TABLE XI (*Continued*)

Psocus (Maki 1938)	*Stenopsocus* (Badonnel 1934)	Muscle designations	Remarks
38 60	E E E	p–cx 4	
16 36 58	e e′ e′	p–cx 5	
52 ?	H (II–III)	p–cx 8	5
	LVM 2(I–II)	s 11	
21 (I–II)	LVI 3 (II–III)	s 12	
20 (I–II) 45 (II–III)	LVL 2 LVL 3	s 13	
4 (I)	d 1, d 2	s 14	
	LVI 2 (I–II)	s 15	
	lv (III–2A)	s 20	
	X 2 (I–II) X 3 (II–III)	s–cx 1	
	Y (I) Y (II)	s–cx 2	
	J (I)	s–cx 4	
	J (II) J (III)	s–cx 6?	6
17 39 61	A A A	t–tr 1	
40 62	A′ A′ A′	p–tr 2	
41 (II) 63 (III)	a a	s–tr 1	

REMARKS (Table XI)

(1) These muscles are prothoracic tergopleural muscles, which are not homologized.

(2) Arising from the subalare, these muscles are attached on the remotor apodeme on the posterolateral coxal margin.

(3) Badonnel (1934) thought that h 3 was serially homologous with h 2, but h 3 is obviously inserted on the furca, and h 2 is on the spina.

(4) U in the pterothorax of *Stenopsocus* arises from the ventral margin of the phragma.

(5) In fig. 17 of Maki (1938) 52 appears to represent p-cx 8, although his description does not agree with his figure.

(6) J in *Stenopsocus* appears to be s-cx 6 or 3, not s-cx 4.

THE MALLOPHAGA

Of the genera referred to in the following discussion, *Tetrophthalmus* (Cope 1941), *Trimenopon*, and *Myrsidea* (Mayer 1954) belong to the suborder Amblycera; *Esthiopterum* (Cope 1940b), *Bovicola*, and *Columbicola* (Mayer 1954) belong to the suborder Ischnocera.

The neck region: The more generalized lateral cervical sclerite in *Columbicola*

occipital process; posteriorly the sclerite is connected with the episternum. Thus, in *Columbicola* the lateral cervical sclerite is not very different from that in Psocoptera.

In *Esthiopterum* (Fig. 97A) the lateral cervical sclerite is represented by a small sclerite that unites the head and the precoxal bridge of the propleuron. Peculiarly, in this genus, an additional dorsolateral cervical sclerite is present. In *Bovicola* the lateral cervical sclerite is absent.

In *Tetrophthalmus* (Fig. 98A), among Amblycera, the lateroventrally continuous cervical sclerite appears to represent a fusion of the lateral cervical sclerite and the dorsolateral cervical sclerite, which are present in *Esthiopterum* (Fig. 97A). In *Trimenopon* (Fig. 98E) and *Myrsidea* the lateral cervical sclerite is a small single plate, which connects the postoccipital ridge with the anterior end of the dorsally displaced pleural ridge. In these genera the sclerotized episternum and the epimeron have been lost, and the lateral cervical sclerite has acquired a direct connection with the pleural ridge.

The pronotum: In *Columbicola* (Fig. 97C) and *Esthiopterum* (Fig. 97A) the pronotum is a simple plate without subdivision, and it is clearly separated laterally from the pleuron. In *Bovicola* (Fig. 97B) a subtriangular plate is separated from the pronotal anterior margin, and the pronotum is laterally indistinguishably fused with the propleuron.

In amblycerous Mallophaga the process of modification of the pronotum appears to have been quite different. In *Trimenopon* (Fig. 98E), *Myrsidea*, and *Tetrophthalmus* (Fig. 98A), the pronotum has a median transverse ridge; and the ridge in *Trimenopon* is crossed by a longitudinal ridge.

In *Tetrophthalmus* (Fig. 98A) the pronotum is simply laterally fused with the propleuron, and the pleural ridge is bent caudad from a point near the presumed dorsal anterior angle of the propleuron. In *Myrsidea* the pleural ridge lies obliquely caudad and meets the transverse ridge of the pronotum. In *Trimenopon* (Fig. 98E) the dorsally displaced pleural ridge demarcates the lateral edge of the definitive pronotum, and its connection with the coxal margin has been lost. It is by its association with the furcal end and with the lateral cervical sclerite (as in *Trimenopon*) that this apparent pronotal lateral ridge can still be homologized with the pleural ridge. This pleural ridge appears at first glance to be serially homologous with a lateral ridge on the metanotum of the same species.

