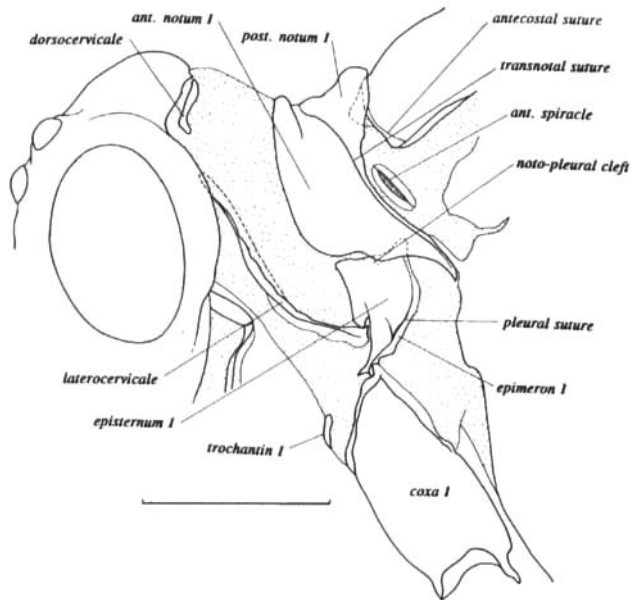


Figure 1. *Panorpa communis*, ♀: Skeletal morphology of the cervix and prothorax, left lateral view. Scale bar 1.0 mm.

Epimeron I, separated from the larger episternum I by the pleural suture, is much reduced in Mecoptera (Fig. 1) other than Nannochoristidae (pers. obs.). In the



Figure 2. *Panorpa communis*, ♀: Noto-pleural and some laterocervical musculature of the cervix and prothorax, left lateral view. Scale bar 1.0 mm.

ground pattern of Diptera (Figs 4-6, 11, 17), epimeron I is a shallow sclerite which reaches the mesopleuron by a pointed extension.

#### *The noto-pleural musculature*

A number of noto-pleural muscles, presumably more than three in the ground pattern of Endopterygota (unpubl. obs.), suspend and control the position of the propleuron under the overhanging lateral margin of the pronotum. These muscles, classified as *t-p?* by Matsuda (1970), arise laterally from the pronotum and insert on the apodeme formed along the dorsal margin of the propleuron. No more than two prothoracic noto-pleural muscles (Fig. 2: Mm. 9 and 10; Tables 1 and 2) are developed in the ground pattern of Mecoptera (and Antliophora). M. 9, which lies mesally and inserts anteriorly to M. 10, is in *Panorpa* (Fig. 2), a strong muscle divided in two close-set fascicles. A similar division of M. 9 may explain why Storch & Chadwick (1968: Mm. 14-16), contrary to Mickoleit (1968: Mm. 12, 13), counted three noto-pleural muscles in *Bittacus*.

Despite the incomplete separation of the pronotum and propleuron in Diptera, it was observed here that several basal groups of nematocerous Diptera, i.e. Trichoceridae, many Tipuloidea (Figs 5, 6), Tanyderidae, Ptychopteridae and Blephariceridae, possess a deep noto-pleural cleft crossed by two noto-pleural muscles. These muscles (Mm. 9, 10) which arise from the anterior notum I and insert on top of episternum I, appear definitely homologous with the corresponding muscles found in Mecoptera.

In some groups of Diptera, very notably in tipuline Tipuloidea (Mickoleit, 1962: M. 16) and Culicomorpha (Fig. 7: M. 9; Owen, 1977: M. 10), episternum I is dorsally forming a thumb-like prominence which accommodates a single, often hypertrophied noto-pleural muscle, M. 9. This development has caused a shortening of the noto-pleural cleft and disappearance of one of the noto-pleural muscles.

In all Psychodidae (Fig. 9; Crampton, 1925a: figs 9, 10), the anterior notum I is extremely short and laterally fused together with episternum I; thus the noto-pleural cleft has been replaced by a suture. Accordingly, both noto-pleural muscles were found to be absent in psychodine and trichomyiine (Fig. 9) Psychodidae. As expected, this applies to the ground pattern of the family.

The notable specializations pertaining to the noto-pleural musculature of Neodiptera are detailed below.

#### *The episterno-dorsocervical musculature*

The cervical cuticle immediately behind the laterodorsal postocciput, or the laterodorsal postocciput proper, accommodates in the ground pattern of most endopterygote orders muscles arising from episternum I and furcasternum I. Matsuda (1970) classified these muscles as *op-p* 1, 2 and *op-s* 2, of which the former typically arises from the anterodorsal episternal angle and the latter from the furcasternal arm. Both muscles have here been observed in Hymenoptera (Tenthredinidae), Trichoptera (Rhyacophilidae, Polycentropodidae) and Lepidoptera (Micropterigidae). Kristensen (1968: Mm. 2, 4) described these muscles in eriocraniid Lepidoptera.

A single muscle, the one arising from episternum I (Fig. 2: M. 1; Tables 1 and 2), is retained in the ground pattern of Antliophora. In *Bittacus* (Mickoleit, 1968) this muscle has a normal origin from the anterodorsal episternal margin. In *Panorpa*

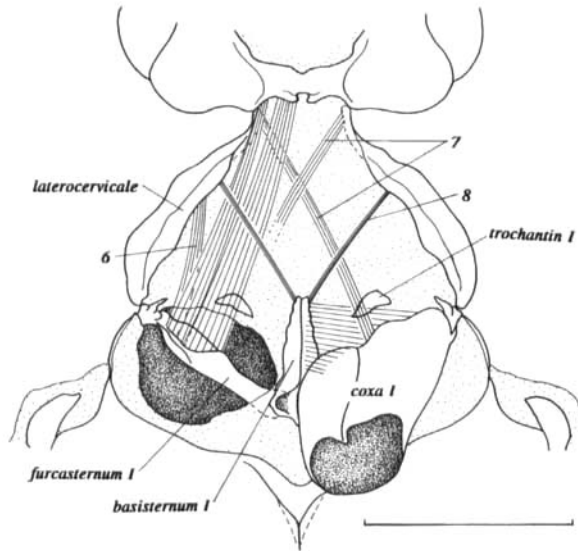


Figure 3. *Panorpa communis*, ♀: Cervix and pronotum in ventral view (right coxa I removed) showing the musculature of the ventral cervical region. Scale bar 1.0 mm.

(Fig. 2: M. 1; Hasken, 1939), it has attained a more posterior origin, from the transition zone between the pleural apophysis and furcasternal arm. For that reason, Matsuda (1970) misidentified it as the furcasterno-dorsocervical muscle (*op-s* 2).

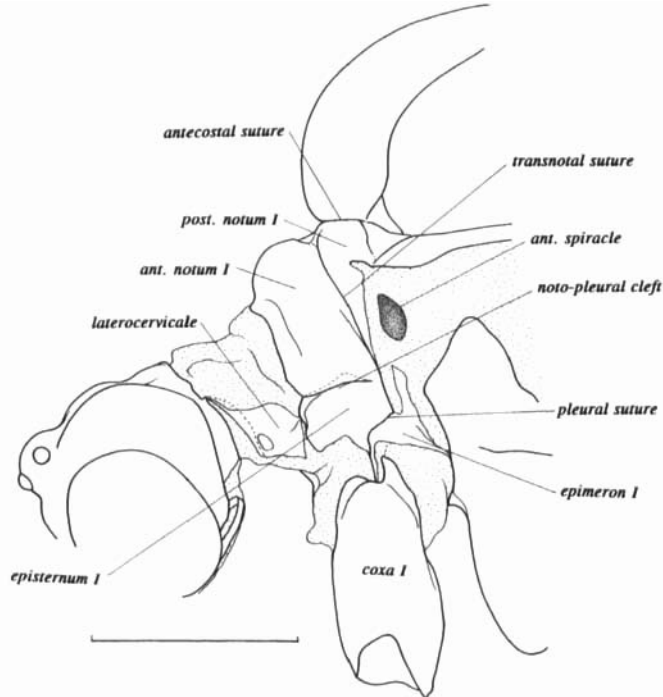


Figure 4. *Trichocera major*, ♀: Skeletal morphology of the cervix and prothorax, left lateral view. Scale bar 0.5 mm.

In Diptera the episterno-dorsocervical muscle has previously been identified in *Tipula* (Mickoleit, 1962: M.3), where it arises from episternum I immediately dorsally to the episterno-laterocervical articulation. The same configuration has here been observed in the following groups of nematoceros Diptera: Trichoceridae, several major groups of Tipuloidea (Fig. 5: M. 1) and Ptychopteridae. A minor portion of M. 1 actually arises from the adjacent part of the laterocervical sclerite in some Tipuloidea, e.g. *Ula sylvatica* (Pediinae). This shift in the origin of the episterno-dorsocervical muscle has been accentuated in Tanyderidae and limoniine Tipuloidea (Fig. 6: M. 1), in which M. 1 arises entirely from the laterobasal part of the laterocervicale.

In all Mecoptera and Diptera examined so far, a postoccipital muscle (Figs 2 and 5: M. 2; Tables 1 and 2) originates on the laterocervicale. This muscle, which tends to be divided in several fascicles, was classified by Matsuda (1970) as *op-cv* 1, 2, 3. It inserts on or immediately behind the dorsal postocciput. In many Bombyliidae and Schizophora, the insertion of M. 2 is accompanied by a sclerotized tendon attached to the lateral angle of the dorsal postocciput.

