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THE VENTRAL INTERSEGMENTAL THORACIC MUSCLES OF COCKROACHES

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The cockroaches, which have persisted in much their present outward form since the Carboniferous, are admittedly rather primitive in many structural respects. Although one dares not take for granted that their musculature also retains a primitive configuration, there is a good *a priori* chance that this is the case; and comparisons with other primitive types, such as *Grylloblatta* (Walker, 1938, 1943), the larvae of *Dytiscus* (Speyer, 1922) or *Cybister,* and larval or adult Megaloptera, to my mind leave no doubt that the muscular pattern of blattids displays many primitive characteristics.

In this paper attention will be called to certain of these features, as they are seen in the ventral intersegmental musculature of the thorax. This system of muscles, though far from homogeneous morphologically, provides a convenient segment of the total thoracic musculature for analysis. It may also be regarded as itself a relatively primitive component of pterygote anatomy, for study of the more recently evolved, highly specialized flying insects shows the ventral intersegmental muscles of the thorax gripped in an evolutionary trend that has already led to the drastic reduction of these muscles and that may ultimately result in their total disappearance. In contrast, the cockroaches and other less advanced forms still exhibit a wealth of muscles in this category, and thus afford some conception of this portion of the ancestral basis from which the more adept flying insects of today have developed.

Descriptions of the thoracic musculature have already been published for three blattid species: *Blatta orientalis* L., by Miall and Denny (1886); *Periplaneta australasiae* (L.), by Maki (1938); and *P. americana* (L.), by Carbonell (1947). Miall and Denny purposely gave only a general account; and comparisons of the reports by Maki and Carbonell discloses more numerous and in some instances more

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striking differences among the ventral intersegmental muscles than one would ordinarily expect from members of the same order, not to say genus. Since a precise knowledge of the distribution of the ventral muscles is essential if one is to draw from them conclusions concerning thoracic evolution, a reinvestigation of these species was made, in the course of which it became apparent that familiarity with a wider variety of blattids would be helpful. Eventually 19 species were examined. The discussion below attempts to extract from this material information that illuminates certain important facets of the evolution of the thorax in winged insects.

METHOD AND MATERIAL

Specimens from culture were etherized, pinned venter-down in a wax dish, and covered with water. Under binoculars, the dorsal integument was carefully cut away from thorax and abdomen, after which the ventral system of muscles was gradually exposed by removing structures that interfered with the view. A few details were checked from other angles. Liberal staining with 1 percent methylene blue from time to time in the course of dissection proved helpful, and brief hardening in 70 percent alcohol was occasionally resorted to. The magnification used was 12.5 to 50 times. At various stages of dissection drawings were made to scale on squared paper with the aid of a micrometer eyepiece.

P. americana (L.), *Blaberus craniifer* (Burm.), *Blatta orientalis* L., *Blattella germanica* (L.), and *Supella supellectilium* (Serv.) were available in our laboratory. Cultures of the following species were supplied through the generosity of F. H. Babers, J. H. Fales, W. L. Nutting, L. M. Roth, P. R. Ruck, C. N. Smith, and E. R. Willis: *P. australasiae* (L.), *P. brunnea* Burm., *P. fuliginosa* (Serv.), *Blaberus giganteus* (L.), *Blattella vaga* (Heb.), *Cryptocercus punctulatus* Scud., *Diploptera dytiscoides* (Serv.), *Eurycotis floridana* (Walk.), *Leucophaea maderae* (Fabr.), *Nauphoeta cinerea* (Oliv.), *Neostylopyga rhombifolia* (Stoll), *Parcoblatta pennsylvanica* (DeGeer), and *Pycnoscelus surinamensis* (L.). A single preserved specimen of *Macropanesthia rhinocerus* Sauss. also was dissected. The 19 species investigated were chosen mainly on the basis of availability and are but a small fraction of the more than 3,500 species of cockroaches that (*fide* Rehn, 1951) have been described.

Nymphs and adults of both sexes were examined for most species, although few differences attributable to stage or sex were found among the msucles to which the present investigation was confined. For comparison, data were obtained from the literature or from the writer's dissections for representatives of a number of other orders. All observations cited in this paper without a statement as to source are from my own work.

Each morphologically distinct muscle was given a designation formed by hyphenating the accepted abbreviations for the skeletal parts between which the muscle is stretched. Under this system, if an attachment is segmental, the segment is identified by an arabic or roman postsubscript for the thorax or abdomen, respectively, while the designations of intersegmental structures are preceded by the appropriate arabic numeral, beginning with *0* for the cervical intersegment. *Exception:* the customary abbreviations *1cv, 2cv* . . . for the cervical sclerites, and *1ax, 2ax* . . . for the axillary sclerites of the wing, the latter with segmental subscripts, are retained. Cruciate muscles, with origin and insertion on opposite sides of the longitudinal body axis, are distinguished by adding X to the usual designation. The skeletal abbreviations used are for the most part those given currency by Snodgrass (1929, and numerous other publications).

Examples: $2sps\text{-}eps_3$, a muscle stretched between the second (postmesothoracic) spina(sternite) and the metepisternum; $fu_3\text{-}s_{IIA}$, the longitudinal ventral muscle from the metafurca to the second abdominal sternum; $eps_2\text{-}cx_1X$, a cruciate muscle of the procoxa, with origin on the contralateral mesepisternum.

A glossary of abbreviations is given at the end of the text.

OBSERVATIONS AND INTERPRETATION

The ventral intersegmental muscular system of the blattid thorax includes elements with primary attachments on the spinae (*sps*) or on the intersegmental laterosternites (*ils*), as well as furcal (*fu*) muscles that run between successive segments. This report is divided accordingly into three main sections.

I. THE SPINAE

Cockroaches have two authentic spinae (*1sps, 2sps*), and in addition possess in the third thoracic intersegment a common junction of serial homologs of the more anterior spinasternal muscles that lacks the median connection with the integument but obviously represents a postmetathoracic spina. This junction (*"3sps"*) is attached by fibrous ligaments (figs. 4, 6, 7, 9, 10, 18: *27*) to the bases of the metathoracic furcal arms (fu_3), between which it floats above the nerve cord. Comparative evidence leaves little doubt that these noncontractile ligaments, which now usually appear as $fu_3\text{-}fu_3$, have been derived from former muscles, $3sps\text{-}fu_3$. A true third spina, which occurs in some Apterygota (Maki, 1938), is known among pterygote insects only in *Grylloblatta* (Walker, 1938, 1943), but an arrangement much like that of blattids has been reported for larval *Dytiscus* (Speyer, 1922) and has also been seen in larval *Cybister,* in *Zootermopsis* (fig. 6), and in larval and adult *Corydalus.* Other vestiges of the third spina and its musculature have been found but not recognized as such by several students in a number of other insects. Altogether, the facts constitute strong evidence that a third spina was present in the ancestral Pterygota, and probably in early hexapods generally.

More thoroughly documented, since much of the testimony is still available in a variety of living forms, is a general tendency toward loss of the remaining spinae and their associated musculature during the post-Carboniferous evolution of the pterygote thorax. Certain cockroaches, however, have gone contrary to this trend, and have experienced a prodigious extension of the first spina and, to a lesser extent, the second, in the direction of the body axis. Compare, for example, figure 1 with figure 2, or 17 with 18. This spinal elongation is related, in part, to hypertrophy of the transverse spinal musculature ($1sps\text{-}eps_2$, $2sps\text{-}eps_3$); and it is probably no coincidence that several species that manifest this development have also exceptionally large transverse muscles of the first abdominal intersegment, $s_{IIA}\text{-}s_{IIA}$ (figs. 1, 8, 11, 12: *34*). My judgment that these characteristics are secondary rests partly upon the fact that they are peculiar to some blattids, being unparalleled in others and absent, so far as I know, in any other group of insects; and partly upon the presence in the musculature of these same cockroaches of other trends away from a primitive condition, such as a tendency toward loss of certain spinacoxal muscles. (See c, this section, below.)

Table 1 provides a composite list of the spinasternal muscles of blattids, as these are now known, and is so arranged as to indicate the probable serial homologies. Most species possess a very large fraction of the total complement. The relatively few exceptions are summarized in footnotes to the table, and some of them are discussed briefly in the text. Included in the spinasternal musculature are (a) transverse spinal muscles; (b) spinal muscles of the preceding or succeeding furca; (c) spinal muscles of the preceding or succeeding coxa; (d) muscles stretched between successive spinae; and (e) spinabdominal muscles. Each of these groups is discussed under the corresponding subheading below.

a. *Transverse spinal muscles.*—The transverse muscles of cock-

TABLE 1.—*Spinasternal muscles of cockroaches*

In this composite list, muscles that appear on the same horizontal line are considered serially homologous. Question marks indicate uncertain homologies. Symbols such as M*40*, C*103* refer to the numbers given the corresponding muscles in *P. australasiae* by Maki (1938) and in *P. americana* by Carbonell (1947). Each of the 19 species investigated here has all muscles shown in the table, except as stated in the notes below or in the text. For muscles without spinasternal attachments, see table 2.

