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**The external morphology and phylogenetic position of the
woodland cave cricket (*Ceuthophilus brevipes* Scudder;
Orthoptera; Tettigoniidae)**

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THE EXTERNAL MORPHOLOGY & PHYLOGENETIC
POSITION OF THE WOODLAND CAVE CRICKET
(CEUTHOPHILUS BREVIPES SCUDDER, ORTHOPTERA, TETTIGONIDAE)

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THE EXTERNAL MORPHOLOGY AND PHYLOGENETIC POSITION OF THE
WOODLAND CAVE CRICKET
(Ceuthophilus brevipes Scudder; Orthoptera; Tettigoniidae)

by

Ashley Buell Gurney

Thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
Massachusetts State College
Amherst, Massachusetts
June, 1935

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Introduction

The purpose of this paper is to furnish, in one work, the detailed external morphology of an orthopteron which, from an evolutionary standpoint, is among the most primitive of all saltatorial Orthoptera. Although published accounts of portions of the external anatomy have been made available by Drs. Crampton, Walker, and others, no complete morphological study of a native American Rhaphidophorine has been made.

Since Scudder erected the genus Ceuthophilus in 1862 more than fifty species have been described. From the point of view of a systematic study of these insects, therefore, it is well to have available a complete account of the morphology of one species to use as a basis for indicating the true relationships of the structures used in the taxonomy of the group.

Crampton (1923c) has suggested that Ceuthophilus may be involved as a carrier of disease organisms. If such should prove to be the case, as appears reasonable, any information regarding the biology and relationships of such a vector may be considered worthy of recording.

Probably the morphology of Ceuthophilus is most interesting to the student of insect phylogeny. The close relationships of orthopteroid insects were recognized by Packard (1883) but at that time a careful comparative analysis of the sclerites had not been made. Even earlier, Scudder

(1869) had written on the arrangement of the families, but he placed the Gryllidae and Tettigoniidae in advance of the Acrididae because of the greater development of songs, social habits, and the elongate nature of the ovipositor.

Marcovitch (1920) summarized the subject of orthopterous phylogeny and the tree shown by him (fig.4) indicates the probable phylogenetic position of the principal groups. The one correction to be made in this tree is that the Tettigoniidae seem to be directed along the lines of the Acrididae, with the Gryllids branching in the opposite direction from a point near the base of the Tettigoniids, rather than that the crickets and katydids followed parallel lines apart from the grasshoppers as his tree indicates.

Throughout the present study of Ceuthophilus a comparative study of the sclerites has indicated the close relationship of the Grylloblattids, Rhaphidophorines, Gryllacrine, and Stenopelmattines. The crickets clearly have close affinities with the primitive Tettigoniids while such forms as the Tridactylines show qualities in their makeup which indicate an origin in the same stock, but these characters develop further in the higher Tettigoniids and thus lead directly to the grouse-locusts and finally to higher grasshoppers.

The main features of the head and abdominal structures of Ceuthophilus have been described by Crampton, Walker, and Yuasa in the papers cited, together with a discussion of evolutionary sequence. The chief original work of this paper is the part dealing with the thoracic sclerites and these are among the most important of all the body structures.

It is hoped that by bringing together the available information on the morphology of this primitive insect a better understanding of its phylogenetic position will result; also that it may aid future taxonomists within the group to locate the structures important in classification.

The Head

The head capsule and its appendages do not differ greatly from the corresponding structures of Stenopelmatus, which Crampton (1930) has discussed in detail. The head capsule of Stenopelmatus in its general features appears rather more broadly rounded in the dorsal area than in the case of Ceuthophilus; the antennae are decidedly more centrally located in Ceuthophilus. In these respects Ceuthophilus has departed further than Stenopelmatus from the primitive type of head capsule represented in Grylloblatta. The migration of the eyes toward the vertex points to the higher Tettigoniid type such as Scudderia, Orchelimum, and Neoconocephalus which leads up to the Acrididae. At the other end of the evolutionary scale the eyes are located far down the genae, as in Isoptera and Dermaptera, which lead to Grylloblatta, as discussed by Crampton (1926,1932) and Yuasa (1920).

Head capsule: As shown in fig.3, the dorsal region of the head capsule of Ceuthophilus is oval in outline. The coronal suture cs is plainly but not strongly demarked and terminates in a small triangular spot near the eyes. In this connection the fastigium of the Stenopelmatine Licodia cerberus Rehn of

Cuba (see Rehn, 1930, fig. 2) should be mentioned. There are no frontal sutures or epicranial arms in Ceuthophilus as there are in Gryllus, Stenopelmatus, or Grylloblatta. The entire region about the eyes and coronal suture is smooth and rather hard. The parietals par are the areas on each side of the coronal suture. The areas above the eyes e are known as the temples te. The frons f is just below and between the antennae while the genae ge are the areas each side above the subgena or basimandibulare bm. The latter is a small sclerite which is closely associated with the small basimandibular membrane bmm, and lies above the base of the mandible md. The margins of the frontal pits fp are somewhat more heavily sclerotized than the surrounding clypeus c and gena. The frontal pits represent the external openings of the invaginations which form the forward arms of the tentorium or pretentorium pt shown in fig. 1.

Eyes: The compound eyes e, like those of Stenopelmatus and Grylloblatta, are rather small in comparison to the eyes of most other primitive types of Orthoptera such as Dictyoptera and Gryllidae. Crampton (1930) has suggested that this reduction of the eyes may be in keeping with the nocturnal habits of these insects (Ceuthophilus is nocturnal) and his suggestion is given support by the fact that the eyes of Gryllotalpa, which tunnels in soil, are distinctly smaller than those of Gryllus, a diurnal surface dweller. The number of facets in each compound eye of Ceuthophilus is about three hundred. Ocelli are lacking.

Antennae: The antennae are long and filiform and vary in number of segments from seventy-five to one hundred and sixty

or more in some cases. In some individuals the antennae are twice the body length. The antennale an (fig.2) is a delicate ring which bounds the membrane at the base of the scape sc. A small projection of the antennale is known as the antennifer af. The scape sc is the largest segment and rather flat. The pedicel pd is short and somewhat bulbous. The next segment, the postpedicel ppd, is considerably longer than the pedicel and assumes the cylindrical form which occurs in the remainder of the antennal segments. The shorter intermediate segments are called short brachymeres sb and the more slender ones toward the tip slender dolichomeres sd. Additional names have also been applied to the segments in allied Orthoptera because of the differences in size and shape.

