Morphology, Evolution and a Classification of the Gerridae (Hemiptera-Heteroptera) *

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ABSTRACT: This work is a study of the morphology, evolution and classification of the Gerridae of the World. Fifty genera and sixteen subgenera out of fifty-three genera and sixteen subgenera known were examined.

In the section on morphology it is attempted to establish homologies and a terminology for as many external structures as possible. In the section on the structural evolution the process of evolutionary change of each structure is traced, and its taxonomic significance is discussed. The postembryonic development of the antennal and leg segments has been studied in representative species of each major group to see how the different proportional lengths of antennal and leg segments are realized ontogenetically; how the ontogenetic growth patterns for these segments have been carried over to adult phylogeny; and how the growth patterns themselves have evolved. It was found that (1) the antennal and leg segments show roughly a simple allometric growth, with either an appreciable increase or decrease in growth ratio at the final stage of development; (2) often lengths of the leg and antennal segments of adults in a great majority of species within a genus fall roughly on the growth lines for the corresponding segments in a representative species of the same genus, indicating that species within a genus share very similar growth patterns for corresponding segments; (3) a hypothetically primitive growth ratio for the antennal segments \((k = 1.142)\) is suggested; (4) a process of development of the proximo-distal gradient in growth ratios for the antennal segments in the phylogeny of the Gerridae is traced; (5) for certain segments, such as the hind tibia, there is evidence in many genera that the growth patterns vary among species of a genus, thus forming the secondary phylogenetic allomorphic lines; (6) as a result of the formation of the secondary allomorphic slope for the hind tibia, which is always steeper than that for the hind femur, the tibia is shorter in relation to the femur in the smaller species of a given genus, and this tendency occurs in most major groups of the Gerridae; (7) since there is a striking tendency toward smaller body size in the structurally more specialized forms at all taxonomic levels, and the congeneric species often appear to have

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very similar allometric growth patterns for corresponding antennal and leg segments, the lengths of antennal and leg segments in the early postembryonic developmental stages in larger and primitive species roughly approximate the lengths of the same in adults of related but phylogenetically more advanced forms. In the light of the knowledge gained from the study of evolution of the leg and antennal segments, the taxonomic status of all groups of the Gerridae (subfamilies, tribes, genera and subgenera) is evaluated.

The arrangement of genera in the proposed new classification of the Gerridae follows. Trepobatinae is described as a new subfamily and Hermatobatinae is excluded from the Gerridae.

(1) Gerrinae.

Gerrini, including Gerris (Gerris s. str., Aquarius, Limnogonus), Gerriselloides, Gerrisella, Gigantometra, Tenagogerris, Eurygerris, Limnogonus (Limnogonus s. str., Limnogonellus), Tachygerris, Tenagogonus (Tenagogonus s. str., Limnometra, Tenagometra), Tenagometrella.

Cylindrostethini, including Cylindrostethus, Potamobates, Platygerris.

Charmatometrini, including Charmatometra, Brachymetra, Eobates.

Eotrechini, including Eotrechus, Onychotrechus, Chimarrhometra, Amemboa, Rheumatotrechus(?)

(2) Ptilomerinae, including Ptilomera (Ptilomera s. str., Proptilomera), Potamometra, Rhyacobates, Heterobates, Potamometroides, Potamometropsis, Rheumatogonus, Pleciobates.

(3) Halobatinae.

Halobatini, including Asclepios, Halobates.

Metrocorini, including Metrocoris, Eurymetra, Eurymetropsiella, Eurymetropsielloides, Eurymetropsis, Ventidius (Ventidius s. str., Ventidioides), Esakia.

(4) Rhagadotarsinae, including Rhagadotarsus (Rhagadotarsus s. str., Carpivia), Rheumatobates (Rheumatobates s. str., Hynesia).

(5) Trepobatinae, including Trepobates, Telmatometra, Trepobatoides, Halobatopsis, Ovatometra, Rheumatometroides, Stenobates, Cryptobates, Naboaundelus, Hynesionella, Metrobates, Rheumatometra, Metrobatopsis.
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INTRODUCTION

The objective of this work is to elucidate the structural evolution of the Gerridae of the World on a morphological basis, and to establish a new classification of the higher categories of this group of insects.

To attain these objectives the external morphology of some representative species of the Gerridae was studied with frequent comparison with other Hemiptera and other major groups of insects in order to establish homologies and a terminology of structures.

Having established the homologies and terminology of structures, the next step was to compare series of forms so as to trace the evolutionary changes of as many structures as possible. For certain structures, such as the antennae and legs, postembryonic development, in representative species of major groups, was studied to see how the different proportional lengths of the leg and antennal segments are realized ontogenetically, and how the ontogenetic growth patterns of these structures have been carried over to adult phylogeny, and how the growth patterns themselves have evolved.

In tracing the evolutionary changes of structures the following morphological principles were borne in mind: (1) that evolution has been continuous, each change being based upon stages that have gone before; (2) that evolutionary changes are to be accounted for by modification of pre-existed structures, by fusion of pre-existed structures, or by loss of pre-existed structures; (3) that evolution has not been merely endless change involving all structures of the body. There are structures which have remained relatively stable while others have changed. It is these stable structures which constitute the bases upon which we can depend for the tracing of continuity.

To decide which of the alternative characters is more primitive or specialized is a matter of probability in morphology, since pale-ontological data either to prove or disprove the morphological interpretations are often lacking or inadequate. This is especially true of the group of insects such as the Gerridae treated in this work. Therefore, the decisions that have been made in regard to which of two or more alternatives is more primitive or specialized can, by their very nature, not be final. The reliability of interpretations based on morphology, however, increases with increase of material with which to make comparison. Entomologists are in an almost ideal position in this respect, since the diversity of forms in insects is unparalleled in the animal kingdom, as stressed by the late Professor G. F. Ferris (1948).
In the third part of this work a new classification of higher
categories of the Gerridae has been attempted with discussion of
the phylogeny of the group thus defined. In discussing phylogeny
of groups all significant characters were tabulated at the end of
the description of each major group to show the over-all degree
of primitiveness or specialization of each group or tribe, and to
determine the number of characters each genus or tribe has in
common with others. The characters selected, however, include
those apparently resulting from parallelism. It was found that
tabulation often prevents the errors that would result from more
subjective judgments based on fewer, often prejudiced characters.
The subfamilial, tribal and generic descriptions have been made
quite full and include discussions of evolutionary changes of struc-
tures at the specific level, whenever enough species were available
to allow observations on structural modifications. In describing
subfamilies, tribes, and genera all characters are described in a
parallel fashion in so far as possible. For three genera, however,
no specimens were available for study, and in these cases the origi-
inal descriptions have merely been repeated. Also any characters
peculiar to a given group (genus, tribe, subfamily) are italicized,
and these characters are excluded from the descriptions of the
other groups.

In table 16, 82 units are equal to 10 mm. For those values with
asterisks, 173.7 units are equal to 10 mm.; the figures under each
leg correspond to the femur, tibia, and the first and second tarsal
segments. The measurements of the third and fourth rostral seg-
ments were made as indicated by broken lines in figure 65. The
relative lengths of leg and antennal segments given as characters
125, 126, 127, 128, 129 are based on the data for both sexes. In
the tables of characters for major groups (+) indicates a primiti-
tive alternative; (−) a specialized; (±) an intermediate condition
between the primitive and specialized alternatives, and (±)\(^\times\) is
the condition in which the primitive or specialized alternative is
shared only by certain species or genera within a given group.

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EXTERNAL MORPHOLOGY

Gerris remigis Say was selected as the standard gerrid for the study of morphology of the external structures of the Gerridae because of its relative abundance, convenient size for dissection and relative primitiveness in structure. Other species were also studied to facilitate the interpretation of structures in this family. Unless otherwise stated the structures below are those of Gerris remigis Say.

The head
(Figs. 65-71)

The head is directed forward apically. The four segmented antennae are also directed anteriorly; the third and fourth segments are always pedunculated at bases in all species of Gerridae except for the fourth segment in Rhagadotarsinae. The rostrum is four segmented, is placed on the ventral surface of the head when at rest; the first segment is thick, about as long as wide; the second is shortest in all species of Gerridae; the third is longest also in all species of Gerridae, with a small apical lobe superposed on the dorsal basal region of the fourth segment; the lobe is clearly defined by the weak membranous region basally, which can be seen upon treatment with KOH. The fourth segment is always black in all species of Gerridae. The rostrum or beak is generally conceived to be labial in origin, the basal two segments corresponding to the postmentum and prementum and the apical two segments being represented by the paraglossa and the ligula in generalized insects.
The labrum is short, subtriangular, apically inserted into the dorsal basal region of the first rostral segment, basally well defined from the apical margin of the clypeus. The epipharynx arises from the clypeal region, is basally continuous with the food pump, apically inserted beneath the labrum into the second rostral segment. This prolonged epipharynx is said to be characteristic of Gerridae, Hydrometridae, and Veliidae (Servadei 1946).

The mandibular plate is externally separated from the maxillary plate by the transverse suture, which ventrally reaches inside the antennal cavity. The basal margin of the mandibular plate bears internally the elongate, subtriangular lever, which is in turn connected with the mandibular stylet; the mandibular stylet (seta) at its base is rectangularly curved behind the basal margin of the lever for the attachment of the muscle (fig. 70).

The maxillary plate lacks the maxillary lever; the maxillary stylet (fig. 71) is basally ensheathed by the setal pouch, which extends beyond the middle of mesothorax (foh. in the figures by Ekblom, 1926). This stylet is supported by the tendenous rod arising from the lateral angle of the foramen magnum. Ekblom (1926) regarded this rod as the tentorium (posterior tentorium). He recognized this enormously prolonged maxillary stylet and the rod (tentorium of Ekblom) in Gerris asper and Velia currens. A similar condition is also known in Trepidotylus of Plataspidae (Poisson 1951). The anterior tentorium is absent.

The salivary syringe is well sclerotized posteriorly, with a piston arising from the posterior end. The food pump is ventrally supported by a single, well-sclerotized, long plate. This is probably homologous to the hypopharyngeal wing in some groups of Heteroptera and Homoptera.

The clypeus is basally well defined. The eyes are indented and the ocelli are absent. The antenniferous tubercles are located far in front of the compound eyes. The two anterior pairs of trichobothria are located anterior to the eyes, and the basal pair is located near the basal angles of the compound eyes.

The thorax

The thorax of the Gerridae was studied by Taylor in Gerris sp. (1918), and by Larsén (1945) in Gerris rufoscutellatus Latreille. Matsuda (1957) studied the pterothoracic sutures of representative species of the Gerridae and discussed their taxonomic significance.
The prothorax

The pronotum is always prolonged in the winged forms, as well as in wingless forms of most groups of the Gerridae. The pronotum is divided into two areas, separated by an obscure transverse suture. The suture usually obsolete when the pronotum is more or less greatly prolonged, but distinctly marked when the pronotum is not greatly prolonged, as in *Eurygerris* (figs. 263, 264). The first phragma arises from beneath the suture. Thus the suture represents roughly the point where the prolongation starts, and it corresponds to the posterior margin of the pronotum in the wingless forms of the genera in which the pronotum is not prolonged. In the winged forms of all genera the pronotum is more or less widened and elevated above the point of the wing base. This point is called the humerus; in wingless forms the humerus is absent or only feebly developed when the vestigial wing pad occurs. It is common practice in the taxonomy of this group of insects to call the area anterior to the humeri the anterior lobe, and the area posterior to the humeri the posterior lobe in the winged forms, but this is inconvenient because the humerus is not produced in wingless forms. The transverse suture demarcating the point of origin of prolongation of the pronotum is more or less distinct, or at least traceable in both winged and wingless forms; therefore, the terms anterior and posterior lobes are applied to the regions anterior and posterior to the suture respectively in this work. The prosternum is indistinguishable from the propleural region and narrower than the meso- and metasternal regions. The prosternal apophysis is present but small.

The mesothorax and Wing bases

The mesothoracic spiracle is hidden beneath the pronotum, located lateral to the intersegmental membrane arising from beneath the transverse suture of the pronotum. In the mesonotum the antecostal suture demarcates the anterior margin except medially where the small lobate acrotergite extends forward. Paired parapsidial sutures run posteriorly from the anterior margin of the mesonotum. The area between these sutures was thought to be the prescutum by Taylor (1918) and Larsén (1945), but the prescutum by definition (Snodgrass 1935) is the area of the mesonotum or metanotum between the antecostal suture and prescutal suture, when the latter is present. In the Gerridae the true prescutum was found to be defined only in *Ptilomera* (fig. 72). The area bounded laterally by
the parapsidial sutures is labelled the scutum (fig. 88). The scutocutellar suture, which separates the scutum from the scutellum, is absent. The posterior region of the mesonotum continuous with the scutal region is thus labelled the scutellum (fig. 88). The postnotum is rather strongly drawn in, bearing the phragma beneath. Its posterior margin is nearly straight, with a small produced area at the middle. There is a narrow sclerite of unelucidated morphological significance along the scutellar region behind the tergal split, which Larsén (1945) called Gelenkkopf. The posterior margin of the postnotum is greatly produced medially in Metrocoris (fig. 76), nearly straight in Ptilomera, Telmatometra, Rheumatosabtes (figs. 72, 78, 80). Neither basalar nor a subalar sclerite is present. The longitudinal lateral membranous suture between the mesonotum and mesopleuron in the winged form is lost in winged forms in most species of Gerridae including Gerris remigis. The pits (fig. 88) on the posterolateral angles of the postnotum denote the presence of the phragma, which is less developed in the wingless forms than in the winged forms.

Heymons (1899a) observed that the tergum in Heteroptera develops from paired anlagen. In the nymphs of many species of Heteroptera the thoracic terga are divided into two more or less well-defined lateral plates by a median longitudinal impression, and both plates become more and more fused together in the later stages of postembryonic development. In the Gerridae also each tergal plate is well defined by the median longitudinal impression, and this impression becomes increasingly obscure in the later stages of development, but the original impression is still retained in varying degrees as the longitudinal sutures on the pro-, meso-, and metanota in many species of the Gerridae. This suture is called the median longitudinal sulcus in this work.

The mesosternum is indistinguishably fused with the mesopleural region in a majority of species of the Gerridae, but the suture separating the mesosternum from the mesopleuron is distinct in such a primitive genus as Eotrechus (fig. 86). The suture, when complete, leads posteriorly to the point of origin of the mesosternal apophysis. The mesocoxal (supracoxal) cleft, or mesoacetabular cleft (fig. 93) extends considerably forward in all species of the Gerridae. The second phragma (figs. 89, 90) in the winged form is well developed and laterally connected with the bases of the mesothoracic sternal apophyses; the posterolateral arms of the phragma in Metrocoris however, in the absence of the meso-
thoracic sternal apophyses, are attached to the inner dorsal angle of the mesoacetabula.

The wing base (figs. 84, 85): In the forewing the first axillary sclerite is articulated with the anterior notal process which is the anterior lateral angle of the tergal split; the second axillary sclerite is located along the first axillary sclerite; the third axillary sclerite is articulated with the acute base of the wing below the anal fold; the median plates are obscurly defined. The tegula is absent. In the hind wing the axillary sclerites are more reduced. The first axillary sclerite is located along the anterior notal process (Gelenkkopf of Larsén, 1945). The individuality of the other two sclerites are also maintained; the median plate with its proximal margin darker. Neither the humeral plate nor the tegula is recognized.

The wing venation: For the naming of the forewing venation I have followed Hungerford and Matsuda (1958a). In fig. 83 R+M and Cu are fused basally, separated into R+M and Cu, respectively, beyond the middle of the forewing. The former, in turn, branches into R and M, respectively, of which R is united with Sc by an oblique vein Sc₂; Cu is apically joined by the vein A and further with M. A is connected with the lower margin of the wing by a short cross vein. In the hind wing (fig. 82) R+M and Cu are clearly separated basally. Cu is apically joined with M. Cu and A are not joined together apically.

The metathorax
(Figs. 72-81, 86-90)

The metanotum in the winged form is defined laterally by the longitudinally elevated carina (fig. 88). This carina probably contains at least partly the element of the first abdominal segment, since the carina is continuous from the abdominal connexivum. The anterior encroachment of the first abdominal segment is also most clearly seen in Rhagadotarsinae (fig. 97), in which the true first connexival segment reaches the definitive intersegmental suture between the mesonotum and metanotum. In the Veliidae also, Esaki and Miyamoto (1955) have shown that the so-called metanotal triangle is actually the first abdominal pleurite. The encroachment of the pleurite of the first abdominal segment into the metathoracic region is thus a fairly common feature in the Gerroidea. In some groups of the Gerridae the first abdominal tergite has its anterior margin straight and the
metanotum does not appear to contain the element of the first abdominal segment, as will be discussed in the next chapter. The metanotal longitudinal sulcus is shown in fig. 88. The third phragma does not occur in the Gerridae. The metathoracic spiracle is conspicuous, placed cephalo-caudad, occupying the intersegmental position between the mesonotum and metanotum laterally.

There occur two sutures in the metapleural region in the Gerridae. The one is the primary intersegmental suture between the meso- and metanota which goes in line with the metathoracic spiracle laterally. Another suture goes dorsally behind the metathoracic spiracle, and this suture is here called the metacetabular suture. The metacetabular suture occurs in the metapleural region, but this suture is definitely not homologous with the pleural suture in lower pterygote insects which leads dorsally to the wing base. This suture is dorsally connected with the posterior margin of the mesonotum in some groups of the Gerridae. Matsuda (1957) called this composite suture "the secondary intersegmental suture." More detailed investigation in this work has revealed more information about the nature of the definitive intersegmental suture between the mesonotum and metanotum occurring in the Gerridae. Comparing the tergum of the winged form and that of the wingless form of *Ptilomera* species (figs. 72, 73) it becomes immediately obvious that the intersegmental suture between the meso- and metanota in the wingless form very likely represents the posterior margin of the postnotum in the winged form dorsally; laterally the suture goes anteriorly then again posteriorly to the metathoracic spiracle, which is located on the intersegmental region between the mesothorax and metathorax. The intersegmental suture in the wingless form of *Ptilomera* is thus the veritable intersegmental suture and it is complete dorsolaterally. In *Gerris remigis* (figs. 74, 75) the intersegmental suture in the wingless form apparently corresponds to the posterior margin of the mesothoracic postnotum dorsally; laterally the suture is directly connected with the conspicuous metathoracic spiracle which is located more dorsally than in *Ptilomera*. In *Metrocoris stalli* (?) (figs. 76, 77) the definitive intersegmental suture appears to represent the posterior margin of the scutocutellum, instead of the postnotum, dorsally. The suture defining the greatly produced postnotum in the winged form, by all criteria, seems to have been lost in the wingless form. In *Telmatometra whitei* (figs. 80, 81) apparently another kind of combination of sutures is responsible for the production of the definitive inter-
segmental suture in the wingless form. It is noticed that the postnotum in the winged form is large and subquadrangular in shape, its posterolateral angles are closely approximated to the dorsal end of the metacetabular suture. From this condition in the winged form it will be a simple step for the metacetabular suture to become connected with the posterolateral angle of the postnotum in the wingless form, thereby producing the nearly straight, long dorsal margin of the definitive intersegmental suture between the meso- and metanota. For the production of the definitive intersegmental suture in Rheumatobates crassifemur the same combination of the sutures most probably are involved, as will be understood by comparing figures 78 and 79 with 80 and 81. There are thus three different kinds of definitive intersegmental sutures in the wingless forms of the Gerridae. Behind the metathoracic spiracle the metacetabular suture is internally marked off by the carina (Pleuralintersegmentalhaken (Larsén, 1945), which leads internally to the base of the mesosternal apophysis (fig. 93).

The metasternum in Gigantometra gigas (fig. 87) is provided with the median unpaired omphalium and the lateral groove leading laterally to the opening on the metacetabula; the opening is covered with a tuft of hairs; the median omphalium is retained in many genera, but the lateral groove is lost in most genera of the Gerridae. The supracoxal cleft does not occur in the metathorax. The basal part of the coxa is inserted beneath the supracoxal lobe. The basal margin of the coxa is oblique in all legs. The paracoxal sclerites are above the ventral and dorsal basal margins of the coxa and thin membrane is attached to each sclerite (fig. 91, 92). The anterior tip of the middle coxa is articulated with the base of the supracoxal cleft and two small black sclerites are loosely connected to each other. The trochanter is narrow and elongate; the trochanteral apodeme bears a large thin membrane for the attachment of muscles, and is present in all legs.

The abdomen

The pregenital segments
(Figs. 94-106)

One of the peculiarities of the hemipterous abdomen, according to Heymons (1899a), is the progressive loss of the pleural element during the embryonic development. The tergite and the sternite become fused and the spiracle, which was originally in the pleural region, becomes located in the sternal region. In addition to this
peculiarity, the fused plate, which is composed primarily of the tergite and sternite, has a tendency to produce a secondary lateral division by sutures either dorsally or ventrally or both. Heymons called the secondarily divided lateral region the paratergite, and the ventral plate the parasternite respectively.