Footnote number	*First spina*	*Second spina*	*"Third spina"*
1,a	*1sps-1ils*	*2sps-2ils*	---
1,b	*1sps-*eps_2 M*40*; C*103*	*2sps-*eps_3 M*74*; C*149*	—
2	*1sps-*fu_1 M*8*; C*99*	— M*41*	*"3sps"-*fu_3 M*105* (*partim*)
3	—	*2sps-*fu_1 C*101*	—
4	*1sps-*fu_2 C*104*	*2sps-*fu_3 M*73*; C*151*	? *"3sps"-*s_{IIA} M*104*; C*191* ?
5	—	*2sps-*s_{IIA} C*189*	—
6	*1sps-*cx_1 M*24, 25*; C*98*	*2sps-*cx_2 M*56*; C*134*	? fu_3-cx_3 *post. rot.* (*partim*) M*88, 89*; C*171*
7	*1sps-*cx_2 C*105*	*2sps-*cx_3 C*173*	—
8	*1sps-2sps* M*39*; C*106*	*2sps-3sps* M*72*; C*152*	? *"3sps"-ventr. diaphr.* M*105* (*partim*)

[1] *Cryptocercus* has both 1,a and 1,b; other species 1,b only. The abdominal transverse muscle, s_{IIA}-s_{IIA} (M*112*, is a serial homolog.

[2] Muscle *2sps-*fu_2 is lacking; Maki's record (M*41*) is probably an error of transcription. (See text.)

[3] No comment.

[4] Carbonell (1947, p. 20) describes muscle *191* in *P. americana* as follows: "Oblique ventral muscle. . . . From the base of the sternal arm to the anterior edge of the first [sic!] abdominal sternum."

[5] Abdominal insertion wholly or partly on s_{IIIA} in *Eurycotis, Macropanesthia, Neostylopyga,* and *Periplaneta brunnea.* (See text.)

[6] Several species have two definitive muscles, *1sps-cx1*, one of which is probably equivalent to the eps_2-fu_1X of other species. (See figures and text.) In listing two furcal posterior rotators of the third coxa, Maki (1938) suggests that one of them may be serially homologous with the spinal posterior rotators of the other legs. (See text for discussion.)

[7] *Blaberus, Diploptera, Cryptocercus, Leucophaea, Macropanesthia, Nauphoeta,* and *Pycnoscelus* lack *1sps-*cx_2; the last five genera also lack *2sps-*cx_3.

[8] The fibers from *"3sps"* to the ventral diaphragm were not found in several species, but were possibly destroyed during dissection in some of these.

roaches are regularly present in the first two thoracic intersegments but absent in the third, where their failure to appear is no doubt related to the near obliteration of the ventral region of the first abdominal segment, reduction of which is a very general and probably very early feature of pterygote reorganization. However, the transverse muscles are represented in the abdomen by the muscular attachments of the ventral diaphragm on the anterior lateral angles of the second abdominal sternum. A striking development of these abdominal fibers is seen in the series *Pycnoscelus, Diploptera, Nauphoeta, Leucophaea,* in which last they attain the status of a powerful transverse muscle, s_{IIA}-s_{IIA} (figs. 1, 8, 11, 12: *34*). The function of such a muscle is unknown. Curiously, *Blaberus, Cryptocercus,* and *Macropanesthia* (figs. 5, 10, 17), which share other peculiarities of the four genera just mentioned, do not show any tendency toward hypertrophy of the transverse muscle of the ventral diaphragm, and in this respect are more like the other species included in this study. The lateral suspensions of the ventral diaphragm are not evident in the abdominal intersegments posterior to the first; and in general the ventral diaphragm of cockroaches is much less extensive than that of some other insects, e.g., phasmids and the acridid Orthoptera.

Some authors have listed as transverse muscles structures such as the ligament fu_3-fu_3, whose affinities are, however, with the spinafurcal muscles.

b. Spinafurcal muscles.—Cockroaches all have the muscle $1sps$-fu_1 and "$3sps$"-fu_3, the latter represented, as a result of loss of the third spina, by fibrous ligaments that often appear as a single transverse band, fu_3-fu_3. A corresponding $2sps$-fu_2 does not occur in any blattid I have examined, and I believe Maki's record of this muscle (1938, fig. 6, No. 41) in *P. australasiae* must rest on an error of transcription, since all cockroaches have another, larger muscle, $2sps$-fu_1, that is omitted from his figure and description.

Miall and Denny's (1886) statement that the muscle $2sps$-fu_1 is inserted on the base of the first leg in *B. orientalis* is misleading, for the connections in *B. orientalis* (fig. 2: *16*) are identical with those of other cockroaches; but the description reflects Miall and Denny's awareness of a structural difference between the prothoracic sternal arm and those of other segments, a distinction that seems to have escaped comment by most others who have investigated the musculature of cockroaches. (See section 3, below.)

The muscles $1sps$-fu_2 and $2sps$-fu_3 are also universally present in blattids as is their possible serial homolog, "$3sps$"-s_{IIA}, which is here discussed under the spinabdominal muscles. (See e, this section, below).

c. *Spinacoxal muscles.*—The first and second spinae both carry posterior rotators (or remotors) of the preceding coxa ($1sps\text{-}cx_1$, $2sps\text{-}cx_2$) in all blattids examined. A corresponding muscle of the third spina is absent as such, but may be represented, as already suggested by Maki (1938), in the muscle $fu_3\text{-}cx_3$ *post. rot.*, which frequently shows signs of a dual composition. In some specimens, a few of the fibers of $fu_3\text{-}cx_3$ *post. rot.* appear to be continuous with those of the ligament $fu_3\text{-}fu_3$. Only in larval *Dytiscus* (Speyer, 1922), in *Grylloblatta* (Walker, 1938, 1943), in *Zootermopsis* (fig. 6: *29*), and in the larvae of *Cybister* and *Corydalus* has a distinct muscle, $3sps\text{-}cx_3$, been found; and in these species the muscle $fu_3\text{-}cx_3$ *post. rot.*, which is also present, seems to be a single band.

Spinal *promotors* of the mesocoxa and metacoxa ($1sps\text{-}cx_2$, $2sps\text{-}cx_3$) also occur frequently in cockroaches, as they do in other primitive forms. However, the mesocoxal promotor is absent in *Blaberus, Diploptera, Leucophaea, Macropanesthia, Nauphoeta,* and *Pycnoscelus;* and the last four of these genera also lack the metathoracic homolog. Both spinal promotors are likewise missing in *Cryptocercus,* which shares to some extent the tendency of these genera toward hypertrophy of the transverse muscles of the first spina although it differs markedly from them in certain other respects. In some other cockroaches, e.g., in *Blattella,* the spinal promotors, though present, are weak. Thus, the trend toward obliteration of these muscles, which has gone far among higher orders of insects, is evident even among the Blattariae.

d. *Spinaspinal muscles.*—The muscles *1sps-2sps* and *2sps-"3sps"* were found in all the species studied here, although they are at times weakly developed and easily overlooked; this is particularly true of *2sps-"3sps."* The first of these muscles is present also in most Orthoptera (*sensu stricto*) and Mantodea, but not in other orders with the possible exception of Isoptera, where it was recorded by Fuller (1924, fig. 9, muscle *n*) for *Termes latericius* Hav. Since this muscle does not occur in other termites studied by Maki (1938) and the writer, it may be that Fuller misjudged the posterior attachment of his muscle *n,* which perhaps represents $1sps\text{-}fu_2$, a muscle missing from Fuller's account but present in all Isoptera studied by others.

The muscle *2sps-"3sps"* has so far been recorded only from blattids, where its general occurrence may be taken as one more indication of primitive structure. What is probably a vestige of this muscle has been found in the immature mantid, *Tenodera sinensis* Sauss. (fig. 7: *23*).

The spinaspinal muscles are the only portion of the longitudinal ventral musculature that has obviously retained its primary relationships in blattids. Both attachments are still unmistakeably intersegmental. Like the other somatic muscles, the spinaspinal muscles are paired bilaterally; but the right and left bands of *1sps-2sps* are often so closely appressed in the midline that they seem like a single element, and they have been so described by some authors. The posterior insertions of *2sps-"3sps"* are usually well separated on the ligament fu_3-fu_3 (e.g., fig. 9: *23*), and in some instances may even seem to be on fu_3 at the site of attachment of the ligament. Care must be taken, therefore, not to confuse them with the usually better developed spinafurcal muscles, *2sps-*fu_3, from which they are morphologically distinct.

The ligament fu_3-fu_3 also serves, in several cockroaches, as a base of attachment for paired muscular strands that course posteriorly to join the meshwork of contractile fibers and membrane that constitutes the ventral diaphragm (figs. 2-5, 8, 11, 18: *30*). These strands, *"3sps"-ventr. diaphr.*, may be serial homologs of the muscles *1sps-2sps, 2sps-"3sps."* I did not succeed in finding these delicate strands in all species, but could not be sure, in the cases where they seemed absent, that I had not destroyed them.