Tentorium: The inner supporting framework or tentorium of the head capsule of Ceuthophilus is formed according to the generalized type discussed by Comstock and Kochi (1902) and Imms (1929,p.45) in which the chief structures are posterior, anterior, and dorsal arms, and the body of the tentorium. Just as furcae and apodemes are invaginations of the external wall of the thorax and abdomen, so the tentorium represents invaginations of the head capsule.

When a potash preparation of the head capsule is studied in frontal aspect the anterior arms pt (fig.1) are seen extending backward from the frontal pits where the invaginations occur. The support given to the mandibles which perform the most important work of the appendages of the head may be easily understood. The dorsal arm st is a small branch which is

attached distally, in Ceuthophilus, near the cephalo-mesal margin of the eye. The posterior arms poc, resulting from invaginations, the external manifestations of which are the gular pits gp near the base of the basicardo, fuse with the anterior arms to form a broad central plate, the body of the tentorium or eutentorium eu. The posterior arms are the chief strengthening elements of the margins of the occipital foramen. The postgenal process pp bears the postgenal acetabulum pga and is separated from the gena ge by the postgenal suture pgs. The parastomium psto is a marginal area extending along the inner ventral edge of the postgenal process.

The commissures connecting the dorsal brain with the suboesophageal ganglion pass through the neuroforamen nf, an incision at the bases of the anterior arms. The commissures leading from the suboesophageal ganglion to the prothoracic ganglion pass between the flaring rims of the occipital foramen to the thorax. The semi-circular neuroforamen nf is probably evolved from the closed structure found in Dictyoptera which leads finally to the entirely fused type exhibited by Gryllus. It may be noted that Grylloblatta, figured by Walker (1931b), is more like Gryllus in this respect than Ceuthophilus or Stenopelmatus.

Occipital region: The occipital condyles occ are the points of articulation of the head capsule with the laterocervicale lc (fig.13). When the external features of the occipital foramen are examined, a flaring band is seen along each side near the gula. This band is the "maxillaria" of Yuasa (1920,p.262).

Dorsad of the condyles the occipital foramen is less heavily sclerotized and the rim is little more than the strengthened margin of the cranium. As Walker (1933,p.317) states, the occipital suture is not complete at this point.

The paroccipital tendon pat and euoccipital tendon eot are attached to the rim of the cranium, and the tendons serve as points of attachment for muscles moving the head.

Clypeus and labrum: The clypeus c is separated from the frons f by a well-marked fronto-clypeal suture. The postclypeal and anteclypeal areas are not plainly apparent in Ceuthophilus. The outline of the labrum la is shown in fig.3. The union with the clypeus is strong but allows some movement.

Mandible: Fig.7 shows the insect's right (dextral) mandible as it appears in posterior view. There are three faces and a somewhat triangular base. The ginglymus gi is a shallow pit at the base of the frontal face of the mandible. The pit forms an imperfect hook which fits into a niche at the base of the clypeus. The gnathocondyle or hypocondyle h is a rounded projection which articulates in the postgenal acetabulum pga borne on the postgenal process pp. The chief tendons which move the mandible on its "rocking" points, the ginglymus and gnathocondyle, are the flexor ft which is the heavier of the two because it performs the actual crushing operations of chewing food and the extensor et which moves the mandible into an open position. Anyone interested in the powerful muscles extending from the tendons into the head capsule may be guided by the work of Walker (1931b) who has

figured in detail the musculature of the head of the allied Grylloblatta. The gnathite gn is a small sclerite which supplies the attachment of the flexor tendon to the base of the mandible. The extensor tendon et is attached directly to the mandible proper at the epignath or extensor prominence ep. The gnathapex ga is a sharp, curved hook for grasping and tearing. The molar region m appears as in fig.7 and is best adapted for grinding processes. The interior of the mandible is hollow.

Labium: The ventral aspect of the labium is shown in fig.5. Fig.4, a dorsal view, shows how the glossae gl arise from the glossigers gg near the point where the latter joins the labial stipites li. The paraglossae pg are also borne by the glossigers. The palpigers ppg bear the three-segmented labial palpi lp. The mentum mn is composed of two regions the posterior of which is more darkly sclerotized. The gula gu and submentum sm comprise one sclerite, but the former portion is darker colored so that it appears distinct.

The labial structures of Ceuthophilus resemble very closely those of Stenopelmatus and Gryllus.

Maxilla: When the ventral surface of the head is examined, the maxilla appears as in fig.5. The stipes s and the narrow parastipes ps are separated internally by a ridge which affords a place of muscle attachment. The basimaxillary membrane b bounds the parastipes ps laterally. Fig.6 shows a view of the internal surfaces of the cardo which is divided into basicardo bc and disticardo dc. The point labelled d is attached to the

postgena near the gular pits and probably functions like a condyle. The cardo-process cp is an arm to which the cardo tendon ctn is attached. Crampton (1930) describes the manner in which the tendon probably moves the maxilla on the point d. The endocardo ec is an internal ridge which gives support to the sclerites and offers a place for muscle attachment. The palpifer pf is a small sclerite bearing the slender five-segmented maxillary palpus mp. The basigalea bg is well demarked and bears the galea g. The lacinia l is toothed as shown in fig.5 and is rather strongly sclerotized.

Crampton (1916a,1923b), Walker (1933), and Yuasa (1920) have discussed in some detail the development of maxillae in orthopteroid insects. The maxillae of Ceuthophilus are very like those of Grylloblatta and Gryllus, but differ from those of the Blattidae on account of the hood-like scoop borne by the galea of the latter. The Decticine genus Peranabrus (figured by Crampton,1923b) shows galea and lacinia somewhat broader than those of Ceuthophilus. An examination of specimens of Conocephalus and Neoconocephalus shows an additional width of the latter appendages which points toward the broad structures found in Acrididae. With respect to maxillae, therefore, Ceuthophilus exhibits a primitive form.

