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The anatomy of the armoured ground cricket, Acanthoplus speiseri Brancsik 1895 (Orthoptera: Tettigoniidae, Hetrodinae)

Keith Japhet Mbata
Iowa State University

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THE ANATOMY OF THE ARMoured GROUND CRICKET, ACANTHOPLUS SPEISERI BRANCSIK 1895 (ORTHOPTERA: TETTIGONIIDAE, HETRODINAE)

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The anatomy of the armoured ground cricket, Acanthoplus speiseri Brancsik 1895
(Orthoptera: Tettigoniidae, Hetrodinae)

by

Keith Japhet Mbata

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of the Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major: Entomology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

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Members of the Committee:

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For the Graduate College

Iowa State University
Ames, Iowa

1985
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Studies on the anatomy of the armoured ground cricket, Acanthoplus speiseri Brancsik 1895, were conducted. The external morphology and endoskeletal processes are of the generalized tettigoniid type except that this species is apterus, ocelli are absent and the eyes bear fixed stalks. In the males, the mesonotum has modified tegmina that serve as stridulating organs, while in the females these structures are absent being represented only by vestigial wing pads. The thoracic musculature of A. speiseri is similar to that of Acridoeza reticulata Guerin, Neoconocephalus robustus (Scudder) and Homorocoryphus nitidulus vicinus (Walker), however, there are a few differences. The male A. speiseri bears a large tergo-pleural muscle in its mesothorax that is absent in its metathorax and completely lacking in the female, while both sexes of A. reticulata and N. robustus possess the muscle in both segments of their pterothorax. Like H. n. vicinus, A. speiseri has single basalar and subalar muscles while A. reticulata has three basalars and two subalars. However, in A. speiseri, the muscles only occur in the mesothorax.

The tergo-trochanteral muscle is large in A. speiseri while it is very small in N. robustus and of moderate size in A. reticulata. The abdominal musculature closely resembles that of Neoconocephalus exiliscanorus (Davis) and Ceuthophilus lapidicola Burm., with only minor exceptions. The alimentary canal resembles that of Amblycorpyha rotundifolia (Scudder) and Neoconocephalus ensiger Harris, while the dorsal blood vessel is similar to that reported for Eugaster spinulosus Johnnson.
The respiratory system closely resembles that of *Phasgonura viridissima* L., with one major exception. Whereas in *A. speiseri*, the wing tracheae are much reduced due to its apterus nature, *P. viridissima* bears a full complement of wing tracheae with complex basal connections. The nervous system is similar to that described for *Conocephalus fasciatus* De Geer, except that in *A. speiseri* the ocelli are absent and the optic lobes are linked to the protocerebrum by long thick stalks. The internal reproductive organs of the female are simple and generalized. In the male, these structures are similar to those of *Orchelimum minor* Brunner, although in the latter, the epididymis-like convolutions of the vas deferens occur a short distance from the testis. In *A. speiseri*, the epididymis-like convolutions are located immediately behind the testis.
GENERAL INTRODUCTION AND LITERATURE REVIEW

Comprehensive reviews on the morphology and anatomy of insects in general are given by Snodgrass (1927, 1928, 1929, 1935a, b, 1937, 1956, 1960, 1963) and Matsuda (1960, 1963a, b, 1965, 1970). The biology, morphology, and anatomy of the Tettigoniidae and/or selected species in the family are also well-documented in the literature (Rigalleau, 1936; Matthey, 1941; Blenton, 1943; Kramer, 1944; Eluwa, 1970). Leroy (1972) reported on the ultrastructure of the integument of visible surfaces of the members of the superfamily Tettigoniioidea.

The evolution of the head (Matsuda, 1965) and the structure of the tentorium (Snodgrass, 1947, 1956) have been well studied. Slifer (1973) reported on the ultrastructure of the antennae of the Tettigoniid, Neoconocephalus ensiger (Harris).


Studies on the anatomy of the alimentary canal (Judd, 1948; Anadon, 1949; Malabre, 1973; Anstee, 1975; Cantarella and Sammartino, 1976) are well-documented in the literature. Mohamed and Murad (1977) reported on the structures of the Malpighian tubules of the tettigoniid, Conocephalus indicus Redt.
Also well-documented in the literature are studies on the nervous system (Nesbitt, 1941; Steinman, 1961; Schmitt, 1964), the musculature (Josephson and Halverson, 1971; Elder, 1971; Matsuda, 1964; Schumacher, 1978), the reproductive system (Browning, 1947; Gupta, 1950; Leroy, 1969), and the respiratory system (Hsueh, 1938; Wigglesworth, 1950, 1972; Richards and Anderson, 1942; Nocke, 1974).

Snodgrass (1935a, b) classified the thoracic muscles of an insect into 15 categories: dorsal, tergo-pleural, tergo-sternal, axillary, epipleural, lateral intersegmental, pleuro-sternal, ventral, tergal promotor(s) of the leg, tergal remotor(s) of the leg, sternal promotor(s) of the leg, sternal remotor(s) of the leg, pleuro-coxal, adductor(s) of the coxa and extracoxal depressor(s) of the trochanter. This categorization of the thoracic muscles is based on their location, function, and points of origin and insertion in the thorax. According to Snodgrass (1935a, b), not all muscles listed above are present in all insects, but many are in all insect species studied. Tiegs (1955) identified the tergal, dorso-ventral, pleuro-tergal, pleural, and axillary thoracic muscles as the important ones in the operation of the insect wing. The same muscle groups are reported to serve important functions in the operation of the stridulatory organs in the Tettigoniidae (Elder, 1971; Josephson and Halverson, 1971; Schumacher, 1978).

The abdominal musculature in the Orthoptera primarily serves a respiratory function, except for specialized muscles that operate the genitalia (Ford, 1922). Three muscle groups, the tergal, sternal, and pleural muscles, are important in the abdomen. All three groups, plus
their various combinations, occur in the genital segments of both sexes, but some muscles are so specialized that they are difficult to homologize with the muscles of the visceral segments.

In the tettigoniid abdomen, Ford (1922) reported the presence of inner and alary tergal muscles. The sternal musculature includes transverse sternal, inner sternal, lateral sternal, median sternal, and outer sternal muscle groups. The pleural region bears tergo-sternal, sternopleural, antagonistic spiracular and spiracle occlusor muscles.

Many studies have been made on the orthopteran digestive and circulatory systems. Comparative studies of the alimentary tract (Gangwere, 1965), the proventriculus (Judd, 1948), and the heart (Nutting, 1951) have been done.

Gangwere (1965) classified the orthopteroid families he studied into four categories based on the gross external features of their digestive tract. The first category includes those families whose alimentary canal is linear and bears no caeca (e.g., Phasmatidae). The second category involves those families in which the alimentary canal is curved or convoluted and its ventriculus bears eight tubular caeca (e.g., Blattidae and Mantodea). In the third category, the canal is curved or convoluted but its ventriculus only bears two bulbous caeca (e.g., Gryllodea and Tettigoniodea). The last category includes those families in which the canal is semilinear and the ventriculus possesses usually six conical caeca (e.g., Acridoidea).

The Tettigoniodea possess an alimentary tract that can be subdivided antero-posteriorly into a mouth, short pharynx, oesophagus,
crop, proventriculus, two bulbous gastric caeca, ventriculus, Malphigian
tubules, intestine, and rectum. Judd (1948) observed that the proven­
triculus in the superfamily bears a short neck and that, internally,
both the neck and the globular proventriculus below it have six lon­
gitudinal folds that are continuous. Each fold has cushions of hair and
sclerotized appendages along its length. The folds are separated from
each other by partitions that may or may not be sclerotized. The pro­
ventriculus has been determined to play many different roles in the
digestive systems of different insect groups. These range from food
shredding and triturating roles to multipurpose functions including
that of filtering food and the prevention of large food particles from
entering the ventriculus (Gangwere, 1965).

Among the members of the Tettigonioidea investigated by Judd (1948),
two categories were erected based on the structure and armature of the
proventriculus. The first category included those families in which
the appendages are covered with hairs and the barbated lobes bear a
small spine surrounded by a tuft of hair (subfamily, Phaneropterinae).
In the second category were included those subfamilies whose members
possess appendages that lack hair but possess barbated lobes that are
strongly sclerotized without hair tufts (Phasgonarinae, Copipherinae,
Conocephalinae, and Decticinae).

The insect circulatory system bears, in addition to the well­
documented aorta and heart, some accessory structures. Nutting (1951)
reported the occurrence of phagocytic organs and segmental vessels in
some orthopteroid subfamilies. In the Tettigoniidae, phagocytic organs
occur in the subfamilies Pseudophyllinae (True Katydid) and Phaneropterinae (Bush Crickets), while no segmental vessels were found in all other subfamilies investigated. The members of the tettigoniid subfamily of armoured crickets, Hetrodinae, are reported to possess 12 pairs of alary muscles, 12 pairs of ostia, and no phagocytic organs or segmented blood vessels (Nutting, 1951).

The respiratory system consists of a complex network of internal tubes (tracheae) that supply air to all parts of the body. Air enters the system via paired stomatal openings that are segmentally arranged, on the pleural regions of the thorax and abdomen.

The tracheal system originates as tubular invaginations of the integument in the embryo. The complex organization of the tracheae characteristic of the adult insect results from the ramifications of the invaginated tubes, coupled with the formation of various anastomoses among them (Snodgrass, 1935). Being ectodermal in origin, each tracheal tube, except for the finest tracheal ramifications (the tracheoles), is lined with cuticle internally, that is periodically shed during growth.

Kennedy (1922) outlined the following sequence of events during the embryonic development of the tracheal system in insects. First, the spiracles develop in each segment followed by the invagination of a spiracular pit from which a spiracular trachea is formed. The latter reportedly then branches off to give rise to an anterior dorsal and a posterior dorsal connective that associate with the muscles of the respective regions of the segment. At about this stage in the
development, three additional tracheal ramifications form from the spiracular pit, namely, an anterior spiracle connective, a posterior latero-tergal trachea, and a leg trachea. The latter projects caudo-ventrally before subdividing to form an antero-tergal branch to the body wall, a pleural branch to the pleural fold, a ganglionic branch (the ventral segmental trachea of Snodgrass), and a sternal branch.

The tracheal plan characteristic of an adult insect of a given insect group derives from the basic tracheal branches named above (Kennedy, 1922; Snodgrass, 1935a, b). For example, the lateral plurisegmental tracheal trunk common in some insect orders develops by the fusion of the anterior spiracular connective of one segment with the leg tracheal branch of an adjacent segment. The ventral plurisegmental tracheal trunk results from the union of the sternal trachea with the ventral segmental trachea of a succeeding segment. Finally, the dorsal plurisegmental tracheal trunk of some insect groups forms by the fusion of the anterior and posterior dorsal connectives of the dorsal segmental tracheae of adjacent segments.

The organization of tracheae in the thorax is much more complex than it is in either the head or abdominal tagmata. This is due, among other things, to the absence of the prothoracic spiracles, the occurrence of legs and, in winged insects, the presence of wings in this tagma (Carpentier, 1927; Kennedy, 1922; Snodgrass, 1935a, b). The first thoracic (mesothoracic) spiracular pair is associated with tracheal trunks that not only supply the pro- and mesothorax but also the head. The tracheae issuing from the second (metathoracic) spiracular pair
supply air to the metathorax in addition to forming anastomoses with tracheal branches from the mesothorax and abdomen.

The number of tracheal trunks entering the head from the mesothoracic spiracles varies in different insect groups. However, at least two primary tracheal pairs are known commonly to enter the cranium from these spiracles in nearly all insect groups described to date. These are the dorsal and ventral head tracheal trunks (one of each type from either spiracle). The head tracheal trunks may give off branches prior to or after entering the head. These ramifications supply air to the brain, muscles of the cranium, and the gnathal appendages.

The tettigoniid mesothoracic spiracle differs from that of other Orthoptera in that it is a compound structure bearing two separate spiracular openings, the truncal and femoral stigmata. The truncal stigma is smaller, always cephaled to the femoral spiracle, and is associated with the tracheae that supply the head, pro- and mesothorax. Its aperture size is regulated by a lip-type closing mechanism. The femoral spiracle, on the other hand, is large, wide and open to the outside without an aperture closing mechanism. The tracheal trunks connected to it supply the foreleg and are associated with the auditory organ in the foretibia. Zeuner (1936) studied the evolutionary relationships of the lower portion of the femoral tracheal system in the Gryllacrididae, Prophalangopsidae, Gryllidae, Gryllotalpidae, and the Tettigoniidae. He found that the system serves as a sound receiving apparatus in addition to supplying air to the foreleg. Nocke (1974) reported that the sometimes horn-shaped or trumpet-shaped femoral
tracheae, occurring in some members of the Tettigoniidae, serve both as tuners of the tympanal organs and as direction sensors of the sources of sounds received.

The metathoracic spiracle in the Tettigoniidae is generally large and bears a lip-type stomatal aperture regulating mechanism. The abdominal spiracles, on the other hand, are of a different kind. They bear an internal or inner-type closing mechanism. The latter consists of two parts, the closing bow and the closing band. These components are operated by the antagonistic and occlusor spiracle muscles that act alternately to open and close the atrial pore, respectively (Mbata and Lewis, 1985c, in press).

The tracheal system in some orthopteran species is sometimes modified in various regions to form tracheal air sacs. These are thin walled vesicles of differing sizes and shapes that serve, among other functions, to increase the volume of tidal air during respiration (Wigglesworth, 1963).

Nesbitt (1941) studied the nervous systems of several representative members of the Orthoptera and related orders. He divided the system into four anatomical regions: 1) the brain or supraoesophageal ganglion, 2) the ventral nerve cord (consisting of the suboesophageal ganglion and the thoracic and abdominal ganglia), 3) the stomodaeal or stomatogastric system, and 4) the peripheral nervous system.

The peripheral nervous systems of the orthopteran prothorax (Steinman, 1961), the mesothorax of *Locusta migratoria migratorioides* Reiche & Fairm. (Albrecht, 1953; Campbell, 1961), the pregenital
abdominal segments of *Neoconocephalus exiliscanorus* (Davis) and *Ceuthophilus gracilipes gracilipes* (Haldeman) (Schmitt, 1964), the migratory locust (Albrecht, 1953), the tettigoniid, *Orphania scutata* Pussard (Malabre, 1973), the tree locust, *Acanthacris ruficornis* (fab.) (Ewer, 1972), and the Indian house cricket, *Gryllodes sigillatus* (Walker) (Narula, 1977) are well-known.

A typical orthopteran brain has three main anatomical subdivisions, the protocerebrum, deutocerebrum and tritocerebrum. The protocerebrum occurs dorsally and constitutes the largest subdivision. It bears optic lobes that may be broadly linked to it or are associated with it via stalks. Also arising from this subdivision of the brain are the ocellary nerves (*Nervi ocellarii*) in those species bearing ocelli.

Ventral to and broadly linked to the protocerebrum is the second subdivision, the deutocerebrum. The latter gives rise to the antennal nerves (*Nervus antennalis*), the accessory antennal nerves (*Nervus antennalis accessorius*) and the tegumentary nerves (*Nervus tegumentalis*).

Below the deutocerebrum is the tritocerebral subdivision. Ventrally it bears a pair of circumoesophageal nerve connectives that link the brain to the ventral nerve cord. Also located ventrally are the labro-frontal nerves that ramify to form the *pars frontalis* nerve to the frontal ganglion, and the *pars labralis* nerve to the labrum. The ventro-lateral regions of the tritocerebrum are linked below by a tritocerebral commissure.

The ventral nerve cord consists of a chain of ganglia that are interlinked by paired nerve connectives. The suboesophageal ganglion
is the largest and is located below the oesophagus and corpotentorium. It supplies nerves to the gnathal appendages and the neck muscles. There are three thoracic ganglia (one to a segment) and a number of abdominal ganglia. The number of ganglia occurring in the abdomen of a given orthopteran group varies, depending on the number of ganglia that have fused with each other during the course of evolution. It ranges from as few as four in *Mantis religiosa* L., to as many as seven in *Diapheromera femorata* Say (Nesbitt, 1941). The tettigonid *Conocephalus fasciatus* De Geer bears six abdominal ganglia. The first definitive ganglion is reported to have fused with the metathoracic ganglion. A similar situation exists in *Neconocephalus exiliscanorus* (Davis) (Schmitt, 1964).

The stomatogastric nervous system includes the frontal ganglion, the oesophageal ganglia, the hypocerebral ganglion, and the gastric or ingluvial ganglia (Nesbitt, 1941). The frontal ganglion occurs anterior to the brain on the pharynx, to which it is tenaciously attached. The oesophageal and hypocerebral ganglia occur immediately behind the brain on the oesophagus. The former communicate with the protocerebrum via occipital nerves (Nervus occipitalis) and with the corpora allata by the *Nervi corporum allatum*. The hypocerebral ganglion is linked to the oesophageal ganglia by short nerves and to the ingluvial ganglia (these are located in the region of the proventriculus on the crop wall) by long nerves, *Nervi recurrens posterior externus*. Also issuing from the caudo-ventral portion of the hypocerebral ganglion, in some orthopteran groups, are a pair of shorter nerves termed *Nervi recurrens posterior internus*. The latter innervate the oesophagus.
Nesbitt (1941) grouped the Orthoptera he studied into two subdivisions based on whether one or two pairs of recurrent nerves are present. Families whose members bear only one pair of recurrent nerves include the Mantidae, Blattidae, Phasmatidae, and Grylloblattidae. Two pairs of recurrent nerves are characteristic of the Rhaphidophoridae, Gryllidae, Acrididae, and the Tettigoniidae.

The internal reproductive organs of female tettigoniids are simple and generalized. They include a pair of ovaries that lie on either side of the digestive tract, a pair of lateral oviducts, a common oviduct, a spermatheca, and an accessory gland. In the male, the internal reproductive structures are more complex and varied. They include a pair of testes, which, like the ovaries in the female, lie on either side of the alimentary canal, paired vas deferentia, one or several kinds of accessory glands, and an ejaculatory duct with its associated pair of vesicles.

Explanation of Dissertation Format

This dissertation is a compilation of papers on the anatomy of the armoured ground cricket, *Acanthoplus speiseri* Branksic 1895, that have been submitted for publication to the Iowa State Journal of Science. The senior author conducted the research under the supervision of the junior author, Dr. R. E. Lewis, who served as his major professor while the former was pursuing doctoral degree studies at Iowa State University. The specimens were collected in Zambia, Southern Africa, by the senior author during 1981 and 1982 and brought to I.S.U. where the study was conducted.
Acanthoplus speiseri belongs to the family Tettigoniidae in the order Orthoptera. It is in a subfamily of armoured ground crickets called Hetrodinae. This subfamily contains some economically important pests of crops in Southern Africa. Very little is known about the anatomy of this group and this study was meant to bridge this gap in our knowledge of the Orthoptera. The major objective of this investigation was to describe the anatomy of the armoured ground cricket A. speiseri and to compare and contrast it with those of selected tettigoniids reported in the literature.

The format of this dissertation is as follows: Section I deals with the external morphology of the ground cricket. Section II describes the endoskeletal processes while Sections III and IV are on the internal anatomy. Section III is concerned with the general musculature and the gross morphologies of the alimentary canal and the circulatory system. Section IV gives a description of the gross structures of the respiratory, nervous, and reproductive systems, followed by a summary discussion of the whole study.

At the end of the dissertation, all references used in the investigation are given and two appendices are presented. Appendix A is a map of Africa showing the distribution of the genus Acanthoplus Stål., and other genera of the subfamily Hetrodinae in Africa as reported by Weidner (1941). Appendix B shows the distribution of A. speiseri in Zambia, determined by the senior author during the preliminary studies.
THE ANATOMY OF THE ARMoured GROUND CRICKET,

Acanthoplus speiseri BRANCSIK 1895.

I. EXTERNAL MORPHOLOGY

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SECTION I. EXTERNAL MORPHOLOGY

Abstract

Studies on the external morphology of *Acanthoplus speiseri* Brancsik were conducted. *Acanthoplus speiseri* possesses a generalized tettigoniid external form with the thoracic and abdominal tagmata exhibiting notable subfamilial specializations. The protergum is a spiniform, sexually dimorphic shield covering the mesoscutum. In the male, it houses beneath a pair of stridulating organs that are reduced and modified tegmina borne on the mesoscutum. The left organ (length, 6.3 mm; width, 4.6 mm; N = 30), overlaps the right (length, 5.9 mm; width, 4.2 mm; N = 30) and both bear beneath a file and plectrum. Females lack stridulating organs; possessing instead, vestigial wing pads on their mesoterga. The ovipositor is short, closely resembling that of *A. bechuanus* Per. In the male, three membranous phalIomeres are specialized for spermatoaphore formation.

Introduction

The armoured ground cricket *Acanthoplus speiseri* Brancsik 1895 belongs to the family Tettigoniidae in the order Orthoptera. The species has been placed in the subfamily Hetrodinae, a group endemic to Africa (Caudell, 1914; Peringuey, 1928; Skaife, 1953; Weidner, 1941, 1955). Although commonly referred to as crickets, members of the Hetrodinae are not true crickets and the common name arose erroneously due to their general resemblance to the latter. All members of the subfamily are adorned or "armoured" with a complex system of spiniform ornaments on
their bodies (Skaife, 1953; Caudell, 1914). Both sexes are heavy bodied, apterous, ground dwelling insects that exhibit a characteristically clumsy gait.