1. The first abdominal segment.

The first abdominal segment is dorsally clearly retained in all species of the Gerridae. The entire (i.e. not laterally obliterated) anterior margin of the first abdominal tergite is present in some groups of the Gerridae. In Brachymetra (fig. 527), for instance, the anterior margin of the first tergite is horizontal, meeting with the anterolateral angle of the first definitive connexival segment, embracing the spiracle behind at the anterolateral angle of the first tergite; the spiracle is also bounded by an oblique suture which reaches the middle of the anterior margin. In some other groups of the Gerridae the anterior margin of the first tergite is bisinuate and laterally not reaching the anterior end of the first connexival segment (e.g. Gerris, fig. 95). The lateral longitudinal ridge (suture) of the metanotum in fig. 95 is probably partly the first segment (pleurite) as discussed previously. It should be noted that in Brachymetra, in which the connexivum is anteriorly defined by the straight anterior margin, no such ridge occurs in the metanotal region. The first segment is always completely lost ventrally except for the Rhagadotarsinae. Lundblad (1933) has already noticed this fact. Matsuda (1957), however, identified the anterior margin of the first ventrite in Rhagadotarsus (fig. 96) as the omphalial groove leading to the metacetabular region, chiefly because of the preconception that the first abdominal segment is always incorporated ventrally into the formation of the metasternal wall of the coxal cavity in Heteroptera. I now think this interpretation is wrong on the basis of the following evidence: (1) the first abdominal pleurite is distinctly incorporated into the metathoracic region; (2) the median omphalium is absent in Rhagadotarsinae; (3) there is at least no lateral opening of the omphalial groove on the metacetabular region, although the opening is obliterated in some forms of Gerridae in which the omphalial groove occurs. The Rhagadotarsinae is a quite abnormal group of the Gerridae combining highly specialized with highly primitive characters, as will be pointed out in the next chapter.
2. The second to seventh abdominal segments.

The connexivum is the paratergite dorsally and the parasternite ventrally according to Heymon’s findings (1899). The connexivum is dorsally well defined by the longitudinal suture from the tergal region. The connexivum is always present in the second to the seventh segment but is never present in the eighth segment; in Rhagadotarsinae it is clearly present in the first segment. Ventrally the connexivum (parasternite) appears to be defined by the longitudinal suture which runs more ventral to the abdominal spiracle (fig. 94). The suture is more distinct and more complete in the primitive genera of the Gerridae, totally disappearing in some highly specialized groups. The seventh connexival segment is more or less greatly produced, forming the connexival spine (fig. 94). In many species of the Gerridae the ventral apical margin of the seventh segment is concave.

The genital segments
(Figs. 98-106)

1. Origin of the male external genitalia in Hemiptera.

Before describing the external genitalia of the Gerridae, it appears to be necessary to mention a recent development of opinions in regard to the origin of the external genitalia of insects, with special reference to Hemiptera. The external genitalia of insects are generally conceived to be the derivatives of the segmental limbs, that is, coxal in origin. Recently Dupuis (1950) elaborated a theory that the male genitalia of insects are derivatives of the tenth abdominal limbs. He coined the terms euphalic and pseudophalic organs, referring to the phalic organs including the parameres (tenth coxite) and to the structures from the ninth coxites respectively. He applied his theory to Heteroptera (1955). He disagreed with Bonhag and Wick (1953) who have shown that the male phalic organs arise from the ninth sternum in Oncopeltus (Lygaeidae, Heteroptera). Snodgrass (1957, December) indicated that the male insect genitalia including those of Heteroptera are the derivatives of the ninth sternum. Matsuda (1957 August, 1958 January) discussed the origin of the insect external genitalia in some detail and came essentially to the same conclusion as Snodgrass, but he credited the discovery to Heymons (1896-1899) who maintained the sternal origin of the external genitalia of insects over a half century ago. Woodland (1957, December) also has
shown in his embryological study on *Thermobia domestica* that the external genitalia in this morphologically important species has nothing to do with coxites in their developmental origin.

As noted from the foregoing brief review on the recent development of opinion in regard to the origin of the external genitalia the overall indication is that the male external genitalia of insects are not the derivatives of the appendages. However, Dupuis' work (1955) is so important for hemipterists and so excellent in gathering the widely scattered information about the male genitalia of Heteroptera that his work, especially his basic concept in regard to the origin of the male genitalia, needs to be taken seriously. Dupuis (1955) refutes Bonhag and Wick's study by pointing out that "Ce point de vue conduit à une numérotation erronée des sternites postgénitaux (δ ci-après), se fonde sur une observation myologique dépourvue de signification (a) et sur une interprétation ontogénétique sans valeur (β) qui méconnaît les faits essentiels de la morphogénèse des genitalia mâles des insectes (γ)."

As to (a) the myological evidence here at issue is the muscle of the stylos on which Bonhag and Wick relied for determination of the gonostylus. This muscle, in my experience also, is highly stable throughout many orders of insects and can be used as a good landmark in determining the stylus. As Dupuis states many muscles appear to be highly unstable in regard to their points of origin and insertion when we examine highly specialized forms of insects; but the musculature in lower groups of many orders maintains stable relationships as regards origin and insertion. This is what I have experienced in my studies of musculature associated with certain structures, such as the tentorium, the thoracic sternum, etc. The musculature can be a very important guide in morphological studies if the materials are carefully chosen and systematically studied in series of forms from more generalized to more specialized groups. If Dupuis' statement is generally true, morphology as a study of homology cannot exist.

As to (β), Dupuis believes that what Bonhag and Wick thought to be the ninth sternite is actually the tenth sternite on the ground that the larval structures do not necessarily coincide with the imaginal structures in location. This appears to contradict him in two ways. First, it should be remembered that his theory is based exclusively on the embryological evidence and on the data of postembryonic development of the male genitalia, which trace the development of the structures from stage to stage up to the adult.
If the larval (or nymphal) structures do not coincide with imaginal structures, how can his method of homology be justified? Secondly, even if the area which Bonhag and Wick observed to be the ninth sternite is actually the tenth sternite as Dupuis maintains, this sternite was observed to give rise to the male phalic organs. How can the sternite give rise to the male genitalia in Dupuis' theory?

As already discussed in detail by Snodgrass (1957) and Matsuda (1957, 1958), the theory which derives the male external genitalia from the tenth abdominal appendages is at least not well founded and it harbors many contradictions. Therefore, Dupuis' statement (\(\gamma\)) to the effect that Bonhag and Wick have misunderstood the essential facts of morphogenesis of the male genitalia is not valid.

Although Bonhag and Wick's study almost convincingly shows that the ninth sternite gives rise to the male genitalia, Qadri's study on the innervation of the genitalia in *Dysdercus* (1949) shows that the tenth abdominal nerves innervate the accessory gland, the median ejaculatory duct, and the intromittent organ. In *Dysdercus*, however, all the thoracic and abdominal ganglia are fused, forming a ganglionic mass in the thoracic cavity, so that the result is not highly reliable. The study of innervation is important in deciding segmentation but it will become reliable only by studying the series of forms from less specialized (less number of fused segmental ganglia) to more specialized. In Neuroptera the anterior seven abdominal ganglia are clearly separated from each other and only the ganglia from the eighth segment on are fused. This is the most generalized condition known in adult pterygote insects. Neuroptera will be the most suitable for this purpose as the basic material to work on.

In any case while the sternal origin of the male genitalia is well supported by evidence, it is less conclusive as to whether they are derived from the ninth or tenth segment. In this work Bonhag and Wick's finding and interpretations are provisionally followed.

2. *The male external genitalia of the Gerridae*.

Following Bonhag and Wick, the pygophore (figs. 98, 100) is the fusion product of the ninth coxites, and it covers ventrolaterally the genital chamber, enclosing the invaginated phallic organs. The pygophore is dorsally fused at its base, forming a narrow sclerotized bridge. The suranal plate (fig. 100) is usually considered to be the tenth segment or the tenth tergum by morphologists (Peytoureau 1895, Heymons 1899, Ekblom 1926 etc.) as well
as by taxonomists. Bonhag and Wick, however, found this to be the ninth tergum in Oncopeltus. One great advantage attached to Bonhag and Wick's interpretation is that it is the ninth tergite in the male that bears apically the anus, and this is the condition in the female in the Gerridae. Thus, if we follow Bonhag and Wick, the homology of the genital segments between the two sexes becomes much easier than in the other theories. Although more studies, with this particular problem in mind, are necessary to either prove or disprove Bonhag and Wick's findings, their interpretation is followed in this work and so labelled.

The male phallic organs of the Gerridae were studied by Poisson (1922, 1924) Singh-Pruthi (1925), Ekbloom (1926), Schroeder (1931), etc. Dupuis' excellent summary of the male genitalia in various groups of Herteroptera (1955), apart from its theoretical aspect, is also very useful.

The basal plate is attached laterally to the pygophore, sustaining the phallotheca within the genital chamber. The parameres arise from the point of connection of the basal plate to the pygophore. The phallotheca lies in the genital cavity with the basal end caudad and resting on and partly surrounded by the basal plate. During the copulation the phallotheca is raised and pushed backward then down, transcribing almost a complete circle. The phallotheca of Gerroidea is peculiar in that it contains the invaginated endosoma within. The endosoma is further divided into the proximal and distal membranous segments, and the conjunctiva between the two. In the resting position the phallotheca surrounds and encloses the endosoma and conjunctiva, its base attached to the basal plates and communicating with the body cavity through the basal foramen. The phallotheca is usually somewhat barrel-shaped, open at the distal end, through which the endosoma is extruded. The conjunctiva joins the phallotheca to the endosoma, being connected with the distal end of the former and the basal part of the latter. In the resting position it serves as lining between the two, and is turned inside out; the distal segment of the endosoma is usually provided with three pairs of sclerotized plates. They are (1) the median dorsal plate; (2) the ventral plates, and (3), the lateral plates. The median dorsal plate appears to be the fusion product of originally paired plates; the ventral plates appear to carry the ejaculatory duct. The number of plates are reduced in some groups of Gerridae, due to loss and fusion of plates.

As Matsuda (1958) pointed out, Christopher and Cragg's study on the development of the female genitalia in Cimex (1922) very convincingly supports the view maintained by Heymons (1896-1899) that the gonapophyses arise from the primary sternum. The study also supports Matsuda's contention (1957, 1958) that the valvifer is the modified sternum. Gillet's observation (1935) on the postembryonic development of the genitalia in Rhodnius and Rawat's observation (1939) on the development of the genitalia in Naucoris clearly indicate that a pair of buds arise on the eighth and ninth sternites. Each pair differentiates into outer and inner pairs, the inner pair on the eighth segment developing into the first valvulae, while the outer pair remains and forms only the first valvifers. The inner pair of buds on the ninth segment develops into the second pair of valvulae, while the outer pair develops into the third pair of valvulae and their bases form the second valvifers. These structures, however, are theoretically the gonocoxites of the eighth and ninth segments of Rawat. They can, however, also be the sternal structures as Christopher and Cragg's more detailed study on Cimex indicates. As far as embryological evidence indicates (Heymons, 1899a), there occur no embryonic abdominal appendage rudiments which might give rise to the external genitalia in Nepa, Notonecta, Cimex, and Pyrrhocoris.

It is clear from the foregoing discussion that there is no factual evidence whatsoever which supports the theory of the appendicular origin of the female genitalia in Heteroptera. The valvulae and the valvifers in Rhodnius and Naucoris studied by Gillet and Rawat should be regarded as sternal structures.

4. The structural plan of the female genitalia in Hemiptera, with special reference to the Gerridae.

Snodgrass (1933) summarized the basic structural patterns of the female external genitalia of Hemiptera. Certain parts of his summary important to our study are given here:

(1) The shaft of the ovipositor is formed of the first and second valvulae, the first being external and ventral, the second internal and dorsal. The second valvulae are generally united with each other, either for a part or for most of their length.

(2) The first valvifers have a pleural position below the tergum on the sides of the eighth segment, though their posterior angles
may be flexibly attached to the ninth tergum. The dorsal muscles of the first valvifers arise on the eighth tergum.

(3) The first valvulae have each two proximal rami. The outer ramus is flexibly attached to the ventral angle of the first valvifer; the inner ramus expands in a small plate solidly united with the anterior ventral angle of the ninth tergum.

(4) The ninth tergum is exposed, and usually large. Its anterior ventral angles are produced forward as extensions to which are united the inner rami of the first valvulae.

(5) The second valvifers have a pleural position on the sides of the ninth segment beneath the lateral margins of the ninth tergum. Each is movably articulated with the tergum at the point near the middle of its dorsal margin.

(6) The second valvulae are attached proximally, each by a single arcuate ramus, to the anterior end of the second valvifer, and the ramus slides on the concave margin of the inner ramus of the corresponding first valvula.

(7) The third valvulae are well differentiated from the second valvifers; they form a pair of lobes ensheathing the distal end of the shaft of the ovipositor; rarely they are absent.

Among the species of the aquatic Hemiptera examined in this study, *Salda* sp. and *Mesovelia mulsanti* have structural plans closer to the above general structural plan in Hemiptera outlined by Snodgrass than the other species. In *Mesovelia mulsanti* (fig. 105) there occurs clearly the second valvifer and the third valvula, but they are absent in the great majority of the Gerridae, as typically seen in *Gerris remigis* (fig. 106). In *Gerris remigis* the first valvula is divided into the inner shorter and the outer longer lobes, the base of the outer lobe being directly connected with the first valvifer, which is a broad sclerite exposed behind the seventh sternite. The thick and membranous ramus, arising from near the apex of the outer lobe, goes cephalad then turns again caudad to be indistinguishably fused with the process of the ninth tergite. The ramus is distinct from the process by different degrees of pigmentation in some species of Gerridae and in *Mesovelia mulsanti* (fig. 105). The vulva is located between the inner lobes of the first valvulae. The second valvulae are connected by the interval-vulvar membrane, the apical margin of which is approximated near the apices of the second valvulae, while the ramus of the second valvulae arises along the inner margin of the second valvula near its apex, goes cephalad and turns
laterally along the inner margin of the ramus of the first valvula. The apical end of the ramus is loosely attached to the inner margin of the ramus of the first valvula due to loss of the second valvifer. In some groups of Hemiptera including *Mesovelia mulsanti* the distal end of the ramus of the second valvula is attached to the base of the second valvifer, which bears apically the third valvula.

**EVOLUTION OF STRUCTURES**

In this section the evolution of each structure is discussed together with its taxonomic significance. While this section is devoted primarily to the study of structural evolution itself at the level above species, it has a secondary purpose to give reasons why I think certain characters are primitive or specialized. A list of characters with their primitive and specialized alternatives thus decided is given at the end of this section. This list of characters is in turn used in tabulating the characters in each group in the following section (classification) by referring to the number for each character in the list. Sometimes recourse was taken to a circular reasoning in deciding primitive or specialized alternative for a character. That is when its alternative, whether primitive or specialized, cannot be decided on morphological bases the decision was made only by its association with other primitive or specialized characters. For instance, when the short pronotum occurs consistently in relatively specialized species or genera the short pronotum is regarded as a specialized, reduced condition. For these characters a symbol (*) was put in the list of characters.

I. **EVOLUTION OF THE STRUCTURES OTHER THAN THE LEGS AND ANTENNAE**

The shape of the body

In the subfamilies which are subsequently shown to be generalized, such as Gerrinae and Ptilomerinae, the shape of the body is elongate; it is shorter and rounder in more specialized subfamilies such as Halobatinae and Trepobatinae. That the primitive gerrids must have been elongate is convincingly evidenced by the fact that the shapes of the bodies of the structurally very primitive existing genera, *Eotrechus* and *Gigantometra*, are strongly elongate. The shortening of the body appears to have been brought about primarily by the reduction of the metasternum and abdomen. In *Eotrechus* the mesosternum is only about one
and a half times as long as the metasternum. In *Gigantometra* and a few other primitive genera of Gerrinae the mesosternum is about twice as long as metasternum and relatively longer than in the other genera of the Gerridae. The extreme reduction of the metasternum is seen in the Halobatinae, in which the metasternum is represented merely by a subtriangular plate which usually does not even reach the metacetabular region.

In *Eotrechus*, *Gigantometra*, and larger species of some other primitive genera of Gerrinae, the abdominal segments are long and the second to seventh segments are subequal in length to each other; slightly more reduced abdominal segments are seen in the more specialized genera of Gerrinae, Ptilomerinae and in *Rhagadotarsus* of the Rhagadotarsinae; the strongest reduction of abdominal segments is evident in Trepobatinae, Halobatinae, and a few highly specialized genera of Gerrinae such as *Amemboa*, *Platygerris*, etc. In these groups the seventh and sixth segments together are often much longer than all the preceding segments together, due to shortening of the more anterior segments.

In the *Limnometra-Tenagogonus s. str.* complex of Gerrini, *Limnometra* is definitely longer than *Tenagogonus s. str.*; in *Gerris* the subgenus *Aquarius*, which is more primitive in the abdomen, is also definitely longer than *Gerris s. str.*; in the *Limnogonus s. str.-Limnogonellus* complex, the former is longer than the latter. In all these groups the metasternum and abdominal segments are relatively longer in subgenera of larger size. Noteworthy also is the fact that *Gigantometra* is relatively longer in the metasternum and abdominal segments than other genera within the tribe Gerrini, and it is the largest species in the Gerridae. In the Charmatometrini, *Charmatometra* has a relatively longer metasternum and abdominal segments than *Brachymetra*, which is structurally less primitive. In the Eotrechini the most primitive genus, *Eotrechus*, has relatively longer metasternum and abdominal segments than the other genera. In the smallest genus (in body length), *Amemboa*, the metasternum as well as most pregenital segments are greatly reduced in length. In the Cylindrostethini the length of the body has become progressively shorter in a phylogenetic series of *Cylindrostethus*, *Potamobates*, and *Platygerris*, and this is beautifully correlated with reduction of the metasternum and abdominal segments.

In the Halobatinae the metasternum has already been greatly reduced as mentioned previously, but it reaches laterally to the metacetabular region in the marine tribe Halobatini and it
does not do so in the fresh-water tribe Metrocorini. The abdomen also has been greatly reduced. Thus, there is no striking difference in body length among genera of the subfamily, but if one compares two related genera, e.g., the larger Ventidius and the smaller Esakia, it can be seen that reduction of abdominal segments is generally responsible for the shortness of Esakia.

Also in the Trepobatinae, the metasternum and abdominal segments are strongly reduced although to a lesser extent than in Halobatinae, and in Trepobatinae there is no striking difference in length among genera. In the related but structurally more primitive subfamily, Rhagadotarsinae, the metasternum and abdomen are relatively longer and the first abdominal segment is ventrally retained, and the subgenus Caprivia of the genus Rhagadotarsus is longer than any species of Trepobatinae. Rhagadotarsus, especially the subgenus Caprivia, is longer than Rheumatobates of the same subfamily which is structurally much more specialized. In the Ptilomerinae, Ptilomera, which is relatively large in size, has generally longer abdominal segments than in the other genera.

It is apparent from the foregoing discussion that among related genera of Gerrinae the reductions in lengths of the metasternum and pregenital segments are responsible for diminution of the body. In other subfamilies this is not so clear, but the smaller size in Trepobatinae and Halobatinae has evidently been brought about by the same mechanism. In these subfamilies the reductions of the metasternum and abdominal segments have reached their functional maximum. The same tendency at the species level is also clearly seen within most genera of Gerrinae if one arranges the species from larger to smaller size.

Concomittant with the reductions in lengths of the metasternum and abdomen, the body becomes relatively widened in the more specialized groups. A conspicuous example is the Cylindrostethus-Potamobates-Platygerris series. Platygerris, though presumably derived from a Potamobates like ancestor, is flattened and wider in shape. Another example is the Ventidius-Esakia complex. Esakia is generally considerably shorter than some species of Ventidius, and the body is more flattened. In Rhagadotarsinae the body is nearly cylindrical in the subgenus Caprivia of Rhagadotarsus and the hind coxae are so approximated to each other that they are not visible dorsally, but they are visible dorsally in Rhagadotarsus s. str. and Rheumatobates which are structurally more specialized as well as shorter and wider in the general shape of the body. All species
of Halobatinae and Trepobatinae are much rounder and rather constant in shape, and much shorter than the species of Gerrinae and Ptilomerinae. It is interesting to call attention in this connection to a well-known classical example given by D'Arcy Thompson (1917), who has ingeniously shown that the sun-fish Orthogoriscus is a close relative of such elongate types as Diodon by applying the principles of Cartesian-co-ordinates. The great difference in general shape of the body between Cylindrostethus and Platygerris, for instance, must have been brought about by the same mechanism, i.e., alteration in the anteroposterior growth gradient along the body axis.

Accompanied by the formation of the rounder general shape of the body in the higher subfamilies, the middle and hind leg bases have become more and more widely separated. A conspicuous example is seen in the Rhagadotarsus(Capricia)-Rhagadotarsus(Rhagadotarsus)-Rheumatobates series, as noted previously. Obviously, the leg bases are much more widely separated from each other in the shorter and rounder Trepobatines and Halobatines than in the species of Gerrinae and Ptilomerinae. Probably the more lateral location of the leg bases have been favored by natural selection, since with more laterally placed leg bases more efficient locomotion on water might have become possible.

Certain deviations from the above mentioned general trend should be noted. In the marine Halobatinae, Asclepios and Halobates, the body size is evidently smaller in the structurally more primitive genus, Asclepios, than in Halobates; in Ptilomera also the structurally more primitive subgenus, Proptilomera, is smaller than in the more specialized subgenus, Ptilomera s. str. At the species level structurally (especially appendages and antennae) less specialized species are smaller than the more specialized species in Rheumatobates. In Gerriselloides the body length is about as long as one of the shortest species of closely related, more specialized Gerris. s. str.