Hypopharynx: The hypopharynx hp is a more or less fleshy structure attached to the base of the labium and situated between the labrum and labium as shown in lateral view in fig. 9. It appears as in fig.8 when, with the labrum cut away, it is viewed from above. There are several lobe-like portions of the hypopharynx the apical portion of which is the disti-

lingua dl. The dorsolingua or surlingua sl is the basal portion. The basilingua bl is a membrane which forms part of the basal attachment and is the location where the common salivary duct discharges fluid into the mouth cavity. The oral opening of the oesophagus is near the dorsolingua so that ingested food passes above the hypopharynx. The lingualora ll is a small triangular sclerite at the base of the hypopharynx.

Epipharynx: The epipharynx is divided into posterior and anterior regions, labelled poe and pre respectively in fig.9. The epipharynx is the roughened inner surface of the labrum and clypeus which is modified to assist in the manipulation of food.

Thorax

While investigators have done less work upon the thorax of Ceuthophilus than upon the head and abdomen, this region is thought to offer even more valuable clues regarding the phylogenetic position than in the case of the latter. Tegmina and wings are entirely absent. Legs may be reasonably expected to show adaptation to mode of living and so are of scant evolutionary importance. The plates of the neck, pleura and sterna are of the greatest significance and will be discussed as the parts of the thorax are taken up in order.

Prothorax

Neck Region: The precervicale prc (fig.13) is a small divided plate which is hidden beneath the pronotum pn. The important cervical sclerite is the laterocervicale lc. Its anterior extremity articulates with the occipital region of the head.

Crampton (1926b, 1933, pp. 140-142) has shown that Blattids, Isoptera, and Mantids are very closely related because of the similarly divided laterocervicale and the mesally extending intercervicale. This latter condition is much different from that exhibited by Ceuthophilus. However, figs. 65, 68, 80, 81, 86, and 94 of Crampton's 1926b paper show that with respect to this sclerite Ceuthophilus is a primitive member of the Saltatoria. It is similar to Gryllacris but most like Grylloblatta. Among the Gryllids, Tridactylus has an undivided laterocervicale which is directed mesally similarly to that of roaches. Gryllus has a partially divided sclerite which comes nearer Ceuthophilus in form, while Oecanthus is very like Ceuthophilus except for the division of the sclerite. Apparently the condition in Oecanthus leads to that occurring in Tettix and other Acridids.

Pronotum: The pronotum pn of Ceuthophilus completely covers the episternum es₁ and epimeron em₁, but as Duporte (1919) has indicated, this is the result of the growing over of the pronotum rather than the forcing out of the pleural sclerites. The pronotum is smooth and polished. A like condition prevails in Gryllacris but in the related Stenopelmatus the beginnings of pronotal sulci are visible and in the remaining subfamilies of Tettigoniidae both the presence of sulci and the form of the pronotum point toward the condition found in Acrididae. The effect of wing muscles is of course entirely absent in Ceuthophilus. The pronotum of Grylloblatta does not extend ventrally so as to completely cover the pleural sclerites but is more like that of Dermaptera. Neither does the Gryllid pronotum show consistent similarities to that of Ceuthophilus. The pronotum

of Gryllotalpa and Tridactylus is not very different from the Ceuthophilus-like forms but that of Gryllus is more flattened dorsally and that of Oecanthus is more suggestive of Grylloblatta or even of a Mantid. With respect to the pronotum, therefore, it appears that Ceuthophilus stands near the base of the whole Tettigoniid line leading directly to the Acrididae while the Gryllids represent an offshoot, possibly from a point near Stenopelmatus. It should be noted that although the Gryllids are an offshoot from the stem which leads to the Acrididae, they may exhibit qualities which constitute examples of development inherited from primitive Tettigoniids. Any such inheritance is interesting because certain of the same qualities were developed in the main Tettigoniid line leading to the Acrididae.

Propleuron: The episternum es₁ of Ceuthophilus is somewhat striking in appearance because of the bilobed condition. At the base it is fused with the precoxale pr and is closely affixed to the base of the pronotum pn.

The epimeron em₁ is a narrow curved sclerite at the base of which there is a tapering prolongation toward the spiracle sp. The episternum es₁ and epimeron em₁ are separated externally by the pleural suture and a narrow fold projects inwardly to form the endopleuron or lateral apodeme. This serves for the attachment of muscles and one-third of its length from the base an apophysis apop is attached which extends to it from the furcasternum fs.

The trochantin tr is a narrow sclerite between the base of the coxa cx and the precoxale pr.

Prosternum: The presternum has entirely disappeared in Ceuthophilus. The basisternum bs is fused with the precoxale pr

and is present as a narrow transverse sclerite. The furcasternum fs is shaped like the basisternum and, as shown in fig.13, bears the apophyses apop which extend internally to the endopleuron already mentioned. The spinasternum ss is represented externally only by a small crescent-shaped sclerite in the midst of membrane. Internally, a small four-armed spina of the spinasternum is present, the anterior arms of which are each weakly forked again.

It is difficult to make a phylogenetic evaluation of the propleural and prosternal sclerites of Ceuthophilus upon a basis of present information. The chief available papers are those of Crampton (1926b), Duporte (1919), and Voss (1905). Grylloblatta, Gryllus, Periplaneta, and other forms have been figured, but in some cases the sclerites hidden by the overlapping pronotum have not been shown. A study of several Tettigoniid genera would be very helpful.

The roach represents a rather complex condition as compared to Ceuthophilus. The existence of both precoxale and antecoxale, the division of the trochantin, the frequent division of the precoxale and its separation from the basisternum, and the large size and frequent union of the sternal elements are characteristic of roaches.

A condition contrasted to that of the roach is found in the grasshopper Dissosteira (see Crampton, 1918c; Duporte, 1919). The episternum and epimeron are reduced to narrow, tapering sclerites. A basal spur of the epimeron extends posteriorly as in Ceuthophilus. The pleural suture is vertical. The elements of the prosternum are united to form a triangular sclerite connected laterally to the episternum.

The condition exhibited in Ceuthophilus is intermediate between these two extremes, but distinctly nearer Dissosteira. Grylloblatta is both roach-like and grasshopper-like in these respects. The condition of the prosternum of Gryllus, Gryllotalpa and Tridactylus indicates a transition to the grasshopper-like condition from a condition much like that of Ceuthophilus.