In pterygote insects, there is no homolog of the spinaspinal muscles anterior to *1sps;* but Maki (1938) has recorded muscles that are probably homologous in the prothorax of some Apterygota.

e. *Spinabdominal muscles.*—The spinabdominal muscles of cockroaches include only *2sps-*s_{IIA}, *"3sps"-*s_{IIA} and *"3sps"-ventr. diaphr.* The last two have already been mentioned in this section, b and d, above. They arise on the ligament fu_3-fu_3, and not on the base of fu_3 as some have stated. The muscle *2sps-*s_{IIA} is characteristic of blattids, and is present in all of them I have seen, though it is weak in *Leucophaea.* Elsewhere, it has been recorded only from *Grylloblatta* (Walker, 1938, No. *111b*). It is interesting as an example of a muscle more than one segment in length, a type that is of infrequent occurrence in pterygote insects. In *Macropanesthia, Periplaneta, Eurycotis,* and *Neostylopyga* the abdominal insertion of some or all the fibers is actually on s_{IIIA}. Apparently this modification may occur readily because *2sps-*s_{IIA} is ordinarily inserted along the antecosta of s_{IIA} dorsal to the usual longitudinal bands, s_{IIA}-s_{IIIA}, with which *2sps-*s_{IIA} is more or less continuous. Dissolution of the integumental attachment at s_{IIA} adds one segment of muscle to the length of $2sps\text{-}s_{IIA}$; and this step, to judge by various instances observed, leads to an intervening stage in which the now floating muscle is still divided by a transverse septum at the original level of attachment on s_{IIA} (figs. 3, 17: *21*). Subsequently, all signs of the septum are lost. Reduction of the ventral region of the first abdominal segment has doubtless contributed to developments of this nature, which are not confined to cockroaches or to the particular muscle in question (cf. fig. 11 : *32*).

2. THE INTERSEGMENTAL LATEROSTERNITES

Intersegmental laterosternite (*ils*) is a term here introduced for sites of muscle attachment that lie at the lateral extremities of the ventral intersegmental folds. Such sites are believed to have been characteristic features of the anatomy of early arthropods in all intersegments. In existing forms, extensive modification of the original relationships is the rule, as will be seen below; nevertheless, recognition of the presence and nature of these sites is helpful in understanding the manner in which the ventral musculature and associated structures have evolved.

Primitively, the musculature of the *ils* included (1) the transverse muscles, which, with or without interruption by a median spina, stretched between the two *ils* of the same intersegment; (2) the outermost bands of the ventral longitudinal body musculature; (3) certain dorsoventral muscles; and probably (4) other muscles of various types, some of which will be noted below. However, the original muscular relationships of the *ils* are still not fully understood; and this fact, together with their varied fate in different lines of descent and in different parts of the body, presents the comparative morphologist with many perplexing problems. Hence, it is not surprising that structures equivalent to the *ils* as here defined have been overlooked by some workers and variously named in different situations by others. Several have referred to them as "intersegmental pleurites," a term which is unsatisfactory both because of the obvious sternal nature of the structures in question and because use of the name "pleurite" in reference to intersegmental elements is self-contradictory. Crampton (1926) avoided these objections by employing the term "furcilla." Unfortunately, this usage of "furcilla" seems likely to cause confusion, because the name had been applied in various other senses by earlier workers and because it suggests a nonexistent affinity with the segmental sternal apophyses, or "furcae" (*fu*). For these reasons, we have substituted the more accurately descriptive designation *"ils."*

The principal primary muscular relationships of the *ils* are tolerably well preserved in the typical abdominal intersegment, granted that a secondary extension of sclerotization has here merged the intersegment indistinguishably with the following segmental sternal plate, of which the former intersegment now forms the antecosta (Snodgrass, 1929). The *ils* are here represented in the anterolateral angles of the definitive abdominal sterna, which in many insects display the muscular relationships outlined above (Ford, 1923; Maki, 1938).

In the intersegments that follow each of the three thoracic segments, the situation is rarely so transparent. One gains the impression that, even in the most primitive forms that have come to hand, the musculature of the *ils* has already been subject to extensive shifting and reduction, while in more recent insects only a few scattered remnants suggest the original role of the *ils* as attachment sites for part of the longitudinal body muscles. Moreover, where the transverse muscles have been preserved, their lateral attachments now usually appear to be on segmental parts. In addition, we find a few muscles that originate on the thoracic *ils* or on their present equivalents, whose insertions are segmental and which have no counterparts in the legless abdomen.

Equally difficult to analyze, because of the extremely varied skeletal and muscular relationships that exist in different groups, is the situation in the cervical intersegment. Here one must be content for the present with the assurance that the former *Oils* are usually somehow represented, most often as part of one or more of the definitive cervical sclerites.

These problems are well illustrated in the cockroaches, in which the musculature of the *ils,* though rich in comparison with that of more recently differentiated orders, can only be considered vestigial in relation to the inferred ancestral condition.

Ventral muscles of cockroaches that appear to belong to the *ils* complex include (a) transverse muscles; (b) cruciate coxal and furcal muscles; (c) certain other furcal muscles; and (d) spinasternal muscles of the abdominal *ils.* (See tables 1 and 2.)

a. *Transverse muscles.*—The transverse muscles of the thorax ordinarily have a median attachment on the spina, and have therefore been discussed under section 1,a, above. The nature of their lateral attachments remains to be considered. As already noted, abdominal relationships support the view that the lateral attachments of the transverse muscles are morphologically intersegmental, i.e., on the *ils.* Comparative evidence from other arthropods and the scanty embryological data on insects (Heymons, 1895; Roonwal, 1937) justify this inference. In the postembryonic cockroach, however, the definitive connection in the thorax is usually with the anterior margin of the succeeding episternum, and the muscles are therefore to be designated as $1sps$-eps_2, $2sps$-eps_3, even though Maki (1938, p. 58) describes the attachment as "on the small sclerite before the [mes]episternum" in *P. australasiae*. If this were all the evidence available, one would conclude that in blattids the *1ils* and *2ils* had fused with eps_2 and eps_3, respectively. The arrangement of the cruciate muscles of the profurca and procoxa in *P. americana* and in *Cryptocercus* (see below) is also consistent with this interpretation.

TABLE 2.—*Ventral intersegmental muscles of cockroaches: muscles without spinasternal attachments*

Symbols such as M6, C55 refer to the numbers given the corresponding muscles in *P. australasiae* by Maki (1938) and in *P. americana* by Carbonell (1947). For muscles with spinasternal attachments, see table 1.

Footnote number	*Muscle type*			
1	Cruciate muscles	$1cv$-cx_1X	eps_2-cx_1X C97	eps_3-fu_1X C102
2	Postcoxal ligaments	$1ils$-fu_1	$2ils$-fu_2	$3ils$-fu_3
3	Furcal muscles	fu_1-*tent.* M6; C55	fu_1-$2cv$ M7; C84	
		fu_1-fu_2 (2 bands) M38; C100		
		fu_2-fu_3 (2 bands) M71; C148		
		fu-s_{IIA} (usually 3 bands) M103; C192, 193		

[1] The 3 cruciate muscles are not serially homologous. For discussion of shifts in origin of eps_2-cx_1X and eps_3-fu_1X, see text sections 2,a and 2,b. The three muscles or their equivalents are present in all species examined.

[2] The three postcoxal ligaments are serially homologous. For variations in their occurrence, see text section 2,c.

[3] The furcal muscles are probably all serially homologous, at least in a broad sense. For variations in the abdominal insertion of fu_3-s_{IIA}, see text section 3. Carbonell (1947) records the abdominal attachment of muscles number 192 as on s_{IA} in *P. americana*. All the furcal muscles listed are present in all species investigated.

However, the full story is not that simple, for *Cryptocercus* possesses not only muscles $1sps$-eps_2, $2sps$-eps_3 that are clearly homologous with those of other blattids, but has in addition fibrous ligaments (figs. 10, 13: *4, 17*) that run from the spinae to small sclerites in the intersegmental membrane well in advance of the episternal margin. These transverse ligaments have evidently been derived from former muscles, and their lateral attachment sites not only occupy the position of true *ils* but also carry the dorsoventral muscles typical of these structures.

Furthermore, careful dissection of most cockroaches discloses a second series of straplike ligaments, also of muscular derivation, that run from the postcoxal membranes (i.e., from the intersegments) to the furcal arms of the respective preceding segments. These ligaments, here designated $1ils\text{-}fu_1$, etc., are inserted on the furcal arms near the seat of the furcophragmatal muscle (see figs. 2, 10: *13, 24, 31*).

It appears, then, that in the thoracic intersegments of cockroaches the former *ils* may now be represented by as many as three seemingly distinct sites: (1) the following episternum; (2) the original *ils;* and (3) the origin of the postcoxal ligament. How this separation came about is by no means obvious.