Present observations suggest that the apparent absence of the episterno-dorsocervical muscle (M. 1), as seen in the majority of Diptera, is a consequence of this muscle having changed its point of origin from episternum I to the laterocervicale. Accordingly, M. 1 has previously been confused with the laterocervico-postoccipital muscle (M. 2), cf. Table 2. However, M. 1 is a smaller muscle which arises laterally to M. 2 and its insertion point lies lateral to the dorsal postocciput, primarily in the laterodorsal cervix which may either be membranous or equipped with a dorsocervical sclerite. In the empidoid, *Empis tessellata*, M. 1 is divided in three separate fascicles; one has an insertion on the dorsocervicale, the others insert separately by thin tendons on the laterodorsal postocciput. In many Schizophora, the fascicles of M. 1 insert on a long tendon which arises from a depression of the laterodorsal postocciput.

The laterocervical origin of M. 1 has evolved convergently at least three times: (1) limoniine Tipuloidea, (2) Tanyderidae, and (3) a group combining Psychodidae (Fig. 9), Blephariceroidea, Culicomorpha (Fig. 7), and Neodiptera (Figs 12, 14, 16, 18, 22). In Chironomidae (Culicomorpha), M. 1 actually arises from an apodeme of the lobe-like extension of episternum I with which the laterocervicale articulates. This is interpreted as a reversal.

#### *The laterocervical musculature*

In most endopterygote orders the principal pair of cervical sclerites are situated ventrolaterally in the cervical membrane and articulate anteriorly with the occipital condyles and posteriorly with the proepisterna. As convincingly demonstrated by Matsuda (1970), the lateral cervical sclerites, or laterocervicalia, are homologous with the propleural preepisterna. In the ground pattern of Antliophora, four or five muscles insert on each laterocervicale and thereby act as indirect remotors and rotators of the head:

*M. 3, antecosta-laterocervical* (Tables 1 and 2). Arises laterally from the mesonotal antecosta; inserts at the mesal margin of the laterocervicale. This long, slender muscle, classified by Matsuda (1970) as *t-s(cv)*9, actually inserts on the tentorium in the ground pattern of Endopterygota. Hence, a laterocervical insertion may be autapomorphic for Amphiesmenoptera + Antliophora + Hymenoptera. However,



this muscle has disappeared recurrently and, when present, it often appears to be a transient muscle found in teneral individuals only. In Mecoptera, M. 3 appears to be permanently present in *Panorpa* (Fig. 2; Hasken, 1939) while it is reportedly absent in Boreidae (Füller, 1955) and Bittacidae (Mickoleit, 1968).

M. 3 has not previously been recorded from any Diptera, but it does occur as a transient muscle in various groups, e.g., pediciine Tipuloidea (Fig. 5) and scatopsid Neodiptera (Fig. 12).

*M. 4, pronoto-laterocervical* (Tables 1 and 2). This muscle, *t-cv1, 2, 3* of Matsuda (1970), is present in most endopterygote orders. It typically arises at midlength on the pronotum and inserts on the mesal margin of the laterocervicale anteriorly to M. 3.

M. 4 is present in Mecoptera (Fig. 2; Hasken, 1939; Mickoleit, 1968) and in the majority of Diptera. Tipuline Tipuloidea (Mickoleit, 1962; pers. obs.) and Culicidae (Fig. 7) provide exceptions. In Mecoptera and in the ground pattern of Diptera (e.g. Figs 5, 9, 12, 18), M. 4 arises from the transnotal crest. The origin of M. 4 has been forwardly displaced to the middle of the anterior notum I in limoniine Tipuloidea (Fig. 6) and backwardly displaced to the posterior notum I in most Brachycera (Fig. 22). Exceptionally, an accessory muscle which inserts on the lateral margin of the laterocervicale is split off from M. 4. The accessory muscle has only been found in

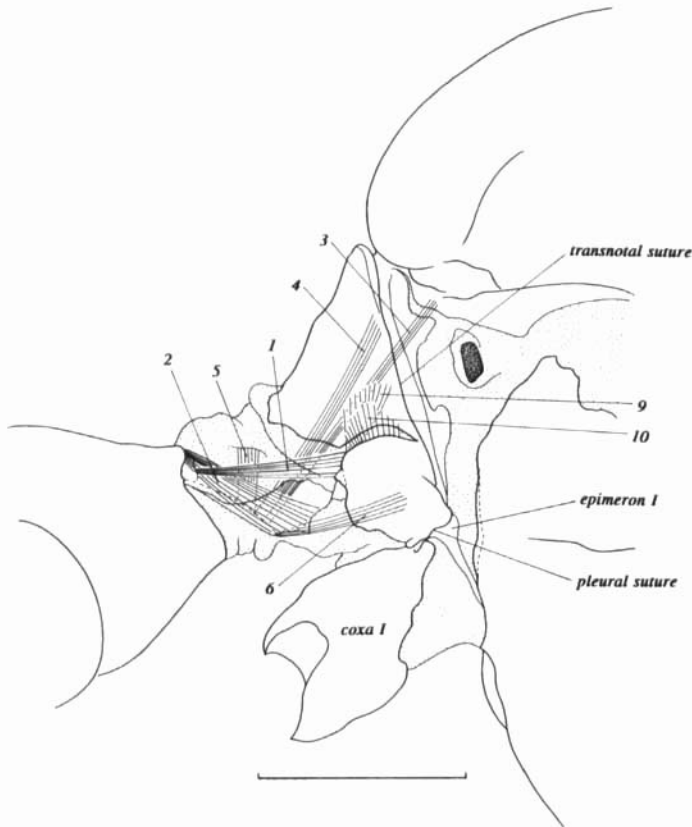


Figure 5. *Tricyphona immaculata*, ♀: Skeletal morphology, noto-pleural and laterocervical musculature of the cervix and prothorax, left lateral view. Scale bar 0.5 mm.

limoniine Tipuloidea (Fig. 6: 4ac), chironomine Chironomidae, and a group of Neodiptera (see below). M. 4ac has obviously been independently gained in these groups.

*M. 5, dorsocervico-laterocervical* (Tables 1 and 2). This muscle, which appears uniquely acquired in Antliophora, may represent a portion of M. 4 which has moved its origin from the pronotum onto the laterodorsal cervical cuticle.

M. 5 is reported from bittacid Mecoptera (Mickoleit, 1968) and was presently encountered in the following groups of Diptera: Peditine Tipuloidea (Fig. 5), chironomid and culicid (Fig. 7) Culicomorpha, and Neodiptera of the families Scatopsidae (Fig. 12), Anisopodidae (Fig. 14) and Axymyiidae (Fig. 16). This distribution pattern suggests that M. 5 has been lost (or gained?) several times in Antliophora.

*M. 6, furcasterno-laterocervical* (Tables 1 and 2). This muscle, *cv-s1* of Matsuda (1970), is present in most endopterygote orders. M. 6 arises from the arm (= apophysis) of furcasternum I and inserts on the mesobasal angle of the laterocervicale.

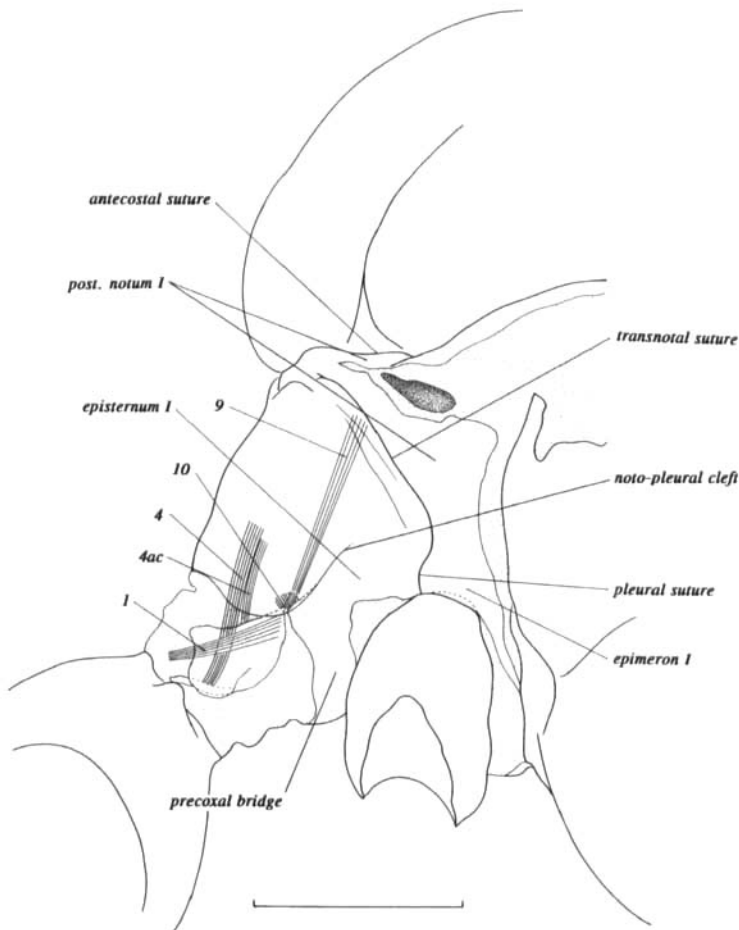


Figure 6. *Limonia nubeculosa*, ♀: Skeletal morphology, noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left lateral view. Scale bar 0.5 mm.