The genus *Acanthoplus* Stål has been reported to be restricted in its geographical distribution to Africa, south of the Sahara. It ranges from the Cape province of South Africa, north to approximately 13° S latitude in Mozambique to the east, to approximately 8° S latitude in Angola to the west (Weidner, 1941). In Zambia, members of the genus are reported to occur commonly in the southwest of the country, close to its borders with Angola, Namibia, and Zimbabwe.

The genus is known to possess some economically important pests of crops in southern Africa (Allan, 1930; Bevis, 1964). However, except for systematic studies (Caudell, 1914; Peringuey, 1928; Weidner, 1941, 1955) and some observations on the biology of *Acanthoplus bechuanus* Per. (Power, 1958) very little is known about the biology and ecology of species belonging to this genus.

Preliminary observations by the senior author on the distribution, bionomics, and feeding habits of *A. speiseri* in Zambia revealed that it is more widely distributed in the country than was previously reported (Weidner, 1941). It is an important pest of corn, its damage to the crop being greatest in small traditional fields surrounded by Savanna vegetation.

Lack of information on this potentially important pest of corn in Zambia, and possibly neighboring countries, prompted this investigation. The anatomy, and later, the acoustic behavior of *A. speiseri* have been
studied with the view of contributing towards the basic research necessary if pest management programs need be initiated to control the species.

Following is a description of the external features of *A. speiseri*. As nearly as possible, the terminology of Snodgrass (1935) has been followed. Lists of these terms and their abbreviations appear in the legends accompanying plates.

**Body Tagmata**

**The head**

The head of *Acanthoplus speiseri* is of the hypognathous type in that the long axis is vertical with the mouthparts directed ventrally. It is dorso-ventrally elongated and oval in outline when viewed *en face* (Figure 1).

Following is a description of the external structure of the head. The descriptions of the internal structure of the cranium and the endoskeletal processes of the thorax and the abdomen will be presented in another article.

**The cranium (head capsule)**

**The frontocylypeal area**

The frontocylypeal or face region of the cranium consists of a large but poorly defined frons (Fr) dorsally and an oblong clypeus (Clp) ventrally. The two sclerites merge into each other in the region between the anterior tentorial pits (at). This is due to the absence of a well-defined epistomal suture (es). The relative position of the epistomal suture can be approximated by the course followed by the underlying frontocylypeal ridge, indicated by the dotted line between the anterior tentorial pits, in Figure 1.
Figure 1. Anterior view of the head

Ant, antenna; AntS, antennal socket; as, antennal suture; ASc, antenna sclerite; at, anterior tentorial pit; c, anterior articulation of mandible; Clp, clypeus; cls, clypeolabral suture; cs, coronal suture; E, compound eye; es, epistomal suture; fgs, frontogenal suture; Fr, frons; fs, frontal suture; Ge, gena; Lbplp, labial palp; Lm, labrum; Md, mandible; Mxplp, maxillary palp; os, ocular suture; OSc, ocular sclerite; Plst, pleurostoma; s, stalk of ocular sclerite; sgs, subgenal suture; Tbc, tubercle; ts, temporal suture; Vx, vertex
The antennal (as) and frontal (fs) sutures form the dorsal limits of the frons, while the sclerite is partially limited by the frontogenal sutures (fgs), and partially merges with the genae (Ge) laterally. The composite frontoclypeal sclerite is bounded below by the clypeolabral suture (cls), which separates a large, oval labrum (Lm) from the triangular clypeus.

The parietals The parietals extend laterally on either side of the cranium, from the vertex (Vx) to the subgenal sutures (sgs). Each is limited anteriorly by an incomplete frontogenal suture, and posteriorly by the occipital suture (Figure 2, ocs). Each parietal supports a small, hemispherical, stalked, compound eye (E). These stalks are mesal extensions of the ocular sclerites (Figure 1, s, OSc). They are fixed to the cranial walls, making the eyes immovable. There are no ocelli on the parietals.

Each antenna is inserted meso-ventrad to a compound eye. Between the antennal bases arises a prominent tubercle (Figure 1, Tbc). Just below the tubercle, the coronal suture (cs) branches into two short frontal sutures. These short frontal sutures then merge with the antennal sutures (as).

Above the compound eye and antennal base is a branched temporal suture (ts'), and below these structures are the lateral sclerites of the head termed the genae (Figure 1, Ge).

The subgenal areas (Plst) The subgenal region on either side of the head consists of a narrow, elongated sclerite, the pleurostoma, that lies beneath the subgenal suture (Figures 1, 2, Pist).
Figure 2. Lateral view of the head

a', a'', a''', primary cranial articulations of mandible, maxilla and labium, respectively; Ant, antenna; c, anterior articulation of mandible; Clp, clypeus; Cv, cervical sclerite; Cvx, cervix or neck; E, compound eye; es, epistomal suture; fgs, frontogenal suture; Fr, frons; Ge, gena; Lb, labium; Lm, labrum; Md, mandible; Mx, maxilla; Oc, occiput; ocs, occipital suture; Pge, postgena; Plst, pleurostoma; Poc, postocciput; pos, postoccipital suture; pt, posterior tentorial pit; sgs, subgenal suture; ts', temporal suture; Vx, vertex
The mandibles (Md) articulate with this sclerite both anteriorly and posteriorly.

The mandibles are short, stout, and of unequal size, the left being larger than the right. This gives the head a slightly lopsided appearance when viewed from the front (Figure 1).

The occipital arch (Oc) and the postocciput (Poc) are seen in the lateral (Figure 2) and posterior (Figure 3) views of the head. The gnathal appendages are also distinct from the lateral and posterior aspects.

**The occipital arch (Oc)** This area of the cranium forms the back of the head and consists of a horseshoe-shaped sclerite that is bounded anteriorly by the occipital suture (ocs) and posteriorly by the postoccipital suture (pos). The sclerite is narrow above, where it is transected by the temporal sutures (Figures 2, 3). It widens below, on either side of the head, into triangular plates that merge with the posterior articulations of the mandibles (Figure 2, a'). The narrow region of the sclerite above is known as the occiput (Oc), while the wider area below forms the postgena (Pge). Wide posterior tentorial pits (pt) occur on the mesal margins of the postgena, at the lower ends of the postoccipital suture.

**The postocciput (Poc)** The postocciput consists of a narrow sclerite forming the rim of a large circular opening from the head into the neck, the occipital foramen (Figure 3, For). The neck or cervical membrane (Cvx) is attached to this rim anteriorly and to the prothorax
Figure 3. Posterior view of the head

a'', a''', primary cranial articulations of maxilla and labium, respectively; cs, coronal suture; E, compound eye; For, occipital foramen; Ge, gena; Lb, labium; Md, mandible; Mx, maxilla; Oc, occiput; occ, occipital condyle; ocs, occipital suture; Pge, postgena; Poc, postocciput; pos, postoccipital suture; pt, posterior tentorial pit; ts', temporal suture; Vx, vertex
posteriorly. Small occipital condyles (occ) occur ventrolaterally on the postocciput, to which cervical sclerites articulate (Figure 2, Cv).

**The antennae (Ant)** The antennae arise below the compound eyes (Figure 1). They average 54.9 mm (range, 44–59.2 mm; N = 15), or about 5 mm longer than the mean body length of the male ($\bar{X} = 32.5$ mm; range, 29–36 mm; N = 30), and about half a centimeter longer than the average body length of the female ($\bar{X} = 38.5$ mm; range, 33–43 mm; N = 30). Each has an average of 123.83 segments (range, 94–184; N = 12).

The first antennal segment, the scape (Figure 4, Scp) is cylindrical and about twice as long as wide. It is inserted in the cranium at the base, through a small, ellipsoidal, membranous socket (Figure 1, AntS). The socket is surrounded by a narrow sclerite (ASc) that is set off from the rest of the cranium by the antennal suture (as). On the mesal margin of the antennal socket, the antennal sclerite is appressed to the narrow stem of the compound eye stalk (Figure 4, s). At its base, the scape bears a slender, fingerlike process (Figure 4, ap) which articulates with a pivoting process (n) on the antennal sclerite.

The pedicel (Figure 4, Pdc), or second antennal segment, is also cylindrical but only half as long as the scape. It articulates with the latter via a small circular membrane.

The rest of the antennal segments form the flagellum of the antenna (Figure 4, Fl).

**The gnathal appendages**

**The mandibles (Figures 5, 6)** The mandibles are short and stout. The larger, left mandible has a mean length of 5.0 mm. Each
Figure 4. Antenna

Figure 5. Anterior view of left mandible

Figure 6. Posterior view of left mandible

Figure 7. Posterior view of right maxilla

ap, antennal pivoting process; 8 Ap, abductor apodeme of mandible; 9 Ap, adductor apodeme of mandible; as, antennal suture; ASc, antenna sclerite; br, brustia; c, acetabulum; Cd, cardo; Co, condyle; e, articulation of maxilla with cranium; fgs, fronto-genal suture; Fl, flagellum; Ga, galea; Lc, lacinia; n, articulation point (antennifer); o, incisor lobe of mandible; p, molar lobe of mandible; Pdc, pedicel; Plf, palpifer; Plp, palpus; q, suture near inner margin of stipes from the posterior aspects; s, stalk of ocular sclerite; Scp, scape; St, stipes; t, suture separating palpifer from stipes.
mandible is roughly triangular in cross-section, thus presenting lateral, anterior and posterior faces. These faces form a wide triangular base by which the mandible is attached to the subgenal region of the cranium. The anterior and posterior faces unite mesally to form the gnathal surface. The latter is divided into an anterior cutting and tearing incisor lobe (o) and a posterior grinding molar lobe (p). Behind the molar region is the brustia (br) of the mandible, bearing strong, short bristles (Figure 5).

The dorsolateral junction of the anterior and posterior surfaces bears a cup-shaped acetabulum by which the mandible interacts with the anterior portion of the cranium (Figure 5, c). On the mesal angle is a large apodeme (9 Ap) to which the massive mandibular promotors attach.

The lateral mandibular surface is broadest at its base and tapers off ventrally. It bears a small apodeme (8 Ap) at its posterior junction with the caudal face to which the extensor muscles attach.

The posterior mandibular angle bears a small, protuberant condyle dorsolaterally (Figure 6, Co) which articulates with the pleurostoma posteriorly.

**The maxillae (Figures 7, 8)** The maxillae arise behind the mandibles. They are linked to the cranium adjacent to the posterior tentorial pits (Figures 2, 3, pt, a'). The basal segment of a maxilla is the cardo (Figure 7, Cd). It is subdivided into two small sclerites by the cardinal suture (Figure 8, cds). The base of the cardo bears a triangular condyle (e) and a mesal apodeme (10 Ap).
Figure 8. Anterior view of right maxilla

Figure 9. Anterior view of hypopharynx

Figure 10. Posterior view of hypopharynx

Figure 11. Posterior view of labium

Figure 12. Anterior view of labium

10 Ap, apodeme of promotor of cardo; bl, basilingua; Cd, cardo; cds, cardinal suture; dl, distilingua; e, articulation of maxilla with cranium; Ga, galea; Gl, glossa; Lc, lacinia; Mt, mentum; Mth, mouth; Pgl, paraglossa; Plg, palpiger; Plf, palpifer; Plp, palpus, Pmt, prementum; se, sensilla; slc, salivarium; Smt, submentum; St, stipes; w', suspensoria of hypopharynx
Ventral to the cardo is the second maxillary segment, the stipes (St). The stipes supports a palpifer (Plf) laterally, on which is borne a five-segmented maxillary palpus (P1p). The terminal segment of the palpus is slightly longer than the penultimate and possesses a rounded end. Posteriorly, the stipes bears a sutural groove that forms an internal inflection for muscle attachment (Figure 7, q).

At the distal end of the stipes are two lobes, an outer galea (Ga) and an inner lacinia (Lc). The latter possesses three teeth at its apex. The terminal tooth is the largest and is movable.

The hypopharynx (Figures 9, 10) The hypopharynx lies between the mandibles and maxillae in the preoral cavity. The food channel occurs anterior to the hypopharynx and the salivary meatus occurs behind it. It is divided into two regions, the basilingua (bl) at the base and the distilingua (dl) anterior to it. Both regions of the hypopharynx bear sensory hairs on their upper surfaces.

The mouth opens behind the basilingua (Figure 9, Mth). It is flanked by peg-like sensilla (se) laterally. Beneath the distilingua is the salivarium (slc).

Both lateral lobes of the hypopharynx are strengthened internally by sclerotized suspensoria (w').

The labium (Figures 11, 12) The labium or lower lip is composed of a basal submentum, a median mentum, and a distal prementum (Figures 11, 12, Smt, Mt, Pmt). The proximal ends of the submentum articulate with the cranium while, distally, the segment is separated
from the mentum by a flexible membrane. The mentum and prementum are separated from each other by a suture.

On the lateral margins of the prementum are palpigers (Plg) which bear three-segmented labial palpi (Plp). The distal end of the prementum possesses two pairs of lobes, the larger, semicircular, outer paraglossae (Pgl) and the inner glossae (Gl).

The thorax

The prothorax

The pronotum The pronotum forms a large shield with an average length of 14 mm (N = 12) in the male and 12.5 mm (N = 12) in the female. It is divided into anterior and posterior regions by a transverse furrow (Figures 13, 14, 16, APR, PPR, tf). The furrow has a corresponding internal inflection on which some prothoracic muscles attach.

The lateral margins of the anterior pronotal region are each adorned with two stout spines (S). The posterior region bears six spines, four on its lateral margins and two postero-laterally. In both sexes, the posterior pronotal region covers the mesoscutum. This region displays sexual dimorphism in that it is elevated and dome-shaped in the male, while it is flat but elevated in the female (Figures 13, 14). In the male, the dome of the posterior pronotal region houses a pair of stridulating organs that are borne on the mesoscutum (Figures 13, 18, 19, 21, Sps). Females lack sound producing structures. The relative position of the latter in the female is occupied by wing pads or stubs of vestigial wings (Figures 20, 22, Vg).
Figure 13. Lateral view of male thorax and abdomen

a, pleural articulation of coxa; APR, anterior pronotal region; Bs, basisternite; Cer, cercus; Cx, coxa; dpg, dorsopleural groove; Epm, epimeron; Ept, epiproct; Eps, episternite; PPR, posterior pronotal region; PS, pleural suture; S, spine; scl, scutellum; sct, scutum; sgp, subgenital plate; sl, lateral sternite; sp, abdominal spiracle; Sps, sound producing structure (stridulating organ); St, abdominal sterna; T, abdominal tergite; tf, transverse furrow of pronotum
Figure 14. Lateral view of female thorax and abdomen

a, pleural articulation of coxa; APR, anterior pronotal region; Bs, basisternite; Cer, cercus; Cx, coxa; dpg, dorsopleural groove; Epm, epimeron; Eppt, epiproct; Eps, episternite; Ovp, ovipositor; Papt, paraproct; PPR, posterior pronotal region; S, spine; scl, scutellum; scu, scutum; sgp, subgenital plate; sp, abdominal spiracle; St, abdominal sterna; T, abdominal tergite; tf, transverse furrow of pronotum
Figure 15. Lateral view of the male pterothorax

Bs, basisternite; Epm, epimeron; Eps, episternite; F, file; F, parapterum (basalar); Pla, root of pleural apophysis; Ps, presternal plate (presternum); PS, pleural suture; Sp, thoracic spiracle; SpS, stridulating organ; St, abdominal sterna; T, abdominal tergite; Tn, trochantin; u, external groove on episternum; w, line dividing tergum into two plates; WP, wing process
Figure 16. Dorsal view of the male head and thorax

Ant, antenna; APR, anterior pronotal region; cs, coronal suture; E, compound eye; Ge, gena; Ma, clear areas of cuticle indicating regions of muscle attachment internally; Poc, postocciput; PPR, posterior pronotal region; S, spine; scl, scutellum; T, abdominal tergite; Tbc, tubercle; tf, transverse furrow; ts', temporal suture; Vx, vertex
Figure 17. Ventral view of the thorax and first three abdominal segments

Acx, precoxal bridge; Bs, basisternite; Cv, cervical sclerite; Cs, coxa; Eps, episternite; j, submarginal suture; K, furcal suture (groove); Ps, presternum; Sa, sternal apophyseal pit (furcal pit); Sl, sternullum; sp, abdominal spiracle; Sp, thoracic spiracle; Spn, root of spins (spinal pit); St, abdominal sterna; Tn, trochantin
Figure 18. Dorsal view of the male pterothorax

Figure 19. Dorsal view of the male pterothorax showing the mesonotum

ANP, anterior notal process; Ax, axillary sclerite; AxC, axillary cord; e, intertergal sclerite; Epm, epimeron; Eps, episternite; F, file; Plm, plectrum; PNP, posterior notal process; Prsc, prescutum; scl, scutellum; sct, scutum; Sps, stridulating organ; ts, transverse notal suture; vs, scutoscutellar or V-shaped suture; w, groove dividing tergum into two plates
Figure 20. Dorsal view of female mesonotum

Figure 21. Lateral view of the male stridulating segment

Figure 22. Lateral view of the female mesothoracic segment

ANP, anterior notal process; Bs, basisternite; Cs, coxa; Epm, epimeron; Eps, episternite; F, file; Mer, meron; P, parapterum (basalar); Prsc, prescutum; PNP, posterior notal process; PS, pleural suture; Pla, root of pleural apophysis; Ps, presternum; scl, scutellum; sct, scutum; Sps, stridulating organ; Sp, thoracic spiracle; Tn, trochantin; ts, transverse notal suture; u, external groove on episternum; Vg, vestigial wing pad; w, groove dividing tergum into two plates; WP, wing process
The dorsal surface of the pronotum is rough. Several grayish spots are observed in specimens that have been preserved in alcohol for a long time (Figure 16, Ma). These are areas to which tergo-steranal and tergo-pleural prothoracic muscles attach internally.

**The propleuron** The propleuron occupies but a small area on the antero-ventral corner of the pronotum (Figures 13, 14). It is divided into an anterior episternum (Eps 1) and a posterior epimeron (Epm 1) by a short pleural suture (PS 1). The epimeron is firmly fixed to the pronotum dorsally. The postero-ventral edge of the episternum and the antero-ventral edge of the epimeron project downward, forming the pleural articulation of the forecoxae (Figures 13, 14, a, Cx 1).

**The prothoracic leg (Figure 23)** The basal segment of the foreleg is the coxa (Figure 23, Cx). It bears a small spine (cxsp) above. The coxa articulates with the trochanter (Tr) distally, via a flexible membrane. The trochanter is smaller than the coxa and is firmly fixed to the stout femur (Fm) that follows it. The femur is smooth and lacks ornamentation. Distal to the femur is the tibia (Tb). The proximal region of this segment is enlarged and bears the auditory organ. The location of the auditory organ on the tibia is not unique to this species; it is characteristic of all members of the family Tettigoniidae.

Externally, the auditory organ possesses a tympanum (tym) that is surrounded by a membrane (me) on both the inner and outer faces of the tibia. Both tibiae of the forelegs possess auditory organs.
Figure 23. Foreleg
Figure 24. Midleg
Figure 25. Hindleg

bcs, basicoxal suture; Cx, coxa; cxsp, coxal spine; Fm, femur; Mer, meron; me, auditory membrane; pu, pulvillus; Tar, tarsus; Tb, tibia; Tr, trochanter; tym, tympanum; Un, claw
Below the auditory organ, the tibia bears two kinds of processes; a row of short immovable spines on its inner face and a pair of terminal spurs. A four-segmented tarsus (Tar) follows the tibia. Distal to the latter is a pretarsus that bears two well-developed claws (Un) terminally. The tarsomere pads, or tarsal pulvilli (pu), are also well-developed.

**The prosternum (Figure 17)** The sternum of the prothorax in the ground cricket is primitively divided into a large anterior basisternite and a very small posterior sternum (Figure 17, Bs 1, St 1). The basisternite is continuous with the pre-coxal bridges (Axc) anterolaterally. In front of the basisternite, a very narrow sclerite (Ps) is cut off by the submarginal suture (j).

A broad transverse groove (K) between the bases of the prosternal apophyses, represented by the furcal pits (Sa 1), separates the basisternite from the sternum. The latter plate is confined to the mesal region, behind the prosternal transverse groove.

**The mesothorax**

**The mesonotum (Figures 18, 19)** Though apterus, the mesonotum exhibits a structure typical of a generalized wing bearing segment, especially in the male. It consists of a single plate that is modified to support sound producing structures (Figures 18, 19, Sps). The stridulating organs are modified mesothoracic wings.

The anterior margin of the mesonotum has a small sclerite, the prescutum (Prsc) that is limited posteriorly by the transverse notal suture (ts). This suture has a corresponding internal ridge which
strengthens that region of the tergum. In the male, the rest of the mesonotum is subdivided into two antero-lateral scuta (sct) and the posterior scutellum (scl), by a scutoscutellar or V-shaped suture (vs). The tip of the V-shaped suture is directed forward and lies very close to the transverse notai suture on the anterior margin of the tergum. In the female, the rest of the mesonotum is simple. It is partially divided into an anterior scutum (sct) and a posterior scutellum (scl) by an external groove (Figure 22, w). This groove is represented internally by a phragma on which dorsal longitudinal muscles of the mesothorax attach.