Mayer (1954) called the narrow area cut by the pleural ridge in *Trimenopon* and *Myrsidea* the paranotum. This paranotum naturally cannot be homologized with the paranotum in lower insects. The area may represent the proepimeron, since it is demarcated by the pleural ridge. In Amblycera an unpaired sclerite (prothoracic postnotum of Mayer) is present between the pronotum and the mesonotum.

The propleuron and prosternum: In *Columbicola* (Fig. 97C) the well-retained episternum is a simple plate, being undivided by sutures. Its anterior articulation with the coxa is either pleurocoxal or trochantinocoxal. The epimeron extends ventrally and forms a condyle that articulates with the coxa. The furcal arm is continuous with the posterior dorsal angle of the propleuron. In *Bovicola* (Fig. 97B) the strongly developed pleural ridge represents the anterior margin of the propleuron, and its ventral end is articulated with the coxal margin. A process from the posterior ventral margin of the coxa fits into a socket on the ventral anterior margin of the strongly ridged posterior margin of the epimeron, which merges with the sternum behind the coxa. A similar postcoxal bridge is formed in *Esthiopterum* and *Columbicola* (Fig. 97C), and a process from this area articulates with the ventral posterior margin of the coxa.

Among Amblycera, *Tetrophthalmus* (Fig. 98A) has a more generalized propleuron in which the sclerotized episterum and epimeron are well retained. The furcal arm is joined with the ventral part of the pleural ridge; the ventral articulation with the coxa is absent. Cope (1941) showed that in this genus the first thoracic spiracle lies in the proepimeron. In *Myrsidea* and *Trimenopon* the propleuron is nearly membranous. In
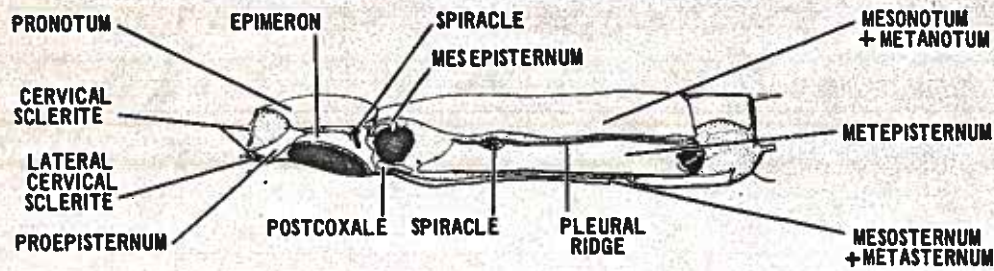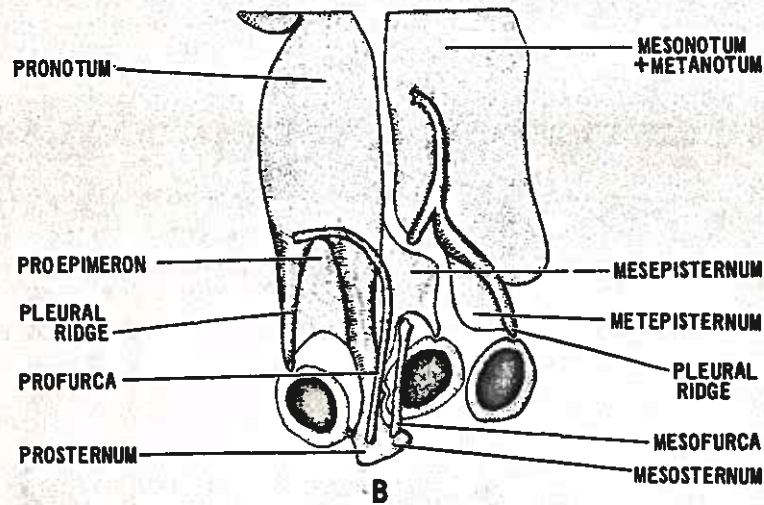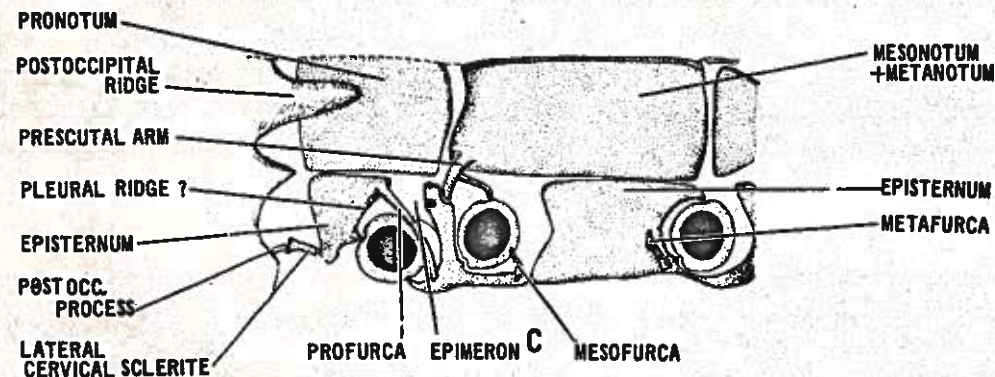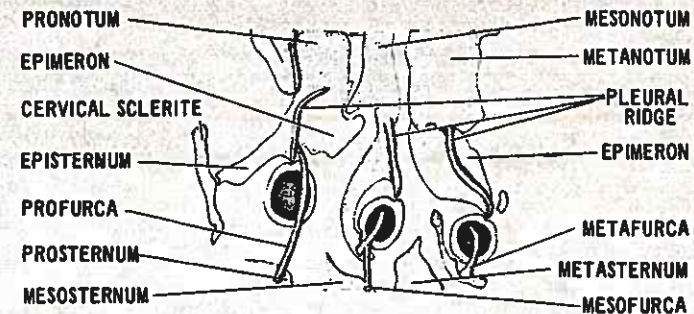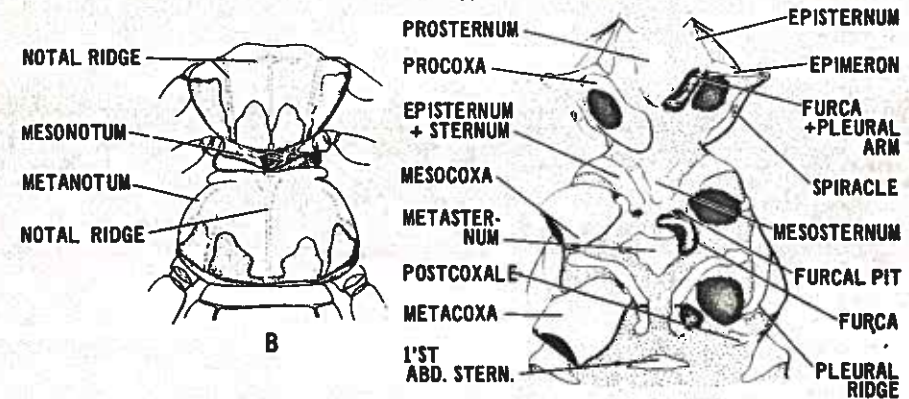
Fig. 97. A, lateral view of thorax in *Esthiopterum diomedeae* (from Cope); B, lateral view of thorax in *Bovicola caprae* (from Mayer); C, lateral view of thorax in *Columbicola columbae* (from Mayer).

Fig. 98. A, lateral view of thorax in *Tetrophthalmus* sp. (from Mayer); B, dorsal view of meso- and meta-thorax in *Trimenopon hispidum* (from Mayer); C, ventral view in *Tetrophthalmus* sp. (from Cope); D, ventral view in *Trimenopon hispidum* (from Mayer); E, lateral view of thorax in *Trimenopon hispidum* (from Mayer).