As already stated, the often straplike but still fibrous transverse ligaments *1sps-1ils,* etc., are evidently derived from former muscles, and are even now represented in whole or in part by muscles in some species. However, again in the light of relationships found in other primitive groups (e.g., *Dytiscus* larva (Speyer, 1922), *Corydalus* larva, etc.), these transverse muscles seem to have served also (after loss of their contractile nature ?) as suspensory ligaments for a portion of the longitudinal ventral intersegmental musculature. Vestiges of this or an analogous arrangement are still present in the first thoracic intersegment of some cockroaches.

In *Cryptocercus,* which in this respect is the most primitive blattid I have seen, both the ligament *1sps-1ils* and the muscle $1sps\text{-}eps_2$ are present and are, laterally, quite distinct (fig. 13: *4, 5*). However, the mesal portion of *1sps-1ils,* incidentally still composed of contractile tissue, is so confluent with the adjacent fibers of $1sps\text{-}eps_2$ that a separation of the two muscles in this region is hardly possible. Thus, the anterior portion of the muscle $1sps\text{-}eps_2$ could be described as "$ligament\text{-}eps_2$." Similarly, it is difficult to specify the origin of the cruciate profurcal muscle eps_2fu_1X (*8*), for part of its fibers arise on eps_2 while the more ventral ones, not visible in figure 13, originate on the ligament *1sps-1ils,* from which they run with the others to the insertion on the contralateral furcal apodeme fu_1.

Variations of these relationships are exemplified in a number of other genera, viz, *Periplaneta, Neostylopyga, Eurycotis, Blatta,* and *Blattella.* In none of these is the peripheral attachment of the ligament *1sps-1ils* preserved; but the central portion of the ligament is present and extends anterolaterally from the spina as a noncontractile septum on which fibers from eps_2 are attached and from which originate muscles ("eps_2"-fu_1X, "eps_2"-cx_1X) that insert on the contralateral profurca and procoxa. These conditions in *P. brunnea* are illustrated in figure 14. Here it will be noted that the origin of the cruciate furcal muscle (*8*) is more central than that of the cruciate coxal muscle (*9*). In *P. australasiae* (fig. 15: *8*) the more dorsal bands of the furcal muscle originate so near the midline that they appear to arise from the spina; and they are so recorded in Maki's (1938) description.

The contrasting arrangement of the corresponding muscles in *P. americana* is apparent in figure 16. In this species, there is no visible remnant of the ligament *1sps-1ils,* and the cruciate muscles (*8, 9*) originate far laterally, on the anterior margin of eps_2, as they were described by Carbonell (1947). Hence the structure of *P. australasiae* and *P. americana* is superficially quite distinct. Access to intervening forms, such as *P. brunnea,* etc., shows, however, that in *P. australasiae* and *P. americana* we are merely confronted with rather extreme variations in the arrangement of morphologically identical elements.

Cryptocercus is unique among the cockroaches studied in that the most dorsal fibers of the transverse muscle of the first intersegment, *1sps*-eps_2, continue across the body without attachment on the spina (fig. 13: *5*). This development is almost certainly secondary, for the more ventral fibers of this muscle have the usual spinal connection.

The several variants we have seen in the cruciate muscles are such that all of them could have been derived, by gradual transition, from any one chosen as a starting point. There is also at present no bar to the alternative assumption that any or all of them might suddenly have arisen *de novo* from each other or from an unknown basic pattern as a result of gene mutation or recombination. Therefore, a decision as to which of the existing configurations portrays the most primitive condition is not warranted on the basis of the evidence so far presented. Although *Cryptocercus* shows some very primitive features in the first thoracic intersegment, it is even here less primitive in other respects than certain other cockroaches, and should not be regarded as the prototype for the arrangement of the cruciate muscles unless independent confirmation can be produced. Other data that bear on this question are cited in this section, b, below.

At the present time, it also does not seem possible to decide whether muscles such as *1sps-1ils* and *1sps*-eps_2 are fundamentally distinct, or whether the episternal branch is no more than a hypertrophied offshoot from an originally single transverse band. Both elements are present simultaneously in a few other insects, not all of which are closely related to the cockroaches. An example is shown in figure 6: *4, 5*. There is some indication also, in various other primitive groups, that there existed muscles of the type $1ils\text{-}eps_2$; if so, these too may have contributed to the arrangements now seen in blattids, for they could conceivably account for the lateral portions of the cruciate muscles that run in some species from eps_2 to the transverse ligament $1sps\text{-}1ils$ or to the septum that has replaced it.

b. Cruciate coxal muscles.—Mention of the cruciate coxal muscle, $eps_2\text{-}cx_1X$ (*9*), has been made in the preceding section. This muscle is inserted together with the spinal posterior rotator $1sps\text{-}cx_1$ (*7*), from which it is morphologically distinct. However, species such as *P. australasiae,* in which the origin of "eps_2"-cx_1X is far mesad, could properly be described as having two definitive spinacoxal posterior rotators, as was done by Maki (1938, fig. 6, Nos. 24, 25). In most instances these two muscles may still be distinguished by the fact that the true spinal muscle originates along the side of the spina ventral to the other spinal musculature, whereas the muscle equivalent to $eps_2\text{-}cx_1X$ has a more dorsal origin, anterior to the transverse muscle $1sps\text{-}eps_2$. Yet the distinction is not always clear; and in some blattids one or the other of these two muscles may even have been lost.

Serial homologs of the muscle $eps_2\text{-}cx_1X$ do not occur in cockroaches so far as is known, but homologs with origins on the *ils* are found in all three thoracic segments of larval *Dytiscus* (Speyer, 1922) and in larval *Cybister*. In larval *Corydalus,* which lacks such muscles in the first intersegment, cruciate posterior rotators of the second and third coxae originate on the corresponding furcal arms. This shift in origin is easily understood from the fact that the furcal arms are here fused with the succeeding *ils,* evidently, as judged by conditions still found in some other Megaloptera such as *Sialis* spp., in consequence of sclerotization along the line of the postcoxal ligaments $2ils\text{-}fu_2$, $3ils\text{-}fu_3$. One infers from the position of the cruciate coxal muscles in these primitive forms that the attachments of the cruciate muscles of cockroaches on $1ils$ or eps_2 are more likely the primary ones than any of the other variants observed in blattids. If so, *Cryptocercus* and, for some strange reason, *P. americana* but not its congeners have more nearly preserved the original condition.

Cruciate promotors of the first coxa have been described from a number of orders, and are apparently present in a much reduced state in all cockroaches, although on account of their delicacy they have escaped the notice of myologists. In the adult insect, which is the stage usually chosen for dissection, they are extremely slender and transparent. They are more easily seen, though not immediately recognizable as muscles, in the nymph, where they were first discovered by Scharrer (1948) as the bearers of the prothoracic glands. The glandular tissue, which encases the tenuous contractile filament and thus renders it more visible (fig. 7: *3*), degenerates soon after metamorphosis, but the muscular core persists throughout life. The origin is near the anterior end of the first cervical sclerite, *1cv,* which for this and other reasons is to be regarded as incorporating the cervical *ils;* and the insertion is on the proximal margin of the contralateral coxa vera, just laterad of the coxotrochantinal articulation. Corresponding cruciate promotors of the second and third coxae have not been identified in any pterygote insect, but there is a possibility that they are represented in the usual spinal promotors $1sps\text{-}cx_2$, $2sps\text{-}cx_3$.

c. *Lateral furcal intersegmental muscles.*—In cockroaches furcal muscles whose origins are on the *ils* or on their present equivalents include only the cruciate muscles $eps_2\text{-}fu_1X$ of the first intersegment; and the three postcoxal ligaments $1ils\text{-}fu_1$, etc. The cruciate muscle has been discussed in the preceding sections.

The postcoxal ligaments are often frail and transparent, and therefore easily overlooked in dissection; and they dissolve rapidly in alkali. These characteristics no doubt explain why the ligaments have not received more attention from morphologists, for they are quite frequently present in primitive insects. (See fig. 6: *13, 24, 31,* and fig. 7: *24,* as well as the figures of cockroaches.)

By a process that has many analogies in the evolution of the pterygote thorax, the postcoxal ligaments have often been replaced, in phylogeny, by apodemal growths, a course of development that culminates in a firm skeletal union between the furcal arm and the succeeding *ils.* Such unions constitute, or at least contribute to, the postcoxal bridges, whose interpretation has interested several previous students of insect morphology.

Cockroaches, however, show little or no indication of the trend toward formation of a postcoxal bridge by sclerotization along the line of this former muscle. Only in *Blaberus,* of the blattids I have seen, is the distal end of the ligament $2ils\text{-}fu_2$ converted into a stiff, well-sclerotized apodeme; whereas the usual course of evolution of a postcoxal bridge in other Ptergygota seems, contrariwise, to have been via sclerotization from the furcal attachment outward.