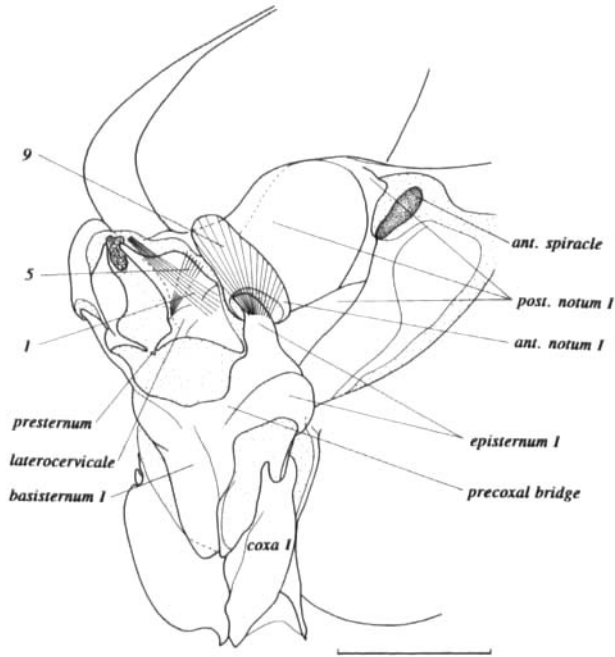


Figure 7. *Culiseta annulata*, ♀: Skeletal morphology, noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

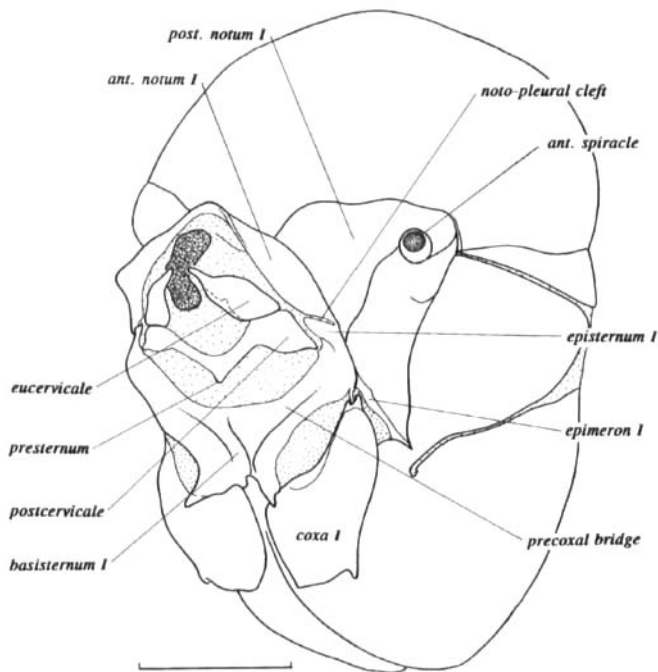


Figure 8. *Mallochohelea nitida*, ♀: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.25 mm.

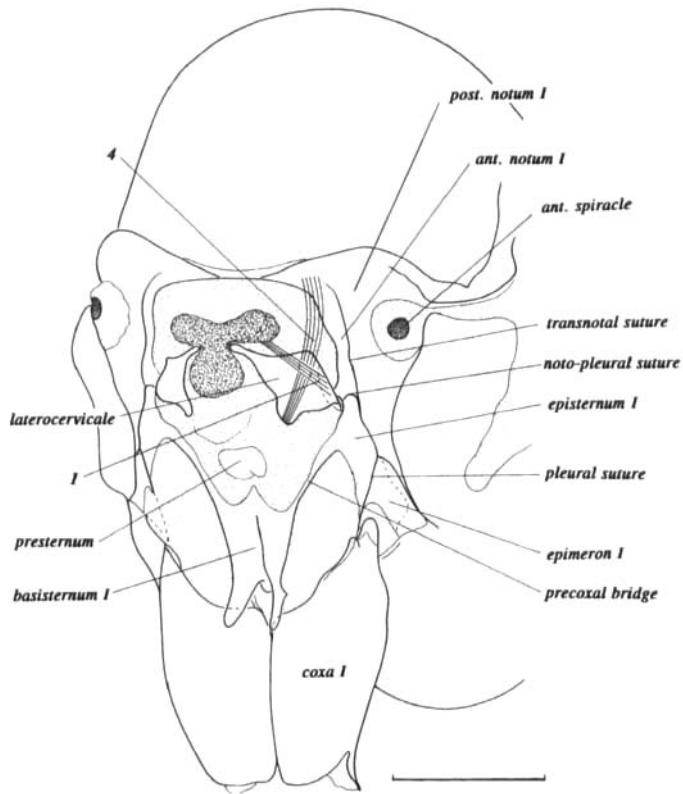


Figure 9. *Trichomyia urbica*, ♀: Skeletal morphology and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left anterolateral view. Scale 0.25 mm.

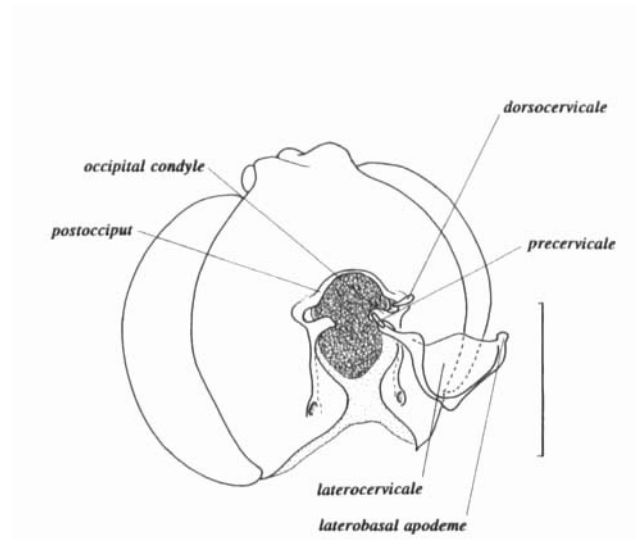


Figure 10. *Pachyneura fasciata*, ♂: Skeletal morphology of the head and cervical sclerites, left posterolateral view. Scale 0.5 mm.

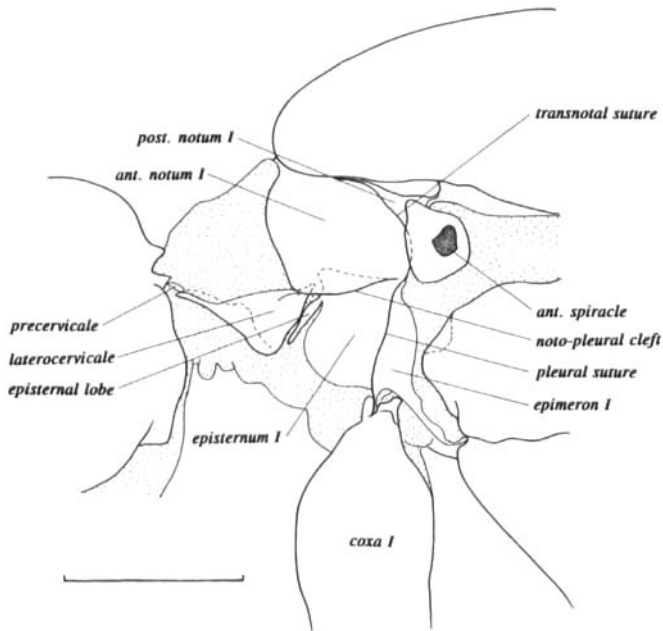


Figure 11. *Scatopse notata*, ♀: Skeletal morphology of the cervix and prothorax, left lateral view. Scale 0.25 mm.

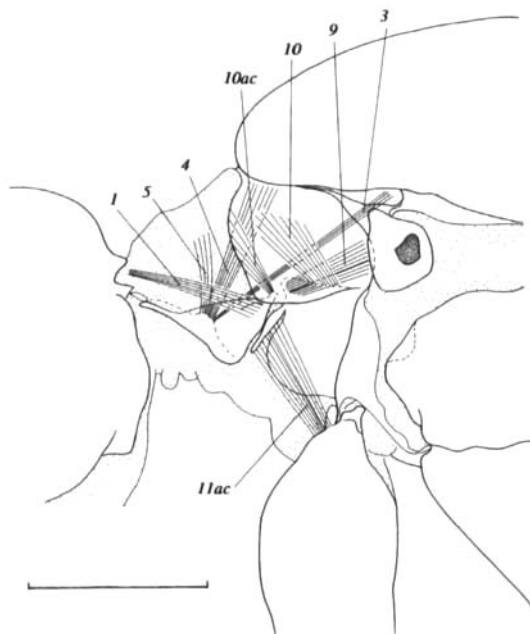


Figure 12. *Scatopse notata*, ♀: Noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left lateral view. Scale 0.25 mm.

M. 6 is a single muscle in Mecoptera (Fig. 2; Hasken, 1939; Mickoleit, 1968) and in the ground pattern of Diptera, viz., Trichoceridae, Tipuloidea (Fig. 5; Mickoleit, 1962), Ptychopteridae, and Tanyderidae. In the remaining Diptera, this ventral cervical muscle consists of two discrete parts with slightly different points of insertion.

*M. 7, coxo-laterocervical, crossed* (Tables 1 and 2). This peculiar muscle, *cv-cx I(X)* of Matsuda (1970), is well known from Hymenoptera (e.g. Markl, 1966: *mcr*). In *Tenthredo*, I have observed that M. 7 consists of a pair of long, slender fascicles which arise from the basicostal margin of coxa I, cross in the neck region dorsal to the ventral nerve cord, and extend to the anterior end of the laterocervicale on the opposite body side. A crossed cervical muscle with this combination of origin and insertion has elsewhere among endopterygote insects only been reported from panorpid Mecoptera (Maki 1938: M. 13; Fig. 3). Hasken (1939) also found this muscle in *Panorpa* but did not notice its crossed configuration. M. 7 is absent in bittacid Mecoptera according to Mickoleit (1968) and Storch & Chadwick (1968). According to Hepburn (1970), whose results do not always appear reliable, M. 7 (not mentioned to be a crossed muscle) occurs in all mecopteran families apart from Meropeidae and possibly Nannochoristidae.

The absence of M. 7 is characteristic of Diptera and Siphonaptera. This is evidently a secondary state.