Leg: The outline and proportions of the fore leg are shown in fig.10. The coxa articulates with the base of the pleuron and the chief muscles concerned in allied species are discussed by Duporte (1919). The coxa cx is somewhat elongate and is grooved to receive the conical trochanter tch which articulates with it. Fig.26 shows the mesal surface of the coxa cx and the tendons ten which pull the trochanter tch.

The femur fe is firmly joined to the trochanter tch and little movement is possible. The femur is grooved beneath and unarmed except for a single small spur near the apex on the inner side of the groove.

The tibia ti is cylindrical and of uniform diameter. It is armed with a pair of small apical spurs dorsally and four pairs of similar spurs ventrally.

The four-segmented tarsus ta is loosely articulated and in lateral view appears as in fig.10. The first, which may result from the fusion of two segments, and fourth segments are longest. The ventral surfaces of the tarsal segments are membranous and slightly dilated to form a pad-like or pulvilli-form condition.

Fig. 11 shows the chief structures important to the articulation of the claws or unguis. The unguis ung is curved,

slender and unarmed. It articulates with the dorsal apical margin of the distitarsus ta₄ and is moved by the action of the tendon ten which pulls the retractile plate rp. There is no arolium. These structures compose the pretarsus of de Meijere (1901,p.423) and are similar on the other two legs. The pretarsi of several Orthoptera, including Ceuthophilus, have been figured and discussed by Holway (1935).

The legs are variable in Orthoptera on account of different living habits and so are difficult to interpret from an evolutionary standpoint. However, the very large bilobed pads of the Japanese Galloisiana (see Caudell and King,1924) and the distinctly bilobed pads on the third tarsal segment of Scudderia and allied genera may have some relation to the slightly dilated condition in Ceuthophilus. In general, the fore leg of Ceuthophilus is much like that of Grylloblatta. The number of tarsal segments does not seem to be important since in the Raphidophorine Daihinia the tarsi do not all have the same number of segments (see Caudell,1916,p.685).

Mesothorax

Mesonotum: The mesonotum mnn of Ceuthophilus is narrower and slightly deeper than the pronotum pn but does not otherwise differ materially from it. The complete absence of tegmina and wings accounts for the chief differences between meso- and metanotum of Ceuthophilus and those of most Saltatoria. Grylloblatta does not show so much growth of the notum ventrally and neither does Stenopelmatus, but the nymph of Melanoplus (see Snodgrass,1909,fig.55) is very like Ceuthophilus, showing

that characteristics of Ceuthophilus persist in the ontogeny of much more highly evolved species.

Mesopleuron: A large part of the episternum es₂ is exposed below the over-hanging mesonotum mnn. This sclerite is roughly triangular, is curved anteriorly, and has a prominent prolongation in the direction of the atrophied precoxale. There is a lengthwise suture as shown in fig.13.

The epimeron em₂ is largely concealed, but occurs as a narrow, curved sclerite beside the episternum. The cephalad portion extends beyond the endopleural suture as the endopleuron and is long and curved at the base. A smaller external hook is present at the caudal-ventral extremity.

The trochantin tr is a narrow crescent-shaped sclerite.

Mesosternum: The basisternum bs and furcasternum fs form a single broad transverse plate. The furcal pits mark the position of the internal furcae fur each arm of which is unequally bifurcate while a median spina extends posteriorly and has two curved "horns" on either side. The spinasternum ss is a narrow sclerite which is not connected to the furcasternum.

As in the case of the prothorax, the pleuron and sternum of the mesothorax are considerably different from those of a roach. The pleural suture of Grylloblatta (Crampton,1915) is slightly more horizontal than in the case of Ceuthophilus and the laterosternite is probably fused to the episternum in the case of the latter. In respect to the propleuron Gryllus (Duporte,1919,fig.13) is much like Ceuthophilus, but the prothoracic epimeron is wider. Among the higher Tettigoniids the presence of wings brings about a change of shape and a

specialization for articulation of wing ossicles. As Snodgrass (1909, pp. 537, 557, figs. 43, 55, 56, 57, 70, 71) has brought out, the short-winged Decticine Anabrus has essentially the same form of pleuron as in adult Acrididae although nymphal Acrididae are not yet specialized for flight and so show a more primitive condition. A pleural ridge in the episternum of Ceuthophilus persists in Acridids.

The broad united furca- and basisternum fs bs of Ceuthophilus is intermediate between the very broad condition of Dissosteira and the broadly lobed condition of Grylloblatta. The furca-sternum and basisternum of the roach are more separated than in Ceuthophilus and so in respect to the mesosternum Ceuthophilus occupies a position near Grylloblatta and annectent to Acridids.

Leg: The coxa cx is shaped as shown in fig. 16 and is grooved above. The trochantin tr is an important articulatory sclerite. A mesal view of the coxa cx and trochanter tch is shown in fig. 22. The trochanter is freely jointed with the coxa but the joint with the femur fe is only slightly moveable. The latter is grooved beneath and armed with two small spurs, one apical spur on the mesal surface and the other externally on the ventral margin near the apex. The tibia ti is slender, cylindrical, curved at the base, armed with three small dorsal spurs in an irregular line, three pairs of ventral spurs and two pairs of apical spurs of which the ventral pair is the longer. The four-segmented tarsus ta with ungues ung does not differ materially from the prothoracic tarsus.

Metathorax

Metanotum: The metanotum mtn is attached to the mesonotum mn by a fold of membrane and in life the anterior margin lies below the posterior border of the latter. The metanotum is longer and not so deep as the mesonotum.

Metapleuron: The episternum es₃ is roughly triangular in shape and a pleural ridge extends from the base nearly the entire length. It is very much like the mesepisternum es₂ except that the prolongation corresponding to the laterosternite of allied species is lacking.

The epimeron em₃ is likewise similar to the mesepimeron em₂ but the endopleural apodeme at the base is not so long as in the latter.

The trochanter tr is narrow and curved.

Metasternum: The basisternum bs and furcasternum fs form a semi-quadrate sclerite which is deeply cleft anteriorly. The furcae fur are curved arms which are tri-furcate.

As Snodgrass (1909,p.556) has stated, "Meso- and metapleura closely resemble each other" in Orthoptera. In general, the pleural sclerites of both segments show the same tendencies and a comparison of figures in the references cited leads to almost identical conclusions.