in *Trimenopon* (Fig. 98E) the reverse is true, there being only a ventral articulation with the coxa.
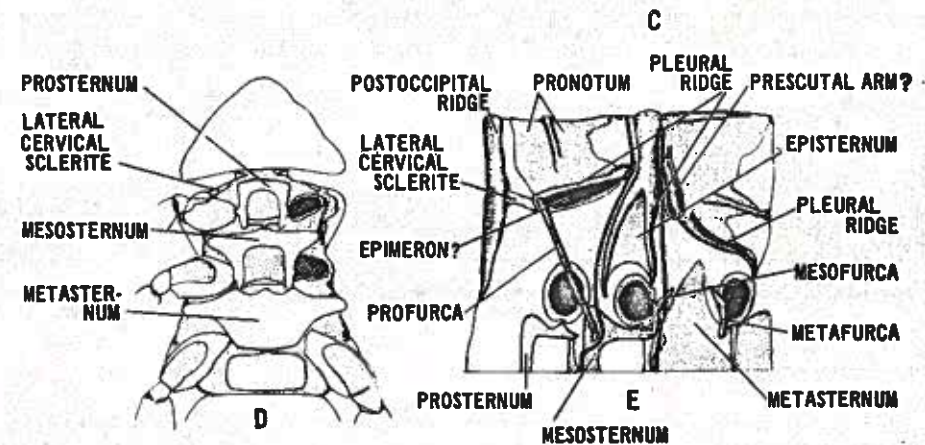
In *Trimenopon* (Fig. 98D, E) the ventral side of the prothorax is provided with a quadrangular sclerotization surrounding the median membranous area; a small median process on its posterior margin fits into a socket formed on the anterior margin of the

articulates with the inner coxal margin. The prothoracic furca arises from the lateral corner of the anterior bridge of this definitive mesosternal sclerotization (Fig. 98E). In *Myrsidea* (Fig. 99B) the sternal sclerotization is without a median membranization, and it has a process on its median posterior end. In *Tetrophthalmus* (Fig. 98C) the furcal bases lie more proximad.

In ischnocerous genera the ventral surface between the coxae is membranous. In *Bovicola* and *Esthiopterum* (Fig. 99A) the furcal pit lies on the postcoxo-sternal

The meso- and meta-notum: The division of the tergum into the prescutal, scutal, and scutellar areas is absent in the meso- and meta-notum of Mallophaga. In *Tetrophthalmus* (Fig. 98A) the meso- and meta-notum are distinctly separated by a membrane. In *Trimenopon* (Fig. 98B) the small mesonotum is strongly sclerotized and has a hollow, median apodeme which invaginates into the metanotum. The border between the metanotum and the metapleuron is strongly ridged. In *Trimenopon* (Fig. 98E) Mayer (1954) recognized the metathoracic prescutal arm (*Tergalarm* of Mayer), which is, however, probably a secondary formation. In *Myrsidea* a sclerotized mesonotal bar extends ventrally along the anterior margin of the mesopleuron to become continuous with the base of the sclerotized sternal bar. In all of these three genera of Amblycera, the mesonotum is smaller than the metanotum. In Ischnocera the mesonotum and metanotum are completely fused. In *Columbicola* (Fig. 97C) and *Esthiopterum* a median longitudinal ridge is present on this fused mesometanotum.

The mesopleuron: In *Tetrophthalmus* (Fig. 98A) the mesopleuron is fused with the mesonotum. The pleural ridge is a strongly sclerotized bar which forms a condyle for articulation with the coxa. The episternum is retained but without division. The anterior articulation with the coxa probably represents the trochantinocoxal articulation; in *Myrsidea* also, the anterior articulation probably represents the trochantinocoxal articulation. In *Trimenopon* (Fig. 98D) the ventral articulation is with the longitudinal sclerotized area along the inner margin of the coxa, and it does not seem homologous with the anterior articulation in *Tetrophthalmus* and *Myrsidea*. Both in *Trimenopon* (Fig. 98E) and in *Myrsidea* the pleural ridge becomes confluent with the transverse ridge of the mesonotum. In all of these three genera the mesopleuron is distinctly retained.