It should be noted that the coxo-tentorial muscle (Matsuda, 1970: *s-cx(cv)*) found in Amphiesmenoptera is surely homologous with M. 7. In the ground pattern of Lepidoptera (Kristensen, 1984), both components of M. 7 insert on a posteromedian process on the tentorial bridge. Accordingly, this is a non-crossed muscle. However, my examination of a 'lower' caddisfly (*Rhyacophila*) confirmed the observation of Kristensen (1984) that M. 7 in the ground pattern of Trichoptera inserts laterally on the tentorial bridge and has maintained the crossed configuration.

Due to the widespread occurrence of a crossed, ventral cervical muscle in non-endopterygote insects (Markl, 1966; Matsuda, 1970), it is currently believed that M. 7 is an archaic muscle in Endopterygota. This idea, however, is not supported by the notable absence of M. 7 in neuropterid orders and Coleoptera. Alternatively, M. 7 could have been independently gained in Antliophora + Hymenoptera + Amphiesmenoptera. This would leave it an open question, whether a laterocervical or tentorial insertion of M. 7 is the derived state.

*M. 8, prosterno-laterocervical/presternal* (Tables 1 and 2). I found this previously unnoticed muscle in panorpid Mecoptera (Fig. 3). It is an extremely delicate muscle which arises anteriorly from basisternum I and inserts on the mesal margin of the laterocervicale. I find it reasonable to believe that M. 8 is homologous with a similarly delicate muscle (Matsuda, 1970: *s?*) which in the ground pattern of Diptera arises proximally from the arm of furcasternum I and inserts on the presternum. In support of this can be mentioned the finding of an intermediate configuration in *Rhyacophila*. In that caddisfly, a tenuous muscle (M. 8) arises from the midlength of basisternum I and inserts on the transition zone between the presternum and the mesal arm of the laterocervicale.

The presternum, always located in the posteroventral cervical membrane, takes a variety of shapes but is typically a diamond-shaped, weakly sclerotized plate. It often has connections with basisternum I or with mesal extensions of the laterocervicalia. Contrary to Matsuda (1970), I do not consider the presternum as an accessory

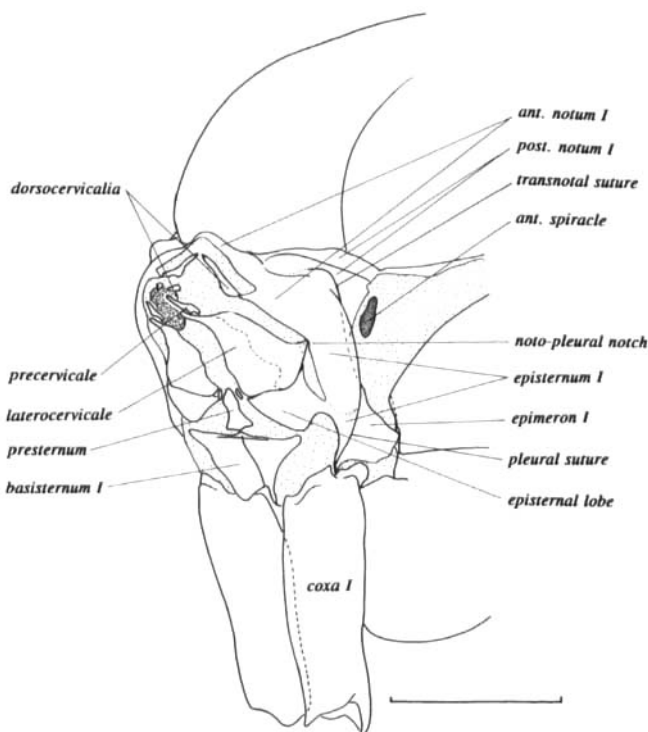


Figure 13. *Sylnicola fuscatus*, ♂: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

sclerite which has been independently acquired by a variety of insects. The situation in endopterygote insects suggests that the presternum could be a primary intersegmental sclerite, possibly serially homologous with the spinasterna (cf. Chadwick, 1959). This would imply that M. 8 primarily inserts on the presternum and that the laterocervical insertion in *Panorpa* is caused by a total reduction of the presternum.

#### *Ground pattern autapomorphies of Neodiptera*

The following text reviews four skeleto-muscular traits of the adult cervical region which are regarded as constitutive for Neodiptera.

*Character 1.* A discrete piece of sclerite, the *precervicale*, is inserted in the articulation between each laterocervicale and occipital condyle.

In the majority of endopterygote insects, the laterocervicalia articulate directly with the occipital condyles. This also applies to the ground pattern of Diptera. The precervicale (Figs. 10, 11, 13, 15, 17, 19 and 21) is a small, oblong sclerite attached by tough, flexible cuticle to the occipital condyle and a subapical area of the laterocervicale, respectively. It appears to be uniquely developed in Neodiptera. As noted by Bonghag (1949), the “first cervical sclerites” (= precervicalia) represent presumably elements detached from the “second cervical sclerites” (= laterocervicalia).

Previously, little attention has been paid to the precervicalia of Diptera, probably because they are often very small and inconspicuous pieces of sclerite which cannot be observed in intact, dry-mounted specimens. In addition, the precervicalia have frequently been confused with the dorsocervicalia, i.e. muscled sclerites belonging to the dorsal cervix. Thus, Mickoleit (1962) identified the dorsocervicale in *Tipula* as "1. Cervicale" (= precervicale) and erroneously stated that it articulates with the occipital condyle. Peterson (1916: figs 97, 115, 133, etc.) provided good illustrations of the precervicalia in various representatives of Neodiptera but made no comments on them. Even Crampton (1925a) paid little attention to these sclerites, though his illustrations show their presence in species of Anisopodidae (fig. 18) and Rhagionidae (fig. 19). The same author (Crampton, 1926) identified the precervicalia in a tabanid (fig. 96), an anisopodid (fig. 115) and a mydid (fig. 116) but he also, in other insects, applied this term for sclerites belonging to the dorsal cervix. A similar ambiguity adheres to the "anterior, lateral cervical sclerite" of Crampton (1942: figs 6A, B).

Bonhag (1949) correctly noted that the precervicale in Tabanidae is unmusculated and articulates anteriorly with the head and posteriorly with the laterocervicale. Ulrich (1971, 1984) made the same observation on the "1. Laterocervicale" (= precervicale) of empidoid flies. Speight (1969), in a comprehensive and well illustrated account of the cervical region in acalyptrate Schizophora, indicated that a vestigial "antero-cervicale" (= precervicale) is generally present. However, Speight's statement that the laterocervicalia establish direct articulations with the head capsule in acalyptrate flies is erroneous (cf. Valdez & Prado, 1990: fig. 49).

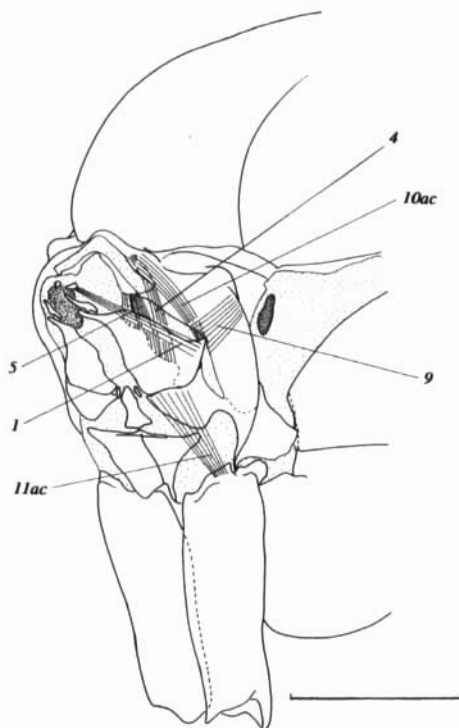


Figure 14. *Sylvicola fuscatus*, ♂: Noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.



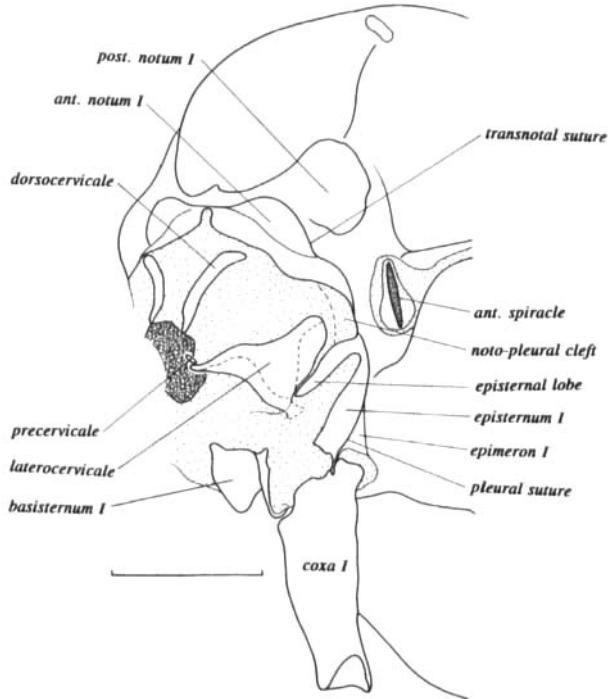


Figure 15. *Axymyia furcata*, ♂: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

Speight (1987) observed that the cervical region of Syrphidae agrees closely with that of Acalyptratae.

**Character 2.** Laterobasal articulation between laterocervicale and episternum I replaced by laterocervical apodeme suspended by an accessory muscle arising from pronotum.