In fact, the general impression left by the blattids is that their tendency is toward obliteration of these ligaments, and this tendency is increasingly manifest as one passes from the prothorax to the metathorax. All the cockroaches studied possess a fairly strong and short $1ils\text{-}fu_1$; and a longer and more slender $2ils\text{-}fu_2$ was found in all but *Pycnoscelus.* The presence of $3ils\text{-}fu_3$ was definitely ascertained only in the genera *Periplaneta* (4 species), *Eurycotis, Blatta,* and *Cryptocercus.* Failure to find a structure of this delicate nature is, of course, no proof of its absence; but the observations cited nevertheless do indicate quite well the tendency for these ligaments to weaken in the more posterior segments. The genera where their presence in the metathorax is most doubtful (*Leucophaea, Nauphoeta,* etc.) are notably those judged to have a more specialized muscular pattern on the basis of other criteria; and several of these are large insects, where such a structure, if present, should be relatively easy to find.

The origins of the postcoxal ligaments of cockroaches, though clearly intersegmental, are at sites anterior and dorsal to the small sclerites indentified as the true *ils* by their reception in *Cryptocercus* of the transverse ligaments and of the usual dorsoventral muscles. In some other insects, the two sites are closer together or even indistinguishable, and I can offer no explanation for their separation in blattids.

d. *Spinasternal muscles of the abdominal ils.*—Only two such muscles have been found in cockroaches, namely $2sps\text{-}s_{IIA}$ and "$3sps$"-s_{IIA}. The usual abdominal attachments for both are near the anterolateral angle of the second sternum, somewhat anterior and ventral to the suspension of the ventral diaphragm. As explained above, this region of the definitive sternite is believed equivalent morphologically to the thoracic *ils.*

Identification of this attachment site with the *ils* renders dubious the homology, indicated as possible in table 1, of "$3sps$"-s_{IIA} with the spinafurcal muscles $1sps\text{-}fu_2$, $2sps\text{-}fu_3$; for it is very unlikely that the *ils* have contributed to the furcal structures of cockroaches. (See this section, c, above.)

The muscle from the second spina $2sps\text{-}s_{IIA}$ clearly has no serial homolog in blattids. It is ordinarily inserted on s_{IIA} somewhat mesad and ventrad of "$3sps$"-s_{IIA}, and is thus two full segments in length. The variant attached on s_{IIIA} has been discussed in section 1,e.

3. THE FURCAE

The consensus of morphologists has been that the furcae (*fu*) of higher insects have been produced, in phylogeny, by the approximation in the ventral midline of paired segmental sternal apophyses (Weber, 1928; Snodgrass, 1929). The resulting Y-shaped structure consists of the infolded furcabasis and the laterally extended furcal arms. In cockroaches, as in other primitive forms, right and left apophyses remain separate. For this reason, purists avoid applying the term "furca" to them, but for convenience we shall continue to refer to them as the furcae or furcal arms, with which they are homologous. Despite the seemingly incontestable segmental nature of these apophyses, they nevertheless carry a large fraction of the surviving longitudinal ventral intersegmental musculature in all pterygote insects. This situation poses a contradiction, long recognized and accepted by students of thoracic structure, that has never been satisfactorily resolved (cf. Snodgrass, 1929).

Weber (1928) surmised that the present furcal intersegmental muscles had been derived from spinasternal muscles. He proposed that, as the furcal arms were gradually elevated in phylogeny, they intercepted the spinasternal muscles, which thereupon acquired furcal attachments and lost their primary connections with the spinae. This hypothesis, which regards the furcal muscles as replacements for the spinasternal muscles, is clearly untenable in the face of the presence of the usual complement of furcal intersegmental muscles in all those primitive forms, such as larval *Dytiscus* (Speyer, 1922) or *Cybister,* larval *Corydalus,* and the cockroaches, which still retain an extensive spinasternal musculature, including (in the blattids) both spinaspinal muscles *1sps-2sps, 2sps-"3sps."* Conceivably, the rising furcal arms could have intercepted some of the more lateral bands of the primary ventral longitudinal intersegmental muscles, for instance those attached on or below the transverse ligaments, *1sps-1ils,* etc.; but even this modification of Weber's hypothesis is unconvincing in the absence of any known situation in insects where interception of a muscle by a skeletal element has led to the development of an attachment between the two. Moreover, the data of Carpentier, Barlet, and others (see Barlet, 1954, for references) show that the essential features of the furcal complex exist in the Apterygota, which also possess an extensive array of muscles homologous with the spinasternal muscles of higher forms. Any notion that the furcal longitudinal muscles have arisen in the Pterygota through transfer of muscles from some other category must therefore be abandoned. How then can they be accounted for?

An answer may be approached, we believe, through realization that the principal endoskeletal structures of insects and other arthropods have all developed as the result of sclerotization along the course of former muscles, and that the present sternal arms are of this nature. Although the genesis of certain endoskeletal structures lies so far in the past that it will probably be impossible forever to document the details of the process in these instances, there are many other cases where the course of evolution can be deduced with reasonable certainty from comparisons of existing forms. The complex endosternal structures of the Apterygota furnish a number of examples, for, as described by the Belgian authors cited above, many endosternal elements that are ligamentous in one species or group are still represented by functional muscles or by apparently degenerate muscles in others. In the opinion of the present writer, yet other parts of the endosternum that are invariably ligamentous in the apterygote species so far studied are homologous with muscles, such as the transverse muscles, that persist as contractile elements in some primitive Pterygota and as ligaments in others. Another clearcut set of examples of the replacement of muscles by endoskeletal structures is found in the later history of the sternal arms themselves, for instance in the development of the furcopleural fusion, which has occurred independently in numerous lines of descent. Here the process can be followed in some detail through several series of intermediate stages provided by existing forms.

As a generalization we offer the hypothesis that all such endoskeletal developments owe their inception to other structural or functional changes that have limited freedom of movement at the insertions of certain muscles. These muscles, deprived of their original effectiveness as contractile organs, are doomed to disappear unless they happen to retain some value in the role of static supports or braces. Furthermore, the organism evidently finds it more economical to construct the braces it requires from other than contractile tissue, which cannot resist compression and which can maintain tension only through a continuous expenditure of energy, so that replacement of bracing muscles or tensors by noncontractile ligaments or by stiffer sclerotized apodemes is the usual evolutionary pattern. In our view, structures originating in this manner constitute the primary endoskeletal rudiments. Once established, these may be variously molded in later evolution in accordance with the mechanical requirements they are called upon to fill; and in the course of such modification their original derivation from muscles may be almost wholly obscured.

Returning to the narrower problem of the nature of the sternal arms and their longitudinal musculature, we may point out that the arms are represented in the Apterygota by ligamentous straps that connect the thoracic endosterna, which are mainly intersegmental in character, with the respective preceding segmental sternal regions (references in Barlet, 1954). In these insects the endosterna provide the attachment sites for almost all the ventral musculature, including, of course, the usual longitudinal intersegmental muscles. We have already indicated our belief that the entire endosternal complex, which is ligamentous in consistency, is of muscular derivation; and we suggest here that the sternal ligaments are merely another example of transformed muscles. We may then regard the endosternum schematically as a point of junction of various intersegmental muscles, among which are the usual longitudinal bands and a muscle to the preceding segmental sternum.

The configuration thus summarized is, however, exactly what is seen in the musculature associated with the sternal arms of pterygote insects. True, the number of elements that impinge upon this focus is less than in the Apterygota; but those elements that do occur in the Pterygota all have their counterparts in muscles that are attached on the apterygote endosternum in proximity to the attachments of the sternal ligaments, or in similarly directed portions of the endosternum itself. Only the fact that the sternal arm of Pterygota is usually a heavily sclerotized ingrowth of the ventral body wall gives the superficial impression of a fundamental difference between the two subclasses.

In cockroaches, even this distinction breaks down; for in the prothorax of blattids the paired furcal pits do not give rise at once to sclerotized apodemes, as they do in the mesothorax and metathorax, or in the prothorax of most Pterygota. Instead, there extends inward from the pit a flexible, fibrous ligament that connects with the apex of a sclerotic bar whose other end articulates firmly with the pleural apodeme. Upon this bar, at or near its junction with the sternal ligament, are inserted the usual muscles of the furcal complex.

On the basis of these facts and the considerations outlined above, we suggest that the sternal arms of pterygote insects represent muscles that formerly ran from the segmental sternal region posteriorly to a common junction of various other intersegmental muscles, including the forerunners of the present longitudinal furcal muscles. In the course of evolution, the sternal muscles were replaced first by noncontractile ligaments, a condition still manifest in the Apterygota and in the prothorax of blattids, and finally by sclerotized apodemes, the form in which they now appear in the pterothorax of cockroaches and in all three thoracic segments of most winged insects. These changes in the sternojunctional muscle have not altered the morphological relationships of the other muscles attached at the junction, which may still be regarded as an intersegmental locus in the morphological sense.

There is thus no problem of explaining a shift of their attachments to a segmental site, for no shift has occurred.

Apart from the structure of the profurca, with its connotations for the evolution of the furcal structures of pterygote insects in general, there is little that is remarkable about the sternal apophyses and their musculature in cockroaches that has not already been touched on in preceding sections. The ventral furcal intersegmental muscles found in the Blattariae may be classified as (a) spinafurcal muscles; (b) furcal muscles from the *ils;* and (c) furcofurcal muscles, including muscles with furcal origins and insertions in the head, neck, or abdomen. If the suggestion offered above is correct, that the definitive furcal apophysis is partly of intersegmental nature, a number of other muscles with furcal attachments, such as those of the appendage, may also be primarily intersegmental. However, further work is needed on the details of such relationships, and it seems best to leave them for future consideration.