In *Columbicola* and *Esthiopterum* a conspicuous process arises from the anterolateral angle of the mesonotum (not shown in Fig. 97A). Mayer (1954) thought this process was the pleural apophysis (arm). In position, however, the process appears to correspond to the prescutal arm that occurs in the corresponding position in the metanotum of *Trimenopon* (Fig. 98E). In *Bovicola* the pleural arm and the pleural ridge are absent; they are apparently replaced functionally by the corresponding pleural arm and ridge of the metathorax (Fig. 97B). The pleural articulation with the coxa is present in all three genera of Ischnocera. In *Bovicola* (Fig. 97B) and *Columbicola* (Fig. 97C) a process on the posterior margin of the definitive propleuron articulates with a socket on the ventral anterior margin of the mesocoxa. In *Esthiopterum*, however, the corresponding process is formed on an isolated plate behind the propleuron, and this condition is probably more primitive than that in *Bovicola* and in *Columbicola*. If the isolated plate in *Esthiopterum* becomes fused with the propleuron, the condition present in *Bovicola* and *Columbicola* would result.

The mesosternum: In *Tetrophthalmus*, as Cope (1941) showed (Fig. 98C), the episternal sclerotization extends ventrally along the inner margin of the coxa, and the furcal pit lies at its caudal end. In *Myrsidea* (Fig. 99B) the sclerotized bar from the pleuron is continuous along the inner margin of the coxa, and merges with the median ventral sclerotization which unquestionably represents the sternum. In *Trimenopon* (Fig. 98D) the sclerotization along the inner margin of the coxa is continuous with the anterior transverse sclerotization.

In *Esthiopterum* (Fig. 99A) a small lateral plate along the inner coxal margin bears the furcal pit; in *Columbicola* this lateral plate is continuous with the episternum; in *Bovicola* (Fig. 98B) the mesosternum is continuous with the prosternum. In both Amblycera and Ischnocera the furcal arm is not fused with the pleural arm or ridge.

The metapleuron: In *Tetrophthalmus* (Fig. 98A) and *Trimenopon* (Fig. 98E) the articulation of the pleural ridge with the coxa is dorsal or posterodorsal, and in *Myrsidea* posteroventral. In *Myrsidea* the anterior articulation lies on the anterodorsal coxal margin; the condyle for this articulation is formed on a narrow sclerite with a strong anterior ridge that Mayer called the trochantin (Fig. 99B). The corresponding anterior articulation with the coxa in *Trimenopon* and *Tetrophthalmus* lies more ventrad than in *Myrsidea*
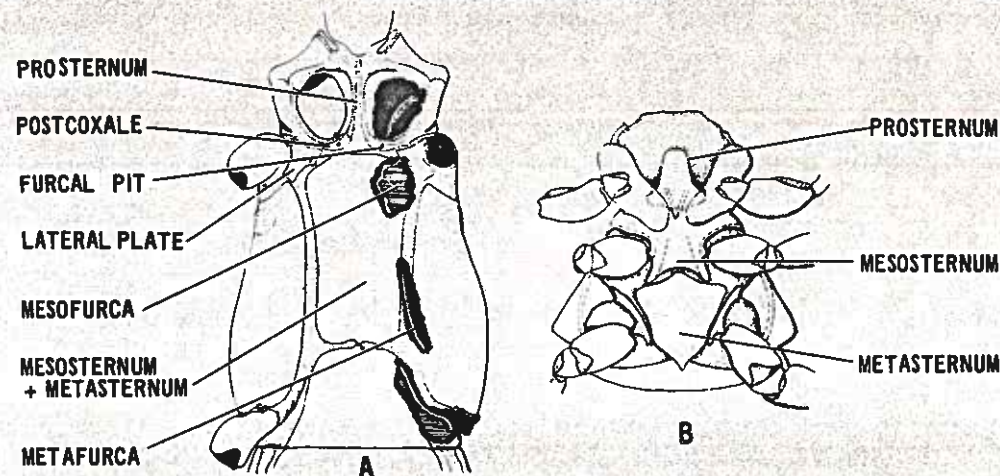
Fig. 99. A, ventral view of *Esthiopterum diomedeae* (from Cope); B, ventral view of thorax in *Myrsidea cornicis* (from Mayer).

In *Esthiopterum* (Fig. 97A) the pleural ridge runs horizontally forward from the dorsal point of articulation with the coxa. The large metapleuron below the ridge is therefore the episternum. The anterior articulation with the coxa, which Cope (1940b) did not show but Mayer (1954) showed, may be the trochantinocoxal articulation, as in Amblycera. As Cope (1940b) showed, the second thoracic spiracle lies on the anterior third of the dorsal margin of the pleuron (i.e. pleural ridge). In *Columbicola* (Fig. 97C) the metapleuron is somewhat similar to that of *Esthiopterum*. According to Mayer (1954), however, a distinct pleural ridge is absent. The second thoracic spiracle lies on the closed membrane between the metanotum and the metapleuron. In *Bovicola* (Fig. 97B) the greatly developed pleural ridge extends into the tergal area, and the anterior articulation with the coxa is absent.