In Mecoptera (Fig. 1) and in the ground pattern of Diptera (Figs 4–9), a point of articulation is established between the anterior margin of episternum I and the laterobasal angle of the laterocervicale. In Neodiptera (Figs 11, 13, 15, 17, 19 and 21), this articulation has been abandoned. Instead, a laterocervical apodeme is developed which accommodates a new muscle, M. 10ac (Table 2; Figs 12, 14, 16, 18, 20 and 22) arising from the anterior notum I. Published descriptions of this apomorphic state refer exclusively to Brachycera, e.g. Bonhag (1949) and Ulrich (1971, 1984) but it has been found to be present as well in the nematocerous Neodiptera.

Ulrich (1984) made the sound suggestion that the accessory M. 10ac of Brachycera represents a former noto-pleural muscle which has attached a new point of insertion. However, as noted in the following, some nematocerous Neodiptera do possess a full complement of noto-pleural muscles (Mm. 9, 10) in addition to the accessory laterocervical muscle. Therefore, the latter is here interpreted as a new muscle, split off from one of the primary noto-pleural muscles, possibly M. 10.

A well developed noto-pleural cleft still separates the anterior notum I and episternum I in the ground pattern of Neodiptera. This is seen in Scatopsidae (Fig. 11), Pachyneuridae and many Sciaroidea (Fig. 17). There exists no published

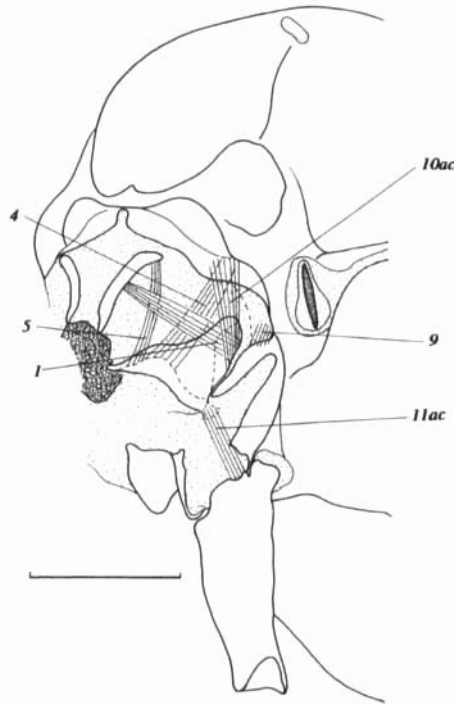


Figure 16. *Axymyia furcata*, ♂: Noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

information on the prothoracic musculature of nematocerous Neodiptera (cf. Ulrich, 1991), but I found that Scatopsidae (Fig. 12) possess a full complement of notopleural muscles (Mm. 9, 10), while a single muscle (M. 10) is retained in Sciaridae (Fig. 18) and Mycetophilidae.

In other groups of Neodiptera, the noto-pleural cleft tends to be more or less obliterated due to shortening and/or fusion of the noto-pleural skeletal parts. This is seen in Anisopodidae (Fig. 13), Axymyiidae (Fig. 15), Cecidomyiidae, Bibionidae and Brachycera (Figs 19 and 21). As noted previously, this development has been paralleled in Psychodidae. A total reduction of the primary noto-pleural musculature, as seen in Psychodidae, has also taken place independently in Cecidomyiidae, bibionine Bibionidae and the vast majority of Brachycera (Fig. 22; Ulrich, 1971, 1984). Rather unexpectedly, a single noto-pleural muscle, which I interpret as M. 9, has been retained in Anisopodidae (Fig. 14), Axymyiidae (Fig. 16) and pleciine Bibionidae. It appears that M. 9 in these groups helps to establish an infolding of the soft cuticle of the laterobasal cervix. Even more remarkably, a tiny noto-pleural muscle (M. 9?) has been found to persist in Tabanidae (not detected by Bonhag, 1949) and in the primitive (mandibulate!) rhagionid, *Symphoromyia crassicornis* (Panzer) (Fig. 20).

**Character 3.** From episternum I arises a flexible, mesally directed *episternal lobe* which attaches broadly to the basal margin of the laterocervicale.

The episternal lobe of Neodiptera lies subvertically in a transverse fold of the ventral cervical cuticle and normally articulates broadly with the basal margin of the laterocervicale. A proximal weakness zone provides this lobe with the ability of pro-

and retraction relative to the remaining episternum. By exception, as in some Mycetophilidae, the episternal lobe is completely detached from the remaining episternum. A sclerotized connection between basisternum I and the ventralmost part of episternum I, known as precoxal bridge, has been established in various groups of Neodiptera (e.g. Fig. 17). This bridge may even coalesce extensively with the episternal lobe, but normally without obscuring the identity of the latter. However, in at least some Cecidomyiidae, the proepisternal lobe is obsolete or absent due to an excessive development of the precoxal bridge.

Crampton (1925a, 1926), in his comparative studies of the cervical sclerites in Diptera and other insects, considered the episternal lobe of Neodiptera as homologous with the postcervicale of simuliid and ceratopogonid (Fig. 8) Culicomorpha, i.e. as a posteriorly detached portion of the primary laterocervicale. This interpretation was adopted, e.g. by Bonhag (1949), Speight (1969), Matsuda (1970) and Ulrich (1971, 1984). For the following reasons I find an episternal derivation of this structure in Neodiptera much more credible: (1) In Neodiptera the episternal lobe is primarily synscleritous with the remaining episternum I; in ceratopogonids etc. the original laterocervico-episternal articulation is maintained between the postcervicale and episternum I. (2) In Neodiptera the laterocervicale shows no sign of having its posterior part set off; in ceratopogonids etc. the eucervicale and postcervicale are readily identified as elements of a formerly entire laterocervicale (cp. Figs 7 and 8). (3) In Neodiptera, except secondarily in empidoid Brachycera (cf.

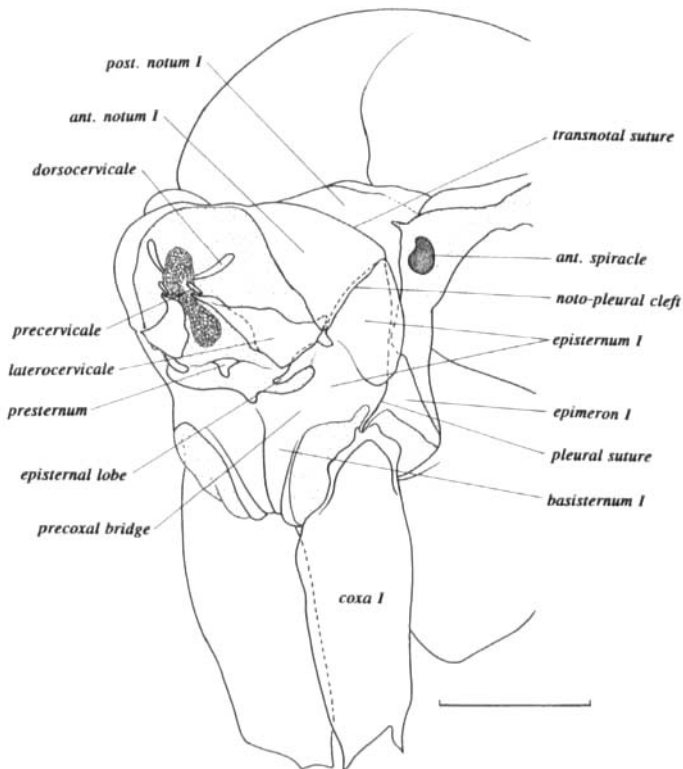


Figure 17. *Bradysia* sp., ♀: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.25 mm.

Ulrich, 1971, 1984), the laterocervico-postoccipital muscle (M. 2) arises solely from the laterocervicale; in ceratopogonids etc. the origin of M. 2 is normally divided between the two cervicalia. (4) A variety of Diptera other than Neodiptera (e.g. some Tipuloidea, Blephariceridae, Psychodidae and Chironomidae) have independently developed lobe-like formations of unmistakable proepisternal origin. However, unlike Neodiptera, these groups have maintained the original cervical articulation as a point of contact between the apex of the episternal lobe and the laterobasal angle of the laterocervicale (or postcervicale).

*Character 4.* Coxa I accommodates a newly developed muscle, an accessory promotor which arises from the episternal lobe.

In the ground pattern of Diptera, the only promotor of coxa I is a horizontal muscle which arises from basisternum I. In addition to this muscle, Neodiptera possess a subhorizontal coxal promotor (M. 11ac; Table 2) which often consists of two closely aligned fascicles. It arises primarily from the episternal lobe and inserts always laterally on the coxal basicosta above the insertion of the basisternal muscle.

The episternal origin of M. 11ac, the accessory coxal promotor of Neodiptera, suggests that this muscle has split off from the episternal coxal abductor, M. 11 (Fig. 22). In neuropterid and amphiesmenopteran orders (pers. obs.), and therefore credibly in the ground pattern of Endopterygota, there are two discrete episternal muscles acting as abductors or promotors of coxa I. However, in Hymenoptera (e.g.

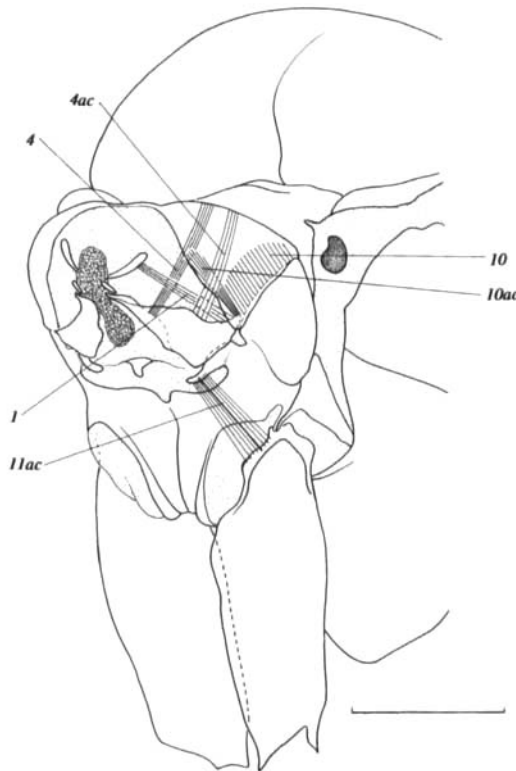


Figure 18. *Bradysia* sp., ♀: Noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax left anterolateral view. Scale bar 0.25 mm.