Leg: The posterior leg is shown in fig.14. The coxa cx is marked by a longitudinal scar externally. Mesally (fig.21) the coxa is divided by a median line into an anterior and posterior area. The trochanter tch is largely concealed as seen from an external aspect and the relationships are better shown in figs. 21 and 15. The trochanter is composed of a wide basal rim and

the trochanter proper. The articulatory process X is connected with the coxa and the tendon ten moves the trochanter. The trochanter fits over a small neck-like process of the femur fe and the femur and trochanter move as a unit just as in the non-jumping legs.

The femur fe is greatly enlarged basally to accommodate the huge muscles which move the tibia ti. The femur is deeply sulcate beneath and both lower margins bear small spines. The apex of the femur is modified to receive the base of the tibia ti which is shown in fig.18. The articulatory processes X,X and the two tendons ten, the lower of which flexes the leg while the upper one performs the action of leaping, illustrate the manner in which simple mechanical processes are utilized by these insects. Blatchley (1920,p.20) states that the ventral apical lobes of the femur prevent the tibia from wobbling in leaping.

The tibia ti is slender and sulcate above. The margins of the groove are lined with small spines and there are five pairs of spurs which are slightly staggered. The three pairs of apical spurs are figured. The number of ventral spurs is variable. Usually there is one very small spur near the apex, but in some cases there is an additional pair nearby. The two hind tibiae of the same individual may differ in this respect. Fig.12 shows a section of tibia with a spur spu removed to give a view of the spur calyx spu c in which it is set.

The four-segmented tarsus ta is very like that of the other body segments.

The form of the hind femora and tarsi is very variable in the genus Ceuthophilus and allied genera. Caudell (1916) has figured some of the forms important to classification.

Abdomen

The anatomy of the abdomen of Ceuthophilus is reasonably familiar to students of comparative morphology, due largely to the researches of Chopard, Crampton, and Walker in the papers listed. The terminal segments of each sex exhibit interesting features from the standpoint of a comparative study and will be discussed separately.

Abdominal segments: The abdomen of Ceuthophilus is sub-cylindrical in general appearance. Crampton (1933) has pointed out that in this respect Grylloblatta (which is much like Ceuthophilus) is more closely allied to primitive saltatorial Orthoptera than to roaches in which the abdomen is strongly flattened. Staining is necessary to show the exact extent of the sclerites. As shown in fig.19, the tergites t₁₋₁₀ are separated by pleural membrane from the sternites s₁₋₉. A similar condition occurs in the Grylloblattids, Stenopelmatus, Camptonotus and, as far as the writer knows, among all higher Tettigoniids also. The tergites of Gecanthus, too, grade into pleural membrane, but Gryllus domesticus L. shows well-defined sclerites and a distinct area of membrane. In Gryllotalpa the membrane is somewhat folded and Tridactylus shows a condition in which the sternites and membrane overlap the tergites. In the Acrididae, however, the opposite condition, in which the tergites have grown over the lateral margins of the sternites, is found.

Under a compound microscope the pleural membrane of Ceuthophilus shows many small spines, most of which bear a seta at the base, and some occur on the tergites. It is interesting to note that these and the dorsal spines of Pristoceuthophilus tuberculatus, described by Caudell (1916, fig.15), may be homologous with those of Galloisiana mentioned by Caudell and King (1924,p.54).

Spiracles: The abdominal spiracles of Ceuthophilus are eight pairs in number and are located as shown in figs. 13 and 19. The seven posterior abdominal spiracles are somewhat smaller than those of the thorax and first abdominal segment. Each spiracular opening is guarded by two small elongate sclerites. The structures of the spiracles have not been examined in detail here, but are described in the work of Vinal (1919) on Dissosteira.

The location of the spiracles of Ceuthophilus seems to be a primitive condition among Saltatoria. In all local Acrididae except the Acrydiinae the abdominal spiracles are borne by the margins of the tergites. As an example of the grouse-locusts, Acrydium has only the eighth spiracle present on the tergite. In Gryllus, Gryllotalpa, and Oecanthus, as in the Tettigoniids, all occur in the membrane, but in Ripipteryx, from Central and South America, the eighth is borne by the tergite and thus the latter and Acrydium are intermediate between the Tettigoniids and higher Acrididae.

Among the Dictyoptera the spiracles of roaches (see Crampton,1925) are borne by small sclerites known as subtergites or pleurites, while Stagmomantis has the spiracles on the tergites.

The exact lines of evolution represented by the different positions of the spiracles are not well understood, but probably the subtergites are portions of the tergites. The subtergites are lost in the Tettigoniids, but in the Acrididae the tergites extend laterally and surround the spiracles.

Terminal Structures of Male

Tergites: The tergites slowly decrease in length toward the apex of the abdomen, but ~~the~~ ninth t_9 is the first to be decidedly smaller than those anterior to it. The dorsal margin of the eighth tergite t_8 shows a variety of specific variations within the genus and is utilized by systematists on this account. In C. brevipes Sc. this margin is smoothly convex and scarcely rises above the level of the other tergites, but in other species it is emarginate, raised in the form of a crescent, or may be distinctly truncate. The ninth tergite t_9 is slightly shorter dorsally than at the lateral extremities. It is sometimes practically concealed by the eighth tergite, depending upon the degree of extension of the inter-tergal membrane. The tenth tergite t_{10} is a very narrow sclerite which is frequently hidden by the ninth.

Sternites: The ninth sternite s_9 differs from the other ventral sclerites in being modified as the subgenital plate. As shown in fig. 19, it is partially divided near the base. An important feature of the subgenital plate is the apical membrane, which is in the form of curved "horns" m s_9 , and which is used as a specific character in systematic work. The beginning student

should not confuse these "horns" with the membranous, horn-like arms of the penis which are called parameres.

In the primitive Grylloblatta the ninth sternite bears a pair of coxites and the latter in turn styli. It may be that the posterior portion of the ninth sternite of Ceuthophilus represents the coxite and that the membranous "horns" are degenerate styli. According to Blatchley (1920,p.602), the subgenital plate of the Gryllacrinae is deeply notched transversely and bears short obtuse styli. Karny (1934) has discussed and figured styli in both sexes of very small nymphs of Rhaphidophora sp. from eastern Asia. In higher Tettigoniids, such as Neoconocephalus and Scudderia, a transverse division of the sternite is not as apparent but styli are present. Gryllids bear no styli. Walker (1922,fig.58) has interpreted the structures of Tettigidea to include coxites and in higher Acrididae they are represented by the apex of the subgenital plate. With respect to the ninth sternite, therefore, Ceuthophilus shows a primitive condition.