The metasternum: In *Tetrophthalmus* (Fig. 98C) the episternal sclerotization extends ventrally along the inner coxal margin and the furcal pit lies on this extension. A triangular, anteromedian sternal plate lies between the lateral sclerotizations. In *Myrsidea* (Fig. 99B) the median subtriangular sclerotization is much more extensive than in *Tetrophthalmus*, and in *Trimenopon* (Fig. 98D) the lateral and median sclerotizations have become indistinguishably fused.

In *Columbicola* and *Esthiopterum* (Fig. 99A) the fused, median mesometasternal plate is separated from the lateral sclerotization continuous from the episternum. The furca arises from the ventral margin of the latter. In *Bovicola* the sternal area is not sclerotized.

The adult musculature: Mayer (1954) described the thoracic muscles of *Trimenopon hispidum*, *Myrsidea cornicis*, *Bovicola caprae*, and *Columbicola columbae*. They are shown in Table XII.

It is difficult to homologize these muscles with those in other orders, because of shifts in points of origin and insertion. The most pronounced shifts have evidently resulted from the great reduction of the mesothorax, and often the mesothoracic muscles have acquired new points of origin on the metathorax. The transsegmental distributions of some other muscles in this order are also secondary.

Generally, the amblycerous genera have retained more muscles than the ischnocerous genera. It is interesting to note that muscle p-s 5 is well retained, a feature that is also shared by Psocoptera. The relative abundance of ventral muscles also indicates a close relationship of this order to Psocoptera, although some of the muscles have shifted their points of attachment.

TABLE XII

Thoracic musculature in Mallophaga

Trimenopon (Mayer 1954)	Myrsidea (Mayer 1954)	Bovicola (Mayer 1954)	Columbicola (Mayer 1954)	Muscle designations	Remarks
	I dlm 2		I dlm 2	op-t 1	
I dlm 1	I dlm 1	I dlm 1	I dlm 1	op-t 3 or cv(d)-t 1	
0, I lm 1	0, I lm 1	0, I lm 1	0, I lm ?	op-p 1, op-s 2	1
0, I lm 2	0, I lm 2	0, I lm 2		t-cv 1 or 2	2
	0, I trm			cv-cx(x) 1	
0, I vlm 1	0, I vlm			s 1 or 2	
I dlm 4 / III dlm 2	I dlm 4 / III dlm 2	I dlm 2	I dlm 3 / III dlm	t 12	
I dlm 2, 3 / III dlm 1	I dlm 3 / III dlm 1	III dlm		t 13	
I tpm 1	I tpm	I tpm	I tpm	t-p?	3
I tpm 2, 3, 4				t-p?	3
II tpm				t-p?	3
III tpm		III tpm		t-p?	3
III tfm	I, II ism 1 / II, III ism 1 / III tfm			t-s 1	4
I dvm 1 / II dvm 1 / III dvm 1?	I dvm 1 / II dvm 1 / III dvm 2	I dvm 1 / II dvm 1	I dvm 1 / II dvm 2(pars) or dvm 1	t-ti(cx) 2	5
II dvm 2			II dvm 1?	t-ti(cx) 3	5
I dvm 2 / II dvm 3 / III dvm 2	I dvm 2 / II dvm 3 / III dvm 1	I dvm 2 / II dvm 2 / III dvm 1	I dvm 2 / II dvm 2 / III dvm	t-cx 6 or 7	5
II pm 2 / III pm 1	II pm 2	III pm 2?		t-cx 8?	
III pfm	III pfm			p-s 1	
I, II ism / II, III ism	I, II ism 2 / II, III ism 2	II, III ism	I, II ism / II, III ism	p-s 5	
I pm 1 / II pm 1	I pm 1 / II pm 1	I pm 1	I pm 1?	p-ti(cx) 2 or 3	
		III pm 1	III pm		
I, II vlm 1 / II, III vlm 1 / III, la vlm 1	I, II vlm / II, III vlm 1 / III, la vlm	I, II vlm	I, II vlm / II, III vlm	s 13	
II, la vlm		II, la vlm		s 15 ? or p-s 10	6
I trm / II trm 1 / III trm 1	II trm 1 / III trm 1	I trm / II trm 1	I trm / II trm 1 / III trm	s 16	
III trm 2	III trm 2			s 20 ?	7
I bm 2 / III bm 2	I bm 1	I bm		s-cx 3	
II trm 2	II trm 2	II trm 2	II trm 2	s-cx 4 ?	8
I bm 1 / II bm / III bm 1				s-cx 5	
II, III vlm (cx)	II, III vlm (cx) 1	II, III vlm (cx) 1	II, III vlm (cx) 1	s-cx 7	
		II, III vlm (cx) 2	II, III vlm (cx) 2	s-cx 7 ?	9
I dvm 3 / II dvm 5 / III dvm 3	I dvm 3 / II dvm 3 / III dvm 3	II dvm 3 / III dvm 2	II dvm 3	t-tr 1	