The scutum bears, an anterior notai process (ANP) and a posterior notal process (PnP), anterolaterally (Figures 18, 19). In the male, the stridulating organs or tegmina articulate with the mesonotum through the notal processes and axillary sclerites (Ax).

In the female, the simpler subdivision of the mesonotum (Figures 20, 22) is due to the absence of the stridulating organs. In their stead, are vestigial, scale-like wing pads (Vg). The latter do not overlap and, consequently, females do not stridulate. However, as in the male, the female mesothoracic wing pads articulate with the tergum via notal processes.

**Stridulation in the male** The stridulating organs in the male (Figure 18) are oval in shape. The left structure overlaps the right when the insect is at rest. Both structures have a parchment-like consistency. Each organ bears a file (F) composed of many cuticular teeth and a hardened edge or plectrum, mesally (Figure 18, Plm). The
file and plectrum are seen as darkened outlines from the dorsal view in situ (Figure 18).

The left stridulating organ has a mean length of 6.3 mm (range, 5.5–6.9 mm; N = 30) and a mean width of 4.6 mm (range, 4.8–5.8 mm; N = 30). It is larger and wider than the right structure, whose mean length is 5.9 mm and is 4.2 mm wide.

The file on the left structure is longer (\(\bar{X} = 27\) mm) and has a greater number of teeth (\(\bar{X} = 28.20\)) than the right (\(\bar{X} = 16\) mm; \(\bar{X} = 17.70\) teeth, respectively).

Stridulation in the male occurs when the file under one stridulating organ is moved back and forth over the plectrum of the other structure. The posterior region of the prothorax is elevated during stridulation.

The mesopleuron The pleura of the mesothorax are nearly the same in both sexes. In the male, however, additional elements for operating the stridulating organs are present (Figures 15, 21, 22).

The dorsal margin of the mesopleuron bears a long wing process (WP). The latter is strengthened internally by the pleural ridge that extends down externally from the wing process to the coxal articulation. Externally, the pleural ridge manifests itself as a pleural suture (PS). At the basal end of the pleural suture ventrally is a pit (Pla) which indicates the origin of an internal pleural apophysis.

The pleural suture divides the mesopleuron into large plates; an anterior episternum (Eps 2) and a posterior epimeron (Epm 2). The episternum is further subdivided into upper and lower plates by an external groove (u). These are sometimes referred to as the anepisternum and katepisternum, respectively, by some authors.
Beneath the episternum and articulating with it are an anterior presternum (Ps) and a posterior trochantin (Tn) sclerites. The trochantin is a reduced, strip-like sclerite that also articulates ventrally with the mesocoxa (Cs 2).

The distinctive feature of the male mesopleuron is the presence of well-developed epipleurites above the episternum (Figures 15, 21, P). Some important muscles operating the stridulating organs attach to these small sclerites.

**The mesothoracic leg (Figure 24)** Except for the absence of the auditory organs and its smaller size (it is the smallest leg on the insect), the mesothoracic leg is similar to the foreleg, already described above.

**The mesosternum (Figure 17)** The mesosternum consists of two distinct plates; a larger rectangular basisternite in front and a smaller sternullum behind (Figure 17, Bs 2, Sl 2). The basisternite articulates with the presternum (Ps) antero-laterally. The presternum, on the other hand, interacts with the episternum (Eps 2).

The basisternite (Bs) is bounded posteriorly by a transverse groove (K) that occurs between the bases of the mesothoracic sternal apophyses. The latter are represented by a pair of pits externally (Sa 2).

The sternullum (Sl) of the mesosternum is a spinasternite. The spina opens to the outside on this sclerite (Spn).

**The metathorax**

**The metanotum** In both sexes, the metanotum is a simple saddle-shaped sclerite that is partially divided into an anterior scutum
(Figures 13, 14, sct) and a posterior scutellum (Figures 13, 14, scl) by an external groove (Figure 15, w).

The metapleuron The metapleuron bears a close resemblance to the mesopleuron except for the size and shape of the plates constituting it. It bears a pleural suture (Figures 13, 14, 15, PS) that divides it into an episternal plate (Eps 3) anteriorly and an epimeral plate (Epm 3) posteriorly. The pleural suture is also strengthened on the inside by a pleural ridge. It terminates ventrally at the base of the metathoracic pleural apophysis, represented by a pit (Figure 15, Pla).

Below the metathoracic episternum is a small oval presternum (Ps) and a narrow trochantin (Figure 15, Th 3). The latter also articulates with the hind leg coxa.

The metathoracic legs This is the largest leg on the ground cricket (Figure 25). It is similar in structure to the mesothoracic leg. However, Acanthoplus speiseri being nonsaltatorial in habit, its femur is not thickened as in the Acrididae. The tibia has two rows of short spines and bears two apical spurs.

The metasternum (Figure 17) The metasternum consists of two plates. A broad anterior basisternite (Bs 3), which is bounded posteriorly by a transverse groove (K), sets off two marginal sternellar sclerites (Sl 3). A transverse groove connects the two external pits (Sa 3) which represents the bases of the metasternal apophyses.
The abdomen

Abdominal segments The abdomen possesses 11 true segments (Figures 13, 14). Each abdominal segment has a generalized structure consisting of a sclerotized dorsal tergite (T), two smaller sclerotized ventral (St) and lateral (sl) sternites, and a membraneous pleural region.

The first eight abdominal segments each bears a pair of spiracles (sp). The latter, according to Snodgrass (1935), lie on the sides of each segment above the dorso-pleural groove (Figures 13, 14, dpg).

The first seven abdominal segments in the female and the first eight in the male are known as the pregenital or visceral segments. They contain most of the internal abdominal organs. The eighth and ninth abdominal segments in the female and only the ninth segment in the male constitute the genital segments. These bear the external organs that serve various activities related to copulation and oviposition. The tenth and eleventh abdominal segments, plus the telson at the posterior end of the body in both sexes, form the postgenital segments.

The visceral segments (Figures 13, 14) The first visceral segment is broadly joined to the thorax. Each segment bears a saddle-shaped tergite on its dorsum and reduced sternites on its venter and on the lateral sides below the spiracles. The pleural region of each segment is membranous. A pair of spiracles occur on the lateral margins of the tergum above the dorso-pleural groove.
The female genital and postgenital segments (Figures 26, 27, 28, 29) The eighth and ninth abdominal segments in the female are the genital segments. Externally, they bear special cuticular modifications of the pleural and sternal regions that facilitate copulation and oviposition in the reproducing adult. The prominent structures on the genital segments in the female are the ovipositors (Figure 14, Ovp). They consist of three pairs of blades or valvulae which work in unison in loosening the soil during oviposition. The dorsal (3 VI) and ventral (1 VI) valvulae are armed posteriorly with spines on their dorsal and ventral aspects, respectively. The inner valvulae (2 VI) are enclosed by the dorsal valvulae (Figures 26, 1 VI, 2 VI, 3 VI).

The eighth abdominal segment bears a tergum that resembles those of the visceral segments before it. However, its pleural region is specialized, bearing a triangular sclerite that is pushed caudally and which appear to be part of the ninth segment. This triangular sclerite is called the first valvifer (1 Vlf). It articulates with a long blade of the ovipositor beneath (1 VI) and with the second valvifer above (2 Vlf). The latter is part of the ninth abdominal segment. Like the first valvifer, it has been shifted backwards on the body to come to lie above the dorsal blades of the ovipositor (3 VI).

The sternum of the eighth segment forms a specialized triangular subgenital plate (sgp). The latter bears a chamber (Gc) on its upper side below the first valvulae. The true external opening of the female reproductive tract lies in the floor of this chamber.
Figure 26. Lateral view of the female genital and postgenital segments

Cer, cercus; dgr, dorsal interlocking groove of ovipositor; dpg, dorsopleural groove; Eppt, epiproct; Gc, genital chamber; Papt, paraproct; sgp, subgenital plate; sp, abdominal spiracle; St, abdominal sterna; T, abdominal tergite; V1, ovipositor valve; Vlf, valvifer
Figure 27. Dorsal view of female genital and postgenital segments

Figure 28. Ventral view of female genital and postgenital segments

Cer, cercus; Eppt, epiproct; Papt, paraproct; St, abdominal sterna; T, abdominal tergite; Vl, ovipositor valve; Vlf, valvifer
Figure 29. Posterior view of female genital and postgenital segments

Cer, cercus; dgr, dorsal interlocking groove of ovipositor; Eppt, epiproct; Papt, paraproct; St, abdominal sterna; T, abdominal tergite; Vl, ovipositor valve; Vlf, valvifer
The ninth tergum is simple in structure. However, as mentioned before, this tergite lies above the first valvifer and as such the latter could be mistaken to be part of the former. It should be borne in mind that both valvifers (1 Vlf, 2 Vlf) have shifted backwards on the body. The first valvifer, which is part of the eighth segment, lies below the ninth tergum, while the second valvifer, which is part of the ninth segment, lies below the tenth tergum.

The second valvifer gives rise to the second or inner valvulae (2 VI). The latter, as mentioned before, are located between the dorsal valvulae with which the second valvifer articulates posteriorly.

The dorsal or third valvulae are the broadest. They bear short spines dorsally and are pointed apically. The ventral valvulae consist of slender blades, each of which has three short spines ventrally. As with the dorsal pair, each blade terminates in a sharp apical spine. Spines on the ovipositor blades serve a dual purpose. They are a protective armor and aid in breaking and loosening soil during oviposition. The dorsal and ventral ovipositor blades interlock by means of a groove located on the dorsal margin of the ventral blades (Figure 26, dgr).

The tenth and eleventh abdominal segments are postgenital in the female. The tenth tergum is small and is fused with the eleventh tergum posteriorly. The pleuron and venter of the tenth segment are membraneous.

The eleventh tergum is the epiproct (Figure 27, Eppt). On either side of the epiproct are large cylindrical and knob-like structures, the paraprocts (Papt). Laterad of the base of each paraproct is a single segmented cercus (Cer). The paraprocts and cerci are parts of the eleventh abdominal segment. The anus opens behind the paraproct.
The male genital and postgenital segments (Figures 30, 31, 32)

In the male, only the ninth abdominal segment is genital. It has a simple tergum (Figures 13, 30, 31, 32, T). Its pleuron is mainly membraneous but bears in the intersegmental region, the external reproductive structures. The sternum of the ninth segment is a modified triangular subgenital plate (Figure 31, sgp). It forms a genital chamber (Gc) that houses the phallus.

The phallic organs in the male include four phallomeres that are separate membraneous lobes. The phallic organs consist of a pair of large lateral phallic lobes (Lpl), a dorsal phallic lobe (Dpl), and a ventral phallic lobe (Vpl). These phallomeres fold together tightly around the posterior opening of the internal reproductive ducts. The wider opening distal to the ejaculatory duct is termed the phallotreme (phtr).

The tenth abdominal segment is reduced in size. It has a small dorsal tergite that is fused posteriorly with the eleventh tergum, the epiproct (Eppt). The pleural and ventral regions of the tenth segment are membraneous.

The cerci (Cer) are borne on the ventro-lateral margins of the eleventh segment. Each cercus possesses a large, curved, ventral plate that is probably used as a clasper during copulation. The anus (A) is flanked by a pair of lobes, the paraprocts (Papt).
Figure 30. Dorsal view of male genital and postgenital segments

Figure 31. Ventral view of male genital and postgenital segments

Figure 32. Posterior view of male genital and postgenital segments

A, anus; bsc, basicercus; Cer, cercus; Dpl, dorsal phallic lobe; Eppt, epiproct; Gc, genital chamber; Lpl, lateral phallic lobe; Papt, paraproct; phtr, phallotreme; sgp, subgenital plate; sp, abdominal spiracle; St, abdominal sternum; T, abdominal tergite; Vpl, ventral phallic lobe
References


THE ANATOMY OF THE ARMOURED GROUND CRICKET,

Acanthoplus speiseri BRANCSIK 1895.

II. ENDOSKELETAL PROCESSES

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SECTION II. ENDO Skeletal PROCESSES

Abstract

Studies on the endoskeletal processes of *Acanthoplus speiseri* Brancsik were conducted. Drawings were prepared with the aid of a 10 mm square grid micrometer ocular disk and 10 x 10 graph paper.

Internally, the cranium bears a large, horizontal, X-shaped tentorium on its lower margins. This consists of a posterior body (the corpo-tentorium) and three pairs of arms diverging from it. Anterior and posterior arms are hollow invaginations of the cranial walls. Their origins are represented externally by pits. Anterior tentorial pits are contained in both the subgenal and epistomal sutures while the posterior tentorial pits occur ventrad of the bases of the postoccipital suture. Dorsal arms are solid and tendinous. They arise near the junction of the anterior arms with the central body and attach to the hypodermis below the antennal sockets. Two pairs of cervical sclerites occur ventrolaterally in the neck membrane. The thorax bears pleural and sternal ridges and large pleural and sternal apophyses. Two large phragmata project into the thoracic cavity from the mesoscutum. A single spina with a pair of bifurcated arms arises from the mesosternum. The ninth abdominal segment in both sexes has a strongly developed antecosta anteriorly. In the female, projecting anterior and posterior, intervalvular sclerites occur on the genital segments.
Introduction

This is the second in a series of reports on studies made on the anatomy of the armoured ground cricket, *Acanthoplus speiseri* Brancsik 1895. The external morphology of the species was described previously (Mbata and Lewis, 1985).

Following is a description of the endoskeletal processes. As nearly as possible, the terminology of Snodgrass (1928, 1929, 1935a, b, 1937) has been followed. Lists of these terms and their abbreviations appear in the legends accompanying the plates.

Body Tagmata

**The head**

The cranium. The most prominent structure inside the cranium is the tentorium. When viewed from the front, on a specimen in which the frons, vertex and parts of the genae have been excised (Figure 1), it is seen as a large, horizontal, X-shaped frame, occupying the lower regions of the cranium. The tentorium serves as a brace for the cranium and provides areas for muscle attachment. Some muscles operating the antennae, labrum, pharynx, and the gnathal appendages attach to this structure.

The tentorium consists of a corpo-tentorium (CT), or the central body, from which the anterior (AT) and posterior (PT) pairs of arms diverge. Near the bases of the anterior arms arise tendinous dorsal arms (DT). The latter are solid throughout their lengths while the anterior and posterior arms are hollow invaginations of the cranial
Figure 1. Anterior view of the cranium showing the corpo-tentorium

Figure 2. Lateral view of the head showing the relationship of the corpo-tentorium with other structures in the head

a', primary cranial articulation of mandible; Ant, antenna; at, anterior tentorial pit; AT, anterior arm of tentorium; c, anterior articulation of mandible; Clp, clypeus; CT, corporotentorium; Cv, cervical sclerite; E, compound eye; es, epistomal suture; Fr, frons; Lb, labium; Lbplp, labial palpus; lcs, clypeolabral suture; Lm, labrum; Md, mandible; Mx, maxilla; Mxplp, maxillary palpus; Oc, occiput; occ, postoccipital condyle; OcR, occipital ridge; OR, ocular ridge; Pge, postgena; Plst, pleurostoma; PoR, postoccipital ridge; PT, posterior arm of tentorium; sgs, subgenal suture; Tor, torma; tsR, temporal ridge
walls that are represented externally by slit-like pits (Figures 1, 4, at, pt).

The anterior tentorial arms (Figures 1, 2, 3, AT) The anterior arms of the tentorium are greatly expanded and buttressed on the anterior wall of the cranium. Posteriorly, they taper off gradually towards the central body. The roots of the anterior arms are represented externally on the face region by silt-like anterior tentorial pits (Figure 1, at). The latter are contained in both the subgenal (sgs) and epistomal (es) sutures. The two sutures are continuous on the face region and are both underlaid internally by the same inflection. Similar positioning of the anterior tentorial pits on the face region has been reported for the cricket, Gryllus assimilis Fabricius (Snodgrass, 1935).

Below the anterior tentorial pits occur small rectangular sclerites, the subgenae or pleurostomata (Plst) with which the mandibles articulate anteriorly (Figure 1, c).

The posterior tentorial arms (Figures 1, 4, PT) The posterior tentorial arms are short and merge with a conspicuous postoccipital ridge at the rear of the cranium (Figure 4, PoR). This ridge is represented externally by the postoccipital suture. The posterior arms open to the outside by way of large, elongated posterior tentorial pits. Their position on the cranium has been outlined by dotted lines (Figure 4, pt). The posterior tentorial pits lie at the basal ends of the postoccipital suture on either side of the head and near the articulation points of the maxilla with the cranium (Figure 4, a'').
Figure 3. Lateral view of the cranium

Figure 4. Posterior view of the cranium

a', a'', primary cranial articulations of mandible and maxilla, respectively; Ant, antenna; AT, anterior arm of tentorium; Clp, clypeus; CT, corpo-tentorium; DT, dorsal arm of tentorium; E, compound eye; es, epistomal suture; Fr, frons; Lm, labrum; Oc, occiput; OcR, occipital ridge; OR, ocular ridge; Pge, postgena; Plst, pleurostoma; Poc, postocciput; PoR, postoccipital ridge; pt, posterior tentorial pit; PT, posterior arm of tentorium; sgs, subgenal suture; Tor, torma; tsR, temporal ridge
The dorsal tentorial arms (Figures 1, 2, 3, DT)  

The dorsal tentorial arms are tendinous and arise near the junctions of the anterior arms with the central body of the tentorium. The arms protrude dorsally and anteriorly to the ventral margins of the antennal sockets, where they attach to the hypodermis of the integument. There is no external evidence of this attachment on the cranium of the ground cricket, although there may be a difference in pigmentation in some other orthopterous insects. Note that in Figures 2 and 3, the dorsal arms do not reach the bases of the antennae. This is due to the fact that the tips of these arms are so delicate that in many preparations they were lost during the clearing process. However, it should be remembered that they actually attach to the cranial walls in the ground cricket.

Other notable endoskeletal processes in the cranium include the mandibular apodemes (Mbata and Lewis, 1985) and various inflections that manifest externally as sutures. Prominent ridges include the ocular (Figures 2, 3, OR), antennal, temporal (Figures 1, 2, 3, 4, tsR), frontoclypeal, subgenal and occipital (OcR) ridges.

The occipital ridge (Figures 1, 2, 3, 4, OcR) demarcates the back of the cranium. Dorsally, the ridge is narrow and comes into contact with the postoccipital (PoR) and temporal (tsR) ridges. Ventrally, the occipital ridge is broader and is continuous with an inflection that incorporates the posterior articulation points of the mandibles with the cranium (Figure 4, a').
The thorax

The neck The neck region or cervix derives from both the labial and prothoracic segments in the embryo (Snodgrass, 1935; Kramer, 1944). In A. speiseri it is composed of cylindrical membraneous walls that bear two pairs of small sclerites ventro-laterally (Figure 11, 1Cv, 2Cv). Anteriorly, the neck membrane is attached to the postoccipital rim at the rear of the cranium and the basal margins of the prementum. Behind, it is attached to the anterior margins of the prothorax.

Internally, the first pair of cervical sclerites consists of simple triangular plates that articulate with the postoccipital condyles anteriorly (Figure 2, lev, occ) and are hinged to the second cervical sclerite posteriorly.

The second cervicial sclerite is larger and spoon-shaped (Figure 11, 2Cv). The stem of the sclerite is directed forward and interacts with the first cervical sclerite. The wider concave part of the sclerite articulates with the anterior margin of the prothoracic sternite.

The prothorax

The protergum (Figures 5, 6) Internally, the anterior region of the protergum bears a number of areas of raised cuticle, dorso-laterally, that bear a specific relationship to muscle attachment (Figures 5, 6, APR, PPR, Ma). Some important prothoracic muscles that insert on the postoccipital ridge anteriorly or the first phragma of the mesotergum or the edges of the mesepisterna posteriorly originate from these protergal cuticular patches. Externally, the protergal patches are represented by small regions of grayish cuticle.
Figure 5. Lateral view of the male thorax and first three abdominal segments

a, pleural articulation of coxa; APR, anterior pronotal region; Bs, basisternite; Cvx, cervix or neck; dpr, dorsopleural ridge; Epm, epimeron; Eps, episternum; j, submarginal ridge; k, furcal ridge; lm, 2M, intersegmental membranes; Ma, areas of raised cuticle on which muscles insert; Ph, phragma; PlA, pleural apophysis; PlR, pleural ridge; PPR, posterior pronotal region; Ps, presternum; S, spine; s, root of pronotal spine; SA, sternal apophysis; scl, scutellum; scu, scutum; Sl, sternullum; sp, abdominal spiracle; Sp, thoracic spiracle; Sps, stridulating organ; St, abdominal sternite; T, abdominal tergite; tfr, transverse furrow ridge; tr, abdominal tergal ridge; u, ridge dividing mesoepisternum into two plates; v, ridge dividing metaepisternum into two plates; 1, 2, 3, pro-, meso- and metathoracic coxal cavities, respectively.
Figure 6. Lateral view of the female thorax and first three abdominal segments

a, pleural articulation of coxa; APR, anterior pronotal region; Bs, basisternite; Cvx, cervix or neck; Epm, epimeron; Eps, episternum; j, submarginal ridge; k, furcal ridge; IM, 2M, intersegmental membranes; Ma, areas of raised cuticle on which muscles insert; Ph, phragma; PLA, pleural apophysis; PIR, pleural ridge; PPR, posterior pronotal ridge; Ps, presternum; s, root of pronotal spine; S, spine; SA, sternal apophysis; scl, scutellum; scut, scutum; Sl, sternellum; sp, abdominal spiracle; Sp, thoracic spiracle; SPN, spina; St, abdominal sternite; T, abdominal tergite; tfR, transferse furrow ridge; Tn, trochantin; tr, abdominal tergal ridge; v, ridge dividing metaepisternum into two plates
Anteroventrally, the protergum bears an angled ridge (tfR) that is represented externally by the transverse sulcus. The latter divides the pronotum into anterior (APR) and posterior (PPR) regions. The bases of the stout spines on the tergum open into the thorax medio-dorsally on the anterior and posterior regions of the tergite (Figures 5, 6, s).