Bianchi (1896) divided the Gerrinae into two subfamilies based on the general shape of the body. These were the Gerrinae, for genera with elongate bodies, and the Halobatinae, for those with shorter and rounder bodies. Actually highly specialized genera of Gerrinae (Platygerris and Amemboa) are shorter than related more primitive genera and have been placed in the Halobatinae, but they are structurally good gerrines, showing that Bianchi's criterion does not hold.
The head

The shape of the head: In the more primitive subfamilies such as Ptilomerinae, Gerrinae, and Rhagadotarsinae, the anterior margin of the head is not smoothly rounded in dorsal view. This is due to the projection of the clypeal region forward, to the well-developed maxillary plates, and to the well-developed antenniferous tubercles laterally. In these groups the rostrum is not tightly appressed to the ventral surface of the head or to the prothorax; it is more or less free from them; the antennae tend to extend forward instead of ventrad in their resting positions. In the more specialized groups the clypeal region tends to be bent ventrally; the mandibular and maxillary plates tend to be fused, and the antenniferous tubercles become obsolete. Accompanying these changes, the rostrum tends to be less free from the ventral surface of the head and prothorax or from the mesosternum; the position of the antennal cavities shifts increasingly ventrad and the antennae tend to be more closely appressed to the ventral surface of the body. This correlated shift of structures is seen at the level of all taxonomic units. In Ptilomerinae the clypeal region forms a rather conspicuous, medially produced region and the antenniferous tubercles are conspicuous developments which are divergent apically in most genera; in Rheumatogonus, however, the clypeal region is more strongly bent ventrad, the antenniferous tubercles are more reduced, and the anterior margin of the head, therefore, is much more rounded in dorsal view than in other genera. In the Gerrinae the clypeal region and the antenniferous tubercles are still well developed in dorsal view, and the antennae arise always from above the anterior margins of the eyes. In the Halobatinae the clypeal region and the antenniferous tubercles are slightly produced on the anterior margin of the head in the marine Asclepios-Halobates complex; in Metrocoris and Eurymetra and few other related genera, the anterior margin of the head is practically not at all produced medially. It is simply broadly rounded in dorsal view, but the antennal cavities still open above the anterior margins of eyes. In the Ventidius and Esakia complex, the shift of the positions of the antennal cavities is beautifully seen in a series from V. malayensis to E. kuiterti (see figures 822, 823, 858). Ventidius malayensis is the largest species, and structurally more primitive than others. In this species the antennal cavities are clearly above the eyes, while in V. kuiterti the cavities are on the line across the anterior margins of the eyes. In E. kui-
terti, the cavities are below the anterior margins of eyes. The antennae and the rostrum in *Esakia* are closely appressed to the ventral surface of the body when they are at rest.

In all genera of Trepobatinae the anterior margin of the head is more or less smoothly rounded. The antenniferous tubercles are a little more developed in *Metrobates* than in others; the antennal cavities open just above the anterior margin of the eyes to a point a little below them. In Rhagadotarsinae the shape of the anterior margin of the head is rather strikingly different from the others. The antenniferous tubercles are conspicuously developed in the subgenus *Caprivia* of Rhagadotarsus; in *Rhagadotarsus s. str.* the structures are less pronounced, and are even much less developed in *Rheumatobates*. In all genera of Rhagadotarsinae the antennae arise from above the eyes, although one sees a continual reduction of the antenniferous tubercles from *Caprivia-Rhagadotarsus s. str.* to *Rheumatobates*. In this subfamily the mandibular and maxillary plates are clearly separated and the latter are so well developed as to form the bucculae, as in some more generalized terrestrial Heteropterons. These bucculae are clearly produced on either side of the clypeal region; the development of the bucculae is strongest in *Caprivia* and weakest in *Rheumatobates*. The clypeal region always projects forward as a median process of the head and the clypeus is basally well defined. The shape of the head in this subfamily is, thus, more like that of generalized Heteroptera and is the most primitive found among the subfamilies of Gerridae.

As the shape of the interocular space is directly associated with the shapes of the inner margins of eyes, it will be discussed in relation to the shape of eyes.

**The eyes:** In the primitive gerrids the eyes were probably indented, more or less globular in shape, relatively small, and not or but little covering on the anterolateral angles of the pronotum as is evidenced by the prevalence of this type of eyes in Ptilomerinae and in the majority of genera of Gerrinae. The eyes appear to have lost indentation and to have become larger and more laterally located, covering a great part of the anterolateral margin of the pronotum, in the more specialized subfamilies, Halobatinae and Trepobatinae. Evolution of the shape and position of the eyes is seen in the series from *Metrocoris* to *Esakia* (figs. 778, 822, 823, 858). In the Gerrinae, *Amemboa* and *Platygerris* have less indented eyes than their more primitive relatives, *Onychotreachus* and *Potamobates* respectively.
The shape of the interocular space of the head is directly dependent upon the shape of eyes. In the species in which the eyes are indented the interocular space is more or less strongly widened posteriorly. This is true of all genera of the Ptilomerinae, and a majority of genera of Gerrinae. The interocular space in Halobatinae and Trepobatinae is considerably less strongly widened posteriorly, due primarily to the absence of the ocular indentations.

As I have already pointed out (1957), the shape of the eyes has been erroneously considered to be a very important subfamily character by previous workers. Thus Amemboa, Platygerris, Charymatometra, Brachymetra and Eobates, because of their relatively short bodies and the shape of their eyes, have been placed in the Halobatinae. Because of the parallelism in evolution of eyes in this family, their shape cannot be used as a subfamily character. More fundamental morphological characters show that the five above-mentioned genera should be included in Gerrinae as will be more fully discussed elsewhere in this work.

The shape of eyes is much the same in the more primitive genera of Gerrinae, and is constant among all genera of Ptilomerinae, but is a character of specific rather than generic importance in the more specialized groups of the Gerrinae, Halobatinae, and Trepobatinae.

The clypeus: The basal margin of the clypeus is evident in the more primitive genera of all subfamilies, but cannot be seen in specialized genera of Gerrinae, Halobatinae and Trepobatinae. The anterior margin of the clypeus is more or less loosely connected with the labrum by means of membranous area. This condition is especially pronounced in the Cylindrostethini of Gerrinae. Whether the basal margin of the clypeus is retained or has been lost is usually generically constant.

The mandibular and maxillary plates, and the labrum: The mandibular plate is distinct from the maxillary plate in the more primitive genera of Gerrinae, Halobatinae, and Trepobatinae. In the Ptilomerinae and Rhagadotarsinae the plates are also quite distinct from each other. The maxillary plate has been discussed in connection with the shape of the head.

Whether the mandibular and maxillary plates are fused or not is usually generically constant. In Rhagadotarsinae the degree of development of the maxillary plate is somewhat significant at the generic or subgeneric level, and can be used as a taxonomic character at these levels. Externally the labrum does not provide any good taxonomic character at any taxonomic level.
The rostrum: The greater part of the rostrum consists of the third and fourth segments. Since these segments are easiest to measure, their measurements for all species available for study are given in table 16. It was found that there exists a strong tendency for the ratio of the third segment to the fourth to be greater in the more primitive and larger (in body length) genera than in related, more specialized smaller (in length) genera. This tendency is noted also at the species level within genera.

In Gerrinae the above tendency is noted in the Aquarius, Gerris s. str., the Limnogon s. str.-Limnogonellus complex, the Limnometra-Tenagogonus s. str. complex, Eurygerris, in the Eotrechini including four genera (Eotrechus, Onychotrechus, Chimarrhometra, and Amemba), in the Cylindrostethini including three genera (Cylindrostethus, Potamobates, Platygerris) and in Brachymetra. In the Halobatinae the tendency is noted in the Ventidius-Esakia complex. In Trepobatinae the ratio of the third to the fourth segment is greater in Telmatometra and Halobatopsis than in the related and smaller (in length) genus Ovatametra. In the relatively primitive, but not the largest (in length) genus Cryptobates and Telmatometra the absolute length as well as relative length of the third segment is definitely greater than in any other genus of the subfamily. This indicates that these genera have a quite different growth pattern for the rostral segments from that of the other genera. In Metrobates, which is relatively large in size and primitive in structures, the relative length of the third segment is greater than in Rheumatometra, Hynesionella, Metrobatopsis, and Naboandellus. The length of the third segment in relation to the fourth segment appears to be directly correlated with absolute size in Rheumatobates and Hynesionella, in which the larger sex (female) has the third antennal segment relatively longer.

The above tendency must have been realized by the persistence of similar allometric growth patterns for these segments among related forms, in which the growth ratio for the third segment is greater than that for the fourth.

The prothorax

The pronotum: Prolongation of the pronotum in wingless forms is known to occur only in Reduviidae and Gerroidea in Heteroptera. In certain gerrids such prolongation does not occur in wingless individuals. That the lack of prolongation in wingless forms is a specialization is indicated by the following facts.

(1) Prolongation of the pronotum in wingless individuals occurs
in more primitive genera or subgenera of Gerrini, such as Aquarius, Gerris s. str., Limnometra, Limnoporus, Limnogonus s. str., Tenagometrella, etc., and the three genera of Charmatometrini.

(2) Varying degrees of reduction of the pronotum in wingless forms occur only in highly specialized species of some more specialized genera or subgenera of Gerrinae, such as Limnogonellus, Eurygerris, Tenagonus, etc.

(3) In the genus Rhagovelia of the Veliidae, there occur varying degrees of prolongation of the pronotum; and the group with more prolonged pronotum in wingless forms has the more primitive wing venation in the winged forms.

If the lack of prolongation of the pronotum in wingless forms is a specialized condition as reasoned above, Lundblad’s (1936) and Matsuda’s (1956) opinions that this feature is primitive should be retracted. Whether the above view is valid for Veliidae in general can be determined only by more extensive study of this family.

A more detailed consideration of evolution of the pronotum in wingless forms of Gerrinae follows:

In Eotrechini the pronotum in wingless forms is not prolonged in any genus although we do not know whether the pronotum is prolonged or not in wingless forms of Eotrechus, since wingless forms of this genus have never been found. The lack of prolongation of the pronotum in wingless forms of the other three genera, however, does not contradict the above view that the prolongation is a primitive condition, since the three genera are structurally much more specialized than Eotrechus. In Gerrini various stages of prolongation of the pronotum are noted. In the large (in size) and structurally primitive genus, Gigantometra, the pronotum is prolonged in wingless individuals (Hoffmann, 1936); in Gerris the pronotum is prolonged in all species examined, but in Gerrisella, which is somewhat related to Gerris s. str., the pronotum is not at all prolonged in wingless forms. In Limnoporus, which is relatively primitive and large in body size, the pronotum is prolonged in wingless forms. In the Limnometra-Tenagogonus s. str. complex, an unprolonged pronotum occurs only in the highly specialized species, T. madagascariensis; interestingly, however, the pronotum is highly modified apically in *fijiensis* from Fiji. The evolution of the pronotum in this genus has taken two quite different courses, one toward reduction in Madagascar and another toward further modification in the Pacific; in the related genus Tenagometra from
Africa the pronotum is not at all prolonged although in another related but relatively primitive genus, *Tenagometrella*, the pronotum is prolonged in wingless forms. In the *Limnogonus s. str.-Limnogonellus* complex there are seen varying degrees of reduction of the pronotum in wingless forms in the specialized, smaller (in size) subgenus *Limnogonellus*. In *Eurygerris*, there also exist varying degrees of reduction of the pronotum from the almost fully prolonged condition in *E. mexicanus* to highly reduced conditions in other species. No wingless forms of the genus *Tachygerris* have ever been recorded.

In Chamaetometrini the pronotum is always prolonged. In Cylindrostethini and all other subfamilies of the Gerridae the pronotum is not prolonged in wingless forms.

Prolongation of the pronotum in wingless forms is a tribal character in Gerrinae except for Gerrini. Since there is a clear indication that the pronotum is in the evolutionary process of progressive reduction independently in various groups of Gerrini, this cannot be used to define natural groups in that tribe, but can be a good species character. Sometimes the color of the longitudinal stripe is a good generic character, *e. g.*, in *Tenagometrella* the pronotum has a median yellow longitudinal stripe instead of a black stripe as in related genera; in *Limnogonus* the pronotum always has a yellow stripe on the apical margin; etc. In the winged forms the shape and the position of the humeri are of taxonomic importance, *e. g.*, the relatively caudal position of the humeri is characteristic of Cylindrostethini.

The Mesothorax

*The lateral longitudinal suture of the mesothorax*: The lateral longitudinal suture separating the mesonotum from the mesopleural region is retained in the Rhagadotarsinae, *Potamometra* of the Ptilomerinae, and *Tenagogonus* (*Tenagometra*) and *Eurygerris* of the Gerrinae in which the pronotum is not prolonged in wingless forms. The suture is completely lost in the other two subfamilies. When this suture is clearly retained it constitutes a good generic, subgeneric or subfamilial character.

*The median longitudinal sulcus of the mesonotum*: This suture, as already indicated, is the exuvial suture. When present, therefore, this is a nymphal character. It is highly conspicuous and represented by a longitudinal groove in females of *Rheumatometra* and *Rheumatometroides*.
The mesosternum: The mesosternum in more primitive genera of Gerrinae is provided with a pair of longitudinal sutures on either side of the median longitudinal axis. That these sutures are probably the ones separating the primary mesosternal region from the lateral mesopleural regions is supported by the facts that the sutures occur only in more primitive genera of Gerrinae and Ptilomerinae, or in more primitive species of some genera of Gerrinae. The sutures are distinct and extend through the entire length of the mesothorax, extending posteriorly to the bases of the sternal apophyses in Eotrechus. The sutures tend to become divergent and obsolescent posteriorly when they occur in other genera. The sutures are present in Gigantometra, all species of Limnoporus, in most species of Aquarius and Gerris s. str., and in some species of Onychotrechus, Eurygerris, Limnometra, Limnogonus, and Cylindrostethus. They are distinct only anteriorly in Limnogonellus when they are present. Also they are distinct in some species of Ptilomera of Ptilomerinae, not recognizable in other genera of Ptilomerinae, and appear to have been completely lost in all other subfamilies.

The mesosternum is often impressed longitudinally on the anterior half of the median longitudinal axis. This suture is apparently a secondary depression to receive the apical portion of the rostrum. In the groups in which the rostrum is short, not extending beyond the prosternum (Cylindrostethini), the anterior margin of the mesosternum is either simply rounded or sometimes even strongly swollen and produced anteriorly at the middle. In females of Heterobates the mesosternum is provided with a median well-demarcated flattened area which extends posteriorly as far as the apical region of the abdomen. Other kinds of modifications seen in Ventidius (Ventidiodes), and Metrobates are described elsewhere. The mesosternum, located between the prosternum and metasternum, appears to have been least modified and least reduced in length during the course of evolution throughout the family.

The intersegmental suture between the mesonotum and metanotum: As the morphological study of this suture has revealed, the nature of the definitive intersegmental suture between the meso- and metanota differs rather widely in different groups of the family. It was also found that two different sutures are involved in the formation of the definitive intersegmental suture, i. e., the primary intersegmental suture and the suture here called the metacetabular suture.

In figure 107 is shown the possible evolutionary history of the
intersegmental suture in wingless forms of the Gerridae. In the hypothetical primitive gerrids the primary intersegmental suture is complete throughout the dorsolateral part of the body, as seen in some genera of Gerrinae and all genera of Ptilomerinae, and the metacetabular suture is only weakly developed dorsally. From this primitive condition the metacetabular suture became united to the anterolateral angle of the first tergite, while the primary intersegmental suture is retained laterally, as seen in Ptilomerinae. In Gerrinae the most primitive condition is seen in \textit{Charmatometra}, in which the primary intersegmental suture is retained dorsolaterally and the secondary metacetabular suture is only weakly developed as in the hypothetically primitive gerrids. In the other two genera of Charmatometrini the primary intersegmental suture is often obsolete laterally. In Eotrechini the primary intersegmental suture is retained laterally and in Gerrini it is more or less obliterated laterally. The metacetabular suture is better developed than in Charmatometrini in these two tribes. From the sutures seen in Eotrechini the condition in Cylindrostethini must have been produced by complete fusion of the metacetabular suture with the dorsal margin of the primary intersegmental suture, while the primary intersegmental suture was still retained laterally. From the type of sutures in Cylindrostethini it is a simple step to produce the type of suture in Rhagadotarsinae and Trepobatinae with the complete loss of the prespiracular part of the intersegmental suture. The type of the sutures in Halobatinae has probably arisen from those in Gerrini by having the suture dorsally (which represents the posterior margin of the mesothoracic postnotum in winged forms) replaced by the posterior margin of the mesothoracic scutellum in winged forms.

The differences in the nature of the sutures are of great taxonomic importance at the subfamilial and tribal levels. The other characters correlated with the different types of the sutures further strengthen their taxonomic values. In fact all the genera included within each subfamily and tribe share very much the same sutures described above.

The metathorax

The \textit{metathoracic spiracle}: The metathoracic spiracle is distinct in all species of all subfamilies, and located always anterior to the metacetabular suture. The orientation of the spiracle—whether it is cephalocaudally or nearly dorsoventrally oriented—is quite constant in each subfamily. In the subfamilies having the primary intersegmental suture between the mesonotum and metanotum more or
less retained laterally, the spiracle is placed cephalocaudally. This orientation of the spiracle is seen in all species of Gerrinae, Ptilomerinae and Halobatinae without exception. In all species of the subfamilies in which the primary intersegmental suture is completely lost laterally (Rhagadotarsinae and Trepobatinae), the spiracle is oriented more nearly vertically, especially in Trepobatinae. Often the anterior end of the spiracle and the metacetabular suture are connected by a faint suture (figs. 80, 81) in Trepobatinae. This suture, in spite of its prespiracular position, is not homologous with the primary intersegmental suture, since it does not reach anteriorly to the wing base in winged forms.

As noted from the above description the orientation of the spiracle is highly correlated with the two fundamentally different types of the intersegmental suture, by which the Gerridae can roughly be divided into two major groups.

The median longitudinal sulcus of the metanotum: This occurs in most genera of Gerrinae, Trepobatinae, Rhagadotarsinae, and some genera of Ptilomerinae. It is the ecdyseal suture. The presence or absence of this suture is usually generically constant.

The lateral longitudinal ridge of the metanotum: The morphology of this ridge (sometimes a suture) has been discussed in some detail previously. It is obvious that the presence of this suture is secondary. In the Ptilomerinae, Charmatometrini, in which the nearly straight and complete anterior margin of the first tergite is retained, this secondary suture does not exist. The presence or absence of this secondary suture is thus correlated with the presence or absence of the straight, laterally unobliterated anterior margin of the first abdominal tergite. As already shown, this suture is especially well developed in Rhagadotarsinae, reaching clearly to the definitive intersegmental suture between the meso- and metanota. It is developed in varying degrees in Halobatinae, Trepobatinae, and Gerrinae except for Charmatometrini.

The metasternum: Since the mesosternum has apparently been least modified in length among thoracic segments during evolution, the relative length of the metasternum to the mesosternum should give a good criterion by which one can judge the degree of reduction of the metasternum. It was found in this study, by applying this method, that the degree of reduction of the metasternum is the least in Eotrechus in the Gerridae, in which the mesosternum is only about one and a half times as long as the metasternum; next are Gigantometra and Cylindrostethus productus, in which
the mesosternum is a little less than twice as long as the metasternum, and the body size is very large and primitive structurally. In *Aquarius* and *Gerris s. str.* the relative length of the mesosternum to the metasternum is 2:1 to 3:1; in the *Limnometra-Tenagogonus s. str.* complex the mesosternum is three to almost six times as long as the metasternum; the metasternum in the larger species of *Limnometra* is relatively longer than *Tenagogonus s. str.* In the *Limnogonus s. str.-Limnogonellus* complex, also, the same relation holds; the mesosternum ranging from three to almost five times as long as the metasternum and being relatively longer in species belonging to the larger (in body size) subgenus *Limnogonus s. str.* than in the smaller *Limnogonellus*. In the Eotrechini the reduction of the metasternum has occurred progressively in the order of *Eotrechus, Chimarrhometra, Onychotrechus, Amemboa*. In the last genus the mesosternum is seven to ten times as long as the metasternum, and the body is the smallest. In the Cylindrostethini the metasternum has also become progressively reduced in the phylogenetic series from more primitive to more specialized, that is in the order: *Cylindrostethus, Potamobates, Platygerris*. In *Cylindrostethus* the ratio of the mesosternum to the metasternum ranges from 1.8:1 to 3.5:1, but it is about 10:1 in *Platygerris*. In the Charmatometrini the ratio is relatively constant, about 5:1 throughout the tribe.

In Ptilomerinae the degree of reduction of the metasternum is generally further advanced than in Gerrinae. The mesosternum is at least several times as long as the metasternum in all genera. In the Rhagadotarsinae the metasternum has not been much reduced; the mesosternum is only a few times as long as the metasternum in the great majority of species of the subfamily. In related subfamily Trepobatinae, the metasternum has been greatly reduced; the mesosternum is ten to twenty times as long as the metasternum in the great majority of the members of the subfamily; only in *Metrobates* is the mesosternum distinctly less than ten times as long as the metasternum. The extreme reduction of the metasternum is seen in Halobatinae, in which the metasternum is represented by a transverse subtriangular plate bearing the omphalium along its posterior margin, and this plate does not even reach the metacetabular region in Metrocorini, and barely reaching it in Halobatini.

Since the degree of reduction of the metasternum overlaps among related genera, it cannot be generally a diagnostic generic char-
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acters, but its highly reduced condition in Halobatinae is a good subfamily character as is its large size and anterior production in Rhagadotarsinae.

The omphalium: The omphalium and the groove leading from it onto the metacetabular region is retained in Gigantometra, Gerrielloides, Charmatometrini, and Cylindrostethini of Gerrinae; the lateral groove is lost although the tuberculous omphalium is retained on the middle of the metasternum in all other genera of Gerrinae, Ptilomerinae, and Halobatinae. The omphalium, as well as the lateral groove, has been lost in Rhagadotarsinae and Trepo- batinae except for Rheumatometroides and Stenobates. The presence of the omphalium and the lateral groove is the primitive condition as seen from the fact that they are retained in more primitive genera of each tribe of Gerrinae, although the groove is lost in Eotrechus.