Except for muscles with spinasternal attachments (table 1), the ventral furcal intersegmental muscles of cockroaches are listed in table 2.

Furcal muscles from the spinae and *ils* have been discussed above, particularly under sections 1,b, 2,a, and 2,c. Like these muscles, the furcofurcal muscles of blattids can be homologized in considerable detail with those of comparable location in other insects. Readily distinguished in most cockroaches are a usually slender mesal band and a more massive lateral band of both fu_1-fu_2 and fu_2-fu_3. Components probably homologous with each of these bands can also be identified in many blattids in the muscle fu_3-s_{IIA}, which often includes an additional more ventral group of fibers. These subdivisions, ordinarily lumped together in descriptions, seem to possess a fair degree of constancy in a number of insect orders, and may be of significance in future more detailed comparative studies.

The fact that the furcabdominal muscles are inserted on the second (never on the first) abdominal sternum, is what would be expected if the furcal attachment is really intersegmental, as has been argued above. Morphologically, these muscles still run from the third thoracic intersegment to the first abdominal intersegment, and have neither lost nor shifted their original attachment sites. However, just as the muscle $2sps$-s_{IIA} has become $2sps$-s_{IIIA} in some species (section 1,e), so is a portion of fu_3-s_{IIA} found, at times, as fu_3-s_{IIIA}, as a result of an analogous development (figs. 1, 5, 8, 11, 12, 17:*32*).

The profurca bears two anteriorly directed longitudinal ventral intersegmental muscles. The stronger, consisting of two or more bands and serially homologous with the muscles fu_1-fu_2, fu_2-fu_3, passes into the head to insert on the tentorium. This muscle, fu_1-*tent* (figs. 1-18: *1*), is commonly considered to be more than one segment in length (Snodgrass, 1935, p. 159). The weaker, usually a thin, flat strap of somewhat degenerate appearance, has a more ventral origin on fu_1 (figs. 4, 5, 9: *2*) and is inserted on the mesal lobe of the ipselateral second cervical sclerite. Possibly this site should be referred to the *Oils,* which are certainly included in the first cervical sclerites, *1cv,* of which the *2cv* may be merely subdivisions (Crampton, 1926); but this question cannot be settled until the constitution and muscular connections of the various cervical structures of insects are better understood.

GENERAL DISCUSSION

Reinvestigation of the ventral intersegmental muscles of the three cockroaches previously studied by others has shown each of the earlier accounts deficient in some respects. The defects are mostly errors of omission. Thus, none of the earlier investigators noted the muscle *1cv*-cx_1X or the three postcoxal ligaments *1ils*-fu_1, etc. That they did not is understandable, for these are hardly muscles in a functional sense, even though the cervicocoxal "muscle" does have a contractile core a few microns in diameter. Carbonell's (1947) exclusion of the ligament fu_3-fu_3($=3sps$-fu_3) and of the bands *"3sps"-ventr. diaphr.* from his description is likely to have been on similar grounds; for in most other details his depiction of *P. americana* is accurate and complete. However, unless Maki's (1938) specimens of *P. australasiae* differed radically from those of this species available to the writer, one must reject Maki's assertions that the muscles *1sps*-fu_1, *1sps*-cx_2, *2sps*-fu_1, *2sps*-cx_3, and *2sps*-s_{IIA} are absent, and that a muscle, *2ps*-fu_2, unknown in any other cockroach, is present. Miall and Denny (1886) stated explicitly that they had not given a complete account of the muscles of *B. orientalis,* so that there is no cause for surprise in the fact that this species has numerous muscles unmentioned in their description.

When these few corrections have been made, it is seen that all species of cockroaches thus far studied have nearly identical complements of ventral intersegmental muscles. The spinasternal promotors of the coxae, *1sps*-cx_2 and *2sps*-cx_3, are absent from some species and show signs of weakness in others. The metathoracic postcoxal ligament *3ils-fu*$_3$ is either lacking or very frail in several genera. *Cryptocercus* alone of the species investigated possesses muscles as yet found in no other blattid; these are the semiligamentous transverse bands *1sps-1ils* and *2sps-2ils,* parts of which seem to have survived as septa in some other cockroaches. With these minor exceptions, the differences among the several species are merely variations in relative size and proportions of the various muscles, or occasionally in their position. Such differences, some of them quite conspicuous, obviously indicate shifts in functional emphasis, although in most instances the details of their interpretation from this viewpoint are obscure.

In contrast with most modern insects, the cockroaches enjoy a relatively rich ventral intersegmental musculature. Some authorities would be inclined, perhaps, to regard this as a consequence of secondary reduction of sclerotization in the ventral regions of the blattid thorax; but acceptance of this view would make it very hard to account for the presence of homologous muscles in a number of other groups in which the thorax is extensively sclerotized. There is no muscle recorded in this paper for which either a direct or a serial homolog has not been found in at least one other order of pterygote insects, and most of them are known from several. Coupled with the fact that those other orders that display a similar degree of complexity in the ventral intersegmental musculature are the ones considered highly primitive in various other respects, the evidence seems more consistently interpreted in the conclusion that the cockroaches also are primitive in this feature, and that the primitive state of the ventral intersegmental muscles was a complex one. As already indicated in the introduction, the various structural patterns preserved for our scrutiny among the more recently evolved orders of insects, which constitute a progressive series of specializations toward greater efficiency in flight, show that improvement in the flight mechanism has been accompanied regularly by reduction in the ventral intersegmental thoracic musculature. These facts also favor the view that the possession of numerous discrete muscles in this category is a primitive characteristic. The results of a more comprehensive inquiry into these problems will be reported elsewhere.

SUMMARY

1. A comparative study was made of the ventral intersegmental musculature of the thorax in 19 species of cockroaches. The observations produced a few corrections, mainly additions, to earlier de-

scriptions of 3 of these species. In general, there are very minor differences among the species in respect to the presence or absence of individual muscles in the category studied, although there are numerous differences, some conspicuous, in the relative size and proportions of the various muscles.

2. The present ventral intersegmental thoracic muscles had their primary attachments on the spinae, on the intersegmental laterosternites, or on the forerunners of the furcal apophyses. Cockroaches still have two typical spinae and definite vestiges of a third. They possess an extensive spinasternal musculature. Remnants of the musculature of the intersegmental laterosternites are present, but some of these muscles now have segmental attachments, and others are represented by noncontractile ligaments. The longitudinal furcal muscles are equivalent to those of other pterygote insects.

3. Attention is called to the postcoxal ligaments that run between the furcal apophysis and the immediately following intersegmental laterosternite in each of the thoracic intersegments, and to the significance of these former muscles in the development of the postcoxal bridges of higher insects.

4. Evidence and arguments are presented for the hypothesis that the furcal apophyses represent former muscles that have been replaced in phylogeny by sclerotized apodemes. It is suggested that one attachment of these muscles was on the segmental sternum, the other at a common intersegmental junction of several other muscles, among them elements of the longitudinal ventral group. Loss of movement at the sternal insertion led first to transformation of the sternojunctional muscle into a fibrous ligament and eventually to the sclerotization of the ligament. Analogous events have occurred frequently in the evolution of the pterygote thorax. The blattid prothorax exemplifies a stage in the evolution of the typical furcal apophysis when the postulated sternal muscle was still in a ligamentous condition. The subsequent sclerotization of this ligament, which has occurred in the other thoracic segments of cockroaches and in all three segments of most Pterygota, in no way alters the morphological relationships of the other muscles inserted upon its central end; morphologically, then, the present attachments of the longitudinal ventral muscles on the furcal arms are still intersegmental, and it is therefore unnecessary to invent mechanisms whereby they might have been shifted from an intersegmental to a segmental site of attachment.

5. The ventral intersegmental thoracic musculature of cockroaches is rich in number of elements, compared to that of more recently

evolved groups. However, direct or serial homologs of all the elements occur in one or more other orders of winged insects. The most extensive complements of these muscles are found in those forms, such as larval dytiscids, Grylloblattodea, and Megaloptera, that are regarded as primitive on the basis of other criteria. It is concluded, therefore, that the blattids also are primitive in respect to the ventral intersegmental muscles; and that possession of a rich ventral intersegmental musculature was characteristic of the early Pterygota.

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GLOSSARY OF ABBREVIATIONS

cv	cervical sclerite
cx	coxa
eps	episternum
fu	furca, furcal arm, segmental sternal apophysis
ils	intersegmental laterosternite
ph	phragma, or the primary dorsal intersegmental fold from which the phragma is derived
post. rot.	posterior rotator, a functional designation used to distinguish certain leg muscles
s	segmental sternum
sept.	septum
sps	spinasternite or spina
t	segmental tergum
tent.	tentorium
ventr. diaphr.	ventral diaphragm
X	cruciate, used of a muscle whose origin and insertion are on opposite sides of the midline

For the way in which these abbreviations are compounded into designations of muscles, see section on Method and Material in text.