Markl, 1966: M. 53; pers. obs.), Mecoptera and in the ground pattern of Diptera, episternum I only gives rise to a single, deltoid muscle which acts as a coxal abductor.

Previously, M. 11ac has only been reported from brachycerous Diptera (Table 2) and was considered as a postcervical (e.g. Bonhag 1949) or cervical (e.g. Ulrich, 1971, 1984) promotor of coxa I. I am now able to confirm the occurrence of M. 11ac in Scatopsidae (Fig. 12), Anisopodidae (Fig. 14), Axymyiidae (Fig. 16), Sciaroidea (Fig. 18), Bibionidae and a wide spectrum of Brachycera (Figs 20 and 22). Ulrich (1971) showed that M. 11ac in several groups of Empidoidea arises in part or entirely from the mesobasal angle of the laterocervicale. A similar origin of M. 11ac has been independently acquired in other groups of Neodiptera showing a regressive development of the episternal lobe: Axymyiidae (Fig. 16), Bombyliidae, and Schizophora (Fig. 22).

### *Internal phylogeny of Neodiptera*

No detailed picture of phylogenetic relationships is presently available for the eight, purportedly monophyletic, fundamental taxa of Neodiptera: Scatopsoidea,

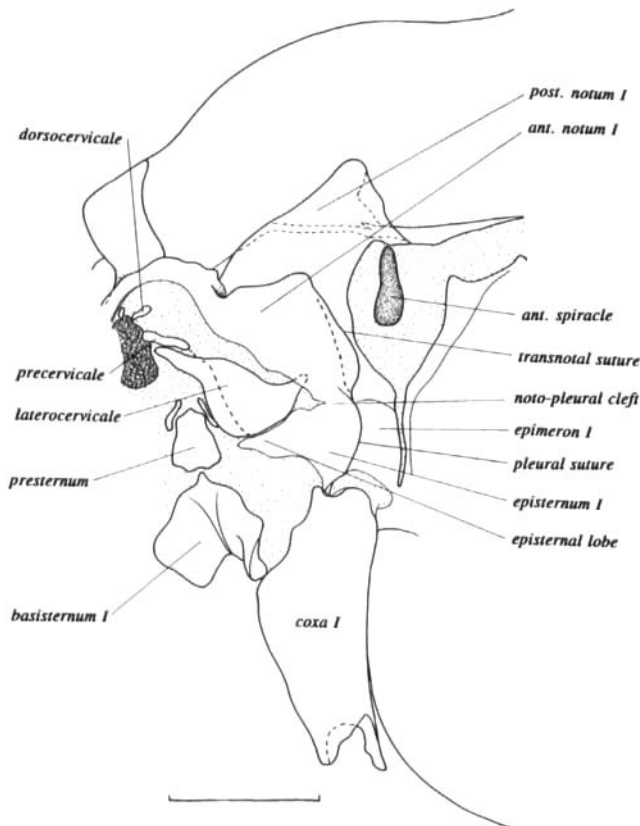


Figure 19. *Symphoromyia crassicornis*, ♀: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

Anisopodidae, Perissommatidae, Axymyiidae, Pachyneuridae, Sciaroidea, Bibionoidea, and Brachycera. However, based on one notable peculiarity of the cervical musculature, I here suggest that a group consisting of Bibionomorpha s.s. (= Pachyneuridae + Sciaroidea + Bibionoidea) and Brachycera is monophyletic. It should be noted, however, that the inclusion of Pachyneuridae is circumstantial due to the absence of soft tissue data.

*Character 1.* Lateral margin of the laterocervicale accommodates an accessory pronotal muscle.

In the ground pattern of Neodiptera, the laterocervicale accommodates two pronotal muscles (Table 2: Mm. 4 and 10ac) inserting on the mesal margin and laterobasal angle, respectively. In all Sciaroidea (Fig. 18), Bibionidae, and Brachycera (Figs 20 and 22) that I have examined, there is an additional pronotal muscle (Table 2: M. 4ac) which inserts on the lateral margin of the laterocervicale anteriorly to M. 10ac. The crossing of this flat muscle externally to the conical M. 10ac is very characteristic.

Previously, M. 4ac has only been reported from various Brachycera (e.g. Bonhag, 1949; Ulrich, 1971, 1984; Valdez & Prado, 1990; cf. Table 2). Ulrich (1984) suggested that this accessory muscle, in the same way as M. 10ac, has differentiated from the noto-pleural musculature. However, I find it more credible to derive this

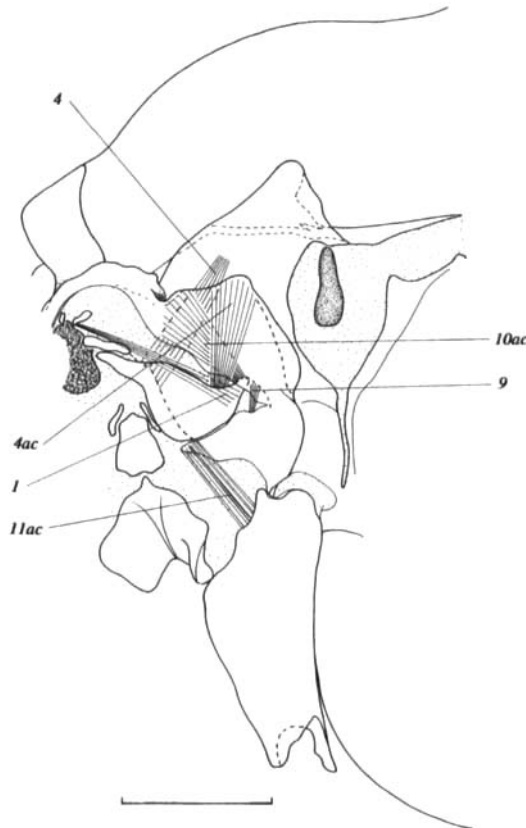


Figure 20. *Symphoromyia crassicornis*, ♀: Noto-pleural and laterocervical musculature (Mm. 2 and 6 omitted) of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

muscle from the primary pronoto-laterocervical muscle, M. 4. This interpretation gains support from limoniine Tipuloidea (Fig. 6: 4ac) which have independently acquired a pronotal muscle inserting on the lateral margin of the laterocervicale. That muscle has obviously been set off from M. 4.

It should be emphasized that the purported monophyly of Bibionomorpha *s.s.* + Brachycera does not provide an argument for the monophyly of Bibionomorpha *s.s.*, but it surely diminishes the possible number of candidates for obtaining the status as the sister group of Brachycera.

*Neodiptera and the higher level phylogeny of Diptera*

Provided that Neodiptera are monophyletic and that Nymphomyiidae rightly belong to Culicomorpha, a fully resolved fundamental phylogeny of Diptera should be within reach. This would allow a total resolution of extant Diptera into only eight fundamental taxa: Trichoceridae, Tipuloidea, Tanyderidae, Ptychopteridae, Psychodidae, Blepharicerioidea, Culicomorpha and Neodiptera.

The basic dichotomy is currently one of the major, controversial items of dipteran phylogeny. Wood & Borkent (1989) suggested that a sister group relationship exists between Tipuloidea and the remaining Diptera (Fig. 23) based on the absence of a "lacinia mobilis" in the larval mandible of the latter group. However, Oosterbroek

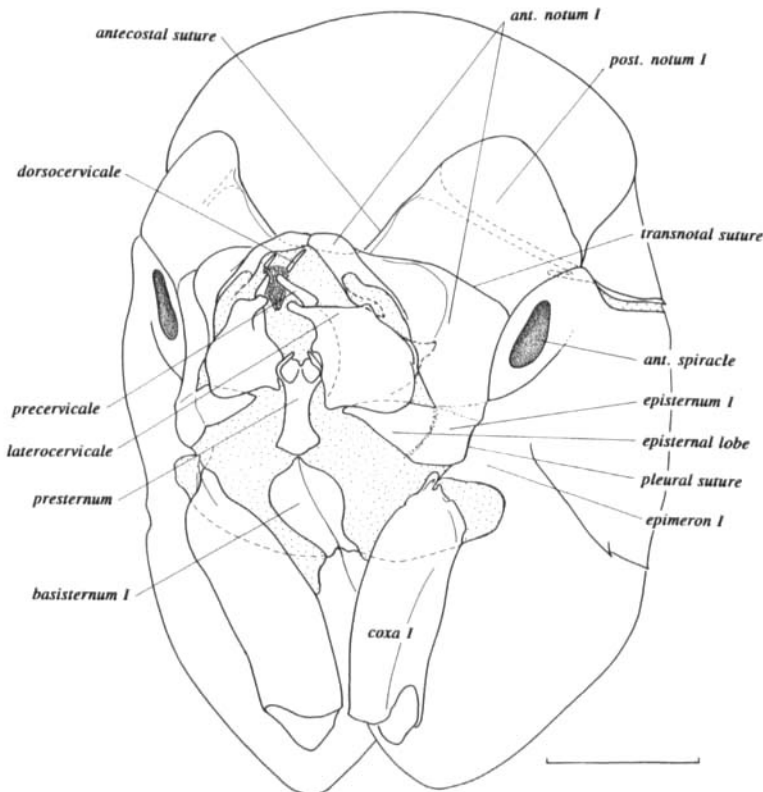


Figure 21. *Hylemya vagans*, ♀: Skeletal morphology of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.