The presence or absence of the omphalium and the groove leading onto the metacetabula offers an excellent generic diagnostic character in the Gerrinae. When only the median tuberculous omphalium is present, the location of the omphalium, whether it is close to or considerably away from the posterior margin of the metasternum, is generically often constant. Occasionally the shape of the omphalium, whether it is located on the more or less swollen surface or not, is a good species character (e.g., Eurygerris). The tuft of hairs which usually covers the lateral opening of the groove on the metacetabula varies in degree of development in various species and this may be a good species character. The total absence of the omphalium is a good subfamily character for Rhagadotarsinae.

The first abdominal segment

The first abdominal tergite: The lateral loss of the anterior margin of the first abdominal tergite must have occurred independently in some or all genera of all subfamilies. In Gerrinae the complete and nearly straight anterior margin is retained in the Charmatometrini; the definitive anterior margin of the first tergite in many genera of Gerrinae is laterally represented by an obscure secondary suture or depression running slightly behind the first abdominal spiracle and by the genuine suture running obliquely forward in front of the first abdominal spiracle, which does not reach antero-lateral angle of the first connexival segment. The anterior margin of the first abdominal tergite in these forms is thus roughly flattened W-shaped or bisinuate (here secondary oblique lateral depressions
The anterior margin of the first tergite is clearly retained in both sexes of *Rhyacobates*, *Potamometroides*, *Rheumatogonus*, *Potamometra*, *Ptilomera* and *Pleciobates* (?). It is obliterated and modified in the females of *Heterobates* and *Potamometropsis*, and the tergite is medially curiously modified in the female of *Potamometra*, though the anterior margin is retained. In Halobatinae the anterior margin is retained rather clearly for its entire width in *Metrocoris* although it runs obliquely forward laterally in front of the spiracle; rather clearly retained laterally, though obliterated medially, in *Asclepios* and *Halobates*; in *Ventidius* and *Esakia*, especially the latter, the anterior margin is obliterated at least in wingless forms of most species. In the Rhagadotarsinae and Trepobatinae the anterior margin tends to be obliterated medially, and in some genera of Trepobatinae (e.g., *Cryptobates*) the anterior margin is even indistinct laterally or lost.

The connexival part of the first abdominal segment: The connexival part of the first segment is distinct from that of the second only in Rhagadotarsinae, in which the connexival part of the first segment encroaches into the lateral region of the metanotum. In the rest of the family the connexivum of the first segment is invariably fused with the second or sometimes indistinguishably fused with the second and third, and encroaches into the mesonotum (lateral longitudinal elevation) in varying degrees in various groups.

The first abdominal ventrite: The first ventral abdominal segment is clearly retained and even longer than the second ventrite in Rhagadotarsinae; in all other subfamilies the first ventrite is completely lost at least superficially, and the first clearly recognizable ventrite is actually the second ventral abdominal segment.

The combination of the characters found in the tergite, connexivum, and ventrite provides good generic or sometimes good subfamily characters. The degree of reduction of the anterior margin of the abdominal tergite, whether it is retained throughout the entire width or obliterated medially or laterally, or whether it is straight or flattened W-shape, etc., are generically constant for most genera, and often constant at the tribal and subfamilial levels. Whether the first connexival segment extends into the metanotal region or not is the character that distinguishes the clearly related genera, *Ventidius* and *Esakia*. The retention of the line separating the connexivum of the first segment from that of the second and the retention of the first abdominal ventrite are important subfamily
characters of Rhagadotarsinae. Matsuda (1955) suggested the taxonomic significance of the basal abdominal tergites in Heteroptera in general; he (1956) also found that the varying degrees of modification of the basal tergites in the winged forms of Rhagovelia (Veliidae) serve as subgeneric characters. In the Gerridae the basal abdominal tergites, especially the first, provide important taxonomic characters at the subfamilial, tribal, and generic levels.

The second to sixth abdominal segments

The second to sixth abdominal tergites and ventrites: Like the mesothorax among the thoracic segments the second to the sixth segments, situated between the proximal and distal genital segments, have had the least modification in evolution. At least dorsally these segments are subequal in length in most genera of all subfamilies. In some genera of Trepobatinae (Cryptobates, some species of Halobatopsis and Ovatametra) and in some genera of Halobatinae (Ventidius and Esakia) the anterior margin of the second tergite is obliterated; in some genera of Ptilomerinae (e.g., Heterobates) the basal abdominal tergites are greatly modified due to strong reflection of the connexivum on the dorsum in the female; in Potamometroides hoogstraali the sixth tergite is provided with the median projection, also the apical angles of the sixth connexival segment in the female is strongly produced. In all other subfamilies the second tergite tends to be produced anteriorly on the anterior margin; this tendency is especially pronounced in Trepobatinae and Halobatinae.

Ventrally the second to sixth segments are subequal and relatively long in the more primitive genera of Gerrinae, such as Eotrechus, Gigantometra, most species of Aquarius, Gerris s. str., Limnometra etc. The segments ventrally are shorter than dorsally though still subequal in most genera of Gerrini. In Eotrechini the abdominal segments are greatly reduced ventrally in Amemboa and Chimarrhometra; among Cylindrostethini the posterior margin of the sixth ventrite in some species of Potamobates and all species of Platygerris is produced anteriorly at the middle in female. In Ptilomerinae the abdominal segments are more often not subequal to each other ventrally. The degree of reduction of the second to the sixth ventrites is generally greater than in Gerrinae; and in genera, in which a large part of the abdomen is telescoped within the thoracic cavity, the male abdominal ventrites are greatly reduced (Potamometroides). In the Rhagadotarsinae the second to sixth segments are relatively long and subequal in length both dorsally and ventrally
in *Rhagadotarsus*, shorter but still subequal in length in *Rheumatobates*. In Trepobatinae the abdomen is as in *Rheumatobates* but at least the sixth segment is a little longer than the fifth segment in a great majority of species of all genera. In the males of *Metrobatopsis* and *Hynesionella* the degree of reduction of the abdominal segments is greatest in the subfamily. In Halobatinae a condition similar to that in Trepobatinae exists, the greatest degree of reduction of the second to the sixth ventrites having been attained in *Ventidius*, *Esakia*, *Halobates*, etc.

**Location of the abdominal spiracles.** There is a consistent tendency for the abdominal spiracles in more primitive species of more primitive genera to be located closer to the anterior margin than to the posterior margin of their respective segments. The spiracles are located more caudad, or even at the middle of the segments in more specialized species with more reduced abdominal segments within the same genus. This process of shift of the location of the spiracles is beautifully seen in such a diverse group as the *Limnometra-Tenagogonous s. str*. complex. In this group the spiracle is placed distinctly closer to the anterior margin than to the posterior margin in species with long abdominal segments. In *T. (L.) anadyomene* and in all species of *Tenagogonous s. str*. the spiracle is at the middle of each segment. A similar tendency is also seen in the *Cylindrostethus-Potamobates* series; in all species of *Cylindrostethus*, in which the abdominal segments are long, the spiracles are placed closer to the anterior margin than to the posterior margin of all segments, whilst in all species placed under *Potamobates* except for *P. thomasi*, in which the abdominal segments are shorter than in *Cylindrostethus*, the spiracles are placed at the middle of each segment, or even closer to the posterior than to the anterior margin; in *P. thomasi* the spiracles are placed closer to the anterior margins than to the posterior margins of abdominal segments, and the abdominal segments in this species are the longest among the species of *Potamobates*. A similar situation to those in the above mentioned genera is also seen in *Aquarius* and *Gerris s. str*. at the specific level. In the Charmatometrini the abdominal spiracles are placed closer to the anterior margin than to the posterior margin in *Charmatometra* and *Eobates*, but at the middle in most species of *Brachymetra*. The spiracles are also placed closer to the anterior margins than to the posterior margins in such primitive genera as *Eotrechus* and *Gigantometra*, but at the middle of each segment in *Tachygerris*, *Chimarrhometra*, *Platygerris*, *Onychotrechus* and probably
Amemboa (not examined), all more or less highly specialized genera of Gerrinae.

In the Ptilomerinae the spiracles are placed at the middle of each segment except for Ptilomera, in which the abdominal segments are relatively long and the spiracles are in front of the middle of the segments. In Rhagadotarsinae the fifth and sixth abdominal spiracles are located closer to the anterior margin than to the posterior margin of each segment in the subgenus Caprivia of the genus Rhagadotarsus; in Rhagadotarsus (Rhagadotarsus) and in Rheumatobates the spiracles are placed at the middle of their respective segments. In Halobatinae and Trepobatinae the abdominal segments are strongly reduced, moreover the basal areas of the metacetabula and the middle and hind legs are so superposed on the lateral region of the abdomen that it is usually very difficult to locate the spiracles under a binocular microscope, but whenever the spiracles are observed they are found to be located at the middle of each abdominal segment.

It is evident from the foregoing description that the primitive position of the abdominal spiracles in the Gerridae is closer to the anterior margin than to the posterior margin of each segment, and that the spiracles have had a tendency to shift their positions to the middles or even beyond the middles of the segments with progressive reduction of the abdominal segments.

The ventral longitudinal suture of the connexivum: The suture is most pronounced in more primitive species of the more primitive genera of Gerrinae in which the suture is only briefly broken at the middle of each segment. The suture extends almost the entire length of each abdominal segment, slightly mesad of the spiracle, but it becomes obliterated in more specialized species within the same genera or in more specialized genera of Gerrinae and is represented by two punctiform depressions. The sequence of obliteration of this suture is seen in such diverse genera of Gerrinae as the Limnometra-Tenagogonus s. str. complex, the Aquarius-Gerris s. str. series, the Cylindrostethus-Potamobates complex, etc. In Gigantometra the suture is well developed; in Eotrechus it is distinct but not as well pronounced as in Gigantometra; in the related but smaller and more specialized genus Onychotrechus it is indistinct; in such highly specialized genera of the subfamily as Amemboa and Platygerris it is very indistinct or completely lost; in the Charmatometrini it is either indistinct or lost. In the Ptiolo-
merinae it is indicated by two oblique impressions mesad of the spiracle of each abdominal segment; it is most distinct in Ptalomera in which the abdomen is more generalized, indistinct or overgrown by silvery adpressed hairs in most other genera. In other subfamilies the suture is further obliterated and even completely lost; the two ill-defined shallow depressions mesal to the spiracle of each segment in Rhagadotarsus is probably the obliterated suture. In Halobatinae and Trepobatinae the suture is almost completely or completely lost.

The seventh abdominal segment

Theoretically, in primitive insects the seventh abdominal segment should be similar in form to the preceding segment. Search for this primitive condition in the Gerridae immediately encountered difficulty in that in no species of the Gerridae is the posterior margin of the seventh segment on the ventral surface straight as is the sixth. It is always either broadly concave or curiously modified, and often the seventh segment at the sides is strongly produced posteriorly as the connexival spines. Since the posterior margin is usually concave and the segment has a strong tendency to be produced laterocaudally, the relative length of the seventh to the sixth segment on the ventral surface is expected to be below 1 in primitive gerrids. It was found that this condition is seen in more primitive species of more primitive genera of Gerrinae, such as Gigantometra, Eotrechus, and more primitive species of Aquarius, Limnometra, etc. In these species the second to sixth abdominal segments are long and subequal to each other in length, and the lateral projections of the seventh are more or less conspicuous except for Eotrechus. In these primitive gerrids the seventh segment on its median longitudinal axis is about two thirds to three fourths as long as the sixth segment ventrally and the posterior margin is more or less strongly concave with resulting laterally produced area. From this primitive condition the seventh segment appears to have undergone various modifications in different groups.

The connexival spines do not occur in Eotrechini and Charmatometrini, but do occur in the more primitive species of the more primitive genera of Gerrini and Cylindrostethini. The absence of connexival spines in the more specialized genera of the latter tribe of the Gerrinae simulate the condition found, e.g., in Eotrechus. In Eotrechus, however, the abdominal segments are generalized and long, while in the species without connexival spines in the Gerrini and Cylindrostethini the abdominal segments are strongly reduced.
The reduction of the abdominal segments are apparently correlated with progressive reduction of the connexival spines in Gerrini and Cylindrostethini. It is therefore likely that the connexival spines never occurred in the Eotrechini and probably also in Charmatometrini, and that the absence of the connexival spines in more specialized species of Gerrini and Cylindrostethini is due to secondary loss.

It is thus impossible to say simply that the absence or presence of the connexival spines is a primitive or specialized condition in the Gerridae; the absence or small size of the connexival spine in Gerrini and Cylindrostethini is evidently a specialized condition, but it is not necessarily so in the other two tribes. Possibly the most primitive condition is the absence of the connexival spines combined with a generalized abdominal form as seen in Eotrechus; this combination of characters has persisted in Eotrechini and Charmatometrini. After the acquisition of the connexival spines in the ancestral group of Gerrini and Cylindrostethini, however, the spines are again subject to loss.

The evolution of the seventh segment is somewhat different in the two sexes. The following descriptions are primarily at the subfamily level, and general problems, whenever encountered, are discussed here. More detailed discussion at the species level is given for each genus in the taxonomic section of this work.

The male: In Gerrinæ the connexival spines occur in the Limnometra-Tenagogonus s. str. complex, in the Limnogonus s. str.-Limnognellus complex, in Aquarius, Limnoporus, and in the Cylindrostethus-Potamobates complex. In these genera the connexival spines have become gradually obliterated with specialization of the abdominal segments. The prolongation of the seventh segment occurs, as in other subfamilies, in more specialized species of more generalized genera and in all species of more specialized genera. The degree of prolongation is indicated by the length of the seventh segment on the median ventral longitudinal axis in relation to that of the sixth segment. In the primitive Gerridae the median length of the ventral surface of the seventh segment is shorter than the sixth segment. The seventh segment has apparently become prolonged simultaneously with the reduction of the second to sixth ventral abdominal segments. This is seen at both the specific and generic levels within the subfamily Gerrinæ. The greatest prolongation of this segment has been attained in Amemboa, Chimarrrometra and Platygerris. In Aquarius, Gerris s. str., and in the
Cylindrostethini the ventral posterior margin of the seventh segment has become more and more emarginated at the middle with specialization (reduction) of the preceding abdominal segments. The two groups seem to share the same evolutionary potentialities in this respect and in retention of the connexival spines in more primitive species; in no other genera of Gerrinae does the median emargination on the ventral posterior margin occur. The process of modification of the seventh segment in the Limnometra-Tenagogonus s. str. complex is peculiar. In this group of subgenera the connexival spines also occur in species with more primitive abdomens. The spines are progressively reduced with specialization of the abdomen and become lost in certain highly specialized species. With further specialization of the preceding abdominal segments, there arise processes like the spines but more ventrally than the connexival spines. These structures migrate more and more ventrally and eventually are located near the median longitudinal axis of the abdomen.

In Ptilomerinae no conspicuous modification of the seventh segment has occurred in the males. The segment has been simply prolonged in more specialized species. The same applies to Rhagadotarsinae, Trepobatinae and Halobatinae. It should be noted, however, that in some species of Halobatinae a depression occurs on the basal region of the ventral surface, as in some genera of Gerrinae and Ptilomerinae.

The female: The connexival spines are more conspicuous in females than in males and are often retained in the female when they are completely lost in the male of the same species (e.g., some species of Limnometra, Gerris s. str., Tachygerris, etc.). The reduction of the connexival spines is in general parallel to that of the males, but is in general less than in males in the Gerrinae. The seventh abdominal segment has undergone no conspicuous modification besides the prolongation of the segment itself and the reduction of the connexival spines.

The degree of specialization of this segment is thus well indicated, in most genera, by the length of this segment, especially its ventral surface, in relation to the preceding segment. In some highly specialized genera such as Platygerris and Tachygerris, however, the ventral apical margin of the segment has been greatly modified while still retaining the distinct connexival spines, and the eighth segment is incompletely concealed beneath this development of the seventh segment. In some species of Eurygerris, such as E. car-
iniventris, the seventh segment is so greatly developed ventrolaterally that the apical region of the connexivum simulates the connexival spines of the more primitive genera. That this is a secondary formation is convincingly evidenced by the fact that no such projection occurs in the more primitive species of the same genus.

In ptilomerinae the seventh segment has undergone even more drastic modification. In such primitive forms as the subgenus Proptilomera of the genus Ptilomera, Rheumatogonus and Potamometropsis there occur no connexival spines and the posterolateral angle of the seventh segment is simply truncate. The absence of the connexival spines appears to be, therefore, a primitive condition in this subfamily. The posterolateral region of the seventh segment, where connexival spines occur in Gerrinae, has become highly modified in more specialized species of Ptilomera and in all other genera except the ones mentioned above. This modification often simulates the connexival spines in Gerrinae but it is not the same, since they occur in more specialized forms in which the seventh segment itself is more or less greatly prolonged. It is of the same secondary nature as that occurring in Eurygerris cariniventris. The process of modification of the posterolateral region of the seventh segment, though somewhat difficult to trace due probably to the much smaller numbers of species available for study, will be discussed elsewhere in the proper place for each genus. The ventral apical margin of the seventh segment is provided with a lobate projection in most genera including such primitive forms as Proptilomera and Rheumatogonus; it does not occur in Rhyacobates and Pleciobates(?).

In Rhagadotarsinae the seventh segment is simply prolonged and without the connexival spines and the ventral apical margin is simply concave. In Trepobatinae the apical projection of the same nature as that occurring in Eurygerris cariniventris occurs in Trepobates knighti, and the ventral apical margin is lobately produced in Metrobatopsis. In all other species of Trepobatinae the seventh segment is as in Rhagadotarsinae. In Halobatinae the connexival spines are absent, and the ventral apical margin is simply concave in all genera except for Metrocoris, in which a lobate development occurs on the ventral apical margin, telescoping the eighth segment above.

The lobate development of the ventral apical margin thus has occurred independently in some of the more specialized genera of
Gerrinae and Ptilomerinae, Metrocoris of Halobatinae and in Metrobatopsis and Rheumatometroides of Trepobatinae. The secondary lateral projections which simulate the connexival spines of the more primitive genera of Gerrinae apparently arose independently in Eurygerris of Gerrinae, in many species of Ptilomerinae and in one species of Trepobates of Trepobatinae.

The absence of the connexival spines on the seventh segment is a good tribal character in Gerrinae and a subfamily characteristic of Halobatinae, Rhagadotarsinae and Trepobatinae. The progressive median emargination on the ventral apical margin in males of some genera of Gerrinae, and the progressive development and migration of processes on the ventral apical margin in males of some other genera indicate the difference in evolutionary potentialities among these groups. The curious modification in females of the ventral apical margin in Platygerris, Tachygerris of Gerrinae, some genera of Ptilomerinae and in Metrocoris of Halobatinae provides good generic as well as specific characters. The absence of this modification even in specialized genera of Rhagadotarsinae and Trepobatinae suggests a difference from the other subfamilies in evolutionary potentialities.

The eighth abdominal segment

Since the female genitalia occur partly in this segment the evolution of this segment is discussed separately for each sex.

The male: The most important evolutionary tendency of the eighth segment is, as for the seventh segment, the prolongation of the segment itself. This is true of all groups of Gerridae. In some of the more primitive genera of Gerrinae, such as Eotrechus, Gigantometra, Limnoporus, Tenagometrella, Charmatometra and Eobates, the eighth segment itself has never become appreciably prolonged. In Brachymetra, Onychotrechus, Chimarrhometra and Amemboa, in which the seventh segment is not greatly modified in shape, the eighth segment also has never become much modified apart from its prolongation in more specialized species of these genera. A similar condition is also noted in Eurygerris and the Limnometra-Tenagogonus s. str. complex. In other genera of Gerrinae evolution has proceeded further, to the point where the ventral surface of the segment is more or less greatly modified. In Cylindrostethini the basal ventral region has become more and more depressed and the ventral apical margin has become progressively asymmetrical with the development of a process on one side of the apical margin;
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In the most highly specialized genus, *Platygerris*, the eighth segment is most prolonged in *P. caeruleus*. In this species it is, in fact, longer than all the preceding segments together. In *Aquarius* and *Gerris s. str.*, the ventral surface of the eighth segment has become more and more longitudinally elevated at the middle in the more specialized species. In the *Limnogonus s. str.-Limnogonellus* complex the ventral apical margin has become increasingly modified with formation of the processes of various shapes in the middle. In some species of *Tenagogonus s. str.* the ventral surface as well as the ventral apical margin have become curiously modified.

In Ptilomerinae the most primitive eighth segment is seen in *Rheumatogonus*, in which the segment is not even appreciably prolonged in the two species examined; in all other genera the segment has been considerably prolonged. At least in some species of *Ptilomera, Heterobates*, and *Rhyacobates* there occurs a depression on the basal region of the ventral surface, as in *Potamobates* and *Platygerris* of the Gerrinae. In these genera (*Heterobates* and *Rhyacobates*) there also occurs a median longitudinal elevation which is more pronounced apically as in *Aquarius* and *Gerris s. str.* of Gerrinae.