Cercus: The cercus ce of the adult is slender, tapers to a fine point, and is non-segmented. As shown in fig.23, the apical portion has small irregular areas of heavier sclerotization which suggest segmentation but actual segments are not demarked. The cercus of the first instar nymph appears as in fig.20. Although difficult to see, three small segments are present. The basipodite or basicercus bas at the base of the cercus is shown in fig.25. In some specimens the two sclerites are imperfectly divided.

The cylindrical eight-segmented cerci of Grylloblatta and the nine-segmented appendages of Galloisiana are more like Plecoptera than the sub-triangular cerci of roaches. As noted above, the cerci of Ceuthophilus show affinities with a multi-articulate adult condition, and in Pristoceuthophilus cercalis (see Caudell, 1916, fig. 17) five small segments are present. Diestrammena and most Gryllids (the cerci of Tridactylus are two-segmented) possess very long, tapering, non-segmented cerci, but those of Stenopelmatus are slightly stouter and shorter than Ceuthophilus and may point toward the short, broad types of most higher Tettigoniids. A comparison of Ceuthophilus nodulosus (see Caudell, 1916, fig. 10) with Amblycorypha or Scudderia, and Pristoceuthophilus celatus (l.c., fig. 13) with Conocephalus shows two types of cerci in the more advanced subfamilies of Tettigoniidae which apparently are presaged in the more primitive Rhaphidophorinae. The broad, often blunt cerci of Acrididae are well known as their modifications, especially in Melanoplus, are used in classification.

Supra-anal plate: The supra-anal plate sa is a sub-triangular flap, the apex of which extends above the anus. It is most heavily sclerotized at the margins and about a central depression. Hubbell (1934, p. 223) refers to a basal portion, the epiproct, and a smaller deflexed distal portion, the suranale. While these terms are in accepted systematic use, the term epiproct in a strict morphological sense applies to the tenth tergite, as it was so used by Crampton (1929, 1933, p. 151).

The supra-anal plate is characteristic of nearly all Saltatoria, though absent in roaches and mantids, and frequently

is absent in Plecoptera. Hebard (1916, figs. 14-16) has figured a small chitinous hook on each side of the supra-anal plate of the adult male Stenopelmatus. In many Gryllids and higher Tettigoniids the supra-anal plate is fused with the tenth tergite and in some Gryllids the line of fusion may be seen. The transverse line of demarcation is conspicuous in many Acrididae, especially in nymphs as Walker (1922, p. 21) has stated. The paired arms, furculae, of Melanoplus are borne by the tenth tergite.

Paraprocts: The paraprocts pa (figs. 25 and 27) are narrow sclerites which give support to the membrane ventrad of the supra-anal plate and between the cerci. They are variously known as laminae subanales and podical and parapodial plates. The drawings are made from stained potash preparations, but in the natural state each paraproct appears as a roughly triangular area. The paraprocts of Grylloblatta are similarly weakly sclerotized and though stronger in other Tettigoniids and crickets they are seldom conspicuous as in Ripteryx and Tridactylus. In Acrididae they have undergone no great change of form except that heavier sclerotization has brought about broad flat plates.

Pseudosternite: The pseudosternite pst is a heavily sclerotized hood-like structure just anterior to the penis. It is supported laterally by rami ra and by endopophyses which extend inward from the arch ar which covers the ejaculatory duct leading to the penis. The postcornua or dorsal lobes pc are folds of the lower margin laterad of the arch. The roof of

the pseudosternite is nearly flat in C. brevipes Sc., but is sharply gable-like in certain species; the arch, postcornua and rami are also subject to specific variation.

Walker (1922, pp. 24-28) has pointed out that, unlike the Rhaphidophorinae, the higher subfamilies of Tettigoniidae do not possess a well developed pseudosternite. Neither is it present in roaches and Grylloblatta, but it is prominent in most crickets and in Gryllus resembles that of Ceuthophilus which suggests that the crickets may have evolved from the lower groups of Tettigoniids. The pseudosternite of the Gryllids, especially in the case of Oecanthus (see Walker, l.c., fig. 46), shows a tendency to be nearer the penis than in Ceuthophilus and this also holds true in Acrydium. The pseudosternite of higher Acridids is well developed, resembles that of Ceuthophilus, and is valuable in systematic work.

Penis: The penis of Ceuthophilus is largely membranous, although the ventral lobe lop is strengthened and spinulose. The parameres pm, which are latero-anterior arms, and the lightly sclerotized area between them frequently are invaginated while in a resting condition and so are examined with difficulty. The ventral lobe is also partly invaginated at times and Walker (1922, pp. 24-28) has discussed the formation of a "spermatophore sac" preparatory to the extrusion of the spermatophore and its attachment to the female.

In order to appreciate the critical features of the female genitalia one must know something of the functions performed. Turner (1916) has outlined in general the breeding habits of the different families of Orthoptera and the question as to whether

the sexual products are inclosed in a spermatophore is readily seen to be important. The latter says that spermatozoa are transferred directly in Acrididae, and so the strong pointed structures described in detail by Walker (l.c.) and Hubbell (1932) are apparently useful. Fulton (1931, pp. 227-231, figs. 4 and 5) has described the structure of the spermatophore in Nemobius and Henneguy (1904, pp. 267-268, figs. 272 and 273) has discussed the spermatophores of various groups and has given figures in the case of Gryllus. The parameres are heavily sclerotized in many higher Tettigoniids and may point toward the condition in Acrididae; the long endapophyses of Ceuthophilus also seem to persist in the more advanced forms.

Terminal Structures of Female

General features: The eighth, ninth and tenth tergites t8-10 (fig. 24) differ rather markedly in shape from the respective sclerites of the male. The eighth sternite s8, which serves as a shield at the base of the lower valves vv, shows modifications in the direction of the egg guides of Acrididae. The cercus, paraprocts and supra-anal plate are similar in both sexes. The important structures are those relating to the ovipositor and since they have been carefully described and figured by Crampton (1929) and Walker (1919b) in papers that are readily accessible, only the main features will be mentioned here.