& Theowald (1991) concluded that the *lacinia mobilis* does not belong to the ground pattern of Tipuloidea but is an autapomorphy for a subordinate group of tipuloids.

Hennig (e.g. 1973) upheld the traditional view of a sister group relationship between Tipuloidea and Trichoceridae and considered this group (Polyneura) to be the sister group of the remaining Diptera (Oligoneura). However, the existing evidence for the monophyly of both groups is not compelling (see Wood & Borkent, 1989; Oosterbroek & Theowald, 1991; and references therein).

Based on admittedly very preliminary evidence, it is here suggested that the primary division of all extant Diptera lies between a 'polyneuran' taxon consisting of Tipuloidea + Trichoceridae + Tanyderidae + Ptychopteridae and an 'oligoneuran' taxon combining all remaining Diptera, i.e. Psychodidae + Blephariceridae + Culicomorpha + Neodiptera (Fig. 24).

One purported autapomorphy for the 'polyneurans' is:

*Character 1.* Laterocervicale mesally provided with an orifice purportedly representing the exit of a cervical gland.

Crampton (1925b: pl. 3 figs 10-17) first pointed to the occurrence of a so-called "laterocervical fenestra" in eriopterine Tipuloidea. Williams (1933: pl. 1 fig. 6) described a homologous "fenestra" in the tanyderid, *Protoplasa fitchii* Osten Sacken. In a morphological account of the apterous eriopterine, *Chionea lutescens* Lundström,

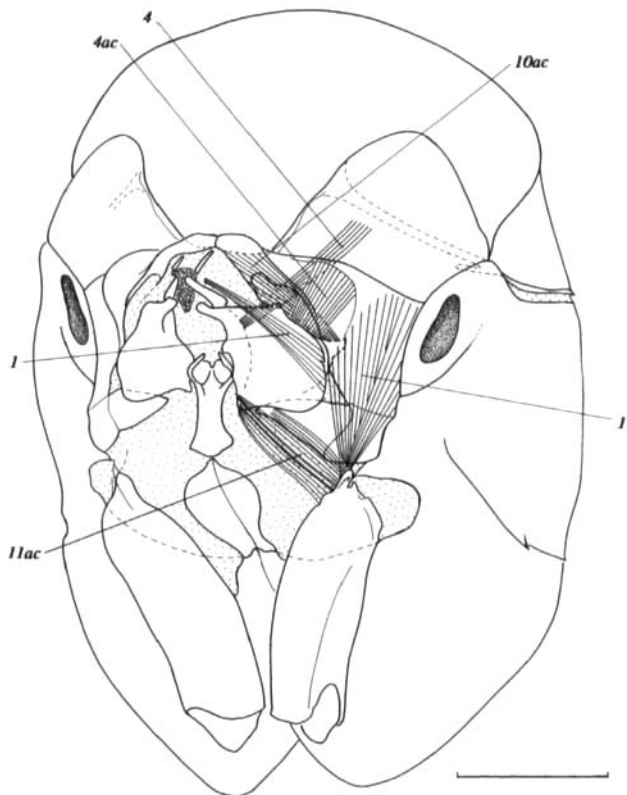


Figure 22. *Hylemya vagans*, ♀: Noto-pleural, laterocervical (Mm. 2 and 6 omitted) and episterno-coxal musculature of the cervix and prothorax, left anterolateral view. Scale bar 0.5 mm.



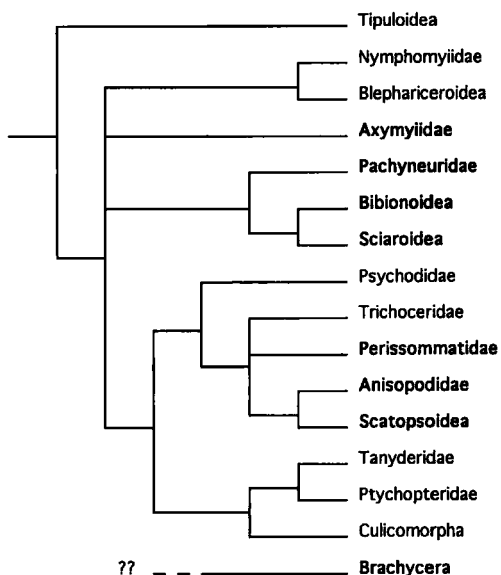


Figure 23. Hypothesized phylogenetic relationships of Diptera, after Wood and Borkent (1989). Bold faced taxa constitute the Neodiptera.

Bitsch (1955) noted the existence of a paired cervical gland provided with an exit in the mesal margin of the laterocervicalia. Obviously, the “fenestra” of Crampton and Williams is homologous with the glandular orifice described by Bitsch. The fine structure and significance of this purported gland remain to be investigated.

A cervical gland has not been reported from any Mecoptera or ‘oligoneuran’ Diptera, which suggests that its occurrence in the ‘polyneurans’ is apomorphic. The cervical gland orifices have here been found in Trichoceridae (Fig. 4), Tanyderidae, and in hexatomine, eriopterine and some limoniine Tipuloidea. This strongly suggests that the organ has been secondarily reduced in pediciine, cylindrotomine, tipuline and most limoniine Tipuloidea. The absence of this gland in Ptychopteridae might as well be secondary.

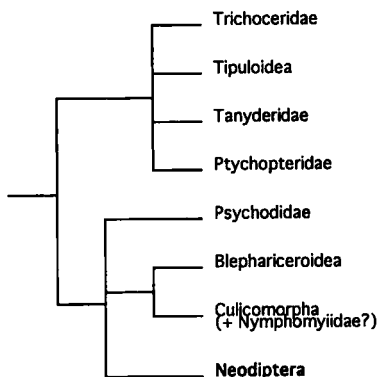


Figure 24. Higher level phylogenetic relationships of Diptera as presently hypothesized.

The following purported automorphies support the monophyly of the 'oligoneurans':

*Character 1.* Origin of the episterno-dorsocervical muscle has been transferred to the laterocervicale.

As noted earlier, episternum I accommodates the origin of a dorsocervical muscle (M. 1: Tables 1 and 2) in the ground pattern of Diptera. This plesiomorphic state occurs in all the 'polyneurans' groups apart from limoniine Tipuloidea and Tanyderidae. A laterocervical origin of M. 1 is characteristic for all 'oligoneurans' apart from Chironomidae (obviously a reversal). Supposedly, the apomorphic state is convergent between Tanyderidae, limoniine Tipuloidea, and the 'oligoneurans'. The independent acquisition of a laterocervical origin of M. 1 in Tanyderidae and Limoniinae is readily seen as a response to the marked prolongation of the cervix and the anterior pronotum, respectively.

*Character 2.* Furcasterno-laterocervical muscle divided into two discrete muscles with slightly different points of insertion.

In the ground pattern of Diptera, as stated earlier, the mesobasal angle of the laterocervicale accommodates a single muscle (M. 6: Tables 1 and 2) arising from the arm of furcasternum I. Without exceptions, M. 6 is single in the 'polyneurans' (Fig. 5), while it is split into two discrete muscles in the ground pattern of the 'oligoneurans' (e.g. Bonhag, 1949: fig. 7; Ulrich, 1984: fig. 11).

The 'oligoneurans', as presently defined, comprise four fundamental taxa (Psychodidae, Blephariceroidea, Culicomorpha, and Neodiptera) with unclarified phylogenetic relationships. Preliminary evidence for a sister group relationship between Blephariceroidea and Culicomorpha (Fig. 24) will be given in this context.

*Character 1.* Basal labial palpomere operated by two muscles arising from the prementum.

The labial palpi of adult Diptera form specialized organs of ingestion, the so-called oral pads or labella. These consist of two more or less discrete articles which, as in Mecoptera, may represent the morphologically 2nd and 3rd palpomeres. In the ground pattern of Diptera, the labium has only two intrinsic muscles which act as abductors of the basal and distal palpomeres, respectively. The former muscle tends to arise from the prementum as two discrete fascicles but these have identical points of insertion on the basal palpomere. This is seen in virtually all groups of Diptera apart from Blephariceroidea, Culicomorpha and Brachycera in which the two fascicles have split into two discrete muscles with different points of insertion. This development has evidently taken place independently in Brachycera because the plesiomorphic pattern is maintained in other groups of Neodiptera. Besides, in Blephariceroidea and Culicomorpha both muscles insert on the basal palpomere as evidenced for Blephariceridae (Imms, 1944; pers. obs.), Dixidae (Imms, 1944), Ceratopogonidae (Jobling, 1928), Culicidae (Jobling, 1976), Simuliidae (Wenk, 1962), and Chironomidae (Hoyt, 1952; pers. obs.), while in Brachycera one muscle inserts on the basal palpomere, the other inserts distally on the sclerotized labial gutter.

## DISCUSSION

*Neodiptera and larval evidence: a phylogenetic conflict?*

The unique share of several novel, relatively complex specializations of the adult cervix provides substantial evidence for the monophyly of Neodiptera. Recognition of this taxon is compatible with the phylogenies proposed by Hennig (1973) and Amorim (1992), but is in conflict with the widely acknowledged phylogenetic hypothesis of Wood & Borkent (1989) which to a major extent relies on larval characters. Their phylogeny has proved very influential as a starting point for cladistic analyses addressing more restricted targets, e.g. Courtney (1991) on Blephariceromorpha and Oosterbroek & Theowald (1991) on Tipuloidea. Proposals on refinement of Wood & Borkent's phylogeny were given by Courtney (1991), Wood (1991) and Sinclair (1992).