In Rhagadotarsinae the eighth segment is greatly prolonged and longitudinally sulcated in the middle in *Rhagadotarsus*, simply prolonged in *Rheumatobates*. In TREPobatinae the prolongation of the segment occurs in many genera, although in the more primitive species of some genera, like *Telmatometra* and *Trepobates*, the segment is not appreciably prolonged. In some more specialized genera the segment is more or less greatly modified, but neither basal depression nor the median longitudinal elevation on the ventral surface occurs in this subfamily. The direction of evolution is more or less peculiar to each genus; e.g., in *Hynesionella* the ventral surface has become elevated conspicuously laterally; in *Metrobatopsis* it is greatly prolonged and is provided with a wide triangularly depressed area in the apical region of the ventral surface; a similar but lesser development occurs in *Trepobatoides*; in *Halobatopsis* the ventral apical margin is greatly produced as a process in one species. In Halobatinae two pairs of processes, dorsolateral and ventrolateral, become more and more conspicuous through the Asclepios-Halobates series. In other genera there exists no such conspicuous modification, and the segment has simply become prolonged in most species.
The ninth abdominal segment

The ninth tergite (suranal plate) in the male: The primitive ninth tergite of the Gerridae was probably rather slender, and the lateral margins more or less parallel to one another as they are in the more primitive existing genera, such as Eotrechus, etc. From this probable primitive condition the tergite has undergone various modifications. In Gerrinae the suranal plate is simple or only feebly widened basally in most genera. Rather conspicuous modifications of the lateral margins are seen in Amemboa. In this genus the basal lateral processes have become more and more conspicuous in the more specialized species within the genus, and in some of the most specialized species there occurs an additional pair of processes inside the lateral pair of the spinous processes. In Onychotrechus and Chimarrhometra there occurs no conspicuous modification of the basal lateral margins of the suranal plate. In Gerrisella the ninth tergite is provided with a pair of conspicuous processes on the lateral margins. The most conspicuous modification of the suranal plate appears to have occurred in Cylindrostethini, in which the basal lateral margins have become greatly modified progressively with production of the asymmetrical processes on the lateral margins in the smaller, more specialized species of Cylindrostethus; and the final stage of modification of the suranal plate attained in the tribe is seen in Platygerris, in which the processes are strongly developed only on the right side and are very conspicuous.

In Ptilomerinae the plate is dilated behind its middle. The dilation becomes progressively more conspicuous in Ptilomera, from a more generalized, simpler condition in the subgenus Proptilomera through a series of species in Ptilomera s. str. In Halobatinae the process of modification of the basal to lateral regions of the suranal plate progresses from a relatively generalized condition in Asclepios to the highly modified conditions in some species of Halobates; while in other genera of Halobatinae no conspicuous modification exists. In Rhagadotarsinae the suranal plate is somewhat dilated but no conspicuous modification occurs. In Trepobatinae conspicuous modifications on the lateral margin exist in Metrobatopsis, Hynesionella, Rheumatometroides and Stenobates. Such modifications of the lateral margins of the suranal plate occur independently in the more specialized genera of all subfamilies except for Rhagadotarsinae.

Among the related genera, the presence or absence of the processes on the lateral margins constitutes a generic character. The
position and shape of the processes also give good taxonomic character at the specific level.

The parameres: The loss of the parameres has occurred independently in some or all genera of all subfamilies except for Ptilomerinae. In Cylindrostethini of Gerrinae the parameres have been virtually lost in the specialized genera, Potamobates and Platygerris, although they have been retained in Cylindrostethus. In Gerrini the parameres are not conspicuous even in the most primitive genus, Gigantometra. They are more or less greatly reduced or completely lost in the Aquarius-Gerris s. str. complex, in Limnopus, Eurygerris, the Limnometra-Tenagogonus s. str. complex, the Limnogonus s. str.-Limnognellus complex, Tachygerris, Tenagometrella, Tenagometra. In Eotrechini the parameres are well developed in Eotrechus, short but robust in Onychotrechus, and completely lost in Amemboa. An interesting fact is that the parameres are greatly developed in the otherwise highly specialized genus, Chimarrhometra. In the related genus Amemboa, however, the basal lateral region of the suranal plate is modified into a conspicuous process but the parameres are absent. The two structures are similar in shape and extend to about the same position, i.e., above the lateral margin of the pygophore. Presumably they replace one another functionally, since when either one is lost or poorly developed the other is well developed. A similar but quite different situation occurs in some species of Potamobates and Platygerris of Cylindrostethini, in which the suranal plate is asymmetrically modified into a spinous process on one side. This process comes in contact apically with an also asymmetrically produced spinous process from the eighth segment. What function these structures perform we do not know. Since in these genera the paramers have been lost, these structures may have something to do with copulation. In Charmatometrini the parameres are simple but retained in all known species.

In Ptilomerinae the parameres have been retained in all genera. Interestingly, the parameres have apparently undergone modification apically in Ptilomera as will be discussed in more detail elsewhere; in the subgenus Proptilomera the parameres are simple apically but in Ptilomera s. str. the apical portions of the parameres are bent and provided with a dense mass of shaggy hairs. In Halobatinae the parameres are distinctly retained in Asclepios, but are reduced and almost unrecognizable in the related, more specialized genus Halobates. In all other genera of this subfamily the parameres are retained and are even somewhat conspicuous. In
Rhagadotarsinae the parameres have been lost in both genera. In Trepobatinae the parameres are unrecognizable in *Metrobatopsis* and *Hynesionella* but in these genera there occurs a conspicuous modification on the basal lateral region of the suranal plate, forming a conspicuous process directed ventrad. In all other genera of Trepobatinae the parameres are conspicuous (*Stenobates* was not examined) or reduced but recognizable (*Rheumatometra*).

The evolutionary tendencies of the parameres in the Gerridae can be summarized as follows:

1. The parameres have had an overall tendency to be lost.
2. The parameres, when lost or reduced, appear to be replaced functionally by the development of the basal lateral region of the ninth tergite (suranal plate) in more specialized genera. This is true of *Amemboa*, *Gerrisella*, *Metrobatopsis*, and *Hynesionella*.
3. When the reduction of the parameres occurs in relatively primitive genera (*Gerrini*), the suranal plate is not modified to form the processes on the lateral margins.
4. With the loss of the parameres both the eighth and ninth tergites are asymmetrically modified (*Cylindrostethini*).
5. The parameres have had a tendency to become modified instead of becoming reduced in certain groups.
   a. In *Ptilomera*, modification of the parameres has had nothing to do with modification (dilation) of the basal lateral margin of the suranal plate into conspicuous process laterally. Both have evolved independently.
   b. In *Chimarrhometra* the parameres have become greatly enlarged, although in a related genus (*Amemboa*) the parameres are lost and the suranal plate is greatly modified.

The shape of the parameres, when present, offers an excellent specific character. The presence or absence of the parameres is constant in most genera.

*The Pygophore:* Prolongation is one of the most important aspects of evolution of the pygophore, as for the preceding segments, and this has occurred in all subfamilies. In highly specialized genera, such as *Potamobates* and *Platygerris* of the Gerrinae and in some species of *Halobates* of Halobatinae, the pygophore is rotated laterally (to the right). The rotation of the pygophore in these genera is always associated with production of more or less conspicuous asymmetrical processes on the suranal plate and the eighth abdominal segment (*Potamobates and Platygerris* of the Gerrinae), or with production of the asymmetrical processes on the ventral apical
margin of the eighth segment (some species of Halobates). A peculiar manner of rotation of the pygophore is noted in two species of Metrobatopsis of Trepobatinae, in which it is rotated anteriorly, instead of laterally, exposing the ventral side of the pygophore sub-vertically. Another feature of the evolution of the pygophore is the modification of its ventral surface and apical margin. The apical margin of the pygophore is very conspicuously modified in many species of Amemboa, Chimarrhometra (figs. 572, 591, 592, 593) and Rheumatotrechus (Kirkaldy, 1908). All these three genera belong to Eotrechini of the Gerrinae, suggesting a peculiar evolutionary potentiality for this particular feature in this tribe. In Ptilomera of the Ptilomerinae the progressive prolongation of the pygophore is conspicuous as will be described elsewhere. In other groups there is a trend for the apical margin of the pygophore, though usually not pronounced, to become more or less concave, and in Eury- metropsis of the Halobatinae the apical prolongation and bifurcation are very conspicuous. In a species of Metrocoris of Halobatinae the apical half is greatly dilated. The occurrence of a median spinous process on the longitudinal axis of the pygophore is a peculiar feature to Metrobatopsis.

The degree of rotation of the pygophore as well as the degree of modification of its apical margin varies considerably in various species within the same genus. Therefore, they are generally more important characters at the species-level than at the generic level.

The styloide: The styloide occurs only in Eotrechus; in all other species the structure has been lost. Whether the styloide in Heteroptera is homologous with the stylus in lower orders of insects or not is still uncertain. The presence of the styloide probably represents a primitive condition, since the structure tends to be either fused with the pygophore or lost in more specialized groups of the same family (e.g., Aradidae, Usinger and Matsuda 1959).

The endosoma (figures 102-104): In the primitive gerrids the number of well-differentiated sclerotized plates in the apical segment of the endosoma was probably three (dorsal, apical and lateral). This is evidenced by the condition in Eotrechus, in which the well sclerotized paired plates number three. Assuming that this is a probable primitive condition in the Gerridae, a general picture of evolution of the sclerotized plates of the endosoma is tentatively suggested in figures 102 to 104.

In hypothetically primitive gerrids each pair (apical, dorsal and lateral) is clearly separated. The next stage in evolution is the
acquisition of the small basal plates at the bases of the dorsal plates with the membranous ventral plates bearing the seminal duct (fig. 102). This condition is seen in some more generalized genera of Gerrinae, such as *Gigantometra*, *Aquarius*, etc. In these forms the definitive dorsal plate extends along the dorsal margin of the endosoma. The paired origin of the resultant plate is clearly indicated by the fact that it is split into two branches at both ends and is more strongly sclerotized on the lateral margins. The apical plate is bifurcate and is located along the apical margin of the endosoma. This plate is separated from the dorsal plate in more primitive genera, such as *Gigantometra*, *Eotrechus*, *Aquarius elongatus* and some genera of Trepobatinae; its paired nature is also well indicated by the condition in Eotrechini, in which paired apical plates are loosely connected to each other. The united definitive apical plate is fused with the definitive dorsal plate in the majority of species of Gerridae, so that what appears to be the dorsal plate is strongly turned backward on the apical margin of the endosoma (fig. 103). The basal plates, originally paired and separated from the dorsal plate, have become fused to the dorsal plate. It is important to point out that the absence of the basal plate is almost always accompanied by the absence of ventral plates. The ventral plates are also paired and appear to be primitively membranous as seen in more primitive species of *Aquarius* and *Limnometra*. A final stage of evolution of these plates is shown in figure 104. It has involved fusion and sclerotization of all four plates except the lateral plates, and the elongation of the resultant fused ventral plates. The lateral plates are always paired (sometimes two pairs present), or the plates are ill-defined, these plates having persisted in all genera.

With the above general picture of evolution of the various plates in the endosoma, the following more detailed processes in their evolution in each subfamily become more intelligible.

In Gerrini of the Gerrinae the apical plate is detached from the apex of the dorsal plate in more primitive forms, such as *Gigantometra*, *Aquarius elongatus*, but the apical plate appears to be fused to the dorsal plate forming an anteriorly directed thick and bifurcate apex of the definitive dorsal plate in most species of *Aquarius*, *Gerris s. str.*, *Limnometra*, *Tenagogonus s. str.*, *Limnogonus s. str.*, *Limnogonellus*, and *Tenagometra*. *Tachygerris* shows an interesting deviation in that the apical plate is clearly detached from the apex of the dorsal plate when it is present, but the tendency
is to become lost so that the apex of the dorsal plate reaches only to the middle of endosoma. The basal plate in this tribe is present in all genera. It is detached from the dorsal plate in some species of *Linmogonus*, while in other genera the basal plate is fused to the dorsal plate. The ventral plate is present in all genera of Gerrini. It is bilobed, indicating its paired origin in *Linnometra* and in some species of *Aquarius*, and it is largely membranous; in all others the ventral plates are fused and not bilobed. In the *Linnometra-Tenagogonus s. str.* complex the ventral plate, though always bilobed, tends to be more sclerotized in more specialized species. The lateral plates are always present although hard to recognize in some species, due to sclerotization along the ventral margin of the endosoma.

In Charmatometrini the apical plate is apparently fused to the dorsal plate, while the basal plate is detached from the dorsal plate in *Charmatometra bakeri*, but fused to the dorsal plate in *Brachymetra*. The original paired membranous ventral plates are completely fused and definitively single lobed, and moderately long.

In Eotrechini there is no well-developed sclerotized basal plate in any genus. The seminal duct appears to be borne on the highly membranous process arising directly from the base of the apical segment of the endosoma. This condition was observed in *Onychotrechus sakuntala* in this study. A well-formed ventral plate, supported basally by the well-developed basal plate, thus does not occur in this tribe. The apical plate is always large, rounded, and loosely connected to the apex of the dorsal plate. In *Amemboae* the apical plate is provided with a pair of processes on the ventral side. The lateral plates are always simple and paired, the ventral plate being highly membranous.

Among the genera of Cylindrostethini, the condition of *Cylindrostethus productus* is peculiar in that the only sclerotized plate is the dorsal plate. In another species of *Cylindrostethus* from the Eastern Hemisphere, *C. naiades*, the basal plate is separated from the dorsal plate and bears the membranous ventral plate. In the species of *Cylindrostethus* from the Western Hemisphere the basal plate is indistinguishably fused to the dorsal plate as in *C. naiades* from the Eastern Hemisphere. The lateral plates in the genus always consist of one pair. In *Potamobates* and *Platygerris* the ventral plate is always sclerotized and prolonged among various species. The lateral plates are often represented by two pairs of sclerotized plates.

In Ptilomerinae the definitive dorsal plate never extends beyond
the middle of the endosoma except for *Ptilomera* and *Potamometra*, in which it reaches the apical margin of the endosoma. The apical region of the dorsal plate in these two genera is very probably the fused apical plate. In some genera, e.g., *Rheumatogonus, Potamometroides, Rhyacobates* and *Potamometropsis*, the apical plate appears to have been lost and the apical end of the definitive dorsal plate represents the apical end of the veritable dorsal plate. In *Heterobates* the apical plate is connected laterally by a transverse bridge. The line of union of the basal plate to the dorsal plate is recognizable by the difference in degree of pigmentation between the two plates. In *Rheumatogonus* the basal plate is apparently loosely connected to the dorsal plate, and in this respect this genus is more primitive than the others. The originally paired ventral lobes are fused to form a single lobe, membranous at least apically in all genera except *Potamometra*, in which the ventral plate is darkly pigmented and very long. The lateral plates, when present, always consist of a single pair. The general evolutionary trend of the plates in this subfamily is toward the loss of the apical and lateral plates, while in no genus does the ventral plate retain the short bilobed form.

In Halobatinae the apical plate is presumably fused to the dorsal plate in all genera. The basal plate at its base is not fused to the dorsal plate in some species (*Esakia kuiterti, Ventidius werneri, Eurymetra natalensis, Halobates sobrinus*). The ventral plate is single lobed, long, and membranous apically. The lateral plates are sometimes consisting of two pairs (*Eurymetra natalensis*). A slender sclerotized loop embracing the dorsal plate occurs in *Eurymetra natalensis, Ventidius werneri, Esakia kuiterti*, and *Asclepios coreanus*. The major evolutionary trend of the various plates of the endosoma in this subfamily is toward fusion of the plates; loss of plates does not seem to have occurred as far as limited number of species examined indicates. The occurrence of the looped, slender sclerite is peculiar to this subfamily.

In Rhagadotarsinae the major trend is toward fusion of the plates. In both *Rhagadotarsus* and *Rheumatobates* the apical, dorsal, basal, and ventral plates are completely fused, forming a round ring within the endosoma; the lateral plates in this subfamily are small.

In Trepobatinae the major evolutionary trend involves the loss of the basal and ventral plates. One may question whether the absence of these plates arose directly from the condition found in *Eotrechus* of the Gerrinae or is a secondary loss. The evidence is
in favor of the latter alternative. First, in the related but generally more primitive subfamily Rhagadotarsinae, both plates, though completely fused, obviously exist; second, in relatively primitive genera of this subfamily (*Trepobates, Cryptobates, Trepobatoides*) as well as in a more specialized genus (*Hynesionella*) the basal and ventral plates are present. The apical plate is always present. It is not fused to the dorsal plate in *Metrobates* and *Halobatopsis* and is fused only by a narrow bridge to the dorsal plate in *Telnatometra*; in all other genera the apical plate is completely fused to the dorsal plate. The lateral plates are long and paired; sometimes they are hardly recognizable due to sclerotization of the endosoma.

**Prolongation of the apical segment of the endosoma:** Prolongation of the apical segment of the endosoma occurs in Gerrinae; in other subfamilies the prolongation is not pronounced. Apically the endosoma is not at all elongated in the primitive genus *Gigantometra* of the Gerrini. In *Aquarius* it is not prolonged in primitive species, such as *G. (A.) elongatus*, but lengthens progressively in a series of more specialized species as is shown in figures 212 to 216. The prolongation of the endosoma is also conspicuous in the *Limnogonus s. str.-Limnogonellus* complex and in *Eurygerris*. In *Charmatometrini* and *Eotrechini* there occurs no conspicuous lengthening of the endosoma. In *Cylindrostethini* the apical segment of the endosoma is prolonged in more specialized genera, such as *Potamobates* and *Platygerris*, but the prolongation in these genera appears to be of different nature from that occurring in Gerrinini in that the endosoma as a whole has been prolonged instead of merely its apical region.

Undoubtedly, the differences in shape of the various plates and presence or absence of certain plates provide excellent specific characters as in other families of Heteroptera. Although the number of species investigated in this study is limited for each genus and often the generic differences are not well marked, it is clear from the foregoing discussion that the general arrangement of the various plates and the evolutionary tendencies noted are more or less peculiar to each subfamily or tribe, and appear to be of taxonomic importance at the subfamilial and tribal levels. Certain peculiar features, *e.g.*, the tendency to lose the apical plate in *Tachygerris* seem to be characters of generic importance.

The female genitalia

A well-developed ovipositor, according to Reuter (1910), is primitive in Heteroptera. In the Gerridae the well-formed long ovipositor is present only in Rhagadotarsinae, in which it serves pre-
sumably for the insertion of the egg into the tissues of plants (Hungerford, 1954). Whether this peculiar development of the ovipositer in this subfamily of the Gerridae is a primary or secondary condition is not certain. In this subfamily the first and second valvulae are greatly prolonged in both genera, but the basic structural plan is the same as in other subfamilies of the Gerridae; the rami of the first and second valvulae are connected to the black subtriangular plate at the apex of the process of the ninth tergite; the second valvifer as well as the third valvulae have been lost as in other subfamilies. In all other subfamilies of the Gerridae the first and second valvulae are less developed than in Rhagadotarsinae. The first valvulae either are not differentiated into the outer and inner lobes or are so differentiated only apically, if at all, in Ptilomerinae. In Gerrinae, Halobatinae, and Trepobatinae they are well differentiated into outer and inner lobes and the latter are usually attached to the vulva; the inner lobe is further split into two slender apical processes in many genera of Trepobatinae, and this is probably a specialized condition. The ramus is attached to a black elongate sclerite above the apex of the process from the ninth tergite in Rhagadotarsinae. This sclerite has apparently reduced to assume a crescent shape in at least some genera of all the other subfamilies, and has been completely lost in many genera. The ramus of the first valvulae has shifted its point of attachment to the outer margin of the usually membranous process arising from the ninth tergite. The ramus of the first valvula is indistinguishably fused to the process in many genera but is often recognizable by different degrees of pigmentation in Ptilomerinae and Trepobatinae.

The second valvulae are pointed apically, forming a complete sheath above the first valvulae in Rhagadotarsinae. In all other subfamilies the valvulae are apically free from each other, connected by the intervalvular membrane. The apex of each valvula usually extends beyond the apical margin of the intervalvular membrane. The ramus is always slender, apparently shifted its position to the inner margin of the thicker ramus of the first valvula accompanied by the loss of the second valvifer. The vestigial third valvulae are retained only in Charmatometrini of Gerrinae. The apical margin of the intervalvular membrane is highly sclerotized in Cylindrostethini, although it is membranous or thinly sclerotized in the other tribes of Gerrini and other subfamilies of Gerridae.

In spite of a limited number of species studied it seems clear that the female genitalia offer excellent taxonomic characters at the subfamilial or tribal level.
The forewing

The most complete, hence the most primitive forewing venation is found in *Ptilomera, Rheumatogonus*, and *Rhyacobates* of Ptilomerinae (figs. 612, 740), in which Sc is well retained without forming the embolium along the costal margin of the wing. Veins R + M and Cu arise independently from very near the base of the wing; R + M joins Sc at the apical one fifth of the wing; Cu is joined with R + M before the middle of the wing by a cross vein. A joins with Cu in their apical thirds. In *Potamometra* (fig. 645) of the same subfamily, R + M and Cu are completely fused basally, R + M + Cu branches into upper R + M and lower Cu at the basal one third of the wing, R + M further diverges into R and M respectively, and each is connected with Sc and Cu apically.

While Sc₂ arises always from near the middle of the costal margin of the wing, the point of separation of the basal R + M into R and M shifts more and more distally in specialized genera of Gerrinae, and this shift of point of separation has evidently occurred independently in three different tribes, *i.e.*, Gerrini, Eotrechini, and Cylindrostethini.

In Gerrini the point of separation of R and M in the most primitive genera (*Gigantometra, Aquarius, Gerris s. str., Limnoporus, Limnometra, Tenagogonus s. str.*, most species of *Limnogonus s. str.*, and *Limnogonellus* and one specialized genus *Gerrisella*) is near the middle of the hemelytron, a point more distal to the point of separation in *Potamometra* of Ptilomerinae, while the point of separation of R and M is more caudal in one specialized genus (*Eurygerris*) and in *Tachygerris*, which deviates in some other characters. In Cylindrostethini the point of separation of R and M is near the middle of the hemelytron as in most genera of Gerrini (fig. 428), but in the specialized genera, *Potamobates* and *Platygerris*, the point of separation of R and M from the basal R + M is much more distal (figs. 463, 484). In Eotrechini the point of separation of R and M is near the middle in two more primitive genera, *Eotrechus* and *Onychotrechus*, but the point of separation is definitely much more distal in a more specialized genus, *Amemboa* (fig. 584), than in the two other genera.