The propleuron (Figures 5, 6) Externally, the propleuron occupies but a small area on the antero-ventral margin of the protergum. Internally, however, the area occupied by the pleuron is larger. It is represented by a stout pleural apophysis that is broad ventrally and tapers off dorsally (Figures 5, 6, PIA 1).

The pleural apophysis is fused at its base to both the ventral portion of the transverse ridge (tfR) and to a short pleural ridge that is represented externally by a short pleural suture. Dorsally, the apophysis is free. The fused portion of the transverse ridge together with the poster-ventral edge of the apophysis project downward forming the knob-like pleural articulation of the forecoxae (Figures 5, 6, a).

The prosternum (Figures 5, 6, 11) The prosternum consists of two plates separated by a wide internal ridge (Figure 11, k). The anterior plate is termed the basistemite (Bs 1) while the posterior plate is the sternellum (Sl 1). On the anterior margin of the basistemite occurs a smaller ridge (j) that cuts off a narrow marginal sclerite, the pre sternum (Ps) from the basistemite. Both basistemite and presternum are continuous with the precoxal bridges (Axc) that lie below the pro-epistemum (Epst).
The internal ridge (k) is represented externally by a groove connecting the two furcal pits. The latter are the bases of internal prothoracic sternal apophyses. These are free, long, and spine-like processes (Figures 5, 6, 11, SAl). Each is thick and broad at the base, adjacent to the furcal pit, but tapers off distally, projecting dorsally and anteriorly with its expanded triangular apex lying close to, but not fused with, the middle of the prothoracic pleural apophysis.

The mesothorax It was shown (Mbata and Lewis, 1985) that the mesothorax exhibits a structure typical of a wing-bearing segment, especially in the male where the mesotergum supports modified tegmina that serve as stridulating organs. The segment is freely attached to the pro- and metathoracic segments by intersegmental membranes (Figures 5, 6, 1M, 2M).

The mesotergum (Figures 9, 10) Internally, the single rectangular plate constituting the mesotergum bears a number of ridges and phragmata. The latter serve in strengthening the tergum and providing areas for muscle attachment.

In the male (Figure 9), a narrow sclerite, the prescutum (Prsc) is cut off anteriorly by a small ridge (ts). The prescutal sclerite widens on either side, ending in triangular plates adjacent to the anterior notal processes. Behind the transverse notal ridge (ts) are two large scutal regions (Sct) that are separated from each other by a V-shaped ridge (vs). Behind the latter is a scutellar plate.

The lateral margin of each scutal area is ragged and bears notal processes with which a stridulating organ articulates. Mesolaterally
Figure 7. Lateral view of male mesothorax
Figure 8. Lateral view of female mesothorax

Ba, basalar; Bs, basisternite; CxP, pleural coxal process (pleural coxal articulation); Epm, epimeron; Eps, episternum; F, file; k, furcal ridge; Ph, phragma; PLA, pleural apophysis; PLR, pleural ridge; Ps, pre sternum; Sa, furcal pit; SA, sternal apophysis; SI, sternellum; Sp, thoracic spiracle; Sps, stridulating organ; St, abdominal sternite; T II, thoracic tergite; WP, wing process
Figure 9. Male mesotergum

Figure 10. Female mesotergum

Ba, basalar; PNP, posterior notal process; Ph, phragma; Prsc, prescutum; Sa, subalar; Scl, scutellum; Sct, scutum; Sps, stridulating organ; ts, transverse notal ridge; vs, scutoscutellar or V-shaped ridge; WP, wing process
is a large phragma (Ph1) that projects into the thoracic cavity. Major coxal muscles attach to this phragma.

A second phragma (Ph2) occurs posteriorly at the junction of the scutal areas with the scutellum. Median dorsal longitudinal muscles attach to this phragma.

In the female, the mesothoracic tergum is a simple plate internally (Figure 10). A prescutal plate (Prsc) occurs on the anterior margin that is bounded posteriorly by a transverse notal ridge (ts). However, the remainder of the tergal plate is only partially subdivided into an anterior scutal region (Sct) and a posterior scutellar region (Scl) by two phragmata (Ph) that are located mediolaterally. These two phragmata are represented externally by grooves.

The mesopleuron (Figures 5, 6, 7, 8) The internal structure of the mesopleuron is a mirror image of its external form, except that the different sclerotized plates are bounded by ridges instead of sutures. The dorsal margin of the mesopleuron bears a wing process (WP) that is continuous with a pleural ridge (PLR 2). Ventrally, the latter gives off a large arm or pleural apophysis (PLA 2) that crosses the coxal cavity. It is also closely associated with a similar arm arising from the sternum, the sternal apophysis (SA 2).

The pleural ridge extends further down into the coxal cavity where it terminates as a knob-like coxal articulation (Figure 7, CxP 2). The pleural ridge is represented externally by the pleural suture and the base of the pleural apophyses by pits above the coxal articulations.
The pleural ridge cuts off an episternal plate (Eps 2) anteriorly and an epimeral plate (Epm 2) posteriorly. Below the episternum are the presternum (Ps) and the trochantinal (Tn) sclerites.

The distinctive feature of the male mesopleuron is the presence of a single epipleurite, the basalar, in front of the wing process (Figures 7, 9, Ba). Another small sclerite, the subalar (Figure 9, Sa), occurs behind the wing process. Some muscles that operate the stridulating organs insert on these small sclerites in the male.

The mesosternum (Figure 17) The mesosternum consists of two distinct plates; a larger, rectangular basisternite in front and a smaller sternellum behind (Figure 17, Bs 2, SI 2). The basisternite articulates with the presternum (Ps) antero-laterally. The latter also interacts with the episternum (Eps 2).

The basisternite (Bs) is bounded posteriorly by a transverse ridge (k) that merges with two palmate sternal apophyses (SA 2) laterally. These project dorsolaterally and are closely associated with the pleural apophyses.

The sternellum (SI) of the mesosternum is a spinasternite. The spina (Spn) opens to the outside on this sclerite. It consists of a pair of highly sclerotized and bifurcated arms that project dorsolaterally in the thoracic cavity (Figure 11, Spn).

The metathorax

The metanotum (Figures 5, 6) In both sexes, the metanotum is a simple saddle-shaped sclerite that is partially divided into an
Figure 11. Ventral view of the thorax and the first three abdominal segments

Acx, anterior coxal bridge; Bs, basisternite; Cx, coxa; Cv, cervical sclerite; dpr, dorsopleural ridge; Eps, episternum; j, submarginal ridge; k, furcal ridge; ls, lateral sternite; PIA, pleural apophysis; Ps, presternum; SA, sternal apophysis; Sl, sternellum; sp, abdominal spiracle; Sp, thoracic spiracle; Spn, spina; St, abdominal sternite; Tn, trochantin
anterior scutum (Figures 5, 6, sct) and a posterior scutellum (Figures 5, 6, scl) by two ridges located dorsolaterally (Figures 5, 6, scl, sct, w).

The metapleuron (Figures 5, 6) The metapleuron bears a close resemblance to the mesopleuron internally, except for the size and shape of the plates constituting it. It bears a pleural ridge (Figures 5, 6, PI R 3) that cuts off an episternal plate (Eps 3) anteriorly and an epimeral plate (Epm 3) posteriorly. Ventrally, the pleural ridge gives off a pleural apophyseal arm that crosses the mesothoracic cavity (PIA 3). It terminates ventrally as a knob-like pleural articulation of the hind leg.

Below the metathoracic episternum is a small oval presternum (Figure 6, Ps) and a narrow trochantin (Tn). The latter also articulates with the coxa of the hind leg.

The metasternum (Figure 11) The metasternum consists of a broad anterior basisternite (Bs 3), and two marginal sternellar sclerites (SI 3) that are separated by a transverse ridge (k). Laterally, the latter gives rise to metasternal apophyses which project dorsolaterally and are closely associated with the metapleural apophyses.

The abdomen

Abdominal segments The abdomen possesses 11 true segments (Figures 12, 13). Each abdominal segment has a generalized structure consisting of a sclerotized dorsal tergite (T), two smaller sclerotized ventral (St) and lateral (Is) sternites and a membraneous pleural region.
Figure 12. Lateral view of female abdomen

a, articulation of antecosta with first valvifer; Ac, antecosta; alv, anterior intervalvular; b, articulation of first with second valvifers; bc, basicercus; c, articulation of second valvifer with the second valve of the ovipositor; Cer, cercus; dgr, dorsopleural ridge; Eppt, epiproct; Papt, paraproc; piv, posterior intervalvular; sgp, subgenital plate; sp, abdominal spiracle; St, abdominal sternite; T, abdominal tergite; Vl, ovipositor valve; Vlf, valvifer
Figure 13. Ventral view of female abdomen

aiv, anterior intervalvular; Ac, antecosta; Cx, coxa; dpr, dorsopleural ridge; Fm, femur; piv, posterior inter-valvular; sp, abdominal spiracle; St, abdominal sternite; Tr, trochanter; t, dorsal wall of genital chamber; Vl, ovipositor valve, Vlf, valvifer
The first eight abdominal segments each bears a pair of spiracles (sp). The latter, according to Snodgrass (1935a,b), lie on the sides of each segment above the dorsopleural ridge (dpr).

The first seven abdominal segments in the female and the first eight in the male are known as the pregenital or visceral segments. They contain most of the internal abdominal organs. The eighth and ninth abdominal segments in the female, and only the ninth segment in the male, constitute the genital segments. These bear the external organs that serve various activities related to copulation and oviposition. The tenth and eleventh abdominal segments, plus the telson in both sexes, form the postgenital segments.

**The visceral segments (Figures 5, 6, 12, 13)** The visceral segments are broadly joined to the thorax. Internally, each segment bears a saddle-shaped tergite that bears internally an anterior ridge on which the median dorsal longitudinal muscles insert (Figures 5, 6, tr). Sternites on its venter (St) and lateral surfaces (ls) are simple. The pleuron is membraneous, bearing a pair of spiracles (sp) above the dorsopleural ridge (dpr).

**The genital and postgenital segments (Figures 12, 13)** The eighth and ninth abdominal segments in the female and only the ninth abdominal segment in the male are the genital segments. Internally, the ninth segment bears a strongly developed antecosta anteriorly (Figures 12, 13, Ac) in both sexes on which some genital and postgenital muscles attach. In the female, the antecosta articulates ventrally with the first valvifer (Figure 12, a, 1 Vlf). The latter is a small sclerite that is part
of the eighth abdominal segment but which has shifted caudally to come to lie below the ninth tergum. The first valvifer also articulates with a blade of the ovipositor ventrally and with the second valvifer dorsally (Figure 12, 2 Vlf, b, 1 VI). The second valvifer is part of the ninth abdominal segment which, like the first valvifer, has shifted backwards on the body to come to lie above the dorsal blades of the ovipositor (3 VI). It gives rise to the second, or inner valvulae, with which it articulates via a ball-and-socket hinge (Figure 12, 2 VI, c). The second valvular pair is sandwiched between the broader dorsal valvulae (3 VI).

The sternum of the eighth segment is a specialized triangular subgenital plate (Figure 12, sgp). It bears a chamber on its upper region below the first valvular pair on whose floor lie the reproductive ducts.

The ninth abdominal sternum is mainly membraneous but bears two important sclerites that link the ovipositor blades. The anterior intervalvular sclerite transverses the ventral valvulae while the posterior intervalvular links the dorsal valvula pair (Figures 12, 13, aiv, piv). The tenth and eleventh abdominal segments in both sexes bear no prominent endoskeletal processes.

References


THE ANATOMY OF THE ARMoured GROUND CRICKET,

Acanthoplus speiseri BRANCSIK 1895

III. GENERAL MUSCULATURE AND THE GROSS MORPHOLOGIES OF THE
ALIMENTARY CANAL AND THE DORSAL BLOOD VESSEL

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SECTION III. INTERNAL ANATOMY I: GENERAL
MUSCULATURE AND THE GROSS MORPHOLOGIES OF THE ALIMENTARY
CANAL AND THE DORSAL BLOOD VESSEL

Abstract

The general musculature and gross morphologies of the alimentary canal and the dorsal blood vessel were studied. The thoracic musculature of Acanthoplus speiseri Brancsik is similar to that of Acridoepaza reticulata Guerin, Neoconocephalus robustus (Scudder), and Homorocoryphus nitidulus vicinus (Walker), except for the following: the male A. speiseri bears a large tergo-pleural muscle in its mesothorax that is absent in its metathorax and completely lacking in the female, while both sexes of A. reticulata and N. robustus possess the muscle in both segments of their pterothorax, though reportedly thinner in the female than in their male counterparts. Similar to H. n. vicinus, A. speiseri has single basalar and subalar muscles while A. reticulata bears three basalars and two subalars. However, in A. speiseri, the muscles only occur in the mesothorax. The tergo-trochanteral muscle is large in A. speriseri while it is very small in N. robustus and of moderate size in A. reticulata. The abdominal musculature closely resembles that of Neoconocephalus exiliscanorus (Davis) and Ceuthophilus lapidicola Burm., with only minor exceptions. The alimentary canal resembles that of Amblycorypha rotundifolia (Scudder) and Neoconocephalus ensiger Harris, while the dorsal blood vessel is similar to that reported for Eugaster spinulosus Johnnson.
Introduction

Apart from the work on the circulatory system (Nutting, 1951) and biological accounts of *Acanthoplus bechuanus* Per. (Power, 1958) and *Eugaster spinulosus* Joh. (Blenton, 1943), no work has been done on the musculature and digestive systems of the Heterodinae. The current study was meant to bridge this gap in our knowledge of the Orthoptera. The digestive, muscular, and circulatory systems of *Acanthoplus speiseri* Brancsik were studied.

Materials and Methods

Material preserved in 70% ethyl alcohol or 40% formalin was used throughout this study. The material was collected in Zambia, Southern Africa, by the senior author, during 1981-82.

The study of the muscular system was not intended to cover all muscles in the insect body but rather the emphasis was placed on revealing the general musculature as would be seen in a sagittal plane. Dissections to study the gross forms of the digestive and circulatory systems were similarly simple; they involved cuttings along the pleural membranes.

All material was dissected under 75% alcohol, stained with basic fuchsin and examined under a binocular microscope with a 10 mm square grid micrometer ocular disk. Drawings were constructed with the aid of 10 x 10 graph paper.

In this study, the terminology for the head and thoracic musculature follows those of Albrecht (1953) and Snodgrass (1929). For the
abdominal musculature, the terminology is that of Ford (1922) and, for the digestive and circulatory systems, terminologies were borrowed from Gangwere (1965), Judd (1948), and Nutting (1951). The use of terminologies from different sources was deliberate but necessitated due to the comprehensive nature of the original descriptions of the systems in question. Lists of these terms and their abbreviations are included in the legends to the illustrations presented.

Observations

The general musculature

The head (Figure 1) The musculature of the head of *A. speiseri* is well-developed. The following muscles are seen in a sagittal plane (see Figure 1).

2. **Anterior Retractor of the Labrum** - This is a large muscle that originates on the subantennal ridge and inserts medially on the anterior wall of the clypeo-labral region.

4. **Elevator of the Antennae** - This muscle occurs in two groups (not shown in the diagram). The muscles arise from the anterior arm of the tentorium and insert on a single apodeme at the dorsal rim of the scape.

5a, 5b. **Depressors of the Antenna** - This muscle occurs in two groups. The muscles arise from the anterior arms of the tentorium and insert on an apodeme on the ventral rim of the scape.

9a, 9b. **Adductors of the Mandible** - These are the largest muscles in the cranium. They take their origin from the large mandibular apodeme (9 Ap) and insert on the cranial walls dorsally
Figure 1. Medial view of the musculature of the right side of the male head, thorax and the first three abdominal segments

Skeleton

Ant, antenna; 9 Ap, adductor apodeme of the mandible; APR, anterior pronotal region; As, tracheal air sac; Bs, basisternite; Clp, clypeus; CT, corpo-tentorium; Lb, labrum; Lm, labium; Md, mandible; Mx, maxilla; PIA, pleural apophysis; PPR, posterior pronotal region; SA, sternal apophysis; So, stridulating organ; St, abdominal sternite; T, abdominal tergite; Vx, vertex

Musculature

2. Anterior retractor of the labrum
4. Elevator of the antennae
5a, 5b. Depressors of the antennae
9a, 9b. Adductors of the mandible
12, 13. Adductors of the stipes
23. Proximal retractor of the labium
32. Retractor of the hypopharynx
42, 43. Ventral dilators of the pharynx
47. First protergal muscle of the head
49. Dorsal longitudinal muscle of the neck and prothorax
50. Cephalic muscle of the neck sclerites
Cst. Cephalo-sternal muscle
52. Protergal muscle of the neck sclerites
55. First ventral longitudinal muscle
58. Tergo-pleural intersegmental muscle
59. Sterno-pleural intersegmental muscle
60. Second ventral longitudinal muscle
62. Tergal promoter of the pro-coxa
63, 65. First and third tergal removers of the pro-coxa
71b. Depressor of the trochanter
M sp. Spina-pleural muscle
Tpl. Tergo-pleural muscle
2 Sp. Sterno-pleural intersegmental muscle
81. Median dorsal longitudinal muscle
82. Oblique dorsal muscle
83. First tergo-pleural muscle
87. Third ventral longitudinal muscle
89. Tergal promotor of the meso-coxa
90. First tergal remover of the meso-coxa
93. Posterior rotator of the meso-coxa
103. Depressor of the trochanter
112. Median dorsal longitudinal muscle
116, 117. Fifth and sixth ventral longitudinal muscles
118. Tergal promoter of the meta-coxa
119, 120. First and second removers of the meta-coxa
122, 123, 124. First, second and third rotators of the meta-coxa
130. Adductor of the meta-coxa
133. Depressor of the trochanter
140. Sterno-pleural intersegmental muscle
143, 144. Seventh and eighth ventral longitudinal muscles
Is. Inner sternal muscle
It. Inner tergal muscle
los. Lateral outer sternal muscle
ptg. Primary tergo-sternal muscle group
stg. Secondary tergo-sternal muscle group
and posteriorly. 9a arises from the anterior branch of the mandibular apodeme while 9b originates on a smaller posterior branch.

12, 13. Adductors of the Stipes - These are large muscles composed of many muscle fibers. They arise from the ventral face of the tentorium and insert on a ridge of the stipes. Muscle 13 arises anterior to 12 and some of its fibers are borne on the ventral surface of the anterior tentorial arms.

23. Proximal Retractors of the Labium - This muscle has its origin on the ventral face of the posterior arm of the tentorium and inserts at the base of the prementum.

32. Retractor of the Hypopharynx - This is a long muscle that arises on the postoccipital ridge (PoR) dorsolaterally and inserts below, on the lateral sclerotized rods of the hypopharynx. Its point of origin is close to the base of the temporal ridge.

42, 43. Ventral Dilators of the Pharynx - Both muscles arise from the anterior edge of the anterior tentorial arm, muscle 43 being dorsal to 42. They attach to the wall of the pharynx.

It should be noted that several muscles that would be visible in a dissection made along the sagittal plane of the cranium have not been illustrated in Figure 1. These muscles include the compressor of the labrum which originates below the anterior retractor muscle of the labrum (2) on the labral wall and inserts on the cranial wall below the subantennal ridge. Other muscles not illustrated are the Posterior
Retractor of the labrum and several muscle groups that operate the stomodaeum in various capacities. The origins and insertions of these muscles in *A. speiseri* are similar to those described for the migratory locust by Albrecht (1953).

**The neck (cervical) and prothoracic musculature**

47. **First Protergal Muscle of the Head (Figures 1, 2, 5)** - A median dorsal longitudinal muscle that originates on the tergal wall of the anterior pronotal region (APR) and attaches on the postoccipital ridge dorsolaterally.

49. **Dorsal Longitudinal Muscle of the Neck and Prothorax (Figure 1)** - This muscle originates on the mesothoracic prescutal lobe and insertion on the postoccipital ridge adjacent to muscle 47.

50. **Cephalic Muscle of the Neck Sclerites (Figure 1)** - This muscle arises from the postoccipital ridge below muscle 49 and inserts on the first cervical sclerite.