The genital aperture opens between the eighth and ninth

sterna into the inner valves iv which are completely inclosed by the larger dorsal valves dv and ventral valves vv.

Ventral valves: At the base of each ventral valve vv is the basivalvula bsv which is partly concealed by the eighth sternite s₈. A small triangular sclerite representing a part of the ninth sternum, the valvifer vf, serves as a point of attachment for both ventral and dorsal valves. Each ventral valve has a decided inner fold along the ventral margin and a narrow fold along the upper margin. The four apical teeth appear as figured. The ventral valve is attached at the base to the basivalvula and by a slim ramus to the valvifer vf.

Dorsal valves: The dorsal valves are equal in length to the ventral valves and when the valves are closed overlap the upper margins of the latter. Near the inner ventral margin of the dorsal valve is a distinct sclerotized projection which may be called the inner hook ih. The superior apophysis sap is a sub-triangular sclerite firmly attached to the base of the valve dv and the anterior point extends within the distal tergites as a point of attachment for tendons.

Inner valves: The inner valves iv are about two-thirds the length of the other valves and are held within the dorsal valves by the inner hooks ih. There are folds near the ventral margins of the inner valves and dorsally the two valves are joined as shown by Walker (1919b, fig. 3). The ramus rm is a short bar at the base of each inner valve which extends within the body as a point of attachment.

Fig.17 shows a ventral view of the developing ovipositor of a small female nymph. The left ventral valve, belonging to the eighth sternite s₈, is cut away to better show the dorsal and inner valves developing from the ninth sternite. Practically a parallel condition prevails in Stenopelmatus and has been figured by Walker (1919b,1919a) in Conocephalus and Grylloblatta. In the first of the two papers cited the latter author has presented a splendid series of figures and a thorough discussion of the types of ovipositors exhibited by the several Orthopteroid families. The advanced form shown by higher Tettigoniids has been discussed; also the differences exhibited by crickets and the way Ripipteryx and Acrydiinae are primitive to higher Acrididae.

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Abbreviations

af	antennifer	em	epimeron
an	antennale	ep	epignath or extensor prominence
apop	apophysis	eot	euoccipital tendon
ar	arch of pseudosternite	es	episternum
b	basimaxillary membrane	et	extensor tendon
bas	basipodite	eu	eutentorium or body of tentorium
bc	basicardo	f	frons
bg	basigalea	fe	femur
bl	basilingua	fp	frontal pits or clefts
bm	basimandibulare	fs	furcasternum
bmm	basimandibular membrane	ft	flexor tendon
bs	basisternum	fur	furca
bsv	basivalvula	g	galea
c	clypeus	ga	gnathapex
cds	cardosuture	ge	gena
ce	cercus	gg	glossiger (Basiglossa)
cp	cardoprocess	gi	ginglymus
cs	coronal suture	gl	glossa
ctn	cardotendon	gn	gnathite
cx	coxa	gp	gular pits
d	articulatory process of basicardo	gu	gula
dc	disticardo	h	gnathocondyle or hypocondyle
dl	distilingua	hp	hypopharynx
dv	dorsal valve	ih	inner hook of dorsal valve
e	compound eye	im	intervalvular membrane
ec	endocardo	iv	inner valve

l	lacinia	pgs	postgenal suture
la	labrum	pl	postlingua or "linguatendon"
lc	laterocervicale	pm	paramere
li	labial stipites	pn	pronotum
ll	lingualora	po	pons valvularum
lop	ventral lobe of penis	poc	parocciput or posterior arms
lp	labial palpus	poe	postepipharynx
m	mola	pp	postgenal process
md	mandible	ppd	postpedicel
mn	mentum	ppg	palpiger
mnn	mesonotum	pr	precoxale
mp	maxillary palpus	prc	precervicale
m s ₉	membranous "horns" of 9th sternite	pre	pre-epipharynx
mtn	metanotum	ps	parastipes
nf	neuroforamen or neural incision	pst	pseudosternite
occ	occipital condyle	psto	parastomium
p	tentorial arch or trabecula	pt	pretentorium
pa	paraproct	ra	ramus of pseudosternite
par	parietal	rm	rami of inner valvulae
pat	paroccipital process	rp	retractile plate
pc	postcornua or dorsal lobes of pseudosternite	s	stipes
pd	pedicel	s ₁	sternites of abdomen
pf	palpifer	sa	supra-anal plate
pg	paraglossa	sap	superior apophysis
pga	postgenal acetabulum	sb	short brachymeres of antenna
pge	postgena	sc	scape

sd	slender dolichomeres of antenna
sl	dorsolingua
sm	submentum
sp	spiracle
spn	spine
spu	spur
spu c	spur calyx
ss	spinasternum
st	supratentorium
t ₁	tergites of abdomen
ta	tarsus
tch	trochanter
te	temples
ten	tendon
ti	tibia
tr	trochantin of coxa
ung	ungues or claws
vf	valvifer
vv	ventral valve
X,X,	fulcral points

Plate I

- Fig.1 Anterior view of tentorium and neighboring parts
- Fig.2 Antenna
- Fig.3 Frontal view of head
- Fig.4 Anterior view of glossae and paraglossae
- Fig.5 Posterior view of back of head
- Fig.6 Inner surface of cardo and stipes
- Fig.7 Posterior view of dextral mandible
- Fig.8 Anterior view of hypopharynx
- Fig.9 Lateral view of hypopharynx and upper and lower lip,
with most of head capsule removed

Plate II

- Fig.10 Lateral view of fore leg
- Fig.11 Ventral view of pretarsus of fore leg
- Fig.12 Section of tibia of rear leg
- Fig.13 Lateral view of thoracic sclerites
- Fig.14 Lateral view of rear leg
- Fig.15 Mesal aspect of rear trochanter
- Fig.16 Lateral view of mesothoracic leg
- Fig.17 Ventral view of terminal abdominal segments of small
nymphal female

Plate III

- Fig.18 Lateral view of base of rear tibia
- Fig.19 Lateral view of abdomen of male
- Fig.20 Apex of cercus of small nymph
- Fig.21 Mesal aspect of base of rear leg
- Fig.22 Mesal aspect of base of mesothoracic leg
- Fig.23 Apex of cercus of adult
- Fig.24 Lateral view of terminal abdominal segments of
adult female
- Fig.25 Latero-posterior view of region about base of cercus
in adult male
- Fig.26 Mesal aspect of base of fore leg
- Fig.27 Dorso-posterior view of terminal abdominal structures
of adult male