Because of this trend the vein Sc₂ becomes united with R + M at the point anterior to the point of separation into R and M in the above mentioned specialized genera. In Charmatometrini, however, the point of separation of R and M is near the middle of the hemelytron and Sc₂ is joined very near or at the point of separation
of R and M in all three genera, as in the primitive genera in the other three tribes. The process of evolution of the veins discussed above is thus beautifully traceable from the most primitive condition in the three genera of Ptilomerinae to the most specialized condition in some specialized genera in Gerrinae, and the mechanism involved is simply the greater degree of fusion of R, M, and Cu veins.

In Halobatinae the wing venation is further reduced and the fusion is more advanced. The embolium is always formed along the costal margin of the hemelytron. In Metrocoris (fig. 779) R + M + Cu is distinct and branches into R + M and Cu; R + M is connected with the embolium by two oblique veins; Cu is connected with A at the apical third of the hemelytron. In Ventidius (fig. 821) the basal region of R + M + Cu is obliterated and the proximal oblique vein connecting the embolium and R + M is lost. In Esakia (fig. 855) the venation is further simplified. Vein R + M + Cu branches into two long simple veins anterior to the middle of the wing, the upper branch going along the costal margin of the wing nearly to the apex and lower vein also, after being joined by A at the middle, extends to the apical margin of the wing. Among Rhagadotarsinae, the venation is similar to that of typical Gerrinae in the genus Rhagadotarsus (fig. 886) except that R + M does not branch into R and M apically, a condition more specialized for these veins than in some most specialized genera of Gerrinae; oblique Sc, the obscure short vein connecting the rear margin of the hemelytron at the middle with A, and Cu are all present. In Rheumatobates the venation is further reduced. The vein A does not continue beyond the middle of the wing and is not joined to Cu. An important feature is a line of weakness which is indicated by a slightly pigmented or white transverse line extending to the middle from the apical margin of the hemelytron in both genera of this subfamily. This line of weakness is limited basally by the vertical line of weakness at a little behind the middle of the wing in Rheumatobates. In Trepobatinae the basal region of the hemelytron is strongly coriaceous, with a well-developed embolium which never extends beyond the basal coriaceous region. The basal coriaceous region occupies only the basal third of the hemelytron in some genera (Metrobatopsis, Naboandelus); R + M + Cu divides into two branches, R + M and Cu. The former is joined to the broad embolium at its apical corner and is continuous nearly to the apex of the hemelytron. The latter joins A beyond the middle of
the hemelytron, then extends apically in most genera. The transverse line of weakness occurs in all genera as in Rhagadotarsinae, suggesting a common ancestry.

Because of its stability, the wing venation in Gerrinae offers excellent subfamily characters. In some genera of Gerrinae, Sc₂ is often joined with R + M before the point of separation into R and M; this varies within genera and is even subject to individual variation in some species, so that this feature may be neither a generic nor a species character. Both in very primitive and highly specialized genera the location at which Sc₂ joins to R + M or R is highly constant and can be of taxonomic importance at the generic level. In Ptilomerinae the venation seems to be a little more variable than in Gerrinae at the generic level. In Halobatinae the venation seems to be of taxonomic importance at the generic level. In Rhagadotarsinae the venation is evidently an important taxonomic character at the generic level. The coriaceous basal region and the broad embolium are characteristics of the subfamily Trepobatinae. As far as the venation is concerned there appears to be very little difference among genera of this subfamily. The occurrence of the transverse line of weakness in the hemelytron in Rhagadotarsinae and Trepobatinae is correlated with the nature of the definitive intersegmental suture between the mesonotum and metanotum occurring only in these two subfamilies.

II. Evolution of the Legs and Antenna

1. Postembryonic development

During the study of structural evolution it became increasingly apparent that the proportional lengths of leg and antennal segments have been altered with change in body size in evolution. This was suspected to be a case of allometry. The next step taken, therefore, was to study the postembryonic development of representative species of each major group to see whether proportional lengths of antennal and leg segments vary ontogenetically in the same manner as they appear to vary phylogenetically among adults of different sizes.

The materials available for study were Metrocoris histrio (Buchanan-White) (Halobatinae) which was kindly sent to me by Professor S. Miyamoto, Japan; Gerris (Aquarius) remigis Say, Gerris (Gerris) marginatus Say (Gerrinae), Trepobates knighti Drake and Harris (Trepobatinae), all collected at Lone Star Lake, near Lawrence, Kansas, and Rheumatobates rileyi palosi Blatchley collected
at a pond on the campus of The University of Kansas by the author. The number of individuals of each stage was sometimes insufficient, but at least a few individuals of each stage were available for study, as noted from table 1.

It was observed that the lengths of antennal and leg segments were more constant than the body size among individuals at each stage. The lengths of the segments are, therefore, more reliable criteria in deciding stages of development than the body size. The inconstancy of the body size at each developmental stage may possibly be due to the fact that different sexes are contained in the materials. In Rheumatobates rileyi palosi *, for which only the female individuals were measured, the body size and the segmental lengths appeared to be more highly correlated than in the other species. Clerk and Hersh (1939) found recognizable sexual and individual differences in relative growth ratios of appendages to the body size in Notonecta. It should be added that the five individuals of the first stage nymph of Gerris (Aquarius) remigis studied may, by sampling error, be represented by relatively large individuals only.

Relative growth: In 1924 J. Huxley put forward an exponential formula which expresses, by means of abstract values, the rate of growth of any one allometrically growing organ (Y) in relation to the total body size or to another organ whose growth is taken as standard (X). The formula is thus $Y = bX^k$ where b is the initial growth index, or the value of Y when X equals unity, and k is the equilibrium constant by which Y grows in relation to X throughout the ontogenetic stages. This constant is also called the growth ratio and this term is used in the following discussion.†

The assumption, implicit in the application of the formula to data, is that differences in size correspond to differences in developmental stage. Hemimetabolous insects such as the gerrids are extremely favorable for the study of relative growth, since in these insects comparable stages (instars) are well marked off and the structures do not undergo drastic modification until the adult stage is reached. Taking the total length of the body as the standard X, and using the lengths of the front, middle, and hind leg segments, as well as antennal segments for the differentially growing parts Y at each developmental stage, the data were fitted to the formula $Y = bX^k$ (From this formula is derived: $\log Y = \log b + k\log X$; this

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* Sexual dimorphism is evident even at the first stage in this species.
† Since the correlation coefficients between the length of body and segments are over 0.99 in the great majority of cases in this study, Imbrie's (1956) bivariate statistical technique is not used.
### Table 1.—Mean values of the body length, antenntal and leg segments.

*Gerris (Aquarius) remigis* Say

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<thead>
<tr>
<th>Stage</th>
<th>No. of individuals</th>
<th>Length of body</th>
<th>Antenntal segments</th>
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<th>Middle leg</th>
<th>Hind leg</th>
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<td>12.9</td>
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Table 1.—Mean values of the body length, antennal and leg segments.—Continued

*Gerris (Gerris) marginatus* Say

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### Table 1—Mean values of the body length, antennal and leg segments—Continued

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<td>Adult g</td>
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<td>34.2</td>
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**Study of the Gerridae of the World**
Table 1.—Mean values of the body length, antennal and leg segments.—*Continued*

*Rhematobates rileyi palosi* Blatchley

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<tr>
<th>Stage</th>
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<th>Length of body</th>
<th>Antennal segments</th>
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<td></td>
<td></td>
</tr>
<tr>
<td>5 ♂</td>
<td>9</td>
<td>91.4 (90-93)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult ♂</td>
<td>5</td>
<td>109.0 (106-111)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage</td>
<td>No. of individuals</td>
<td>Length of body</td>
<td>Antennal segments</td>
<td>Front leg</td>
<td>Middle leg</td>
<td>Hind leg</td>
</tr>
<tr>
<td>-------</td>
<td>-------------------</td>
<td>----------------</td>
<td>-------------------</td>
<td>-----------</td>
<td>------------</td>
<td>----------</td>
</tr>
<tr>
<td>1</td>
<td>10</td>
<td>35.4 (30.6-40.0)</td>
<td>4.3   2.8   3.1   6.7</td>
<td>7.2</td>
<td>6.8</td>
<td>4.4</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>48.2 (42.0-51.5)</td>
<td>6.0   3.7   3.9   8.1</td>
<td>10.6</td>
<td>9.7</td>
<td>5.5</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>65.0 (60.0-70.0)</td>
<td>8.9   5.3   6.2   10.5</td>
<td>15.4</td>
<td>12.6</td>
<td>7.8</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>85.9 (77.0-93.0)</td>
<td>13.0  8.1   8.9   13.2</td>
<td>22.4</td>
<td>18.5</td>
<td>10.3</td>
</tr>
<tr>
<td>5♂️</td>
<td>8</td>
<td>113.38 (101-119)</td>
<td>21.3  12.1  13.9  18.1</td>
<td>36.0</td>
<td>28.0</td>
<td>15.1</td>
</tr>
<tr>
<td>5♀️</td>
<td>6</td>
<td>123.2 (115-128)</td>
<td>20.6  12.2  13.4  18.9</td>
<td>32.2</td>
<td>27.0</td>
<td>16.2</td>
</tr>
<tr>
<td>Adult ♂</td>
<td>10</td>
<td>129.7 (125-132)</td>
<td>36.2  19.1  20.0  20.7</td>
<td>53.3</td>
<td>38.1</td>
<td>19.8</td>
</tr>
<tr>
<td>Adult ♀</td>
<td>5</td>
<td>146.6 (142-150)</td>
<td>29.9  17.7  19.8  21.0</td>
<td>47.6</td>
<td>34.4</td>
<td>21.0</td>
</tr>
</tbody>
</table>
Table 2.—The values of the constants of the relative growth function.

_**Gerris (Aquarius) remigis Say**_

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>$S^2$</th>
<th>b</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st antennal segment</td>
<td>1.2166</td>
<td>0.0060</td>
<td>-1.2487</td>
<td>0.0026</td>
</tr>
<tr>
<td>2nd antennal segment</td>
<td>1.1352</td>
<td>0.0025</td>
<td>-1.3661</td>
<td>0.0010</td>
</tr>
<tr>
<td>3rd antennal segment</td>
<td>0.9423</td>
<td>0.0045</td>
<td>-0.8875</td>
<td>0.0020</td>
</tr>
<tr>
<td>4th antennal segment</td>
<td>0.5329</td>
<td>0.0019</td>
<td>0.1100</td>
<td>0.0008</td>
</tr>
<tr>
<td>Front femur</td>
<td>1.2032</td>
<td>0.0010</td>
<td>-0.9614</td>
<td>0.0005</td>
</tr>
<tr>
<td>Front tibia</td>
<td>1.1256</td>
<td>0.0012</td>
<td>-0.8307</td>
<td>0.0004</td>
</tr>
<tr>
<td>Front tarsus</td>
<td>1.0417</td>
<td>0.0060</td>
<td>-1.0810</td>
<td>0.0003</td>
</tr>
<tr>
<td>Middle femur</td>
<td>1.2258</td>
<td>0.0019</td>
<td>-0.5980</td>
<td>0.0006</td>
</tr>
<tr>
<td>Middle tibia</td>
<td>1.0673</td>
<td>0.0016</td>
<td>-0.3120</td>
<td>0.0009</td>
</tr>
<tr>
<td>Middle tarsus</td>
<td>0.8260</td>
<td>0.0052</td>
<td>-0.0420</td>
<td>0.0023</td>
</tr>
<tr>
<td>Hind femur</td>
<td>1.2191</td>
<td>0.0067</td>
<td>-0.1149</td>
<td>0.0030</td>
</tr>
<tr>
<td>Hind tibia</td>
<td>1.3997</td>
<td>0.0049</td>
<td>-0.7914</td>
<td>0.0022</td>
</tr>
<tr>
<td>Hind tarsus</td>
<td>0.9247</td>
<td>0.0042</td>
<td>-0.5064</td>
<td>0.0019</td>
</tr>
</tbody>
</table>

_**Gerris (Gerris) marginatus Say**_

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>$S^2$</th>
<th>b</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st antennal segment</td>
<td>0.9219</td>
<td>0.0018</td>
<td>-0.6928</td>
<td>0.0007</td>
</tr>
<tr>
<td>2nd antennal segment</td>
<td>0.8855</td>
<td>0.0016</td>
<td>-0.8703</td>
<td>0.0006</td>
</tr>
<tr>
<td>3rd antennal segment</td>
<td>0.7914</td>
<td>0.0052</td>
<td>-0.6643</td>
<td>0.0020</td>
</tr>
<tr>
<td>4th antennal segment</td>
<td>0.4924</td>
<td>0.0034</td>
<td>0.3523</td>
<td>0.0013</td>
</tr>
<tr>
<td>Front femur</td>
<td>0.8764</td>
<td>0.0059</td>
<td>-0.3560</td>
<td>0.0023</td>
</tr>
<tr>
<td>Front tibia</td>
<td>0.8259</td>
<td>0.0042</td>
<td>-0.2979</td>
<td>0.0016</td>
</tr>
<tr>
<td>Front tarsus</td>
<td>0.6509</td>
<td>0.0042</td>
<td>-0.4230</td>
<td>0.0016</td>
</tr>
<tr>
<td>Middle femur</td>
<td>1.0104</td>
<td>0.0032</td>
<td>-0.2518</td>
<td>0.0012</td>
</tr>
<tr>
<td>Middle tibia</td>
<td>0.8223</td>
<td>0.0009</td>
<td>0.0569</td>
<td>0.0004</td>
</tr>
<tr>
<td>Middle tarsus</td>
<td>0.7060</td>
<td>0.0027</td>
<td>0.1574</td>
<td>0.0010</td>
</tr>
<tr>
<td>Hind femur</td>
<td>1.0350</td>
<td>0.0028</td>
<td>-0.3030</td>
<td>0.0011</td>
</tr>
<tr>
<td>Hind tibia</td>
<td>0.9620</td>
<td>0.0017</td>
<td>-0.4399</td>
<td>0.0006</td>
</tr>
<tr>
<td>Hind tarsus</td>
<td>0.6620</td>
<td>0.0020</td>
<td>-0.0447</td>
<td>0.0008</td>
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</table>

_**Metrocoris histrio (Buchanan-White)**_

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>$S^2$</th>
<th>b</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st antennal segment</td>
<td>2.1900</td>
<td>0.0032</td>
<td>-3.0220</td>
<td>0.0014</td>
</tr>
<tr>
<td>2nd antennal segment</td>
<td>1.6240</td>
<td>0.0083</td>
<td>-2.1390</td>
<td>0.0035</td>
</tr>
<tr>
<td>3rd antennal segment</td>
<td>1.2490</td>
<td>0.0029</td>
<td>-1.3519</td>
<td>0.0012</td>
</tr>
<tr>
<td>4th antennal segment</td>
<td>0.7840</td>
<td>0.0032</td>
<td>-0.3850</td>
<td>0.0014</td>
</tr>
<tr>
<td>Front femur</td>
<td>1.5196</td>
<td>0.0056</td>
<td>-1.4726</td>
<td>0.0024</td>
</tr>
<tr>
<td>Front tibia</td>
<td>1.5050</td>
<td>0.0027</td>
<td>-1.5076</td>
<td>0.0011</td>
</tr>
<tr>
<td>Front tarsus</td>
<td>1.2010</td>
<td>0.0069</td>
<td>-1.1470</td>
<td>0.0029</td>
</tr>
<tr>
<td>Middle femur</td>
<td>1.5596</td>
<td>0.0195</td>
<td>-1.2020</td>
<td>0.0054</td>
</tr>
<tr>
<td>Middle tibia</td>
<td>1.4210</td>
<td>0.0157</td>
<td>-0.9600</td>
<td>0.0067</td>
</tr>
<tr>
<td>Middle tarsus</td>
<td>0.6720</td>
<td>0.0171</td>
<td>0.5260</td>
<td>0.0072</td>
</tr>
<tr>
<td>Hind femur</td>
<td>1.6170</td>
<td>0.0073</td>
<td>-1.3026</td>
<td>0.0031</td>
</tr>
<tr>
<td>Hind tibia</td>
<td>1.7820</td>
<td>0.0035</td>
<td>-1.8426</td>
<td>0.0015</td>
</tr>
<tr>
<td>Hind tarsus</td>
<td>0.7340</td>
<td>0.0064</td>
<td>-0.1805</td>
<td>0.0027</td>
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</table>
Table 2.—The values of the constants of the relative growth function.—Concluded.

Trepobates knighti Drake and Harris

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>$S^2$</th>
<th>b</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st antennal segment</td>
<td>1.5780</td>
<td>0.0199</td>
<td>-1.8832</td>
<td>0.0076</td>
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<tr>
<td>2nd antennal segment</td>
<td>1.4525</td>
<td>0.0139</td>
<td>-1.8590</td>
<td>0.0053</td>
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<tr>
<td>3rd antennal segment</td>
<td>1.4321</td>
<td>0.0075</td>
<td>-1.7760</td>
<td>0.0029</td>
</tr>
<tr>
<td>4th antennal segment</td>
<td>0.8196</td>
<td>0.0057</td>
<td>-0.4590</td>
<td>0.0022</td>
</tr>
<tr>
<td>Front femur</td>
<td>1.4985</td>
<td>0.0066</td>
<td>-1.4980</td>
<td>0.0025</td>
</tr>
<tr>
<td>Front tibia</td>
<td>1.3032</td>
<td>0.0052</td>
<td>-1.2150</td>
<td>0.0020</td>
</tr>
<tr>
<td>Front tarsus</td>
<td>1.1590</td>
<td>0.0038</td>
<td>-1.0900</td>
<td>0.0012</td>
</tr>
<tr>
<td>Middle femur</td>
<td>1.1780</td>
<td>0.0014</td>
<td>-0.6822</td>
<td>0.0005</td>
</tr>
<tr>
<td>Middle tibia</td>
<td>1.2970</td>
<td>0.0012</td>
<td>-0.6665</td>
<td>0.0005</td>
</tr>
<tr>
<td>Middle tarsus</td>
<td>1.0863</td>
<td>0.0056</td>
<td>-0.4325</td>
<td>0.0021</td>
</tr>
<tr>
<td>Hind femur</td>
<td>1.4707</td>
<td>0.0017</td>
<td>-1.1575</td>
<td>0.0007</td>
</tr>
<tr>
<td>Hind tibia</td>
<td>1.0523</td>
<td>0.0043</td>
<td>-0.6150</td>
<td>0.0015</td>
</tr>
<tr>
<td>Hind tarsus</td>
<td>0.9611</td>
<td>0.0007</td>
<td>-0.5600</td>
<td>0.0003</td>
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</tbody>
</table>

Rheumatobates rileyi palosi Blatchley

<table>
<thead>
<tr>
<th></th>
<th>k</th>
<th>$S^2$</th>
<th>b</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle femur</td>
<td>1.1396</td>
<td>0.0022</td>
<td>-0.4820</td>
<td>0.0004</td>
</tr>
<tr>
<td>Middle tibia</td>
<td>1.1660</td>
<td>0.0008</td>
<td>-0.5960</td>
<td>0.0002</td>
</tr>
<tr>
<td>Middle tarsus</td>
<td>1.0160</td>
<td>0.0014</td>
<td>-0.4200</td>
<td>0.0003</td>
</tr>
<tr>
<td>Hind femur</td>
<td>1.2587</td>
<td>0.0014</td>
<td>-0.6620</td>
<td>0.0003</td>
</tr>
<tr>
<td>Hind tibia</td>
<td>1.0440</td>
<td>0.0006</td>
<td>-0.6510</td>
<td>0.0001</td>
</tr>
<tr>
<td>Hind tarsus</td>
<td>0.8033</td>
<td>0.0007</td>
<td>-0.5600</td>
<td>0.0003</td>
</tr>
</tbody>
</table>

means that if the logarithms of the sizes are plotted we should expect a straight line, from the slope of which the value of $k$ can also be determined). The values $b$ and $k$ thus obtained are shown in the table 2 (all the data are weighted by the sample sizes at each developmental stage).

In figure 108 four antennal segments ($Y$) and the length of body ($X$) in Metrocoris histrio are logarithmically plotted. It is noted that they conform approximately to the law of simple allometry. Note the nearly straight line as far as the fifth nymphal stage, with a decline in slope at the final stage of development for all four segments. Note also that the broken lines, which indicate the development of the segments in the female, decline more from the fourth developmental stage on. Similar conditions are also noted for all other leg and antennal segments in all species studied, as will be immediately noted from the figures 109, 110, etc.
Simple allometry in the strict sense, i.e., exactly the same growth ratio throughout developmental stages for each segment, apparently does not exist. Differences in growth ratio at different stages sometimes appear to be considerable. It is, however, an overall growth slope throughout the postembryonic developmental stages for each segment as expressed by the regression line and the regression coefficient (the value of k in terms of the allometric equation) that are the primary concern here, so that the growth pattern for each segment at each developmental stage is not analyzed.

It should be pointed out, however, that there is either increase or decrease in growth ratio at the final stage of development for almost all segments in all species studied. The increase occurs consistently in *Trepobates knighti* (fig. 110, etc.) and *Rheumatobates rileyi palosi* (fig. 141, etc.), and the decrease occurs consistently in the two species of *Gerris* studied and in *Metrocoris histrio* (fig. 108, etc.). The data as well as figures consistently indicate that the growth ratio is greater for the males than for the females during the later stages of development for all segments.

Among other aquatic Hemiptera, Clark and Hersh (1939) have shown the existence of approximately single phase allometry in *Notonecta*. Sprague's (1956) study on the postembryonic development of structures in *Hydrometra martini* also indicates the presence of a roughly single phase allometric growth for various structures including legs, although she did not discuss it fully in terms of allometry.