Cst. **Cephalo-ternal Muscle (Figures 1, 2)** - A slender muscle that arises from the postoccipital ridge below muscles 47 and 49. It projects posteroinerally, passing laterad of muscle 62 to insert on the tip of the prosternal apophysis. This muscle has not been mentioned by Snodgrass.

51. **Cephalic Muscle of the Neck Sclerites (Figures 9, 10)** - This muscle shares the same origin with muscle 50 on the postoccipital ridge but inserts on the second cervical sclerite.
Figure 2. Medial view of the male prothorax

Skeleton
APR, anterior pronotal region; Cx, coxa; 1M, 2M, intersegmental membranes; PlA, pleural apophysis;
PPR, posterior pronotal region; SA, sternal apophysis; Tr, trochanter

Musculature
47. First protergal muscle of the head
49. Dorsal longitudinal muscle of the neck and prothorax
52. Protergal muscle of the nec sclerites
Cst. Cephalo-sternal muscle
62. Tergal promotor of the pro-coxa
63, 65. First and third remotors of the pro-coxa
68b. Abductor of the pro-coxa
69. Adductor of the pro-coxa
71b, 71c. Depressors of the trochanter
87. Third ventral longitudinal muscle
52. **Protergal Muscle of the Neck Sclerites (Figure 1)** - This muscle originates on the tergum in the anterior pronotal region (APR) and inserts at the posterior margin of the first cervical sclerite near its junction with the second cervical sclerite.

52X. **Cephalic Muscle of the Neck Sclerites (Figure 9)** - A short muscle that arises near the postoccipital condyle and inserts on the anterior margin of the first cervical sclerite.

54. **Prosternal Muscle of the First Neck Sclerite (Figures 9, 10)** - A horizontal, diagonal muscle that arises from the prosternal apophysis and inserts on the first cervical sclerite of the opposite side of the neck. The two muscles cross each other medially.

55. **First Ventral Longitudinal Muscle (Figure 1)** - A flat muscle composed of a number of fiber bundles. It arises from the base of the posterior arm of the tentorium and attaches to the anterior basal margin of the prosternal apophysis.

56. **Dorsal Lateral Neck Muscle (Figure 6)** - A flat muscle possessing several fiber bundles that arise on the mesonotal antecosta and insert on the cervical membrane anteriorly.

57. **Ventral Lateral Neck Muscle (Figure 9)** - A short, broad muscle that originates on the prothoracic episternum and inserts in the neck membrane.

58. **Tergo-pleural Intersegmental Muscle (Figure 1)** - A broad, flat muscle that arises from the protergum and inserts on the mesonotal antecosta.
59. **Sterno-pleural Intersegmental Muscle (Figures 1, 3, 6, 9, 10)** - An oblique intersegmental muscle composed of many muscle fiber bundles. It is broad at its origin on the antero-dorsal edge of the prosternal apophysis and gradually tapers towards its insertion point on the dorsal ridge of the mesothoracic episternum.

60. **Second Ventral Longitudinal Muscle (Figures 1, 9, 10, 11)** - A flat muscle arising from the posterior edge of the prosternal apophysis. It tapers off posteriorly and inserts on the anterior edge of the mesosternal apophysis.

62. **Tergal Promotor of the Pro-coxa (Figures 1, 2, 9, 10)** - A large tergo-sternal muscle that arises from the tergum on the anterior pronotal region (APR) and inserts at the ventral end of the protrochantin near its junction with the coxa.

63. **First Tergal Remotor of the Pro-coxa (Figures 1, 2, 9, 10)** - A large tergo-coxal muscle that arises medio-dorsally on the tergum and extends ventrolaterally, passing behind the pro-sternal apophysis to insert at the inner posterior angle of the pro-coxa.

64. **Second Tergal Remotor of the Pro-coxa (Figures 5, 9, 10)** - A second tergo-coxal muscle that shares the same point of insertion on the coxa with muscle 63 but lateral to it. The muscle originates lateral to muscle 63 on the tergum.

M Sp. **Spina-pleural Muscle (Figures 1, 3, 11)** - A slender transverse muscle that arises via a small apodeme on the mesothoracic
Figure 3. Medial view of the male mesothorax

Figure 4. Medial view of the male metathorax

Skeleton

Ac, antecosta; Bs, basisternite; Cx, coxa, k, sternal ridge; PlA, pleural apophysis; PlR, pleural ridge; SA, sternal apophysis; So, stridulating organ; Tr, torchanter; tr, abdominal tergal ridge; T, abdominal tergite; w, metathoracic tergal ridge

Musculature

49. Dorsal longitudinal muscle of the neck and prothorax
58. Tergo-pleural intersegmental muscle
59. Sterno-pleural intersegmental muscle
81. Median dorsal longitudinal muscle
82. Oblique dorsal muscle
83. First tergo-sternal muscle
87. Third ventral longitudinal muscle
Tpl. Tergo-pleural muscle
2 Sp. Sterno-pleural intersegmental muscle
92. Anterior rotator of the meso-coxa
93. Posterior rotator of the meso-coxa
97. First pronator-extensor of the stridulating organ
99. Depressor-extensor of the stridulating organ
100. First adductor of the meso-coxa
103. Depressor of the trochanter
M Sp. Spina-pleural muscle
117. Sixth ventral longitudinal muscle
It 1. First inner tergal abdominal muscle
Od. Oblique dorsal muscle
112. Median dorsal longitudinal muscle
118. Tergal promoter of the meta-coxa
119, 120. First and second tergal remotors of the meta-coxa
123, 124. Second and third posterior rotators of the meta-coxa
130a, 130b. Adductors of the meta-coxa
140. Sterno-pleural intersegmental muscle
144. Ventral longitudinal muscle
Figure 5. Medial view of the male prothorax with some inner muscles removed

**Skeleton**
APR, anterior pronotal region; Cx, coxa; IM, 2M, intersegmental membranes; P1A, pleural apophysis; PPR, posterior pronotal region; SA, sternal apophysis; Tr, trochanter

**Musculature**
62. Tergal promotor of the pro-coxa
64. Second tergal remotor of the pro-coxa
68b. Abductor of the pro-coxa
69. Adductor of the pro-coxa
71b, 71c, 71d. Depressors of the trochanter
87. Third ventral longitudinal muscle
Figure 6. Medial view of the male mesothorax with more inner muscles removed

Figure 7. Medial view of the male metathorax with some inner muscles removed

Skeleton
Ac, antecosta; Bs, basisternite; Cx, coxa; Eps, episternite; k, sternal ridge; PL, pleural apophysis; PLR, pleural ridge; Sa, sternal apophysis; So, stridulating organ; SPN, spina; T, abdominal tergite; tr, abdominal tergal ridge; Tr, trochanter; w, metathoracic tergal ridge

Musculature
49. Dorsal longitudinal muscle of the neck and prothorax
56. Dorsal lateral neck muscle
58. Tergo-pleural intersegmental muscle
59. Sterno-pleural intersegmental muscle
81. Median dorsal longitudinal muscle
82. Oblique dorsal muscle
89. Tergal promoter of the meso-coxa
91. Second tergal remotor of the meso-coxa
92. Anterior rotator of the meso-coxa
93. Posterior rotator of the meso-coxa
97, 98. First and second pronator-extensor of the stridulating organ
99. Depressor-extensor of the stridulating organ
103. Depressor of the trochanter
112. Median dorsal longitudinal muscle
117. Sixth ventral longitudinal muscle
119, 120. First and second tergal remotors of the meta-coxa
122, 123, 124. First, second and third posterior rotators of the meta-coxa
126. Second abductor of the meta-coxa
130a, 130b. Adductors of the meta-coxa
140. Sterno-pleural intersegmental muscle
144. Ventral longitudinal muscle
it 1. First inner tergal abdominal muscle
Figure 8. Medial view of the female pterothorax and the first six abdominal segments

**Skeleton**

Bs, basisternite; P1A, pleural apophysis; SA, sternal apophysis; St, abdominal sternite; II, III, thoracic tergites; T, abdominal tergite; tr, abdominal tergal ridge

**Musculature**

49. Dorsal longitudinal muscle of the neck and prothorax
60. Second ventral longitudinal muscle
81. Median dorsal longitudinal muscle
83. First tergo-sternal muscle
89. Tergal promoter of the meso-coxa
90. First tergal remotor of the meso-coxa
112. Median dorsal longitudinal muscle
116. Fifth ventral longitudinal muscle
118. Tergal promoter of the meta-coxa
119, 120. First and second tergal remotors of the meta-coxa
123, 124. Second and third posterior rotators of the meta-coxa
133. Depressor of the trochanter
M Sp. Spina-pleural muscle
140. Sterno-pleural intersegmental muscle
143, 144. Ventral longitudinal muscles
is. Inner sternal muscle
it. Inner tergal muscle
los. Lateral outer sternal muscle
mos. Median outer sternal muscle
ptg. Primary tergo-sternal muscle group
stg. Secondary tergo-sternal muscle group
sts. Secondary transverse sternal muscle
ts. Transverse sternal muscle
tso. Origin or insertion point of the transverse sternal muscle
Figure 9. Ventral view of the male cervix, thorax and the first five abdominal segments

Skeleton
Ant, antenna; As, tracheal air sac; cs, coronal suture; CT, corpo-tentorium; Cx, coxa; E, compound eye; Epm, epimeron; Eps, episternum; Fm, femur; g, abdominal nerve ganglion; k, sternal ridge; Ms, mesothoracic nerve ganglion; Mt, metathoracic nerve ganglion; P, prothoracic nerve ganglion; PLA, pleural apophysis; SA, sternal apophysis; St, abdominal sternite; Tbc, tubercle; Tr, trochanter; ts, temporal suture; I-V, abdominal segments

Musculature
47. First protergal muscle of the head
50, 51, 52X. Cephalic muscles of the nec sclerites
54. Prosternal muscle of the first cervical sclerite
55. First ventral longitudinal muscle
57. Ventral lateral neck muscle
60. Second ventral longitudinal muscle
67. Second posterior rotator of the pro-coxa
68b. Abductor of the pro-coxa
71b. Depressor of the trochanter
83. First tergo-sternal muscle
89. Tergal promotor of the meso-coxa
90, 91. First and second tergal remoters of the meso-coxa
94, 95. First and second abductors of the meso-coxa
97, 98. First and second pronator-extensors of the stridulating organ
99. Depressor-extensor of the stridulating organ
Tpl. Tergo-pleural muscle
103. Depressor of the trochanter
116, 117. Ventral longitudinal muscles
118. Tergal promotor of the meta-coxa
119, 120. First and second remoters of the meta-coxa
126. Second abductor of the meta-coxa
is. Inner sternal muscle
los. Lateral outer sternal muscle
mos. Median outer sternal muscle
ptg. Primary tergo-ster nal muscle group
sm. Sterno-pleural muscle
Figure 10. Ventral view of the prothorax

Figure 11. Ventral view of the mesothorax

Figure 12. Ventral view of the metathorax

Skeleton
As, tracheal air sac; Cx, coxa; Cxsp, coxal spine; Eps, episternite; Fm, femur; gl, g2, first and second abdominal nerve ganglia; k, sternal ridge; Ms, Mt, P, meso-, meta-, and prothoracic nerve ganglia; P1A, pleural apophysis; SA, sternal apophysis; SPN, spina; Tr, trochanter

Musculature
50,51. Cephalic muscles of the neck sclerites
54. Prosternal muscle of the first neck sclerite
55. First ventral longitudinal muscle
60. Second ventral longitudinal muscle
63, 64, 65. First, second and third tergal remotors of the pro-coxa
67. Second posterior rotator of the pro-coxa
68. Abductor of the pro-coxa
71b. Depressor of the trochanter
83. First tergo-tergal muscle
87. Third ventral longitudinal muscle
89. Tergal promoter of the meso-coxa
90, 91. First and second tergal remotors of the meso-coxa
92, 93. Anterior and posterior rotators of the meso-coxa
94, 95. First and second abductors of the meso-coxa
97, 98. First and second pronator-extensor of the stridulating organ
99. Depressor-extensor of the stridulating organ
103. Depressor of the trochanter
116, 117. Fifth and sixth ventral longitudinal muscles
M Sp. Spina-pleural muscle
Tpl. Tergo-pleural muscle
118. Tergal promoter of the meta-coxa
119, 120. First and second tergal remotors of the meta-coxa
122, 123, 124. First, second and third rotators of the meta-coxa
126. Second abductor of the meta-coxa
129. Depressor of the trochanter
143, 144. Ventral longitudinal muscles
los 1. Lateral outer sternal muscle of the first abdominal segment
mos 1. Median outer sternal muscle of the first abdominal segment
spina and projects dorsolaterally to a wide insertion on the mesothoracic epimeron, near the second or metathoracic spiracle. This muscle is also not mentioned by Snodgrass. Ewer (1954) described a similar muscle in the tree locust Acanthocris ruficornis (Fab.) and Maki (1938) called a similar muscle the anterior transverse muscle and gave it the number 69.

65. Third Tergal Remotor of the Pro-coxa (Figures 1, 2, 9, 10) - This muscle originates lateral to muscle 64 on the tergum and shares the same insertion point with muscles 63 and 64 at the posterior inner angle of the pro-coxa.

67. Second Posterior Rotator of the Pro-coxa (Figures 9, 10) - A flat muscle arising mesally from a minute spinule and inserting at the posterior angle of the pro-coxa.

68a, 68b. Abductors of the Prothoracic Coxa (Figure 5) - Two branches of an abductor muscle of the coxa. Number 68b is the largest, originating from a small ridge adjacent to the root of the third prothoracic spine and inserting at the outer rim of the pro-coxa just before the coxal articulation. Number 68a (not shown in the diagrams) is a smaller branch that arises from the transverse ridge on the tergum. It shares the same insertion point with 68b.

69. Adductor of the Prothoracic Coxa (Figure 5) - A flat muscle arising from the ventral face of the prosternal apophysis and inserting at the ventral base of the trochanter.
Depressors of the Trochanter (Figures 1, 2, 5) — Three branches of a single five-branched muscle. The three arise on the sides of the pronotum (b and d) and on the wall of the prosternal apophysis (c). They all insert via a common apodeme on the ventral rim of the trochanter.

The mesothoracic musculature (Figures 1, 3, 6, 8, 9, 11) — In our previous papers (Mbata and Lewis, 1985a, b), we showed that the mesothorax of the male A. speiseri bears a tergum that supports modified tegmina that serve as stridulatory organs. The mesothorax in both sexes is freely articulated to the pro- and metathoracic segments by intersegmental membranes. The musculature of this segment is slightly different in the two sexes due to the lack of stridulatory organs in the female. The following muscles are identifiable in a specimen cut along the sagittal plane.

Tpt. Tergo-pleural Muscle (Figures 1, 3, 9, 11) — This is the largest muscle in the mesothorax of the male. It is absent in the female (see Figure 8). It arises from the ventral and posterior surfaces of the mesothoracic phragma and inserts on the dorsal flattened face of the meso-pleural apophysis. This muscle is a strong elevator of the stridulatory organs in the male. It raises the tegmina during stridulation.

2 Sp. Sterno-pleural Intersegmental Muscle (Figure 1) — An intersegmental muscle that takes its origin at the distal edge of the mesosternal apophysis and inserts at the anterolateral edge of the metatergum.
81. **Median Dorsal Longitudinal Muscle (Figures 1, 3, 6, 8)** - A flat muscle with many fibers. It arises medio-dorsally on the antecosta and inserts on the metathoracic antecosta.

82. **Oblique Dorsal Muscle (Figure 1)** - A short muscle originating on the scutum lateral of muscle 81. It extends postero-ventrally and attaches on the anterior edge of the metathoracic tergum.

83. **Tergo-steranal Muscle (Figures 1, 3)** - A long muscle that is broad at its origin on the lateral part of the prescutal lobe and narrow at its area of insertion on the mesosternum.

84. **Second Tergo-steranal Muscle (Figures 9, 11)** - A large, long muscle lying lateral to muscle 83. It arises on the prescutum and inserts on the mesosternum before the inner margin of the meso-coxal cavity.

87. **Third Ventral Longitudinal Muscle (Figures 1, 2, 3)** - This muscle originates on the prothoracic spina and inserts on the mesepistemum adjacent to muscle 83.

88. **Tergal Promotor of the Coxa (Figures 1, 3, 8, 9, 11)** - A large tergo-coxal muscle that is divided into two branches. Both insert on a common stalk near the anterior angle of the coxa close to its junction with the trochantin. They arise on the anterior margin of the phragma on the scutum, 89a being mesal to 89b.

90. **First Tergal Remotor of the Coxa (Figures 1, 3, 8, 9, 11)** - A large, long muscle that acts antagonistically to muscle 89.
It arises from the scutum at the posterior face of the phragma and inserts on a common stalk with another tergo-coxal remotor, muscle 91, on the posterior inner angle of the mesocoxa.

**91. Second Tergal Remotor of the Coxa (Figures 6, 9, 11)** - A smaller muscle that shares the same insertion stalk with muscle 90, on the posterior inner angle of the coxa. It lies caudad to 90 and arises from the posterior surface of the phragma on the scutum.

**92. Anterior Rotator of the Meso-coxa (Figures 3, 6)** - A short, broad muscle arising from the sternum adjacent to the insertion point of muscle 89. It attaches to the lateral face of the mesosternal apophysis.

**93. Posterior Rotator of the Meso-coxa (Figures 1, 3, 6)** - Another short, broad muscle that originates from the spina and extends outward to insert on the posterior inner angle of the meso-coxa.

**94, 95. First and Second Abductors of the Meso-coxa (Figures 9, 11)** - These muscles arise on the episternum and attach to the outer margin of the meso-coxa via short apodemes.

**97. First Pronator-extensor of the Stridulatory Organs (Figures 6, 9, 11)** - A basalar muscle that is broad in the male but slender in the female. It arises from the basalar sclerite, extending ventrally to attach to the lateral wall of the sternum, before the coxal cavity.
98. **Second Pronator-extensor of the Stridulatory Organs (Figures 6, 9, 11)** - A muscle arising from the basalar sclerite caudad of muscle 97, it inserts on the lateral wall of the sternum, adjacent to the coxal cavity.

99. **Depressor-extensor of the Stridulating Organ (Figures 3, 6)** - A large muscle that originates on the subalar sclerite and inserts below on the basicoxal ridge.

100. **First adductor of the Meso-coxa (Figure 3)** - This muscle originates from the ventral margin of the mesosternal apophysis, insertion, on the inner rim of the meso-coxa.

103. **Depressor of the Trochanter (Figures 3, 9, 11)** - A long, broad muscle arising on the scutum. It projects downward passing cephalad of the closely appressed mesopleural and mesosternal apophyses and then bends caudally to attach at the ventral rim of the trochanter.

116. **Third Ventral Longitudinal Muscle (Figures 1, 8, 9, 11)** - A flat muscle that originates from the posterior edge of the mesosternal apophysis and inserts on the anterior apophyseal margin of the metathorax.

117. **Fourth Ventral Longitudinal Muscle (Figures 1, 8, 9, 11)** - This is a slender muscle arising from the spina and inserting on the metathoracic apophysis.

**The metathoracic musculature (Figures 1, 4, 7, 8, 9, 12)** The musculature of the metathoracic segment is similar to, but simpler than, that of the mesothorax. In both sexes, a tergo-ster nal muscle homologous
to muscle 84 of the mesothorax is lacking. The depressor of the trochanter (133) is inserted more distally in the trochanter than its homologue (103) in the mesothorax. The following metathoracic muscles were identified from longitudinal dissections.

Od. **Oblique Dorsal Tergal Muscle (Figure 4)** - The muscle originates on the metatergal ridge and inserts on the first abdominal tergal antecosta.

112. **Median Dorsal Longitudinal Muscle (Figures 1, 4, 7, 8)** - A first muscle arising from the antecosta of the metatergum and inserting at the anterior edge of the first abdominal tergum.

118. **Tergal Promotor of the Meta-coxa (Figures 1, 4, 8, 9, 12)** - A muscle homologous to 83 of the mesothorax. It originates on the metascutum and inserts on the lateral part of the sternum before the coxal cavity.

119. **First Tergal Remotor of the Metathoracic Coxa (Figures 1, 4, 7, 8, 9, 12)** - A muscle homologous to 90 in the mesothorax and 63 in the prothorax. It is large with a number of fiber bundles. It arises on the metascutum dorsolaterally and projects ventro-posteriorly behind closely appressed metapleural and metasternal apophyses and inserts on an apodemal stalk on the posterior inner angle of the meta-coxa.

120. **Second Tergal Remotor of the Metathoracic Coxa (Figures 1, 4, 7, 8, 9, 12)** - A moderately wide but long muscle. Its origin is on a ridge that separates the scutal and scutellar
plates on the tergum. The muscle tapers off ventrally and inserts on an apodermal stalk on the extreme posterior angle of the metacoxa.

122, 123, 124. Posterior Rotators of the Coxa (Figures 1, 4, 7, 8, 9, 12) - All arise from the posterior margin of the lateral arm of the metasternal apophysis. Number 122 inserts on the meral region of the coxa, 123 at the posterior angle of the coxa, and 124 on the meral ridge of the coxa.

126. Second Abductor of the Coxa (Figures 7, 9, 12) - A flat sheet of muscle arising from the inner wall of the metepisternum and inserting at the base of the sternum above the coxal articulation.