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EXPLANATION OF FIGURES

All muscles figured are numbered uniformly according to the list below. Instances in which the definitive attachments differ from those given in the list have been discussed fully in the text.

The arrangement of ventral muscles in certain species is such that not all of them can be shown in a single drawing. However, all cockroaches studied have all muscles given in the list, whether the muscles appear in the figures or not, except as noted under tables 1 and 2 or in the text. The termite *Zootermopis* (fig. 6) and the mantid *Tenodera* (fig. 7) have only the ventral intersegmental muscles shown in the drawings.

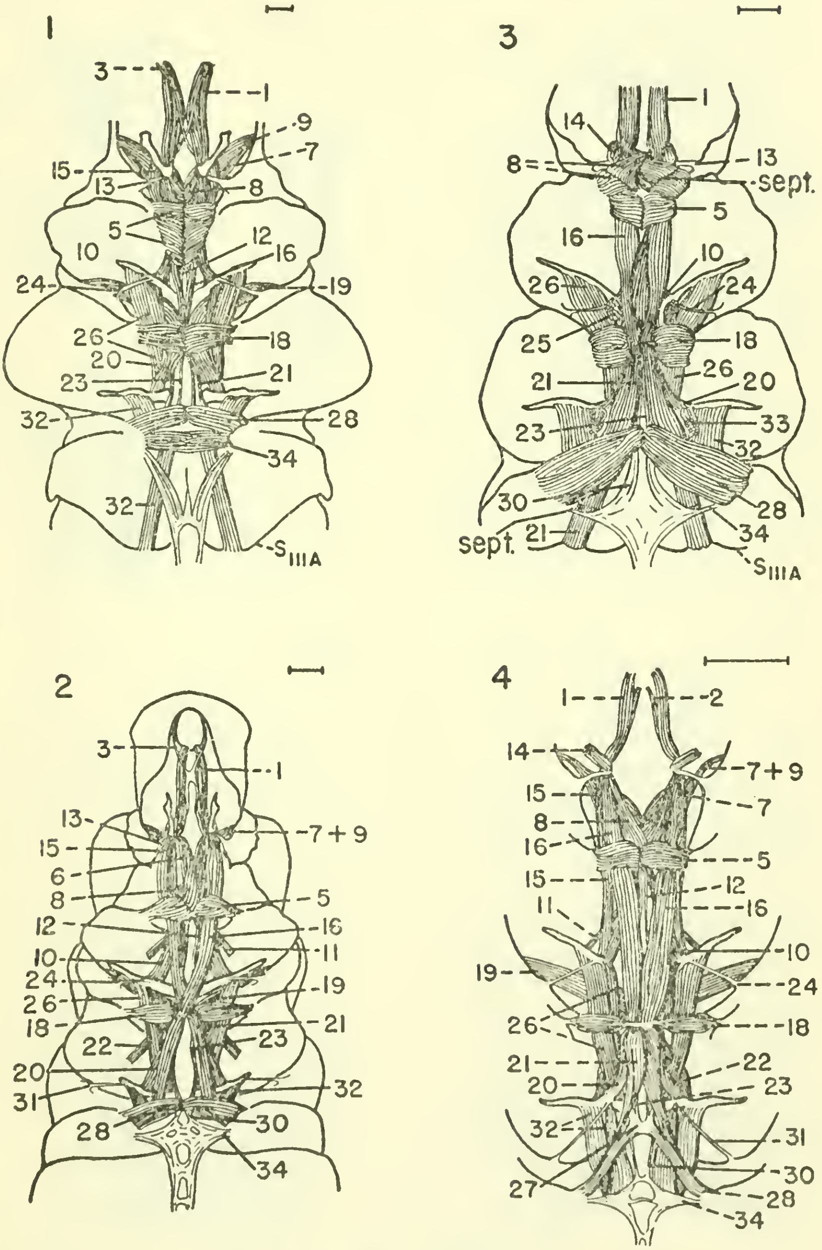
In a few instances different levels of dissection have been shown in different parts of the same figure; this does not imply an absence of the usual bilateral symmetry. To assist in orientation, some figures contain a few muscles that do not belong to the ventral intersegmental category.

The scale indication represents 1 mm.

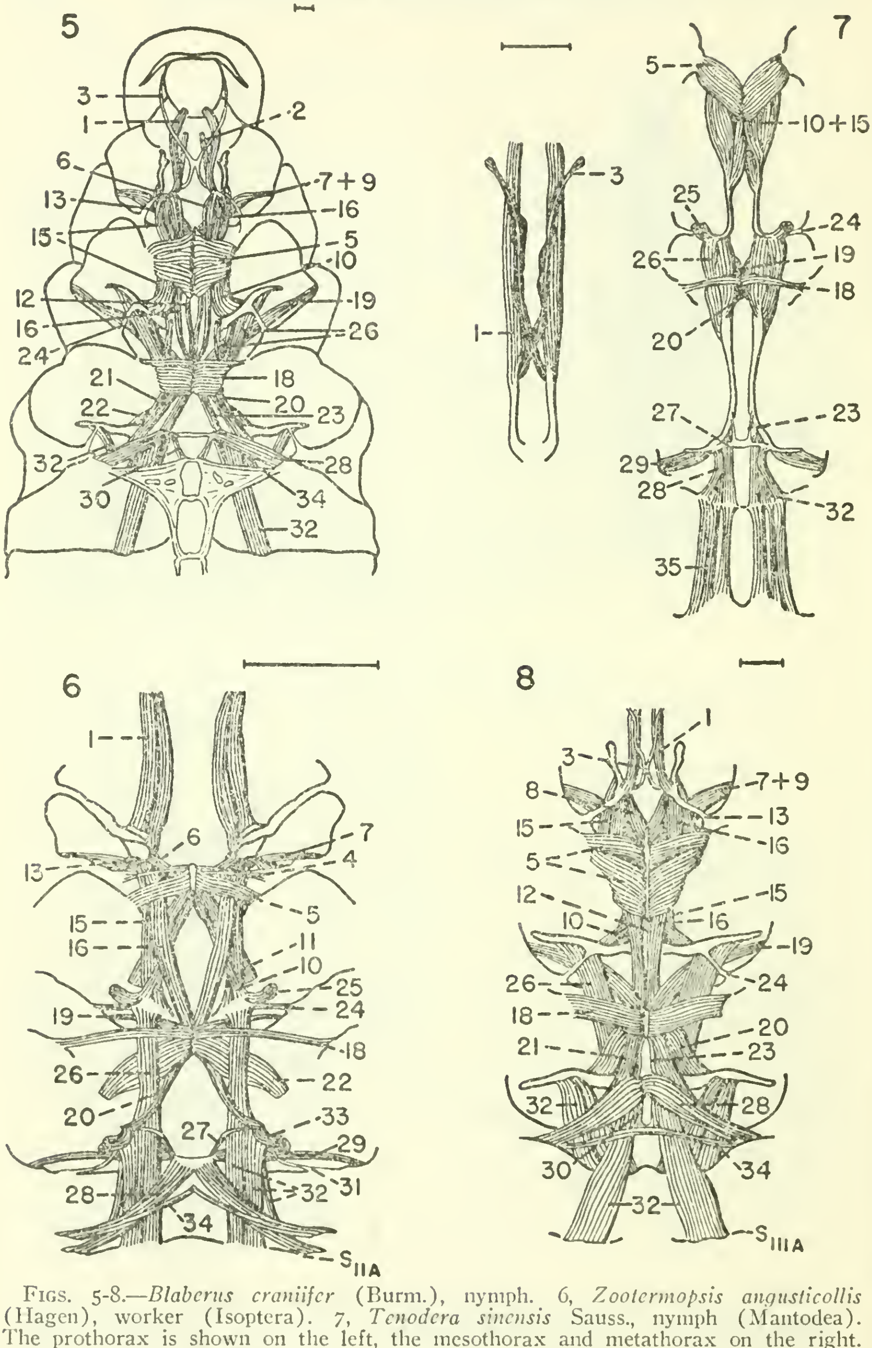
NUMBERING OF MUSCLES IN FIGURES 1-18

Number	*Muscle*	*Number*	*Muscle*	*Number*	*Muscle*
1	fu_1-*tent.*	13	*1ils*-fu_1	25	fu_2-*2ph*
2	fu_1-*2cv*	14	fu_1-*1ph*	26	fu_2-fu_3
3	*1cv*-cx_1X	15	fu_1-fu_2	27	*"3sps"*-fu_3
4	*1sps-1ils*	16	*2sps*-fu_1	28	*"3sps"*-s_{IIA}
5	*1sps*-eps_2	17	*2sps-2ils*	29	fu_3-cx_3 *post. rot.**
6	*1sps*-fu_1	18	*2sps*-eps_3	30	*"3sps"-ventr. diaphr.*
7	*1sps*-cx_1	19	*2sps*-cx_2	31	*3ils*-fu_3
8	eps_2-fu_1X *	20	*2sps*-fu_3	32	fu_3-s_{IIA} *
9	eps_2-cx_1X *	21	*2sps*-s_{IIA} *	33	fu_3-*3ph* (or -t_{IA})
10	*1sps*-fu_2	22	*2sps*-cx_3	34	s_{IIA}-s_{IIA}
11	*1sps*-cx_2	23	*2sps-3sps*	35	s_{IIA}-s_{IIIA}
12	*1sps-2sps*	24	*2ils*-fu_2		