The comparison of growth ratios: The comparison of the relative growth ratios among different segments is shown in table 3. In the table the signs > or < indicate the relation in which the growth ratios between the two comparable segments are significantly different (*P*<0.05 or higher); ≥ or ≤ indicate the relation in which the relative growth ratios between the two segments are different at the level of 0.1>*P*>0.05; = indicates the relation where the growth ratios of the two segments are different at the level of *P*>0.1.

Since the number of individuals measured at each developmental stage is different at different stages and different species, the mean values of body and segmental lengths are used in calculating growth ratios and initial growth indices. Therefore, N = 6 in using the above formulae. If the measurements for all individuals (e.g., when the numbers of individuals at different stages are the same), instead of mean values at each stage, were calculated the value of N increases, and the value of $S^2$ decreases accordingly. It should
Table 3.—Comparison of growth ratio among segments.*

<table>
<thead>
<tr>
<th></th>
<th>G. remigis</th>
<th>G. marginatus</th>
<th>M. histrio</th>
<th>T. knighti</th>
<th>R. rileyi palosi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antenna</td>
<td>1=2&gt;3&gt;4</td>
<td>1=2&gt;3&gt;4</td>
<td>1&gt;2&gt;3&gt;4</td>
<td>1=2&gt;3&gt;4</td>
<td></td>
</tr>
</tbody>
</table>

* To see the difference in initial growth indices and growth ratios t-test were used. The formulae are:

\[ S_{b} = \sqrt{\frac{\sum d^{2}y_{x}}{N - 2}} \]

\[ S_{y} = \sqrt{\frac{\sum d^{2}y_{x}}{N - 2}} \]

therefore be borne in mind in reading the following discussion that the significance levels would be higher than those indicated in the table 3, if the latter method were used in calculation.

Different micrometer units were used for measurements of leg and antennal segments in Trepobates knighti, Rheumatobates rileyi palosi and Metrocoris histrio from those used for the same in the two species of Gerris, so the b values between the two groups are not comparable.

2. Evolution of the leg and antennal segments in adult phylogeny

Westoll (1950) classified several different types of relative growth as follows:

(a) ontogenetic relative growth (heterauxesis), and
(b) absolute size allometry (allomorphosis) of essentially adult material, of several kinds, e. g.,
(i) members of different contemporaneous stocks or races of species (race allomorphosis)
(ii) members of different species of the same genus, without paying attention to difference (usually small) in geological age (species-form allomorphosis, and similarly genera-form allomorphosis, etc.)
(iii) members of a lineage, showing progressive change in size, and of known relative geological age (lineage allomorphosis).

The problem here investigated, as already noted, is primarily to see how the ontogenetic relative growth (heterauxesis) relates to
adult phylogeny, or species-form allomorphosis and genera-form allomorphosis in the above classification by Westoll. If different species of the same genus have essentially similar allometric growth patterns, e.g., for the leg and antennal segments, the points representing the lengths of segments in adults would be expected to be on or close to the growth lines for the corresponding segments in a representative species for which ontogenetic data are available. The locations of points on or along the growth lines would depend on different body sizes reached by different species. The regression lines for different segments of more than one species (often many) of adults would be on or closely parallel to the growth lines for the corresponding segments. The line based on more than one species of adults is here called the allomorphic line, and the allomorphic slope refers to the slope of such a line in distinction from the growth line and growth slope respectively. While the regression lines for many congeneric adult species (allomorphic lines) more or less conform to the growth lines in direction, they sometimes deviate greatly from the growth lines due to specific differences in the allometric growth mechanisms. Allomorphic lines and slopes of this nature are called the secondary allomorphic lines and slopes (fig. 147, B. to F., indicated by a) in distinction from the former type of allomorphic lines and slopes.

The allomorphic line expressed by the regression line also does not always indicate the underlying growth pattern or the secondary allomorphic trend, since the points for the segments tend to aggregate within a certain area when the range of body size is small. It does indicate the underlying growth pattern or the secondary allomorphic trend only when the range of body size among species is sufficiently great and the body sizes are distributed more or less evenly. The allomorphic trend seen in the relations between the segments and the body size in the species with extreme body sizes within a given group of species has, therefore, often more biological meaning than the allomorphic line based on the regression line.

In the following discussion often incomplete data based on the highly limited numbers of museum specimens, and the literature treating the postembryonic development of the body size, legs and antennae (also based on more or less highly limited numbers of individuals, and the number of individuals measured often not recorded) are referred to. These data are, by their very nature, not highly reliable. They were, however, used to see over-all growth patterns for the structures concerned, and they often gave
clues in interpreting what has probably happened to these structures in evolution of various groups of the Gerridae. After the completion of this work I had a chance to collect the nymphs and adults of sixteen species representing eight genera of the Gerridae in Costa Rica and Panama. They are now under study and the data cannot be fully included in this work. The preliminary data obtained from the study of these species, however, are occasionally referred to in the following discussion. In any case the interpretations or suggestions based on the incomplete data need to be verified in the future.

The length of antennal and leg segments of adults are based on one individual of each species taken at random from the museum specimens. They are shown in table 16. For many species only a single specimen or highly limited number of specimens were available.

The antennae

Gerrini: In fig. 111 are shown the postembryonic growths of the first and fourth antennal segments in the two species of Gerris studied, together with data for the same two segments in adults of the other species of Gerris (smaller points for different nympha1 stages). The round black spots representing the first antennal segments in the various species of the subgenus Aquarius conform fairly well in slope to the growth line for the same segment in G. (A.) remigis. Most of the triangular points representing the various species of the subgenus Gerris s. str. also conform fairly well to the growth line for the first segment in G. (G.) marginatus. The allomorphic lines for both subgenera rather clearly reflect a difference in growth ratio for the first segment between the two subgenera (1.2166 and 0.9219 in G. (A.) remigis and G. (G.) marginatus respectively, different at the level of P<0.05).

There is no statistically significant difference in growth ratios for the fourth segment in the two species studied. This suggests that there would be no significant difference in the allomorphic slope for this segment if similar growth ratios have been inherited in the species of both subgenera. The points representing the fourth segments in adults of both subgenera continually fall below and along the growth line for this segment in the two species of Gerris, indicating that the growth ratio for the fourth segment is presumably much the same in all species belonging to two subgenera. The fourth segment in G. (G.) marginatus practically does not grow at the final stage of development and the same may probably be true
of other species, judging from the positions of the points which come considerably below the growth line for the same segment in *G. (G.) marginatus*.

Since the growth ratios for the first segments are much greater than those for the fourth, and the growth ratios for the fourth segments are much the same in the two species belonging to different subgenera, the first segment is relatively longer than the fourth in the larger species (*Aquarius*) and relatively shorter in the smaller species (*Gerris s. str.*). Similarly, since growth ratio for the second segment is considerably greater than that for the third segment in *Gerris (Aquarius) remigis* (0.05 > P > 0.002), it is expected that the second segment is relatively longer in the larger species than in the smaller species, assuming that similar growth patterns for these two segments have been inherited by the other species of *Aquarius*. This assumption appears to be true. It is noticed from table 16 that in a majority of species of *Aquarius* the second segment is distinctly longer than the third, and the second segment is longest (in relation to the third) in the largest species, *G. (A.) elongatus* Uhler. In contrast, there is no statistically significant difference in growth ratios between the second and third segments in *G. (Gerris) marginatus*, and the second segment is about as long as the third in a majority of species of the subgenus *Gerris*.

All the above facts strongly indicate that the species belonging to each subgenus share essentially a similar growth ratio for each segment.

In the subgenus *Limnoporus* of the genus *Gerris* (fig. 111) the points for the first segments fall roughly on the allomorphic line for *Aquarius*, although those for the fourth segments (signs X₄) fall much above the allomorphic line for the same segment in *Aquarius* and *Gerris s. str.*. The second and third segments in *Limnoporus* are considerably longer than those in *Aquarius* and *Gerris s. str.* of equivalent body lengths. In the three larger species of *Limnoporus* the second segment is distinctly longer than the third, but in the smaller species, *G. (L.) canaliculatus*, the segments are equal in length, suggesting the presence of a greater growth ratio for the second than for the third in this subgenus, as in *Aquarius*.

In *Eurygerris* each species has apparently quite different growth patterns for the antennal segments as far as the preliminary data under study indicate. The lengths of second and third segments in *Eurygerris* are longer than those in *Gerris* of equivalent body lengths. In *Gerriselloides* all four segments are about equal in
lengths to those in the species of *Gerris s. str.* of corresponding body sizes, suggesting that the growth ratios for all segments are presumably much the same as in *Gerris s. str.* In *Gerrisella* the fourth segment is much shorter than the fourth segment in *Gerris s. str.* although in *Gerrisella*, which is represented by a single species *G. settembrinoi*, the body length is a little longer than in the smallest species of *Gerris s. str.* In *Gigantometra* the point for the first segment falls approximately on the growth line for the same segment in *Aquarius*, but the fourth segment falls much above the extended growth line for the same segment of *Aquarius*. The second segment is considerably shorter than the third in spite of the gigantic body size. This suggests that the lengths of these two segments in *Gigantometra* are realized from quite different growth mechanisms for these two segments from those in *Aquarius* or *Gerris s. str.*

Hoffmann's data on the development of *Limnogonus fossarum* (1936) indicate the highest growth ratio for the first and second segments and lowest for the fourth segment as in *Gerris*. The first segment is only slightly longer than the fourth in a great majority of species of *Limnogonus s. str.*, and the first segment is about twice or at least one and a half times as long as the fourth segment in the subgenus *Limnogonellus*. If growth patterns for the antennal segments similar to those in *Limnogonus fossarum* are shared by the species of *Limnogonellus*, it is expected that the fourth segment would be relatively longer in *Limnogonellus*, which is generally much smaller in body size. Therefore, the relatively short fourth antennal segment in *Limnogonellus* is presumably realized from quite different growth relations between the two segments from those in *Limnogonus s. str.* The allomorphic slopes for the second and third segments in the *Limnogonus s. str.*-*Limnogonellus* complex, however, appear to reflect the difference in growth ratio between the two segments indicated by Hoffmann's data, i.e., a greater growth ratio for the second segment than for the third segment. In a majority of species of *Limnogonus s. str.*, which are greater in body length, the second segment is longer than the third, while in a few species of *Limnogonus s. str.* (e.g., the smallest species, *L. lundbladi*) and in all species of *Limnogonellus* the second segment is as long as or even a little shorter than the third segment.

In the *Limnometra-Tenagogonus s. str.* complex the incomplete data on *Tenagogonus* (*Tenagogonus zambezinus* suggest a gentle
proximo-distal gradient of decreasing growth ratio for the antennal segments, but the differences among the segments are very slight. These growth patterns appear to persist to a great measure in the other species of the Limnometra-Tenagogonus s. str. complex. As will be noted from the table 15, there is at least no clear tendency for any one segment to be relatively longer or shorter than the other, although the body size varies greatly among species. In Tenagometrella (female), Tenagogonus (Tenagometra), and Tenagogerris the fourth segments are considerably shorter than those of the species of the Limnometra-Tenagogonus s. str. complex of the corresponding sizes, but the first three segments in these three genera are about equal in length to the same segments in the species of the Limnometra-Tenagogonus s. str. complex of corresponding sizes. These facts suggest that the growth patterns for the first three segments in the three genera must be similar to those in the related Limnometra-Tenagogonus s. str. complex. In Tachygerris celocis (fig. 112) the incomplete growth slopes for the first three segments are steep, and the slope for the fourth segment is much gentler. The allomorphic slope for each segment roughly conforms to the growth slope for each segment except for conspicuous deviations in the third segment of T. quadrilineatus and the second segment in T. spinulatus. In the male of Tenagometrella the antenna is over two and a half times as long as in the female (table 16); the proportional lengths of the first three segments are, however, very similar between sexes. This unusually long male antenna is, therefore, presumably realized primarily from an unusually high initial growth index in the male.

The features common to all genera of this tribe appear to be that the growth ratio for the fourth segment is smallest in all genera except possibly for the Limnometra-Tenagogonus s. str. complex, and this segment probably has a high initial size and growth index b. Secondly, there is no conspicuous difference in the steepness of growth slope between the second and third segments, but the growth slope for the second is more often a little steeper than that for the third. Thirdly, there is indication that the more distal segments, especially the fourth, vary more in their growth patterns at the specific level.

Charmatometrini: In one unidentified species of Brachymetra, for which incomplete data on the postembryonic development of antennal segments are available, there is a proximo-distal gradient of decreasing growth ratio among antennal segments. In Brachy-
metra unca, while the growth slope for the first segment is steeper than those for the other three segments, there is no distinct difference in growth ratio among the last three segments as far as the incomplete data indicate. As noted from figure 114, the growth slope for the first segment is obviously steeper than that for the fourth segment (from a large male nymph to an adult male), and the points for the lengths of both segments of the other species of Brachymetra, Eobates, and Charmatometra conform fairly well to the growth slopes for both segments (dotted lines represent the slope that would be realized with enlargement of the body in B. unca). The first segment in Brachymetra shawi, however, obviously deviates. In fig. 113 the postembryonic development of the second and third segments in B. unca and the lengths of these two segments in adults are plotted. It is also noted that the allomorphic lines conform fairly well to the growth lines for these segments in B. unca. Brachymetra lata, however, deviates greatly from the slope.

All the above facts indicate, apart from a few exceptions, that the species belonging to this tribe have essentially similar growth patterns for the antennal segments. Another fact that deserves mentioning is that in this tribe the growth ratio for the first segment is also much steeper than those for the other segments, as is the case with most genera of Gerrini.

Cylindrostethini: In an unidentified species of Cylindrostethus from the Philippines the growth slope (from a large male nymph to a male adult) for the first segment is steepest, and gentlest for the fourth segment; the growth slope for the third segment is only slightly steeper than that for the second (fig. 115). The points representing antennal segments in adults of the other species of Cylindrostethus from the Eastern Hemisphere tend to conform less to the growth lines from the more distal segments. Cylindrostethus sumatranus \((S_1 - S_4)\) makes conspicuous deviations for all segments. This species differs also in the abdominal structures and general color pattern from those in the other congeneric species. In figure 116 the antennal segments in the species of Cylindrostethus from the Western Hemisphere are plotted; no nymphal specimens were available for study. It is noted that the allomorphic lines are below and nearly parallel to the corresponding allomorphic lines for the species of Cylindrostethus from the Eastern Hemisphere (compare with figure 115). This fact suggests that the two groups of Cylindrostethus from different Hemispheres probably differ mainly
in the initial growth index b in terms of the allometric equation.

In *Potamobates* a large male nymph specimen of *Potamobates woytkowskyi* was available for measurement. In figure 117 it is immediately noted that the allomorphic slopes for the first and fourth segments conform fairly well to the growth slopes for the corresponding segments. As in *Cylindrostethus*, the slope for the first segment is much steeper than that for the fourth segment. The data indicate also that the growth slopes for the second and third segments are about equally steep, but in both the largest and smallest species (*P. thomasi* and *P. horváthi*) the second segment is distinctly longer than the third; in all other species both segments are about the same in length. The growth patterns for these two segments in these two species may be considerably different from those in other species. As will be pointed out elsewhere, *P. thomasi* deviates also structurally.

In the postembryonic development of the antennal segments in *Platygerris depressus* (from a large male nymph to an adult male, figure 118) the growth ratio for the first segment is greatest and smallest for the fourth segment; the growth ratio for the third segment is a little greater than that for the second segment, as far as the incomplete data indicate. The points representing the segments in other species of *Platygerris* do not conform to the growth lines of *Platygerris depressus* for all segments. Each species must have different growth patterns for antennal segments. This is the only genus of Gerrinae in which the allomorphic lines for the antennal segments do not at all conform to the growth lines. A possibility exists, however, that this is due partly to enormous prolongation of the eighth abdominal segment in the largest species, *Platygerris caeruleus*.

Eotrechini: A large nymph of *Chimarrhometra orientalis* and a large male nymph of *Onychotrechus rhexenor* were available for study. By comparing them with corresponding adults, it was found that the growth slopes for the first segments are steeper than those for the other segments, and the slopes for the fourth segment are gentlest. The lengths of the first segments in all species of the tribe fall approximately on the growth line for the same segment in *O. rhexenor*. The fourth segments in the species of *Anemboa* and *Eotrechus* fall much above the growth line for the same segment in *O. rhexenor*. The four genera of Eotrechini are not closely re-

*In the specimen of *Eotrechus kalidasa* Kirkaldy the two distal segments are missing. Distant's figure (1904, p. 104), however, clearly indicates that all segments are very much the same in length. Distant's description says "antennae with the first and second joints longest and subequal, third and fourth a little shorter and subequal."
Ptilomerinae: In two nymphal specimens at different developmental stages of an unidentified species of *Ptilomera* from India (fig. 119), the lines connecting the points for each antennal segment at the three stages are nearly straight on the log-log grid, indicating allometric growth for these segments. It is noted that the lengths of the first segments of different species of *Ptilomera* fall roughly on the growth line for the same segment. The species in the other genera, except for *Rheumatogonus*, also fall close to the growth line for the first segment of the *Ptilomera* species from India. In this subfamily the growth slopes for the first segments in all genera, except *Rheumatogonus*, are presumably much the same. Esaki (1923) thought that in this subfamily the proximal segments of the antennae and legs have been prolonged in adaptation to their peculiar habitat (rapid and turbulent streams). This appears to be true. If the first antennal segments in these genera are plotted on the graph for the hypothetically primitive antennal segment (fig. 127) they fall far above the growth line for the latter. The growth ratio k for the first antennal segment in the species of *Ptilomera* from India is 0.89 and b is 0.05*. The k value is considerably smaller than that for the same segment in the hypothetically primitive gerrid, with acquisition of the relatively high b value of 0.05. In two species of *Rheumatogonus* studied, the first antennal segments fall close to the hypothetically primitive growth line for the antennal segment. In this subfamily, therefore, the relatively primitive condition for the first segment appears to have been retained in this genus only.

Among the other three antennal segments in the *Ptilomera* species from India, the growth ratios appear to decrease in proximo-distal order. In *Ptilomera* the slopes for all segments apparently are gentler than, for instance, in *Gerris*. In *Potamometra*, which is somewhat related to *Ptilomera*, all segments except for the fourth, fall below the growth lines for the corresponding segments in the *Ptilomera* species studied. Since the number of species in the other genera is highly limited and the developmental data are not available, they are not discussed here. From figures 119 and 120, however, the degree of conformity of the antennal segments to the growth lines in the *Ptilomera* species can be roughly visualized.

* Comparable with b values in the two species of *Gerris* studied.
Halobatini: Miyamoto's data (1937) on the postembryonic development of Asclepios coreanus miyamotoi indicate that the length of the first antennal segment at the fifth nympha! stage is 3.45 times as long as that at the second nympha! stage; comparable figures for the second, third, and fourth segments are 2.33, 2.09, 1.86 times as long as those at the second nympha! stage. To see whether these differences in growth ratios persist in the Asclepios-Halobates complex or not, the lengths of antennal segments in adults of the species belonging to these two genera were plotted. It was found that the allomorphic lines for the first and fourth segments roughly reflect the difference in growth ratios between the first and fourth segments in Asclepios coreanus miyamotoi.

Metrocorini: In figure 121 the points representing the species of Metrocoris (smaller points represents the lengths at nympha! stages in Metrocoris histrio), except for the largest species, Metrocoris stali(?), conform fairly well to the growth lines for the corresponding segments in Metrocoris histrio. A rather sharp decline of growth ratio at the final stage of development, which occurs in M. histrio, probably occur in all other species as seen from the fact that all points for the first and fourth segments fall below the growth lines for these segments in M. histrio (here represented by regression lines). As already found, the proximo-distal order of decrease of growth ratio is present in M. histrio (P<0.05) and the growth ratios for the basal segments (male) are peculiarly high in the same species. Similar growth pattern probably exists in many or all species of this genus. It was found by plotting that each segment in the related genera, Eurymetra, Eurymetropsis and Eurymetropsiella, falls close to the growth line for the corresponding segment in M. histrio.

In figure 122 the incomplete growth lines (male) for the first and second segments are steeper than those for the third and fourth segments in Ventidius henryi. The degree of conformity of allomorphic lines to the growth lines of the corresponding segments can be seen also from the same figure. In Esakia the points for the first segments fall considerably above the growth line for the first segment in V. henryi. The second, third and fourth segments fall roughly on the allomorphic lines for these segments in Ventidius. In the female of V. henryi the growth slope for the third segment is much steeper than that for the fourth, and even a little steeper than that for the second. In Esakia the female third segment is also relatively longer than in the male as in
Ventidius. Esakia, in this respect, appears to have inherited a similar growth pattern from a Ventidius-like ancestor. In Esakia the male third segment is greatly thickened and modified as if compensating for its relative shortness.

Rhagadotarsinae: In the postembryonic development of the female antennal segments in Rheumatobates rileyi palosi (2nd instar to adult female, figure 123) the growth slopes for the first, third and fourth segments are about equally steep, and they are much steeper than the slope for the second segments. It is noted from the figure that the allomorphic slope for the first segments in the species of Rhagadotarsinae is nearly parallel to the growth slope for the first segment in Rheumatobates rileyi palosi, and all points fall on or above the regression line for the postembryonic development of the first segment in the species studied. Most white points representing the second segments in the species of Rhagadotarsinae also fall roughly in the expected areas. The characteristics of growth patterns for the antennal segments in this subfamily are: (1) The growth ratio as well as the initial size of the second segment is much smaller than those of the other segments. (2) There is no great difference in growth ratios among the first, third and fourth segments. (3) There appears to be increase in growth ratio at the final stage of the development for all segments.