130a, 130b. Adductors of the Coxa (Figure 7) - Two short flat muscle branches that originate from the posterior face of the metasternal apophysis and insert on the posterior part of the inner margin of the coxa.

133. Depressor of the Trochanter (Figures 1, 4, 8, 12) - A large muscle in both sexes that arises from the scutum. It is one of three branches that share a common insertion on the ventral rim of the trochanter.

140. Sterno-pleural Intersegmental Muscle (Figures 1, 4, 7) - An oblique intersegmental muscle that arises from the distal tip of the metasternal apophysis and attaches to the first abdominal tergum antero-ventrally.
143. **Ventral Longitudinal Muscle (Figures 1, 8)** - A broad, flat muscle originating from the posterior face of the metasternal apophysis and inserting on the laterosternite of the first abdominal segment.

144. **Ventral Longitudinal Muscle (Figures 1, 4, 7, 8, 12)** - This muscle originates on the third spina and inserts on the first and third abdominal laterosternites.

**The abdominal musculature (Figures 1, 8, 9, 14)**

A typical tettigoniid abdominal segment bears a tergum, sternum, and two pleural regions. The sternum is further subdivided into a medial eusternite and two laterosternites. In *A. speiseri*, the laterosternites are membranous. The following muscles are distinguishable in dissections made in sagittal and horizontal planes.

**The Tergal Musculature**

*Inner Tergal Muscles (Figures 1, 8, 13, 14, it)* - These are flat muscles composed of many fiber groups. The number of fibers in each group varies and, hence, also the group sizes are diverse. The muscles arise subanteriorly on anterior tergal ridges and insert on the anterior margin of the following tergum in segments 1–9 in the male and segments 1–8 in the female.

*The Alary Muscles (Figure 20, Am)* - Nine pairs of alary muscles are present in the abdomen. They arise medio-laterally on the anterior margin of the tergites and insert medially on the heart. In all, 12 alary muscle pairs are present, three pairs are borne in the thorax.
Figure 13. Medial view of the female genital and postgenital abdominal segments

**Skeleton**

Eppt, epiproct; Gc, genital chamber; Papt, paraproct; spg, subgenital plate; St, abdominal sternite; T, abdominal tergite; VI, ovipositor valve (blade)

**Musculature**

ant. Antagonistic spiracle muscle
ca. Cercal abductor muscle
ce. Cercal elevator muscle
is. Inner sternal muscle
t. Inner tergal muscle
iv. Inner valvular muscle
los. Lateral outer sternal muscle
os. Outer sternal muscle
ptg. Primary tergo-ster nal muscle group
sa. Superior apophyseal muscle
stg. Secondary tergo-ster nal muscle group
ttg. Tertiary tergo-ster nal muscle group
lmos 7. Adductor of the subgenital plate
os 9. Protractor of the ovipositor
ptg 9. Third depressor of the ovipositor
sa 9. Lateral abductor of the ovipositor blades
stg 8. First depressor of the ovipositor
stg 9. First elevator fo the ovipositor
ttg 8. Second depressor of the ovipositor
Figure 14. Medial view of the male genital and postgenital abdominal segments

**Skeleton**
Cer, cercus; Dpl, dorsal phallic lobe; Eppt, epiproct; Gc, genital chamber; Lpl, lateral phallic lobe; Papt, paraproct; sgp, subgenital plate; St, abdominal sternite; Vpl, ventral phallic lobe

**Musculature**
ca. Cereal abductor muscle
ce. Cereal elevator muscle
cs. Cereal muscle from the supra-anal plate
is. Inner sternal muscle
it. Inner tergal muscle
los. Lateral outer sternal muscle
mos. Median outer sternal muscle
mp. Major constrictor of the spermatophore
ptg. Primary tergo-sternal muscle group
rpd. Dorsal retractor of the phallus (ptg 10)
rpv. Ventral retractor of the phallus
spm. Supra-paraproctal muscle
stg. Secondary tergo-sternal muscle group
is 9. Paraproctal muscle
los 9. Suspensory muscle of the spermatophore cup
The Sternal Musculature

Transverse Sternal Muscle (Figure 13, ts) - A segmental muscle occurring in abdominal segments 1-8 in the male and segments 1-7 in the female. The muscle arises medio-laterally on the membraneous laterosternite and inserts on the opposite laterosternite of the same segment. (Transverse sternal muscles are not shown in all diagrams. However, their relative areas of origin and/or insertion on the segment are indicated as tso.)

Secondary Transverse Sternal Muscle (Figures 8, 9, sts) - This muscle occurs in two groups, each composed of short muscle fibers that originate on the laterosternite and insert in the membrane, lateral to the eusternite.

Inner Sternal Muscle (Figures 1, 8, 9, 13, 14, is) - These are intersegmental ventral longitudinal muscles. They are flat muscles composed of various numbers of fiber groups. They arise on the anterior margin of the laterosternite and insert posteriorly on the anterior margin of the following laterosternite. The muscles occur in abdominal segments 1-9 in both sexes.

Lateral Outer Sternal Muscle (Figures 1, 8, 9, 13, 14, los) - Arising on the antero-lateral angle of the eusternite, this muscle tapers off posteriorly to insert on the ventral margin of the laterosternite in segments 1-7 in the male and segments 1-8 in the female.
Median Outer Sternal Muscle (Figures 8, 9, 13, 14, mos) -
This is a slender muscle sharing a common origin with the lateral outer sternal muscle, but medial to it. It inserts on the anterior margin of the following eusternite, medially-laterally.

The Pleural Musculature

Primary Tergo-ternal Group (Figures 1, 8, 9, 13, 14, ptg 9) -
A long, slender muscle that is sometimes partially subdivided into two groups, this muscle arises antero-ventrally on the tergum and inserts on the dorsal margin of the laterosternite in abdominal segments 1-9 in both sexes.

Secondary Tergo-ternal Group (Figures 1, 8, 9, 13, 14, stg) -
The muscle occurs in two groups both of which arise on the tergum, caudad to the primary group. Both insert on the laterosternite.

Sterno-pleural Muscle (Figure 9, sm) - Composed of a number of short fibers that arise on the dorsal edge of the laterosternite and insert on the pleural membrane below the spiracle.

Antagonistic Spiracle Muscle (Figures 13, 14, ant) - This is a short muscle that originates on the posterior margin of the laterosternite and inserts on the closing bow of the spiracle.

Spiracle Occlusor Muscle (not shown in the illustrations) - This is another small muscle that arises on the closing band of the spiracle and inserts on the handle of the closing bow.
The Musculature of the Female Genitalia (Figure 13)

The Sternal Musculature

Segment 8

**Transverse Sternal Muscle (ts)** - Absent in the adult.

**Inner Sternal Muscle (Figure 13, is 8)** - A flat muscle that arises on the subgenital plate anterolaterally. It inserts on the anterior intervalvular sclerite. The muscle is continuous with the inner sternal muscle of the seventh segment. Jointly, they serve as a retractor of the ovipositor.

Segment 9

**Inner Sternal Muscle (Figure 13, is 9)** - A large paraproctal muscle that takes its origin on the first valvifer and inserts on the anterior margin of the paraproct.

**Outer Sternal Muscle (Figure 13, os 9)** - An intervalvular muscle of the first valvifer. It arises from the median apodeme of the posterior intervalvular sclerite and inserts on the first valvifer. This is a protractor muscle of the ovipositor that pulls the ovipositor forward and backward.

**Superior Apophysis Muscle (Figure 13, sa 9)** - A large bundle of fibers originating from the dorsal blades of the ovipositor and inserting on the inner blades.
Inner Valvular Muscle (Figure 13, iv 9) - A slender muscle that originates on the first valvifer and inserts on a ridge of the second valves.

The Pleural Musculature

Segment 8

Primary Tergo-tergal Group (Figure 13, ptg 8) - This muscle is larger than its homologues in the preceding segments. It arises dorsally on the eighth antecosta and inserts on the subgenital plate antero-ventrally.

Secondary Tergo-tergal Group (Figure 13, stg 8) - The largest muscle in the genital segments. It arises from a highly developed antecosta of the eighth tergum, dorsolaterally, and inserts on the antero-dorsal edge of the ventral ovipositor blades. The muscle functions as the first depressor of the ovipositor.

Tertiary Tergo-tergal Group (Figure 13, ttg 8) - A large tergal muscle of the anterior intervalvular sclerite that arises on the antecosta of the ninth tergum and inserts medially on the anterior intervalvular sclerite. This muscle is the second depressor of the ovipositor.

Antagonistic Muscle of the Spiracle (Figure 13, ant) - This muscle arises on the subgenital plate and inserts on the closing bow of the eighth abdominal spiracle.
Segment 9

Primary Tergo-sternal Group (Figure 13, ptg 9) -
The second largest muscle in the genital segments, it arises on the ninth antecosta and inserts on the anterior intervalvular sclerite, adjacent to its antecostal articulation. The muscle is the third depressor of the ovipositor and operates the dorsal blades.

Secondary Tergo-sternal Group (Figure 13, stg 9) -
Originating on the dorsal margin of the posterior intervalvular sclerite apodeme, this muscle inserts on the anterior intervalvular sclerite and is the first elevator muscle of the ovipositor.

Tertiary Tergo-sternal Group (Figure 13, ttg 9) -
This is also referred to as the posterior tergal muscle of the second valvifer. It is a large flat muscle that arises on the anterior and ventral portions of the ninth tergum and attaches to the posterior dorsal apodeme of the second valvifer.

Superior Apophysis Muscle (Figure 13, sa 9) - A short, thick muscle arising on the median apodeme of the posterior intervalvular sclerite and inserting on the second valvifer.
The Musculature of the Male Genitalia (Figure 14)

The Sternal Musculature

Transverse Sternal Muscle - Absent in this segment.

Inner Sternal Muscle (Figure 14, is 9) - A ventral longitudinal muscle that serves as a paraproct dilator, it originates on the ninth laterosternite and inserts on the tenth sternal area of the paraproct.

Outer Sternal Muscle (Figure 14, os 9) - Occurs in two groups:

Lateral Outer Sternal Muscle (Figure 14, los 9) -
Arising antero-laterally on the ninth sternum, this muscle inserts on the ventral phallic organ.

Medial Outer Sternal Group (not shown in the illustrations) - Arising on the ninth sternum, antero-laterally. This muscle inserts on the genital pouch.

Major Protractor Muscle of the Genitalia (Figure 14, mp) -
A cup-like muscle that envelops the genitalia and originates on the tenth antecosta.

Ventral Retractors of the Phallus (Figure 14, rpv) - A short muscle arising on the ninth sternum and inserting on the phallobase.

The Pleural Musculature

Primary Tergo-sternal Group (Figure 14, ptg 9) - Larger than its homologs in the pregenital segments, this muscle arises on the ninth antecosta and inserts on the ninth sternum.
Dorsal Retractor of the Phallus (Figure 14, rpd) - This is a slender muscle that arises laterally on the tenth tergum and inserts on the phallobase.

The Cercal and Paraproctal Musculature

Cercal Abductor Muscle (Figures 13, 14, ca) - This is a large muscle in the male originating on the tenth antecosta and attaching to the rim of the cercus, medio-dorsally.

Cercal Elevator Muscle (Figures 13, 14, ce) - A large muscle arising lateral of ca on the tenth antecosta and inserting on the rim of the cercus ventrally.

Cercal Muscle from the Supra-anal Plate (Figure 14, cs) - A slender muscle originating on the tenth tergum medially and attaching to the rim of the cercus medially.

Paraproctal Abductor Muscle (Figure 13, ttg 10) - A large muscle in the female arising on the antecosta of the tenth tergum and inserting on the rim of the paraproct medio-dorsally.

Paraproct Dilator Muscle (Figures 13, 14, is 9) - Arising on the subgenital plate, antero-laterally. This muscle inserts on the tenth sternal area of the paraproct.

The gross external morphology of the alimentary canal

The alimentary tract of *A. speiseri* (Figure 15) is the curved or convoluted type and is much longer than the body length. It can be subdivided into an anterior stomodaeum, a medial mesenteron, and a posterior proctodaeum.
Figure 15. The gross external morphology of the alimentary canal

an, anus; Ant, antenna; APR, anterior pronotal region; Bs, bassisternite; Ca, caecum; Cer, cercus; Clp, clypeus; Cr, crop; E, compound eye; Eppt, epiproct; Fr, frons; Hyp, hypopharynx; int, intestine; Lb, labrum; Lm, labium; Ma, Malpighian ampulla; Mt, Malpighian tubule; Mth, mouth; Oe, oesophagus; Phy, pharynx; PPR, posterior pronotal region; Pr, proventriculus; r, rectum; So, stridulating organ; Sp, spine; St, abdominal sternite; T, abdominal tergite; Vt, ventriculus; Vx, vertex
The stomodaeum includes the mouth (Mth) that is surrounded by the buccal cavity (BuC). Following the mouth is a short pharynx (Phy) that leads into the oesophagus (Oe). The latter is continuous with a large crop (Cr) that opens posteriorly into a globular proventriculus (Pr), via a short neck. The proventriculus in turn opens into the mesenteron by way of the pyloric valve.

The mesenteron is bounded anteriorly by the pyloric valve and bears two sac-like, bulbous gastric caeca (Ca). The latter are typically located dorsally and ventrally, sandwiching between them the proventriculus of the stomodaeum. Caudal to the caeca is the ventriculus (Vt).

Anteriorly, the proctodeum possesses six fascicles on which are borne the Malphigian tubules (Mt). The fascicles discharge into the same number of ampullae (Ma) that open into the intestine (Int). The last portion of the proctodaeum is the rectum (R) that opens to the outside through the anus (An).

Figure 16 is a sagittal section of the stomodaeum. The intima of the pharynx and oesophagus is very thick dorsally but relatively thin ventrally. The pharynx opens into the oesophagus through a narrow region (PPhy). The intima of the crop is also relatively thin. It is thrown into transverse folds along the length of the structure.

The crop opens into the proventriculus via a spiniform neck. The spines (CT) are borne on cushions of hair. The cushions occur in rows that are continuous with the longitudinal rows bearing sclerotized appendages in the proventriculus below (Figure 16, Ap, Pr). The pyloric valve consists of six membranous flaps that project from each longitudinal row (Oes V).
Figure 16. Sagittal view of the stomodeum

Figure 17. Internal view of the anterior region of the ventriculus

Figure 18. Sagittal view of the rectum

an, anus; Ap, appendage; APhy, anterior region of the pharynx; Ca, caecum; Cr, crop; CT, sclerotized spine; ddr, dorso-lateral dilator rectal muscle; int, intestine; Lm, lamina of caecum; Mth, mouth; Oe, oesophagus; Oes V, oesophageal valve; PPhy, posterior region of the pharynx; Pr, proventriculus; R, rectum; rp, rectal pad; vdr, ventro-lateral dilator rectal muscle; Vt, ventriculus; 42, 43, ventral dilator muscles of the pharynx
Figure 19 is a longitudinal section through the proventriculus. The neck region bears six longitudinal rows of cushions (CC) that are covered with setae. There are eight setal cushions in each row. The anterior cushions are smaller and bear fewer setae while those occurring posterior to them are larger. The first four or five cushions each bear a spine (CT) that projects posteriorly into the lumen of the neck.

The globular proventriculus bears six longitudinal rows of sclerotized appendages. Each row has 16 appendages whose sizes gradually decrease toward the pyloric valve. Each appendage bears a median tooth (MT) that projects into the lumen of the proventriculus. On either side of the median tooth is a sclerotized lateral lobe (LL). The latter is flanked on either side by triangular and pointed, barbated lobes (BL).

Between adjacent longitudinal folds are located highly sclerotized partitions (CP) that run the length of the folds. Each longitudinal row gives rise to a membraneous flap posteriorly that forms part of the phyloric valve. The latter is cylindrical and projects into the ventriculus in the region where the outpocketing of the gastric caeca (Ca) begin (Figure 17). The caeca bear lamillae-like folds internally (Lm).

The rectum bears six well-developed rectal pads (rp) internally that are separated from each other by areas of clear membrane (Figure 18).

The gross external morphology of the heart and aorta

The dorsal blood vessel is associated with twelve pairs of alary muscles (Figure 20, Am) that arise dorsolaterally on each tergite and attach to the heart medially, between expanded pulsating ampullae (Amp).
Figure 19. Sagittal view of the proventriculus

Ap, appendage; Bl, barbated lobe; CC, hair cushion; CH, hair loop; CP, sclerotized partition; CT, sclerotized tooth; LL, lateral lobe; MT, median tooth; OesV, oesophageal valve; Pr, proventriculus
Figure 20. Gross external morphology of the dorsal vessel

Am, alary muscle; Amp, ampulla; Ao, aorta; As, tracheal air sac; DCon, dorsal tracheal commissure; DTra, dorsal plurisegmental tracheal trunk; Ost, ostia; Papt, para-proct; w, metathoracic tergal ridge; I-III, thoracic segments; 1-10, abdominal segments; nx:TH 27
The heart extends from the ninth abdominal segment to the prothorax. It bears along its length, expanded intersegmental ampullae that each bear a pair of ostia (Ost).

Each ostium is a vertical, slit-like opening of the lateral wall of the ampulla. According to Nutting (1951), the tettigoniid ostia open between two layers of the dorsal diaphragm (not shown in the diagram).

The aorta (Ao) is a straight tube that is continuous with the heart. It arises from a spherical ampulla in the prothorax and continues to the head, closely appressed to the dorsal medial surface of the crop. Below the tritocerebral arch (not shown in the diagram), the aorta is expanded and bears a ventral opening, through which the haemolymph flows into the cranium.

Throughout its length, the aorta is bordered by two dorsal pleurisegmental tracheal trunks (DTra). The latter are connected to abdominal air sacs (As) laterally and are linked to each other through dorsal commissures (DCom), located between the ampullae, above the alary muscles.

Discussion

The thoracic musculature of A. speiseri is similar to that reported for Acridopeza reticulata Guerin (Tiegs, 1955), Neoconocephalus robustus (Scudder) (Josephson and Halverson, 1971), and Homorocoryphus nitidulus vicinus (Walker) (Schumacher, 1978), except for the following:

a. Acanthoplus speiseri bears a large tergo-pleural muscle in the male that is absent in the female, while in both A.
reticulata and *N. robustus* the muscle is present in both sexes, though reportedly thinner in the females.

b. Similar to *H. n. vicinus*, *A. speiseri* bears a single basalar and a single subalar while *A. reticulata* has three basalars and two subalars. However, *A. speiseri* differs from the other two in that these muscles are absent in the metathorax due to the lack of wings or stridulating organs in this segment.

c. The tergo-trochantaral muscle (depressor of the trochanter) is very large in both sexes of *A. speiseri*, while the muscle is very small in both sexes of *N. robustus* and moderate in *A. reticulata*.

d. *Acanthoplus speiseri* has larger mesothoracic muscles in the male that are not correlated with the thoracic size, while in *H. n. vicinus* the larger mesothoracic musculature of the male is correlated with the larger thoracic size when compared to its female counterpart.

The abdominal musculature of *A. speiseri* is very similar to that reported for *Neoconocephalus exiliscanorus* (Davis) (Schmitt, 1964) and *Ceuthophilus lapidicola* Burm. (Ford, 1922), with the following exceptions:

a. In *A. speiseri*, the secondary tergo-sternal group inserts in the membrane lateral to the eusternite while in *N. exiliscanorus* and *C. lapidicola* the muscle group inserts on the lateral margin of the eusternite.

b. The inner tergal muscles of *A. speiseri* consist of many fiber bundles forming a flat sheet originating subanteriorly on a
tergal ridge and inserting on the antecosta of the following tergum, while in *C. lapidicola* the muscle spreads out fan-like posteriorly to its insertion region on the antecosta of the following tergum.

c. While female *A. speiseri* possess large paraprocts, *C. lapidicola* has small ones resulting in notable differences in the locations of the operative muscles.

The gross external morphology of the alimentary canal closely resembles that reported for *Amblycorypha rotundifolia* (Scudder) (Gangwere, 1965), and the nature of the proventriculus is similar to that of *Neoconocephalus ensiger* Harris (Judd, 1948). The Malpighian tubules are similar to those described for *Conocephalus indicus* Redt. (Mohamed and Murad, 1977).

The following differences, however, are notable in the structures of the proventriculus of *A. speiseri* and *N. ensiger*. In *A. speiseri*, there are 16 sclerotized appendages on each of the six longitudinal folds and the partitions between the folds are smooth-surfaced, while in *N. ensiger* there are 12 appendages per longitudinal fold and the partitions have scale-like projections on their surfaces.

The gross external morphology of the dorsal blood vessel resembles that reported for another member of the subfamily Hetrodinae, *Eugaster spinulosus* Johannson (Nutting, 1951).
References


THE ANATOMY OF THE ARMoured GROUND CRICKET,

Acanthoplus speiseri BRANCSIK 1895

IV. THE RESPIRATORY, NERVOUS AND REPRODUCTIVE SYSTEMS

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SECTION IV. INTERNAL ANATOMY: RESPIRATORY, NERVOUS AND REPRODUCTIVE SYSTEMS

Abstract

The gross anatomies of the respiratory, nervous, and reproductive systems of the armoured ground cricket, *Acanthoplus speiseri* Brancsik were studied. The respiratory system closely resembles that of *Phasgonura viridissima* L., with one major exception. Whereas in *A. speiseri* there are very reduced wing tracheae due to its apterus nature, *P. viridissima* bears a full complement of wing tracheae with complex basal connections. The nervous system is similar to that described for *Conocephalus fasciatus* De Geer except that in *A. speiseri* the ocelli are absent and the optic lobes are linked to the protocerebrum by long, thick stalks. The internal reproductive organs of the female are simple and generalized. In the male, these structures are similar to those of *Orchelimum minor* Brunner, although in the latter the epididymis-like convolutions of the vas deferens occur a short distance from the testis. In *A. speiseri*, the epididymis-like convolutions are located immediately behind the testis.