TABLE XII   (Continued)

Trimenopon (Mayer 1954)	Myrsidea (Mayer 1954)	Bovicola (Mayer 1954)	Columbicola (Mayer 1954)	Muscle designations	Remarks
I pm 2	I pm 2 / III pm 3	I pm 2	I pm 2	p-tr 1	
I bm 3	I bm 2		I bm	s-tr 1	
	II, III vlm (cx) 2		II, III vlm (cx) 3	s-tr 1 ?	10

REMARKS (Table XII)

(1)   0, I lm in *Columbicola* is inserted ventrally on the coxal margin; 0, I lm 1 in *Bovicola* is inserted on the pleural ridge; 0, I lm 1 in *Trimenopon* and *Myrsidea* is inserted on the dorsally extended furca.

(2)   0, I lm 2 in *Bovicola* is inserted anteriorly on the postoccipital ridge. This is probably due to a secondary shift that has accompanied the loss of the lateral cervical sclerite.

(3)   I tpm muscles cannot be homologized.

(4)   II, III ism 1 in *Myrsidea* arises from the middle of the metanotum. Presumably this is due to shift backward of the origin of the muscles. III tfm in *Myrsidea* arises from near the lateral margin of the metanotum.

(5)   Dorsal and ventral points of attachment of these muscles vary considerably in different genera. Homologizations are based on the positions of muscles on the coxal margin relative to the points of pleurocoxal articulation. The homologies proposed here differ considerably from those proposed by Mayer (1954).

(6)   These muscles extend between the mesofurca and the first abdominal sternum, and may be p-s 10. Usually s 15 extends between the profurca and the second spina.

(7)   III trm 2 in *Trimenopon* extends from the metafurca to the membranous fold between the metasternum and the first abdominal segment; the same in *Myrsidea* stretches the area between the metafurca and the median line of the metasternum.

(8)   II trm 2 connects transversely the mesothoracic coxae. This muscle is probably the derivative of s-cx 4. The loss of the second spina has apparently resulted in the direct connection of mesocoxae by this muscle.

(9)   These muscles connect the basal part of the mesofurca and the posterior margin of the metacoxa.

(10)   These muscles arise from the mesofurca and are inserted on the trochanteral apodeme of the hind leg. The derivation by these muscles is quite unclear.

THE ANOPLURA

Ferris (1951) studied the thorax of *Solenopotes capillatus, Pediculus humanus,* and *Haematopinus suis.* In all three species the tergum, the pleuron, and the sternum of three thoracic segments are continuously fused and largely membranous. Ferris used the internal phragmata, which clearly correspond to the internal ridges in Mallophaga, as the landmarks for determination of segmental boundaries, as well as for determination of original divisions of a segment into the tergum, the pleuron, and the sternum. As Ferris showed, the phragma (ridge) distally (laterally) articulates with the coxal margin of all three segments (Fig. 100A, B). He, therefore, homologized it with the pleural ridge in other insects.

In *Solenopotes* (Fig. 100A) the phragma (ridge) extends dorsally to meet its counterpart from the other side on the median longitudinal axis of the body. Since, according to Ferris, these ridges are homologous with the pleural ridge, Ferris had to