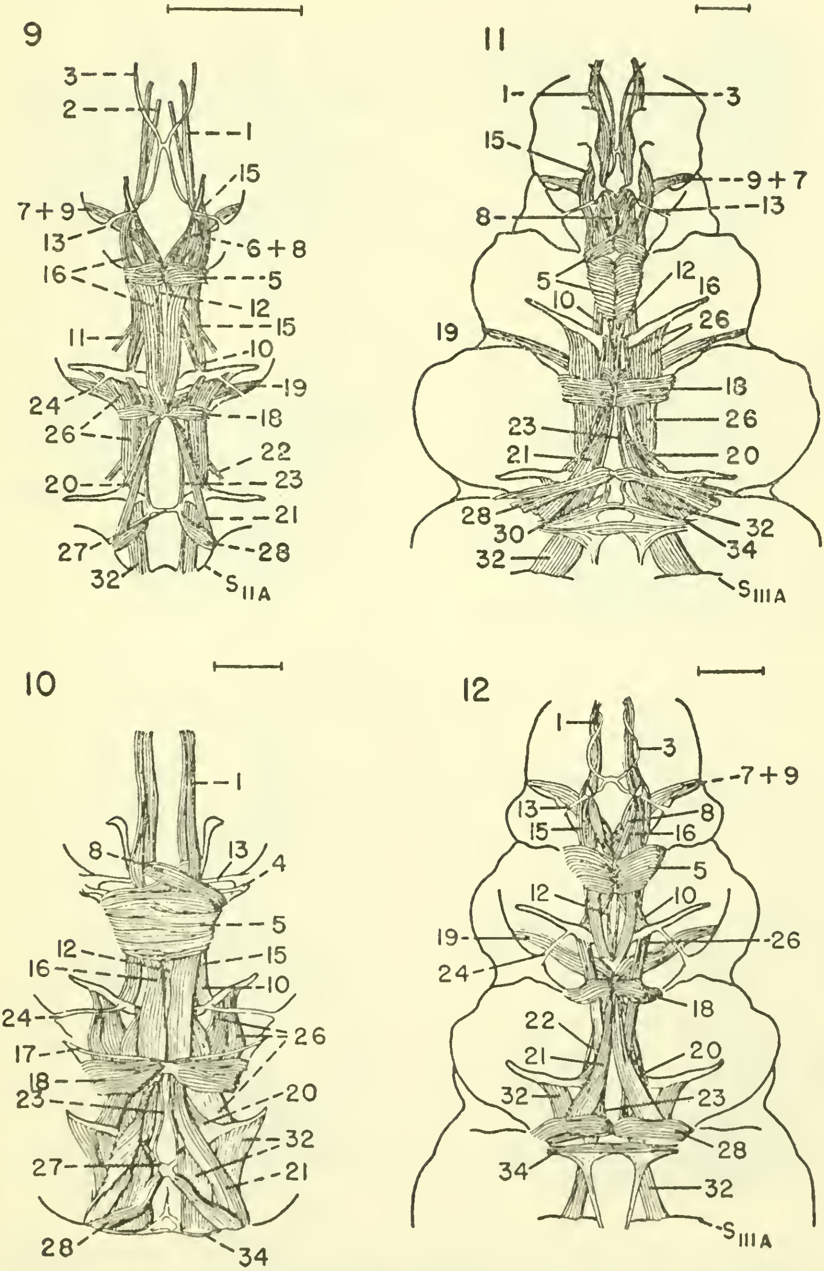
* Variants from these attachments are discussed in the text.



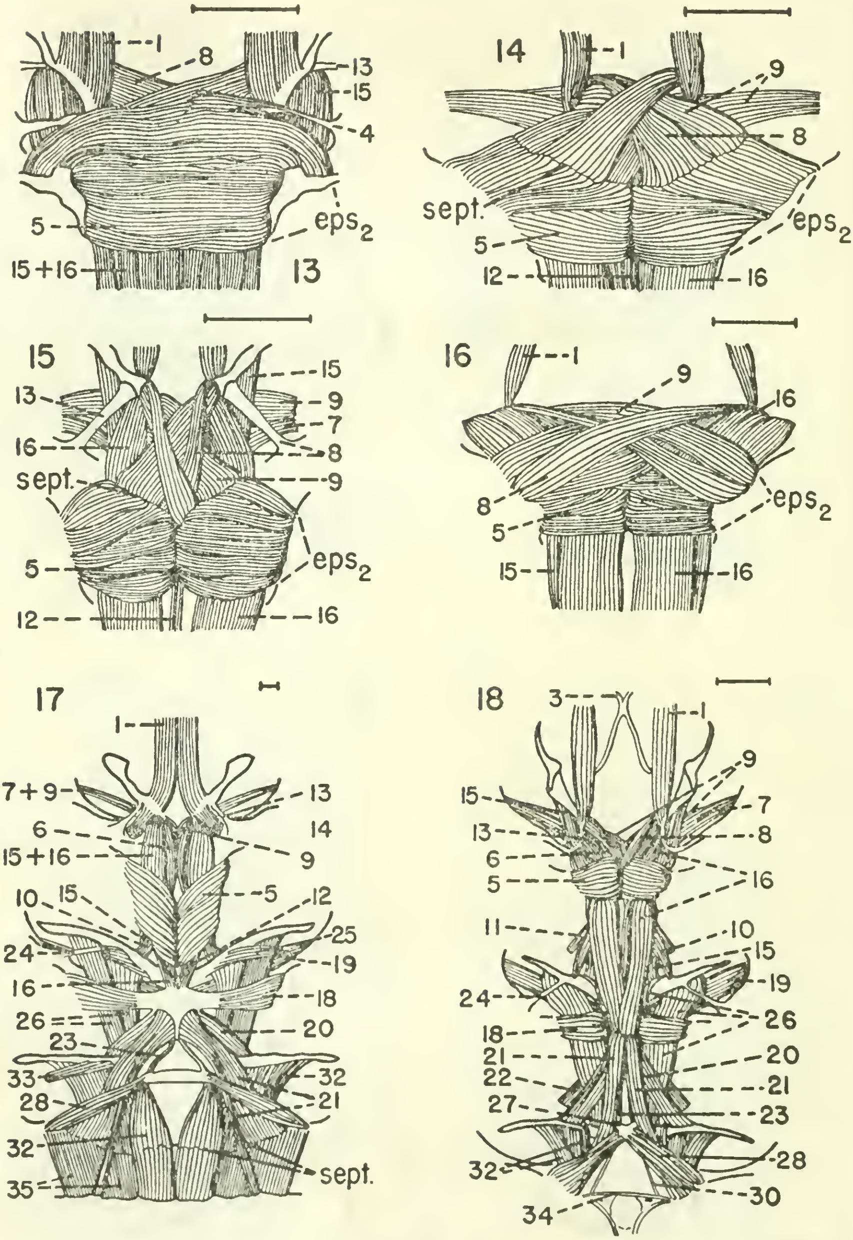
Figs. 1-4.—1, *Leucophaea maderae* (Fabr.), male. 2, *Blatta orientalis* L., male nymph. 3, *Neostylopyga rhombifolia* (Stoll), male. 4, *Blattella vaga* (Heb.), female.



FIGS. 5-8.—*Blaberus craniifer* (Burm.), nymph. 6, *Zootermopsis angusticollis* (Hagen), worker (Isoptera). 7, *Tenodera sinensis* Sauss., nymph (Mantodea). The prothorax is shown on the left, the mesothorax and metathorax on the right. The portion of the prothorax posterior to the sternal arms, which does not carry any ventral intersegmental muscles, has been omitted. Glandular tissue that invests the muscles $lcv\text{-}cx_1X$ (3) is shown in solid black. 8, *Nauphoeta cinerea* (Oliv.), nymph.



FIGS. 9-12.—9, *Supella supellectilium* (Serv.), female. 10, *Cryptocercus punctulatus* Scud., female. 11, *Pycnoscelus surinamensis* (L.), female. 12, *Diploptera dytiscoides* (Serv.), nymph.



Figs. 13-18.—13, *Cryptocercus punctulatus* Scud., female, detail of first thoracic intersegment. 14, *Periplaneta brunnea* Burm., nymph, detail of first thoracic intersegment. 15, *Periplaneta australasiae* (L.), nymph, detail of first thoracic intersegment. 16, *Periplaneta americana* (L.), nymph, detail of first thoracic intersegment. 17, *Macropanesthia rhinocerus* Sauss., female. 18, *Parcoblatta pennsylvanica* (DeGeer), nymph.