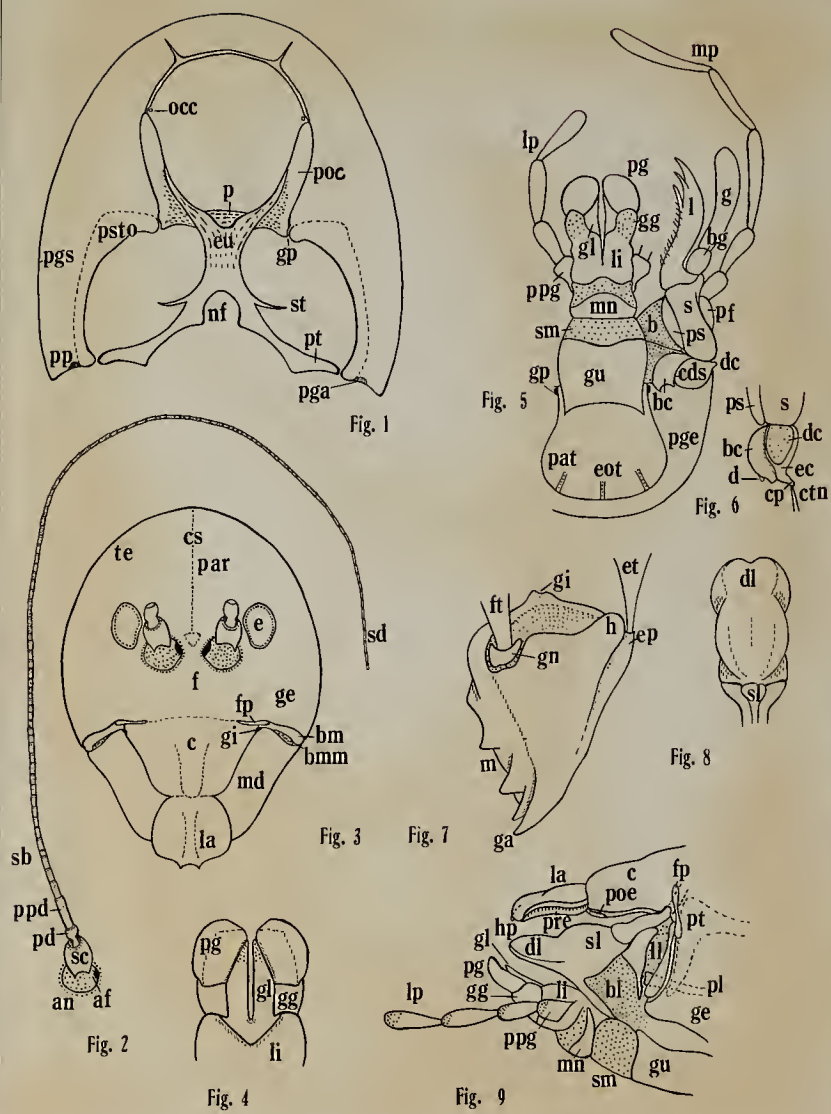


Plate I

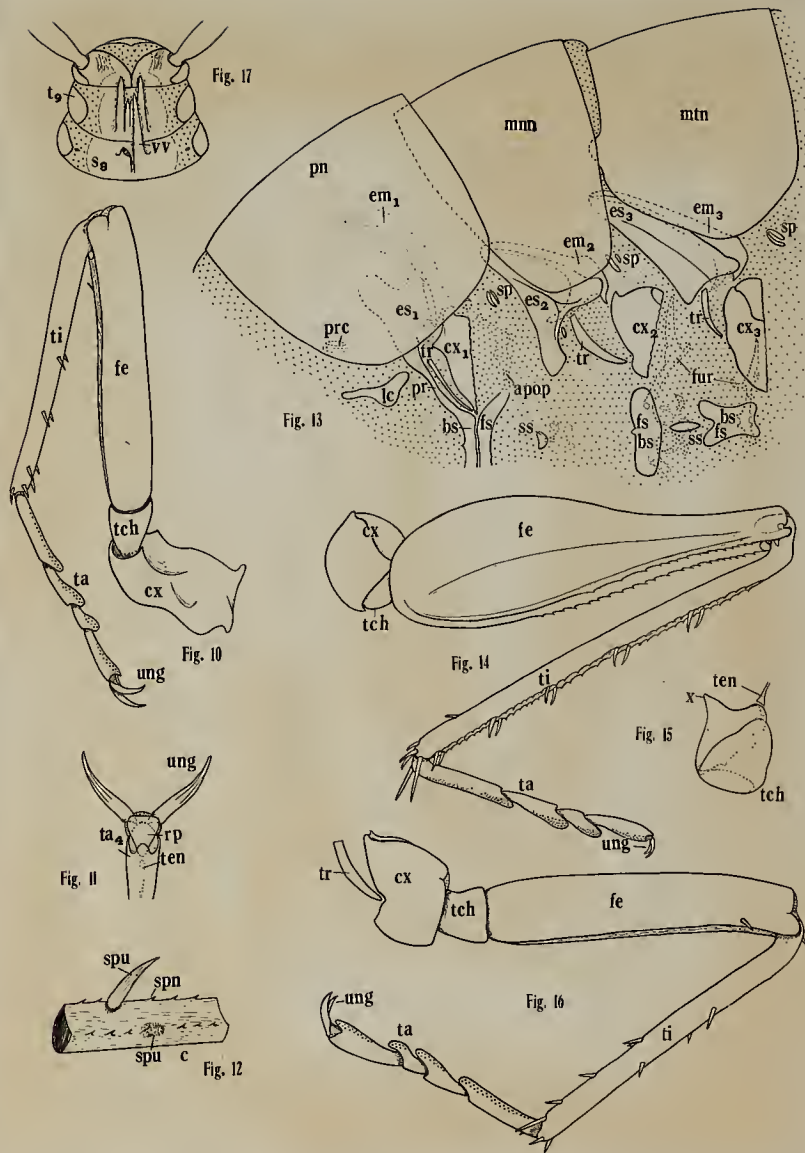


Plate II

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