Introduction

Studies on the anatomies of the respiratory (Albrecht, 1953; Carpentier, 1927; Haber, 1926; Pichard, 1909; Snodgrass, 1935; Vinal, 1919), nervous (Campbell 1961; Ewer, 1972; Malabre, 1973; Nesbitt, 1941; Schmitt, 1964; Steinmann, 1961), and the reproductive systems (Gupta, 1950; Qadri, 1940; Snodgrass, 1937) of representative members of major families of the Orthoptera are well-documented in the literature.
This paper provides an account of the gross anatomies of the respiratory, nervous, and reproductive systems of the armoured ground cricket, *Acanthoplus speiseri* Brancsik. The external morphology, endoskeletal processes, the general musculature, and the gross morphologies of the alimentary canal and the dorsal blood vessel of the species were described previously (Mbata and Lewis 1985a, b, c).

Materials and Methods

Material preserved in 70% ethyl alcohol or 40% formalin was used throughout the study. The material was collected in Zambia, Southern Africa, by the senior author during the period 1981-82.

The study of the respiratory, nervous, and reproductive systems was not intended to cover the fine histological details of the systems in question but rather to reveal their gross anatomies. Therefore, the peripheral nervous system, tracheoles and details of the fine structures of the ovaries and testes are not covered in the present work.

All material was dissected under 75% alcohol, stained with basic fuchsin and examined under a binocular microscope with a 10 mm square micrometer ocular disk. Drawings were originally done on 10 x 10 mm graph paper and later transferred to drawing paper using a light table.

In this study, the terminologies employed in describing the respiratory system are those of Carpentier (1927), Kennedy (1922), and Snodgrass (1935). Terminology for the nervous system has been borrowed from Nesbitt (1941), Albrecht (1953), and Snodgrass (1935), while that used for describing the reproductive system follows Snodgrass (1937)
as closely as possible. Lists of these terms and their abbreviations accompany the legends to the illustrations.

Observations

The respiratory system

The general organization of the tracheal system of the armoured ground cricket will, for convenience, be divided into the cephalic, thoracic, and abdominal subsystems. An account detailing the structures of the thoracic and abdominal spiracles will then follow.

The cephalic tracheal subsystem (Figures 2, 3, 4) The principal tracheal trunks supplying air to the head take their origin from the truncal apertures of the mesothoracic spiracles (Figure 1, Sp 2). The latter occur near the caudo-ventral margins of the pronotum (N1), above the pro-coxal articulations. Each mesothoracic spiracle gives off a dorsal head tracheal trunk (DHTra) and a ventral head tracheal trunk (VHTra), both of which enter the head through the occipital foramen.

The dorsal head tracheal trunk (Figure 1, DHTra) fuses with the dorsal plurisegmental tracheal trunk (DTra) a short distance from the spiracle before proceeding to the head. It divides soon after entering the cranium (Figures 2, 3, 4), forming: 1) a large dorso-lateral trunk (LDHTra) that supplies branches to the adductor muscles of the mandible, the compound eye, and the antenna; 2) a smaller median dorsal trunk (MDHTra) that serves the adductor muscles, the brain, and oesophagus; 3) a short dorsal branch that fuses with a similar branch from the opposite side of the head, forming a dorsal commissure (DCom). The lateral and medial dorsal head tracheal trunks from the two halves
Figure 1. Lateral view of the male thorax and abdomen showing the tracheal system

ACTra, acoustic or femoral trachea; adc, anterior dorsal connective; ALTra, anterior leg trachea; ASVTra, anterior supra-ventral trachea; AWTra, anterior wing trachea; CTra, communicating trachea; Cx, coxa; d, dorsal abdominal trachea; DCom, dorsal commissure; DHTra, dorsal head tracheal trunk; DTra, dorsal plurisegmental tracheal trunk; EPSVTra, external posterior supra-ventral trachea; i, intestinal trachea; N, notum; pdc, posterior dorsal connective; PDLTra, posterior dorso-lateral trachea; PDTra, paradorsal trachea; PLTra, posterior leg trachea; PWTra, posterior wing trachea; SA, sternal apophysis; SO, stridulating organ; sp, abdominal spiracle; Sp, thoracic spiracle; SPN, spina; v, ventral abdominal trachea; VCom, ventral commissure; Vf, vesicula femorals; VHTRA ventral head tracheal trunk; VLTRA, vetro-lateral trachea; VTRA, ventral plurisegmental tracheal trunk; x, X-shaped ventral commissure; 1-8, ventral abdominal tracheal air sacs
Figure 2. Dorsal view of the head

Figure 3. Antero-dorsal view of the head showing the frontal tracheal air sac inosculation

Figure 4. Lateral view of the dorsal and ventral head tracheal trunks

a,b,c,d,e, air sacs of the ventral head trachea; Ant, antenna; AT, anterior arm of the tentorium; AntTra, antennal trachea; Clp, clypeus; CT, corpo-tentorium; DCom, dorsal commissure; DHTra, dorsal head tracheal trunk; E, compound eye; Fr, frons; Lb, labium; LCom, lateral head commissure; LDHTra, lateral branch of the dorsal head tracheal trunk; Lm, labrum; L,M, dorso-ventral commissures of the second branch of the ventral head tracheal trunk; MDHTra, median branch of the dorsal head tracheal trunk; PT, posterior arm of the tentorium; VHTral, ventral head tracheal trunk; VHTral, first ventral branch of the ventral head tracheal trunk; VHTral2, first dorsal branch of the ventral head tracheal trunk; VHTral3, second ventral branch of the ventral head tracheal trunk; VHTral4, second dorsal branch of the ventral head tracheal trunk; 1-7, cephalic tracheal air sacs
of the head form an inosulation with each other and with the branches of the ventral head trunks, creating a system of air sacs medially in front of the brain (Figures 2, 3; 1-4). Tracheal branches issuing ventrally from the fourth air sac in this 'frontal tracheal air sac inosculation' are connected to a chain of smaller sacs in the labrum (Figure 4; 4, 7). The fifth and sixth tracheal air sacs are fused with the dorso-lateral head tracheal trunk just before the latter projects downwards into the mandible.

The ventral head tracheal trunk (VHTra) projects antero-ventral shortly after emerging from the mesothoracic spiracle (Figure 1). It gives off a small branch below that forms part of an X-shaped ventral commissure of the prothorax (Figure 1, X). In the cervical region, the ventral head trunk branches to form an arm that supplies the hypopharynx and labium via a number of small air sacs (Figure 4, VHTra 1, a, b, c, d, e). A second tracheal branch (VHTra 2) is given off just prior to entering the cranium. This branch projects antero-dorsally and sends off smaller ramifications to the adductor and abductor muscles of the mandible and to the neck muscles. Two of its branches form anastomoses with the latero-dorsal and medio-dorsal tracheal trunks (Figure 4, L, M). A third tracheal branch (VHTra 3) is formed ventrally in the genal region. It supplies the gnathal appendages below and also has a ramus that fuses with the latero-dorsal head trunk. A fourth tracheal branch (VHTra 4) is an air sac that, together with the main trunk of the ventral head trachea, fuses to the frontal tracheal air sac inosulation described earlier.
Two other lateral commissures are also observed in the head of A. speiseri. One links the latero-dorsal head trachea (LDHTra) to the third branch of the ventral trachea (VHTra 3). The second one connects the median head trachea (MDHTra) to the fourth branch of the ventral head trunk (Figure 4, LCom).

The thoracic tracheal subsystem (Figures 1, 5) The tracheation of the thorax in the ground cricket is much more complex than that of the other tagmata. This is due to: 1) the presence of only two spiracular pairs (instead of three) serving the three segments in addition to providing the head with tracheal branches; 2) the presence of legs in this region of the body; and 3) the occurrence of stridulating organs (males) and vestigial wings (females) on the mesonota (Mbata and Lewis, 1985a, b).

In addition to its association with the dorsal and ventral head trunks, the truncal aperture of the mesothoracic spiracle sends off tracheal branches to the pro- and mesothoracic organs. From the truncal stigma also issues: 1) a small tracheal branch (EPSVTra) that projects antero-ventrally, passing over a large prothoracic air sac (Vf) before fusing with the ventral head tracheal trunk (VHTra); and 2) an anterior supra-ventral trachea (ASVTra) fine branch of which extends to the mesothoracic tergo-sternal, tergo-pleural, tergo-coxal promotor, trochanteral depressor, subalar, basalar, and ventral longitudinal muscles. Below, it fuses with the ventral plurisegmental tracheal trunk (VTra).

The anterior supra-ventral trachea (ASVTra) described above also forms an anastomosis with a shorter posterior dorso-lateral branch
Figure 5. Ventral view of the thoracic and abdominal trachea

adl, anterior dorso-lateral trachea; ASVTra, anterior supra-ventral trachea; C,D,E,F, ventral thoracic air sac commissures; CTra, communicating trachea; Cx, coxa; EPSVTra, external posterior supra-ventral trachea; pdl, posterior dorso-lateral trachea; PLA, pleural apophysis; SA, sternal apophysis; sp, abdominal spiracle; SVHTr, supra-ventral head trachea; VCom, ventral commissure; Vf, vesicula femoralis; VHTr, ventral head trachea; VLTr, ventro-lateral trachea; VTr, ventral plurisegmental tracheal trunk; X, X-shaped ventral commissure; 1-8, ventral abdominal tracheal air sacs
(PDLTra), a short distance from the truncal spiracle. This branch, in turn, fuses with the posterior wing trachea (PWTra) or, as it is sometimes called, the dorso-lateral tracheal trunk (ADLTra) in the region above which another short dorsal anterior wing trachea originates. The latter unites with the dorsal plurisegmental trunk (DTra) above. The posterior wing trachea (PWTra) is fused to the anterior middle leg trachea (ALTra) ventrally. It also sends off fine branches to the metathoracic tergo-promotor, trochanteral depressor, and other muscles occurring cephalad of the metathoracic pleural ridge. It then proceeds on to fuse with the metathoracic spiracle.

Above the dorsal head tracheal trunk (DHTra) in the prothorax and fused to it is the paradorsal trachea (PDTr). It is expanded along its length into a number of air sacs. It also supplies branches to the prothoracic muscles.

The femoral stigma of the mesothorax is linked internally to a large, bag-like, trumpet-shaped vesicle (Figures 1, 5, Vf). The latter is part of the acoustic or femoral tracheal trunk (ACTra) supplying the foreleg. The vesicle gives off a small communicating trachea (CTra) medially that fuses with a similar branch from the vesicle of the opposite side of the body.

The organization of the trachea associated with the metathoracic spiracle is much simpler than that of the mesothoracic spiracle. Three tracheal trunks arise from the spiracle: 1) a posterior wing trachea (PWTra) described earlier; 2) a ventro-lateral tracheal trunk (VLTra) that projects caudo-ventrally before fusing with the ventral
plurisegmental trunk below; and 3) a posterior dorso-lateral trachea (PDLTra) that forms an anastomosis with the dorsal plurisegmental trunk above. This trachea gives off an anterior hind leg branch (ALTra). The posterior hind leg trachea (PLTra) originates from the first abdominal spiracle.

A number of ventral commissures occur in the thorax (Figures 1, 5, VCom, X). In the prothorax, there is an X-shaped commissure resulting from the fusion of branches of the ventral head trachea and the ventral plurisegmental trunk. A small tracheal ramus arises from each of the anterior arms of the commissure and enters the head. This is called the supra-ventral head trachea (Figure 5, SVHTra). The ventral commissures of the meso- and metathoracic segments are paired tracheal air sacs that are fused medially (Figures 1, 5, B, C, D, E, F).

The abdominal tracheal subsystem (Figures 1, 5) The organization of trachea in the abdomen of A. speiseri is generalized with some minor modifications. Each half of the body bears two main longitudinal trunk, namely the dorsal and ventral plurisegmental tracheal trunks (Figure 1, DTra, VTra). These extend the length of the body from about the seventh segment to the prothorax, where the dorsal trunk is continuous with the head trunk and the ventral trunk terminates in the X-shaped ventral commissure of the prothorax.

The basic tracheal plan for each segment involves the following. A short dorsal trachea (d) arises from the spiracle and projects upward. It forks to form anterior and posterior dorso-lateral branches (Figure 1, adl, pdl). The anterior branch bears a long, narrow,
tapering air sac that fuses above with the posterior branch of the
dorsal trachea of the preceding segment. The posterior branch expands
into a large sausage-shaped air sac the narrower dorsal end of which
bears the embryonic anterior and posterior dorsal connectives
described before (Figure 1, adc, pdc). These connectives fuse with
each other in successive segments to form the dorsal plurisegmental
trunk (DTra) found in the imagine.

The dorsal plurisegmental trachea from the two halves of the body
border the aorta and heart (Figure 6, DTra, Ao). They communicate with
each other segmentally via short dorsal commissures (DCom) located
between the ampullae (Amp) of the blood vessel above the alary muscles
(Am). A ventral trachea unites below with the ventral longitudinal
tracheal trunk (Figures 1, 5, v, VTra). A pair of intestinal or
visceral tracheae (Figures 1, 5, i) ramify on the digestive tract
(Figures 7, 8, 9, 10), the reproductive organs (Figure 29, Tra), the
fat body, and other tissues.

A ventral air sac commissure occurs in the first abdominal segment
(Figures 1, 5, VCom). This commissure is linked to a chain of paired
ventral air sacs caudally (1 pair per segment) that communicate with
each other via short tracheal connectives (see Figures 1 and 5, the
ventral abdominal air sacs are numbered 1-8).

Structures of the spiracles (Figures 11-20)

The thoracic spiracles (Figures 11-14) The mesothoracic
spiracle bears truncal and femoral stigmata that are closely situated
(Figures 11, 12, ts, fs). The truncal stigma has a lip-type closing
Figure 6. Tracheal ramifications of the female thoracic and abdominal dorsum

adl, anterior dorso-lateral trachea; Am, alary muscle; Amp, ampulla of the dorsal blood vessel; Ao, aorta; DCom, dorsal commissure; DTra, dorsal plurisegmental tracheal trunk; I-III, thoracic nota; Papt, paraproct; pdl, posterior dorso-lateral trachea; Ph, phragma; 1-10, abdominal tergites
Figure 7. Lateral view of the left side of the digestive tract

Figure 8. Lateral view of the right side of the alimentary canal

an, anus; Ca, caecum; Cr, crop; dvTra, dorsal visceral tracheal trunk; int, intestine; Ma, Malpighian tubule ampulla; Mth, mouth; Oe, oesophagus; Phy, pharynx; Pr, proventriculus; R, rectum; spl-sp8, abdominal spiracular tracheal branches; Vt, ventriculus
Figure 9. Dorsal view of the alimentary canal

Figure 10. Ventral aspect of the digestive tract

an, anus; Ca, caecum; Cr, crop; dvTra, dorsal visceral tracheal trunk; Ma, Malpighian tubule ampulla; Mth, mouth; Oe, oesophagus; R, rectum; spl-sp8, abdominal spiracular tracheal branches; Vt, ventriculus
Figure 11. External structure of the mesothoracic spiracle
Figure 12. Internal anatomy of the mesothoracic spiracle
Figure 13. External view of the metathoracic spiracle
Figure 14. Internal aspect of the metathoracic spiracle

a, aperture; am, antagonistic spiracle muscle; c, anterior spiracular lip; d, posterior spiracular lip; DHTra, dorsal head tracheal trunk; EPSVTra, external posterior supr-ventral trachea; fs, femora stigma; L, lip; m, manubrium; Nl, pronotum; Ptr, peritreme; q, ventral lobe; ts, truncal stigma; Vf, vesicula femoralis; VHTra, ventral head tracheal trunk
Figure 15. External structure of the first abdominal spiracle
Figure 16. Internal anatomy of the first abdominal spiracle
Figure 17. External structure of the second abdominal spiracle
Figure 18. Internal anatomy of the second abdominal spiracle
Figure 19. External structure of the eighth abdominal spiracle
Figure 20. Internal anatomy of the eighth abdominal spiracle

a, atrial aperture; am, antagonistic spiracular muscle; b, closing bow; c, closing band; d,i,v, dorsal, intestinal and ventral abdominal tracheae, respectively; L, closing lever; m, manubrium; om, occlusor spiracle muscle; PLTra, posterior leg trachea; PTr, peritreme
mechanism (L) externally while the femoral stigma is open to the outside (a).

Internally (Figure 12), the truncal aperture is associated with the roots of the dorsal and ventral head tracheal trunks (DHTra, VHTRA), the extreme supra-ventral trachea (EPSVTRA), and the anterior supra-ventral trachea (ASVTRA). The opening of the truncal atrial pore is achieved through the contraction of the antagonistic spiracle muscle that arises on the mesosternum and inserts on an antero-ventral process of the closing lobe antero-ventrally (Figure 12, am, ts, L). The closure of atrial pore occurs automatically when the antagonistic spiracle muscle relaxes due to the elastic properties of the cuticle surrounding the truncal stigma.

The femoral stigma, on the other hand, is linked internally to a large trumpet-shaped air sac (Figure 12, Vf) that communicates with the acoustic or femoral tracheal trunk of the foreleg (ACTra). The latter, as the name implies, is associated with the auditory organ located on the proximal end of the foretibia.

The metathoracic spiracle (Figures 13, 14) has a typical orthopteran structure consisting of a rigid anterior lip (c) and a movable C-shaped bar (d) that are linked ventrally by a cuticular lobe (q). The two components of the spiracle are surrounded by an oval peritreme (Ptr). Internally (Figure 14), the spiracular opening is connected to the base of the posterior wing trachea (PWTRA), the posterior dorso-lateral trachea (PDLTRA) and the ventro-lateral trachea (VLTRA). One branch of the spiracles antagonistic muscle inserts on the manubrium (m) of the movable
bar, while another branch of nearly equal size inserts on the peritreme antero-ventrally.

The abdominal spiracles (Figures 15-20) The basic structure of the abdominal spiracles is the same although their sizes and shapes vary slightly. Each spiracle bears a thick, oval, elongated closing band and a C-shaped closing bow. Both of these are surrounded by a chitinous ring or peritreme (Figures 15, 17, 19; b, c, Ptr). Internally, the closing mechanism of the spiracle involves antagonistic and occlusor spiracle muscles (Figures 16, 18, 20; am, om).

The opening of the atrial pore is achieved through the contraction of the antagonistic muscle. The latter takes its origin on the posterior margin of the laterosternite of the segment bearing the spiracle and inserts on a manubrium (m) of the closing bow. Closure of the spiracle is the result of relaxation of the antagonistic muscle, followed by the contraction of the occlusor spiracle muscle. The latter arises from a lever (L) on the closing band and inserts on the manubrium of the closing bow, adjacent to the point of insertion of the antagonistic muscle.

The nervous system (Figures 21-26)

The brain or supra-oesophageal ganglion (Figures 21, 22, 23) The supra-oesophageal ganglion of A. speiseri deviates from the typical orthopteran brain in two important respects. It appears to bear only two anatomical regions externally (Figure 21), and its optic lobes possess long stalks (Figure 21, LO, OS). However, all the three
Figure 21. Anterior view of the brain

AT, anterior arm of the tentorium; CA, corpora allata; Cr, crop; D, deutocerebrum; E, compound eye; GF, frontal ganglion; GH, hypocerebral ganglion; GO, oesophageal ganglion; LO, optic lobe; NA, nervus antennalis; Oe, oesophagus; OS, optic stalk; P, protocerebrum; PF, pars frontalis; Phy, pharynx; PL, pars labralis; T, tritocerebrum; 33,34,35,39, dilator muscles of the pharynx
Ant, antenna; Br, brain; CA, corpus allatum; CC, circumoesophageal connectives; Clp, clypeus; Cr, crop; CT, corpo-tentorium; D, deutocerebrum; E, compound eye; Fr, frons; GF, frontal ganglion; GH, hypocerebral ganglion; GO, oesophageal ganglion; Hphy, hypopharynx; Lb, labium; Lbplp, labial palp; Lm, labrum; LO, optic lobe; Md, mandible; NA, nervus antennalis; NM, nervus mandibularis; NM1, pevi maxillae; NM2, nervus labii; NO, nervus occipitalis; NRPE, nervus recurrens posterior externus; NRPI, nervus recurrens posterior internus; OS, optic stalk; P, protocerebrum; PF, pars frontalis; Phy, pharynx; PL, Pars labralis; SOG, suboesophageal ganglion; T, tritocerebrum; TCI, first thoracic nerve connectives; TCom, tritocerebral commissure; Vx, vertex
Figure 24. The ventral ganglionic chain in situ

Figure 25. Dorsal view of the male thoracic and abdominal ganglia

Ab, abdominal connective; AbG, abdominal ganglia; Ac, abdominal nerve connective; Br, brain; g, abdominal ganglion; G, thoracic ganglion; NS, median or subintestinal nerve; lNv2-lNv4, nerves from the prothoracic ganglion; 2Nv1-2Nv4, nerves from the mesothoracic ganglion; 3Nv1-3Nv3, nerves from the metathoracic ganglion; TgNv, StNv, tergal and sternal nerves; 2TgNv, 2StNv, tergal and sternal nerves from the second definitive abdominal ganglion; Tc, thoracic nerve connective; ThG, thoracic ganglia
Figure 26. Dorsal view of the brain and the stomatogastric ganglia

Ant, antenna; AT, anterior arm of the tentorium; CA, corpora allata; E, compound eye; GH, hypocerebral ganglion; GO, oesophageal ganglion; NA, nervus antennalis; NO, nervus occipitalis; NRPE, nervus recurrens posterior externus; P, protocerebrum; T, tritocerebrum
anatomical regions of a typical orthopteran brain, protocerebrum, deutocerebrum, and tritocerebrum are present (Figures 21, 22; P, D, T).