The nematocerous groups presently included in Neodiptera, i.e. Bibionomorpha *s.l. sensu* Hennig (1973), were in the phylogeny of Wood & Borkent (1989, see Fig. 23), moved to three different branches of an unresolved polytomy: Axymyiomorpha, Bibionomorpha *s.s.*, and Psychodomorpha:

- (1) Axymyiomorpha only included the small, supposedly monophyletic family Axymyiidae.
- (2) Bibionomorpha *s.s.* were proposed to include Pachyneuridae, Bibionoidea and Sciaroidea, but evidence for the monophyly of this group was not given by Wood & Borkent (1989). Nevertheless, this restricted concept of Bibionomorpha was adopted by Blaschke-Berthold (1994), and she presented a list of seven purported autapomorphies for the group. Unfortunately, these all appear to be highly homoplasious and widespread among other Diptera, or dubious with respect to homology and polarity. Wood (1991) stated that the aedeagus is without a sperm pump in all Bibionomorpha *s.s.* except Hesperinidae (a family included in Bibionidae by Wood & Borkent, 1989), but this observation was not confirmed by Blaschke-Berthold (1994) who identified a small sperm pump and associated ejaculatory apodeme in an array of bibionid and sciaroid representatives.
- (3) Psychodomorpha *sensu* Wood & Borkent (1989) include Psychodidae, Trichoceridae, Perissomatidae, Anisopodidae and Scatopsoidea, i.e. a heterogeneous assemblage of non-Neodiptera (Psychodidae, Trichoceridae) and Neodiptera. They further suggested that a sister group relationship exists between Psychodidae and the remaining Psychodomorpha and, at a higher level, between Psychodomorpha and Ptychopteromorpha + Culicomorpha. These assumptions are all incompatible with the monophyly of Neodiptera.

Wood & Borkent (1989) proposed a single autapomorphy for Psychodomorpha + Ptychopteromorpha + Culicomorpha, five for Psychodomorpha, and three for Psychodomorpha less Psychodidae. These characters all refer to purported modifications in the larval mouth parts. However, the phylogenetic relationships of Psychodomorpha have been differently assessed by subsequent authors. Courtney (1990, 1991), in a phylogenetic analyses of Blephariceromorpha, proposed that this taxon might constitute the sister group of Psychodomorpha. Alternatively, Sinclair (1992), in a comparative study of the larval mandibles and associated structures of

Diptera, argued for a sister group relationship between Brachycera and Psychodomorpha.

For a critical appraisal of the alleged larval autapomorphies for Psychodomorpha *sensu* Wood & Borkent, see Oosterbroek & Theowald (1991: 215-217). These authors concluded, upon a detailed comparative study of tipuloid larvae, that Psychodomorpha are founded solely on character states which are either strongly subject to homoplasy, variably present within Psychodomorpha, or constitutive for more inclusive groups of Diptera. These conclusions are corroborated by the findings of the present work.

#### *Adaptive significance of neodipteran specializations*

Neodiptera represent a species-rich group of flies (100000+ described species) exhibiting extensive morphological and ecological diversity. They include tiny, fragile gall-midges, giant horse-flies and bizarre, apterous ectoparasites of bats. Nevertheless, the four specialized traits known for Neodiptera have been maintained practically unchanged in all lineages. This provides a weighty argument for considering them as adaptively important. Their association with the neck region also suggests that they could be functionally interrelated.

A soft and flexible neck region is very consistently present in insects, including the most heavily armoured ones. The ability to move the head independently of the thorax is essential for insect mobility notwithstanding drawbacks, such as increased vulnerability to attacks from predators and parasitoids. Devices for decreasing cervical exposure (permanent or temporary) have evolved repeatedly among insects. The ability to temporarily lock the head up against the prothorax may be the most common protective device. The neck region of 'polyneurax' Diptera in particular is comparatively large and exposed and it appears that head withdrawal provides little protection in these forms. It will here be argued that the cervical autapomorphies for Neodiptera are all adaptive, evolved and maintained to increase the protection of the neck region.

A moderate to extreme reduction of the dimensions of the occipital foramen and adjacent cervix seems characteristic of Neodiptera. This in effect diminishes the exposure of the entire neck region. The basis for this may have been the development of the precervicalia. These articular sclerites make the head less susceptible to movements of the laterocervicalia. The restricting effect of the precervicalia is inversely correlated to the distance between the occipital condyles. The other cervical specializations (development of a notal muscle which suspends the lateral basal angle of the laterocervicale; attachment of the laterocervicale to a flexible episternal lobe; development of an episternal muscle which both acts as protractor of coxa I and retractor of the episternal lobe) may function in concert as a device for effective withdrawal of the head tightly up against the prothorax.

The above considerations suggest that the novel, presumably protective, cervical specializations of Neodiptera have contributed to the 'fitness' and evolutionary success of the group. It should be emphasized, however, that some of the oldest branches of Neodiptera are presently poor in species (Scatopsoidea, Anisopodidae), or may even be approaching extinction (Perissomatidae, Axymyiidae). This signals that the innovations contributing most to the total, current success of Neodiptera are those which arose more recently, by adding to the neodipteran morphotype the extra

specializations acquired by the origin of such species-rich subordinate groups as Sciaroidea, Brachycera, Cyclorrhapha, and Schizophora.

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#### NOTE ADDED IN PROOF

After the completion of the present paper, I had the opportunity to examine adults of the eriopterine tipuloid, *Gnophomyia viridipennis* Gimmerthal, a species with well developed 'laterocervical fenestra'. The specimens were newly emerged and therefore possessed a fully developed set of transient thoracic muscles, i.e. muscles that supposedly are active only during eclosion and disintegrate shortly after. One of the transient muscles, the antecosta-laterocervical M. 3, was observed to have its point of insertion coinciding exactly with the 'fenestra'. From this I conclude that Bitsch's (1955) observation of a "canal glandulaire" in *Chionea* actually refers to rudiments of M. 3 arising from the 'fenestra'. It also follows that the evidence for the monophyly of the 'polyneurane' Diptera given in the present paper cannot be upheld.

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## APPENDIX

## Material examined

Taxonomic list of species (adults only) used for comparative study of the skeleton and musculature of the prothorax and cervix. Species marked with an asterisk (\*): only skeletal parts examined.

## TRICHOPTERA

- Rhyacophilidae: *Rhyacophila nubila* Zetterstedt  
 Polycentropodidae: *Holocentropus picicornis* Stephens

## LEPIDOPTERA

- Micropterigidae: *Micropterix aureatella* Scopoli  
 Adelidae: *Adela reaumurella* Linnaeus

## HYMENOPTERA

- Tenthredinidae: *Tenthredo mesomelas* Linnaeus

## MECOPTERA

- Panorpidae: *Panorpa communis* Linnaeus

## DIPTERA

- Trichoceridae: *Trichocera major* Edwards  
 Tipuloidea:  
 Pediciinae: *Ula sylvatica* Meigen; *Pedicia rivosa* Linnaeus; *Tricyphona immaculata* Meigen  
 Hexatominae: *Austrolimnophila ochracea* Meigen; *Phylidorea longicornis* Schummel  
 Eriopterinae: *Eriocnopa trivialis* Meigen; *Rhypholophus varius* Meigen  
 Limoniinae: *Limonia nubeculosa* Meigen; *Metalimnobia quadrinotata* Meigen  
 Cylindrotominae: *Diogma glabrata* Meigen

Tipulinae: *Tipula lateralis* Meigen  
 Tanyderidae: *Mischoderus annuliferus* Hutton  
 Ptychopteridae: *Ptychoptera contaminata* Linnaeus  
 Psychodidae:  
 Trichomyiinae: *Trichomyia urbana* Curtis  
 Psychodinae: *Pericoma nubila* Meigen  
 Blephariceridae:  
 Edwardsiniinae: *Edwardsina chilensis* Edwards  
 Culicomorpha:  
 Culicidae: *Culiseta annulata* Schrank  
 Simuliidae: *Simulium* sp.  
 Ceratopogonidae: *Mallochohelea nitida* Macquart  
 Chironomidae:  
 Tanypodinae: *Anatopynia plumipes* Fries  
 Chironominae: *Chironomus* sp.  
 Scatopsodea:  
 Synneuridae: *Canthyloscelis pictipennis* Edwards\*  
 Scatopsidae: *Scatopse notata* Linnaeus  
 Anisopodidae: *Sylvicola fuscatus* Fabricius  
 Axymyiidae: *Axymyia furcata* McAtee  
 Pachyneuridae: *Pachyneura fasciata* Zetterstedt\*  
 Sciaroidea:  
 Sciaridae: *Bradysia* sp.  
 Mycetophilidae: *Neoempheria lineola* Meigen  
 Cecidomyiidae: *Anarete* sp.  
 Bibionidae:  
 Pleciinae: *Penthetria appendiculata* Hardy  
 Bibioninae: *Bibio hortulanus* Linnaeus  
 Brachycera:  
 Tabanidae: *Chrysops relictus* Meigen  
 Rhagionidae: *Symphoromyia crassicornis* Panzer; *Rhagio scolopaceus* Linnaeus  
 Vermileonidae: *Vermileo vermileo* Linnaeus  
 Xylophagidae: *Xylophagus compeditus* Meigen  
 Stratiomyidae: *Beris chalybata* Forster; *Chloromyia formosa* Scopoli  
 Asilidae: *Dioctria atricapilla* Meigen  
 Therevidae: *Acrosathe annulata* Fabricius  
 Scenopinidae: *Scenopinus fenestralis* Linnaeus  
 Bombyliidae: *Bombylius major* Linnaeus  
 Empididae: *Empis tessellata* Fabricius  
 Platypezidae: *Agathomyia falleni* Zetterstedt  
 Lonchopteridae: *Lonchoptera tristis* Meigen  
 Anthomyiidae: *Hylemya vagans* Panzer