The protocerebrum (P) is the largest subdivision. It occurs dorsally; it is cordate in shape and bears stalked optic lobes (LO) dorsolaterally. No ocellary nerves (nervi ocellarii) are present. Ventrad to the protocerebrum and strongly linked with it is the deutocerebrum (D). This region of the brain is small in the ground cricket and it is not distinctly dermarcated externally. However, its relative position can be approximated by the position of the bases of the antennal nerves that arise from it (Figures 21, 22, 23; NA – nervus antennalis). No accessory antennal nerves (NAA – nervus antennalis accessorius) or the tegumentary nerves (NT – nervus tegumentalis) were observed in the dissections. However, this should not be taken to mean that these nerves are absent in the ground cricket. Further detailed studies are needed.

Below the deutocerebrum is the tritocerebrum (T). Ventrally, it bears a pair of circumoesophageal nerve connectives that link the brain to the suboesophageal ganglion of the ventral nerve cord (Figure 23, CC, SOG). Also arising from the ventral margins of the tritocerebrum are the labro-frontal nerves and the ventral nerve commissure. The pars frontalis labro-frontal nerves from the two sides of the tritocerebrum form a loop to the frontal ganglion on the pharynx (Figure 21, PF, GF, Phy). The pars labralis labro-frontal nerves project ventrad to innervate muscles of the labrum (Figure 21, PL; Figure 22, Lb). The tritocerebral nerve commissure loops around the oesophagus below, linking the two sides of the brain (Figure 23, TCom).
The ventral nerve cord (Figures 24, 25) The first ganglionic mass in the cord is the suboesophageal ganglion (SOG). It lies below the oesophagus under the corpo-tentorium (Figure 22, CT). The circum-oesophageal connectives (CC) linking the brain to it pass in front of the corpo-tentorium between its anterior arms. Nerves arising from this ganglion innervate the mandibles (NM - nervus mandibularis), hypopharynx, maxillae (NM 1 - nervus maxillae), labium (NM 2 - nervus labii) and the cervical region. The suboesophageal ganglion is linked to the thoracic ganglionic masses by a pair of nerve connectives (Figure 23, TC1).

Of the three thoracic ganglia, those of the pro- and mesothorax are nearly equal in size. The metathoracic ganglion tends to be slightly larger due to its incorporation of the first definitive abdominal ganglion. Emerging from the lateral margins of each ganglion are the two principal groups of nerves to the body (Figure 25, Nv2, Nv3). According to Nesbitt (1941), the anterior nerve group (Nv2) provides branches to the tergal promotors, sternal promotors (or the anterior rotators), basalar, subalar, axillary (in winged forms), sternal abductor, and tergo-sternal muscles. The posterior nerve group (Nv3) serves the tergal remotors, sternal remotors (or the posterior rotators), sternal adductor, and the ventral longitudinal muscles, in addition to sending a large branch into the leg. In the migratory locust, nerve group 2 (Nv2) is reported to innervate the hypodermis of the respective segment while nerve group 3 (Nv3) sends branches to the legs (Albrecht, 1953).
Another nerve (Nvl) arises anteriorly from each ganglion near its junction with the thoracic nerve connectives. In the prothorax, nerve Nvl (not shown in the illustrations) fuses with a branch from the suboesophageal ganglion. In the meso- and metathorax, nerve Nvl forms a plexus with nerve Nv4 of the anterior ganglion. Nerves arising from this loop (not illustrated) are reported to innervate the wings. In *A. speiseri*, the courses taken by these nerves were not determined in this study.

There are six free abdominal ganglia occurring in segments 1, 2, 4, 6, 7, and 8 (see Figure 25). The first definitive abdominal ganglion is fused with the metathoracic ganglion. This is evidenced by the presence of a pair of nerves (1 TgNv, 1 StNv) that arise posteriorly from this ganglion which innervate the tergal, pleural, and sternal muscles of the first abdominal segment.

The second definitive or the first free abdominal ganglion (g2) is located in the first abdominal segment. This and the following four ganglia each bear two pairs of lateral nerves. The anterior nerve (TgNv) innervates the tergal and pleural muscles and sends off branches to the dorsal blood vessel. The posterior nerve (StNv) innervates the sternal muscles.

The last or eighth abdominal ganglion is larger than the rest. It is heart-shaped and is a compound ganglionic mass supplying nerves to the eighth, ninth, tenth, and eleventh abdominal segments (Figure 25, 8TgNv, 8StNv, 9TgNv, 9StNv, 10 and 11 Nv). In the male, the nerves of the ninth abdominal segment innervate the phallic organs (not shown in the
diagrams). In the female, the ventral or first pair of ovipositor blades is innervated from branches of the eighth nerves while the inner or the second and the dorsal or third ovipositor blade pairs are innervated from branches of the ninth segmental nerves. In both sexes, however, the nerves of the tenth segment innervate the cerci and dilator muscles of the rectum. Nerves of the eleventh segment supply motor filaments to the epiproct, paraprocts, and the dilator muscles of the anus in addition to supplying large sensory branches to the cerci (Nesbitt, 1941).

In the middle of the ventral nerve cord, between the nerve connectives, are the very thin median or subintestinal nerves (Figure 25, NS). These nerves supply branches that innervate the spiracular muscles in those segments where spiracles are present.

**The stomatogastric nervous system (Figures 22, 23, 26)** This system involves four ganglionic masses, the frontal ganglion, paired oesophageal ganglia, hypocerebral ganglion, and paired ingluvial ganglia (Figures 22, 23, 26; GF, GO, GH). The frontal ganglion is located in front of the brain on the pharyngeal wall (Phy), to which it is firmly attached. The median oesophageal ganglia and the hypocerebral ganglion occur immediately behind the brain attached to the oesophagus. The oesophageal ganglia are positioned above the hypocerebral ganglion and communicate with it via short nerves. Each oesophageal ganglion is shaped like an air-foil and is attached to the protocerebrum at its broad anterior end by the occipital nerve (NO). On the narrow posterior margin arises a large nerve that links it to the large oval corpora allata (CA) attached to the wall of the oesophagus.
Posteriorly, the hypocerebral ganglion gives off two pairs of nerves. One pair is the small, short, median recurrent nerves (NRPI) that innervate the oesophagus. The other pair are large long nerves (NRPE). The latter run along the dorso-lateral walls of the crop (Cr) to the ingluvial or gastric ganglia on the walls of the proventriculus (not shown in the illustrations).

The reproductive system (Figures 27-30)

The female internal reproductive organs (Figures 27, 28) The internal reproductive organs of the female are simple and generalized in structure. They include: two ovaries, paired lateral oviducts, a median or common oviduct, a spermatheca, and a single accessory gland.

The ovaries (Ov) lie on either side of the digestive tract in the abdominal cavity. In gravid females, these are very large organs that occupy most of the abdomen and, due to the large sizes of the developing and matured eggs in them, mature females exhibit highly distended abdomens compared to males. The terminal ligament (Lg) of each ovary attaches to the tergal ridge of the metathoracic segment dorso-laterally.

Posteriorly, each ovary gives off a large lateral oviduct (Odl). The latter unit around the seventh abdominal segment to form a short, wide, common oviduct (Odc). This, in turn, opens into a short genital chamber (GC) that leads to the vulva (Vul) or the external genital opening. The latter occurs between the ventral ovipositor blades and the subgenital plate (Figure 27, lVl, sgp).

A duct from a large, shoe-shaped spermatheca opens on the dorsal wall of the genital chamber caudad to the entrance of the common oviduct
Figure 27. Lateral view of the female reproductive organs

AcGld, accessory gland; Dct, duct of the spermatheca; GC, genital chamber; Lg, ovarian ligament; Odl, lateral oviduct; Ov, ovary; Papt, paraproct; R, rectum; sgp, subgenital plate; Spr, spermathecal aperture; Spt, spermatheca; St, abdominal sternite; T, abdominal tergite; VI, ovipositor blade; Vul, vulva or gonotreme
Figure 28. Dorsal view of the female internal reproductive organs

AcGld, accessory gland; Dct, spermathecal duct; E, egg; Lg, ligament; Odc, median oviduct; Odl, lateral oviduct; Ov, ovary; Spt, spermatheca; Vul, vulva; VI, ovispositor blade
Figure 29. Lateral view of the male reproductive organs

AcGlds, accessory glands; AGS, accessory gland stalk or shaft; Dej, ejaculatory duct (ductus ejaculatorius); DPL, dorsal phallic lobe; ejv, vesicle of the ejaculatory duct; Epdm, epididymis; LPL, lateral phallic lobe; Phtr, phallotreme; r, rectum; sgp, subgenital plate; ST, sperm tube; Tes, testis; Tra, trachea; Vd, vas deferens; VPL, ventral phallic lobe
Figure 30. Dorsal view of the male internal reproductive organs

a, b, two kinds of accessory glands; AGS, accessory gland shaft; Dej, ejaculatory duct; ejv, vesicle of the ejaculatory duct; Epdm, epididymis; LPL, lateral phallic lobe; ST, sperm tube; Tes, testis; Vd, vas deferens; VPL, ventral phallic lobe
A single, unbranched tubular accessory gland (AcGld) opens behind the spermathecal aperture on the dorsal wall of the genital chamber.

The **male internal reproductive organs** (Figures 29, 30) The internal reproductive organs of the male include a pair of testes, paired vas deferentia, two kinds of accessory glands, and a pair of vesicles attached to a short ejaculatory duct.

The testes (Tes) are large, compact, bean-shaped bodies lying on either side of the alimentary canal, extending from the first to the seventh abdominal segments. Each testis bears a large number of short sperm tubes (ST).

Posteriorly, vas deferentia (Vd) emerge from each testis and are thrown into complex convolutions immediately upon emerging, forming compact epididymis-like bodies (Epdm). Beyond the epididymis-like mass each vas deferens is a short, straight tube that opens into a median ejaculatory duct (Dej), together with a pair of stalks (AGS) bearing the accessory glands (AcGlds).

Two types of accessory glands are present. One type consists of large, long, and numerous tubules that occupy most of the posterior and ventral region of the male abdomen, being intermingled with the digestive tract and the fat body. They arise on about the distal two thirds of the accessory gland shaft (Figure 30, a). The second type consists of small, short, closely packed tubules that form compact globular bodies on the proximal third of the accessory gland shaft (Figure 30, b).
The ejaculatory duct opens to the outside via a wide chamber or the phalotreme that is surrounded by phallic lobes (Figure 29, DPL, LPL, VPL, Phtr).

Summary

The gross anatomies of the respiratory, nervous, and reproductive systems of the armoured ground cricket, Acanthoplus speiseri, have been described. The respiratory system closely resembles that described for the tettigoniid, Phasgonura viridissima L., with the following exceptions:

a. Being apterus in nature, the wing tracheae are reduced in A. speiseri, while in P. viridissima a full complement of the wing tracheae are present.

b. Whereas in P. viridissima the dorsal abdominal trachea gives rise to three air sacs, in A. speiseri only two occur, although they are much larger.

The nervous system is similar to that of Conocephalus fasciatus De Geer except for the following differences:

a. Whereas in C. fasciatus the optic lobes join the protocerebrum by short necks, in A. speiseri the structures are linked to this region of the brain by long, thick stalks.

b. Three ocellary nerves arise from the protocerebrum of C. fasciatus, while no ocellary nerves are present in A. speiseri. The lack of ocelli is not unique to the ground cricket. It has been reported in other orthopterans, e.g., Ceuthophilus brevipes Scudder and Diapheromera femorata Say (Nesbitt, 1941).
The female internal reproductive organs are simple and generalized. In the male, the structures are more specialized. They resemble those described for *orchelimum minor* Brunner except that, whereas in the latter species the epididymis-like mass is located a short distance from the testis, in *A. speiseri* this structure occurs immediately behind the testis.

References


SUMMARY DISCUSSION

Geographical Distribution of A. speiseri in Zambia

The geographical distribution of the representative members of the genus Acanthoplus Stål. in Africa is more extensive than was reported previously (see Appendix A). In Zambia, Southern Africa, A. speiseri was found to occur in areas far beyond the northern geographical distribution limit envisaged for the genus in the past (Weidner, 1941). In this country, the species was collected from areas around the following towns: Chilanga, Chipata, Choma, Isoka, Kabwe, Kacholola, Kafue, the Kafue National Park, Kalomo, Kaoma, the Luangwa Game Reserve, Luanshya, Lundazi, Lusaka, Mansa, Mazabuka, Monze, Mumbwa, Ndola, Nyimba, Petauke, and Solwezi, during a preliminary survey by the author (see Appendix B).

The discrepancy between what was reported to be the northern limit of the genus on the African continent and the distribution patterns of A. speiseri as determined for Zambia supports Professor Weidner's contention that available information on the distribution patterns of the Hetrodinae is still insufficient to warrant a conclusive statement on the evolution of the subfamily in Africa. Further research is required before one can do so.

External Morphology and Endoskeletal Processes

The external form and endoskeletal process of A. speiseri are of the generalized tettigoniid type. However, a few features exhibit subfamilial specializations of taxonomic importance. Like all other members of the Hetrodinae, A. speiseri bears spiniform body ornaments,
it is 'armoured' by spines. The ground cricket is heavy-bodied and apterus. The males possess modified tegmina on their mesonota that serve as stridulating organs. In the females, these structures are absent, being represented only by a pair of minute wing pads. Consequently, the females of this species do not stridulate.

Unlike many tettigoniids, the ovipositors of the female are very short and are specialized for ovipositing eggs in the soil. The occurrence of short ovipositors in female Heterodinae has also been reported in a related species, A. bechuanus Per., by Power (1958).

Internal Anatomy

The thoracic musculature of A. speiseri is similar to that of Acridopeza reticulata Guerin, Neoconocephalus robustus (Scudder), and Homorocoryphus nitidulus vicinus (Walker) except for the following:

a. The male A. speiseri bears a large tergo-pleural muscle in its mesothorax that is absent in its metathorax and is completely lacking in the pterothorax of the female, while both sexes of A. reticulata and N. robustus possess the muscle in both segments of their pterothorax, though reportedly thinner in females than in the males.

Tergo-pleural muscles are said to be an important group of muscles in the Ephemerida, Plecoptera, Sialidae, Mecoptera, Trichoptera, and the Aphididae (Snodgrass, 1935a, b). They are indirect wing muscles that also serve in moving the wings during stridulation (Josephson and Halverson, 1971). Tiegs (1955) characterized these muscles as exhibiting a deferred
function and called them pure wing muscles in the Australian mountain grasshopper, *A. reticulata*.

The presence of large tergo-pleural muscles in the mesothorax of male *A. speiseri* is, therefore, not surprising, as this segment bears the stridulating organs. Since the latter are modified wings, it can be expected that these muscles operate the stridulating organs in a way similar to that of normal wings in flight in those species that possess wings. The tergo-pleural muscles are strong elevators of the stridulating organs. They raise the tergmina when the insect is singing. The females lack tergo-pleural muscles since they lack wings or stridulating organs.

b. A single basalar and subalar muscle occurs in *A. speiseri*, a situation similar to that reported in *H. n. vicinus*, while *A. reticulata* bears three basalars and two subalars. However, *A. speiseri* differs from *H. n. vicinus* in that these muscles occur only in the mesothorax of the male.

Basalar and subalar muscles are commonly called the direct wing or flight muscles, since they directly operate the wings during flight. Again, it is not surprising that these muscles are to be found only in the mesothorax of the male *A. speiseri*. They operate the stridulating organs in the same manner as they do the wings in winged insects, causing the back and forth movements of one stridulating organ over the other during singing. Josephson and Halverson (1971) observed that these
muscles fire impulses synchronously, but in an approximate antiphase to the indirect muscles (including the tergo-pleural muscles described above) during flight in H. n. vicinus.

c. The tergo-trochanteral muscle is large in A. speiseri, while it is very small in N. robustus and of moderate size in A. reticulata.

The abdominal musculature in the ground cricket resembles that of Neoconocephalus exiliscarnorusc Davis and Ceuthophilus lapidicola Burm., with only some minor exceptions.

The alimentary canal is similar to that of Amblycorypha rotundifolia (Scudder) and Neoconocephalus ensiger Harris. On the basis of the structure of the proventriculus, Judd (1948) classified the six subfamilies of the Tettigoniidae he studied into two broad categories. In the first group, the proventriculus bore appendages that were covered with hairs and the barbated lobes had small spines that were surrounded by tufts of setae. In this category, he placed Scudderia curvicauda De Geer (subfamily Phaneopterinae). The proventriculus of the second group was characterized by appendages lacking hairs and barbated lobes that were highly sclerotized and without setal tufts. In this category, he included the following species: Neoconocephalus ensiger (Harris) (Copiphorinae), Conocephalus fasciatus De Geer (Conocephalinae), Phasgonura cantans Fuessly (Phasgonurinae), and Atlanticus gibbosus Scudder (Decticinae). In this scheme of classification, A. speiseri falls in the second category, as its proventriculus bears hairless appendages and its barbated lobes are strongly sclerotized without setal tufts.
The dorsal blood vessel of *A. speiseri* is similar to that reported for another member of the Heterodinae, *Eugaster spinulosus* Johnson. In both species there are 12 pairs of alary muscles flanking the sides of the vessel, three thoracic and nine abdominal pairs of ostia, and there are no segmental blood vessels. In other tettigoniids, the number of pairs of alary muscles ranges from 10 in the Copiphorinae and Conocephalinae to 12 in the Pseudophyllinae, Decticinae, and Phanerop terinae (Nutting, 1951). The number of ostia pairs in the thorax and abdomen of all these subfamilies is the same as that found in *A. speiseri* and no segmental blood vessels have been reported in any one of them.

The respiratory system of the ground cricket resembles that described for *Phasgonura viridissima* L., with one major exception, whereas in *A. speiseri* there are very reduced wing tracheae due to its apterus nature, *P. viridissima* bears a full complement of the wing tracheae with complex basal connections.

The nervous system of *A. speiseri* is similar to that described for the tettigoniid, *Conocephalus fasciatus* De Geer, except that in *A. speiseri* the ocelli are absent and the optic lobes are linked to the protocerebrum by long, thick stalks. The absence of ocelli in the Tettigoniidae has also been reported in *Ceuthophilus brevipes* Scudder and *Diapheromera femorata* Say (Nesbitt, 1941). However, *A. speiseri* differs from these two species in that its optic lobes are stalked and its brain has an apparent external appearance of possessing only two anatomical subdivisions. In both *C. brevipes* and *D. femorata*, the optic lobes are tenaciously linked to the protocerebrum and the brain has distinctly three anatomical subdivisions when viewed from the outside.
The internal reproductive organs of the female ground cricket are simple and generalized. In the male, these structures are similar to those of *Orcholimum minor* Brunner (Snodgrass, 1937) and *Leptophyes punctatissima* (Bosc.) (Qadri, 1940), although in the latter two species the epididymis-like convolutions of the vas deferens occur a short distance from the testis. In *A. speiseri*, the epididymis-like body occurs immediately behind the testis.

According to Snodgrass (1937), the occurrence of an epididymis-like mass in the internal reproductive organs of the male Tettigonioida is not uncommon. The structure is said to have attained its largest size in the Gryllotalpidae where, in species like *Gryllotalpa hexadactyla* Perty and *Scapteriscus vicinus* Scudder, the epididymis is as large, if not larger, than the testis.


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APPENDIX A. GEOGRAPHICAL DISTRIBUTION OF SOME OF THE
GENERA OF THE SUBFAMILY HETRODINAE IN AFRICA
Figure A1. Geographical distribution of some of the genera of the subfamily Hetrodinae in Africa (adapted from Weidner, 1941)

- Enyaliopsis
- Gymnoproctus
- Cosmoderus
- Acanthoplus
- Hetrodes
- Cloanthella
APPENDIX B. DISTRIBUTION OF *Acanthoplus speiseri*

BRANCS. IN ZAMBIA
Figure B1. Distribution of *Acanthoplus speiseri* Brancs. in Zambia

- Brachystegia woodlands, Savana woodlands and Savanna grasslands
- Other vegetation mainly Savanna shrub and grasslands
- Areas where *A. speiseri* was collected