Trepobatinae: Figure 124 shows the postembryonic development of the antennal segments in Trepobates knighti, together with the first and second antennal segments in the males of the other species of Trepobates. The growth lines for the first and second antennal segments in T. knighti are expressed by regression lines. Due primarily to the relatively small range in body size among species, the points representing the first and second segments tend to cluster at certain points, thus not suggesting underlying growth slopes. It is, however, interesting to point out that the white points representing the first segments and black points representing the second segments fall above the growth lines (regression lines) for the corresponding segments in T. knighti. This is due probably to an abrupt increase in growth ratio at the final stage of development, as evidently occurs in T. knighti. As already found, the growth ratio k for the first segment in T. knighti is greater than the equivalent in Gerris, but smaller than in Metrocoris histrio. There is no statistically significant difference in growth ratios among the first three segments, and the growth ratio for the fourth segment is lowest in T. knighti.

In figure 125 it is seen that the growth slopes for the antennal seg-
ments from a large male nymph to an adult male in *Telmatometra indentata* are much steeper than those in *Trepobates*, and of all segments the third segment is steepest (other unpublished data also indicates that the ratio is greatest for the third segment). As immediately noted, the allomorphic slopes for the first and second segments conform fairly well to the growth lines for the same segments in *T. indentata*, but the same for the third segment does not at all conform to the incomplete growth slope for the same segment in *T. indentata*. The unusually steep growth slope for the third segment in *T. indentata* coupled with this disconformity between the growth and allomorphic lines lead one to suspect strongly that the growth pattern for this segment might be highly variable at the specific level in this genus. Although not shown in the graph, the data indicate the presence of a similar condition for the fourth segment. In *Trepobatoides* (fig. 125) the antennal segments, except for the second, do not at all conform to the growth line for the antennal segments in *Telmatometra indentata*. In *Halobatopsis* the first and second, especially the former, fall approximately on the allomorphic lines for these segments in *Telmatometra*. In *Ovata metra*, no segment, except for the third, falls close to the growth lines for the antennal segments in *Telmatometra indentata*.

In *Metrobates porcus* the growth slope for the first segment based on large male nymph and an adult male, is remarkably steeper than those for the other segments, and the lengths of the first segments in the other species fall on the graph in conformity to the growth line for this segment in *M. porcus* (fig. 126). In spite of a relatively small range in the body size among the species of *Metrobates*, the allomorphic line for this segment well reflects a very high growth ratio common to all species. The allomorphic slope for the second segment is also nearly vertical, but the growth slope for this segment in *M. porcus* is gentle. The allomorphic slope for this segment never reflects the growth slope for this segment in *M. porcus*. The growth slope of the second segment in another species, *Metrobates denticornis*, was found to be even a little gentler than that in *M. porcus*. The nearly vertical secondary allomorphic slope for this segment in *Metrobates* is apparently formed by a high degree of variation in growth pattern for this segment at the specific level, either in the initial growth index or the growth ratio, or both. A similar condition exists for the third segment in this genus. It should be pointed out, however, that the second and third segments in this genus are always provided with a conspicuous comb shaped
process at their distal ends. This kind of modification might have something to do with alteration in the growth pattern at the specific level, depending on different degrees of modification.

In *Hynesionella omercooperi* there is a proximo-distal gradient of decreasing growth ratios (from a large male nymph to an adult male). In *Cryptobates* the absolute lengths of the first segment in two species studied are very different (7, 13 micrometer units respectively), but this wide difference can easily be conceived if the growth ratio for this segment is very high as in the other genera of this subfamily, taking into account a considerable difference in body size between the two species (42, 55 units). *Stenobates* and *Rheumatometroides* are monotypic genera but they are closely related. The lengths of the first segments in these two genera are also greatly different (25, 13 units respectively), but if these two genera have a high growth ratio for the first segment as in the other genera, this difference in lengths of the first segments would easily be realized, considering a rather great difference in body size between the two genera (72, 55 units respectively). In *Metrobatopsis* the species are highly variable in degree of structural specialization. Correlated with this, each species appears to have a considerably different growth ratio even for the first segment.

From the above account it is clear that the growth ratio for the first segment is remarkably high in at least a great majority of genera of this subfamily. Whether this high growth ratio is of any adaptive advantage or not is open to question. The species belonging to this subfamily usually live in quiet waters, so the relatively long first antennal segment cannot be adaptively advantageous in the same manner as it is for Ptilomerinae which live in swift and turbulent waters. Assuming, however, that the reduction in body size is also at work in the evolution of this subfamily as in the other subfamilies, this high growth ratio could have been a very efficient mechanism in reducing the absolute as well as relative lengths of the first segment, since they do not need extremely long antennae to maintain themselves on the quiet waters. It should be recalled that the long first antennal segment in Ptilomerinae appears to be realized by a relatively high initial growth index b with a relatively low growth ratio k. Therefore, the relatively long first antennal segment in the larger species of most genera of Trepobatinae and the long first antennal segment in Ptilomerinae (except for *Rheumatogonus*) are quite different both in developmental pattern and adaptive significance.
Evolution of the growth gradients for the antennal segments

In the foregoing accounts various types of growth gradients for the antennal segments in various groups have been observed. The next logical step is to search for a possible growth pattern from which various types of gradients might have been derived.

It was found that the four antennal segments in *Eotrechus kalidasa* are strikingly similar in lengths. It may reasonably be assumed that this condition is the primitive one. The assumption is justified by a general criterion in comparative anatomy which regards the more similar condition among homologous structures as more primitive. Moreover, *Eotrechus* is highly primitive in many structures, probably the most primitive, in an overall sense, in the Gerridae. When many structures are primitive, there is a good possibility that the other structures will also be primitive.

The question next arises as to just how this supposed primitive antenna in *Eotrechus* would be realized in terms of allometric growth mechanisms. In fig. 127 we see that in *Eotrochus kalidasa* and *Tenagogonus (Limmometra) ciliatus*, the first segments fall a little above the extended growth line for that segment in *Onychotrechus rhexenor*, a relatively primitive member of *Eotrechini*. This suggests that all three species, in spite of their difference in body size and generic status, have similar growth ratios. Since the growth ratio for the first segment, as already shown, is best stabilized at the generic level and the segment in two primitive species falls close to the extended growth line for this segment in *O. rhexenor*, the regression line for the first segments in *Onychotrechus rhexenor, Eotrechus kalidasa*, and *Tenagogonus (Limmometra) ciliatus* in fig. 127 can reasonably be regarded as representing the most primitive growth line for an antennal segment in the Gerridae. The growth ratio k for this primitive antennal segment is 1.142. This value is also close to the growth ratio for the first antennal segment in another primitive species, *Gerris (Aquarius) remigis* Say (k is 1.216).

For the realization of similar absolute lengths among antennal segments in *E. kalidasa* a very similar growth pattern for each segment presumably exists. This presumption is justified by the facts that the growth ratios for all antennal segments, except for the third, are similar in *Hoberlandt's* (1947) data on *Tenagogonus madagascariensis* and in my incomplete developmental data on the antennal segments in *Tenagogonus zambezinus* which indicate similar growth ratios for all segments. Moverover, there is no
tendency for any one segment to be relatively longer or shorter than the others in *Tenagogonus*, in spite of the fact that the range of the body length is great among species. The similar absolute lengths among antennal segments in *Eotrechus kalidasa* must be realized by similar growth relations among segments to those in *Tenagogonus*. The hypothetically primitive growth ratio for an antennal segment, therefore, should be valid for all segments.

From the hypothetically primitive growth pattern for all antennal segments outlined above, has evolved the proximo-distal gradient of decreasing growth ratios, as diagrammatically illustrated in fig. 128. In figure 128 type A represents the most primitive condition, in which the growth ratios for all antennal segments are the same \((k = 1.142)\). To realize the same or very similar lengths of antennal segments by the same growth ratios for all segments the initial sizes of all segments, or initial growth indices, should be the same or very similar. The growth lines for all segments, thus completely overlap. To see how well the actual growth patterns for the antennal segments in *Eotrechus kalidasa* would conform to this supposed primitive condition remains as an interesting problem to study in the future. *Tenagogonus* is probably near this condition. Type B is the condition in which the growth ratio for the fourth segment alone has been significantly affected. This condition appears to exist in *Gerris s. str.*, *Tenagometra*, *Tenagogerris*, *Tenagometrella*, and some species of the *Limnometra-Tenagogonus* complex. The growth patterns in *Trepobates knighti* and *Tachygerris* are similar to those in *Tenagometra*, *Tenagogerris*, and *Gerris s. str.* in that the growth ratio for the fourth segment only has been greatly lowered, but the growth ratios for the first three segments in *Trepobates knighti* are much greater than in the hypothetically primitive gerrid. Type C is a further affected condition, in which the growth ratios for the last two segments have been lowered in evolution. The growth patterns for the antennal segments in *Gerris (Aquarius) remigis* appear to approximate this condition. Type D is the proximo-distal gradient in decreasing growth ratios. The growth pattern in *Metrocoris histrio* fits this condition, although the growth ratios for the basal segments are very high. Type E is the condition in which the growth ratio for the first segment is very high and the proximo-distal order of decreasing growth ratios is maintained. This condition is suspected to be present in some groups of Trepobatinae. Type F is an exceptional condition in which the growth
pattern for the second segment alone has been significantly affected by evolution. This type is present in Rhagadotarsinae.

The hind leg

Gerrini: In figure 129 the growth slopes for the femur, tibia, and tarsus in G. (A.) remigis are definitely steeper than those in G. (G.) marginatus. (The growth ratios for the tibia and tarsus in G. (A.) remigis are greater than the same in G. (G.) marginatus at the level of P.<0.05). Note how well the points for adults of various species conform to the growth slopes in each subgenus. Although there are no statistically significant differences in growth ratios between the femur and tibia in either species studied, there is a tendency for the tibia to be shorter in relation to the femur in the smaller species at least in *Aquarius*. It may also be said that the points for tarsi deviate slightly more from the growth lines for corresponding segments in both species. In *Gigantometra* the femur falls a little above the growth line for the segment in G. (A.) remigis, but the tibia falls much above and the tarsus considerably below the growth line for the corresponding segments in the same species, suggesting that the growth patterns for these two segments are significantly different from those in *Aquarius*. In the subgenus *Limnopus* of *Gerris* the points for femora and tibiae fall a little below the growth lines for the corresponding segments in G. (A.) remigis, although the points for tarsi fall a little above the growth line for the same segment in G. (A.) remigis. The three segments in *Gerriselloides* fall on or very close to the corresponding segments in *Gerris* s. str., suggesting that this genus has the growth patterns for the hind leg segments very similar to those in *Gerris* s. str. In *Gerrisella* the femur falls quite close to the growth line for the same segment in G. (A.) remigis, but the other two fall much below the growth lines for the corresponding segments in both species of the genus *Gerris* studied. Evidence at hand* indicates that the allomorphic slopes in *Eurygerris* do not reflect the growth slopes for the three segments common to all species.

In figure 130 three leg segments in all species of the *Limnometra-Tenagogonus* s. str. complex were plotted. The regression coefficients for the femur, tibia, and tarsus are 1.016, 1.469, 0.846, respectively (these values reflect allomorphic slopes). Hoberlandt's (1947) data on *Tenagogonus madagascariensis*, however, indicate that the length of the femur in adult male is 1.89 times as long as

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* Complete developmental data for two species under study.
that in a second stage nymph; the tibia and tarsus in an adult male are 1.81 and 1.45 times as long as the same segments in a second instar respectively. These growth ratios thus do not coincide with the regression coefficients for the three segments in the Limnometra-
Tenagogonus s. str. complex noted above. Incomplete data on the
growth of the hind leg segments in Tenagogonus zambezinus (fig. 
130) also show a similar growth pattern to that in T. madagascari-
ensis. In fact, as will be noted from figure 130, there is a tendency 
for the growth slopes of the segments in T. zambezinus to deviate 
progressively more in the more distal segments from the allomorphic 
slopes of the corresponding segments. The absence of coincidence 
between the allomorphic and growth slopes for the corresponding 
segments might have resulted from a progressive decrease in growth 
ratios for the more distal segments in the smaller species (Tenag-
gonus s. str.), or from a decrease in initial growth index with 
growth ratio remaining unchanged in the smaller species. Whatever 
the underlying mechanism may be, the tibia is relatively shorter in 
the smaller species, resulting in the formation of the steeper sec-
derary allomorphic slopes for the tibia than for the femur. The 
three hind leg segments in the genera or subgenera related to the 
Limnometra-Tenagogonus s. str. complex (Tenagometra, Tenago-
metrella and Tenagogerris) fall close to the regression lines for the 
corresponding segments in the Limnometra-Tenagogonus s. str. 
complex.

In figure 131 are shown the growth lines for the femur and tibia 
in males of an unidentified species of Limnogonus (from a large 
nymph to an adult female) from New Guinea. All points for the 
other species are leg segments in the females in this genus. It is 
immediately noted that the deviation of the points for the tibia 
(round points for Limnogonus s. str., triangles for Limnogonellus) 
from the incomplete growth line for the same segment is greater 
than the same for the femur. The same interpretation as given 
above for the Limnometra-Tenagogonus s. str. complex can be made 
for the greater deviation of the points for tibiae from the growth line 
for this segment. Evidence at hand (two species representing both 
subgenera, under study) indicates, however, that the growth pat-
terns for the tibia in these two species is similar. Apart from the 
underlying growth mechanisms, the tibia is shorter in relation to the 
femur in the smaller species, as suggested by the steeper allomorphic 
slope for the tibia than that for the femur. Limnogonus intermedius 
is represented by \( \times \) in figure 131. Note how the leg segments in this
species deviate from the corresponding allomorphic lines for the other species. This species, together with a few other African species, deviates also in other characters.

In figure 132 the allomorphic slopes for the tibia and tarsus do not conform to the growth slopes for the same segments in *Tachygerris celocis*. The growth slopes for the same segments in *Tachygerris spinulatus*, which is larger in size, are much gentler than those in *T. celocis*. These incomplete data suggest that the disconformity of allomorphic slopes to the growth slopes for the tibia and tarsus apparently results from the difference in growth pattern among species. The difference in growth slope for the femur between *T. celocis* and *T. spinulatus* is much less than the differences in the other two segments between the two species, and the allomorphic slope for the femur conforms fairly well to the growth slopes for this segment in the two species. The secondary allomorphic slope for the tibia is steeper than the allomorphic slope for the femur as in the other genera, and the tibia in the shorter species is also relatively shorter in this genus.

**Charmatometrini:** In figure 133 E, E' represent a nymph and an adult (male) of an unidentified species of *Brachymetra* from Ecuador and P, P' represent a nymph and an adult (male) of an unidentified species of *Brachymetra* from Panama. The allomorphic slopes deviate more from the growth slopes in the more distal segments. The allomorphic lines appear to be formed by smaller growth ratios for all segments in the shorter species. Although the growth ratio for the femur is about as great as or a little greater than that for the tibia in all three species, the secondary allomorphic slope for the tibia is even a little steeper than that for the femur, due apparently to a little greater degree of alteration in growth pattern for the tibia at the specific level. The tibia and tarsus are thus relatively shorter in the shorter species in Charmatometrini.

**Cylindrostethini:** In figure 134 the allomorphic lines for the femur and tibia in the species of *Cylindrostethus* from the Eastern Hemisphere (triangle points) conform well to the growth lines for the corresponding segments in an unidentified species of *Cylindrostethus* from the Philippines. The allomorphic lines for the femur and tibia in the Western Hemisphere species of *Cylindrostethus* (round points) are nearly parallel to the equivalents in the Eastern Hemisphere species of *Cylindrostethus*. If these very similar allomorphic slopes for the femur and tibia in the two groups of *Cylindrostethus* really reflect the similarity in the growth slopes
for the segments between the two (no developmental data are available for the Western Hemisphere species of Cylindrostethus), the difference between the two groups lies primarily in the initial growth index b in allometry equation terms, i.e., a lower b value for the Western Hemisphere Cylindrostethus than that for the Eastern Hemisphere Cylindrostethus. The growth line for the tarsus is a little steeper than the allomorphic line for the same segment in the Eastern Hemisphere species of Cylindrostethus. The tarsus tends to be longer in the smaller species of Western Hemisphere Cylindrostethus. It is thus most improbable that the different lengths of tarsi in different species have been derived from a similar growth mechanism common to all species. Since the growth, as well as the allomorphic, slopes for the tibia are steeper than those for the femur, the tibia is relatively shorter (in relation to the femur) in the smaller species in this genus, as in the other genera of Gerrinae.

In figure 135 incomplete postembryonic growth lines for the femur and tibia in Potamobates horváthi and the lengths of three leg segments in all species of Potamobates are plotted. Note how well the segments, in all species except for Potamobates thomasi, conform to the growth lines for the femur and tibia in P. horváthi. All species, except for P. thomasi, probably have much the same growth patterns for these segments. It should be recalled that P. thomasi deviates also in the lengths of antennal segments. The tarsus is missing from the nymph studied. Both the growth and the allomorphic slopes for the tibia in this genus are steeper than those for the femur, and the tibia is also relatively shorter in the smaller species.

In Platygerris, it was found that the allomorphic lines do not at all conform to growth lines for all segments in Platygerris depressus; they rather greatly deviate from the latter, as will be noted from figure 136. The growth slope for the femur is much steeper than the same for the tibia in P. depressus. In almost all genera of Gerrinae the middle and hind femora are about as long as the body, but in this genus they are considerably longer than the body, probably in correlation with their habitat in rapidly running water. These rather extraordinarily long femora are apparently realized from this very high relative growth ratio. Platygerris offers a unique case in which the allomorphic slope for the femur is so much different from the growth slope, but this is partly due to extraordinary development of the eighth abdominal segment
in the largest species, *P. caeruleus*. The secondary allomorphic slope as well as the growth slope (in two species under study) for the tibia are steeper than those for the femur, and the tibia is relatively shorter (in relation to the femur) in the smaller species.

**Eotrechini:** The growth lines from a large male nymph to an adult male for the femur and tibia in *Chimarrhometra orientalis* and *Onychotrechus rhexenor* are nearly parallel to each other. The growth line for the tarsus in *O. rhexenor* is nearly horizontal. Whether allomorphic slopes coincide with growth slopes or not is difficult to see for the reasons mentioned previously. At the generic level, however, there is a tendency for the tibia to be relatively longer in the more primitive and larger (in size) genera. In the largest (in body length) and structurally very primitive genus, *Eotrechus*, the tibia is even longer than the femur. In *Onychotrechus* the tibia is longer in relation to the femur than it is in *Amemboa*, which is smaller in body size and generally more specialized structurally. This tendency, however, is probably realized from different growth patterns in different genera, since the four genera are not closely related to each other. It is interesting to recall that in the largest and structurally most primitive species of Gerrini, *Gigantometra gigas*, the tibia is also much longer than the femur, as in the largest species in *Eotrechini*, *Eotrechus kalidasa*.

**Ptilomerinae:** Since the tibia and tarsus in dried museum specimens of this subfamily are always greatly twisted, the study of these two segments is not attempted. The femur, however, is always robust and straight. In figure 137 is shown the incomplete post-embryonic development of the femur and tibia at three different developmental stages in an unidentified species of the genus *Ptilomera* from Southern India. The femora in all other species of *Ptilomera*, except for one, fall very close to the growth line for the femur. This beautiful conformity suggests that the growth pattern for the femur is much the same in most species of *Ptilomera* studied. Note also the steeper growth slope for the tibia than that for the femur. It was found by plotting that the femur of *Potamometra berezowskii* falls considerably above the growth line for the femur in the *Ptilomera* species from India. The femora in *Rhyacobates, Heterobates, Potamometropsis, Potamometroides*, and *Rheumatogonus* come below the line. *Rheumatogonus* has the shortest femur as is the case with the first antennal segment, and this is probably the least specialized condition in *Ptilomerinae*. In all species of *Ptilomerinae*, however, the hind femur is longer than the length of
the body, and this is presumably the prerequisite for them to survive swift and turbulent currents by maintaining their body with the aid of relatively long proximal antennal and leg segments. In Gerrinae it is only in \textit{Platygerris}, which inhabits similar streams, that the femur is longer than the body. In this subfamily (at least in \textit{Ptilomera}), in contrast to \textit{Platygerris}, the relatively long femur is apparently realized by a rather gentle growth slope, gentler than that for the tibia, with probably a large initial size, or initial growth index in terms of the allometry equation.

\textit{Halobatini}: Miyamoto's data (1937) on \textit{Asclepios coreanus miyamotoi} indicate that the growth ratio for the tibia is a little greater than that for the femur (5th instar femur : 1st instar femur : : 72-23, 5th instar tibia : 1st instar tibia : : 40:12), the growth ratio for the tarsus is much smaller than those for the other two segments (5th instar tarsus : 1st instar : : 15.5:8). In figure 138 it is noted that regression lines for the femur and tibia would be nearly parallel. \textit{Halobates proavus} deviates conspicuously, especially for the tibia and tarsus. The allomorphic slope for the tarsus is much gentler than those for the two preceding segments. The differences among allomorphic slopes thus roughly coincides with the differences in growth ratios among the three segments in \textit{A. coreanus miyamotoi}.

\textit{Metrocorini}: In \textit{Metrocoris} the points representing the femora and tibia in all species, except for the largest, \textit{Metrocoris stali(?)}, fall below and along the growth line for each segment in \textit{Metrocoris histrio} (fig. 139 represented by regression lines). This reflects a possible abrupt decrease in growth ratio at the final stage of development in all species, which evidently occurs in \textit{M. histrio} as seen from the figure. The allomorphic line for the tarsi considerably deviates from the growth line for the same segment in \textit{M. histrio}. All segments in \textit{Eurymetra}, \textit{Eurymetropsis}, and \textit{Eurymetropiella} fall roughly on the allomorphic lines for the corresponding segments in \textit{Metrocoris}. As in \textit{Gerris (Aquarius) remigis}, there is no statistically significant difference in growth ratio between the femur and tibia in \textit{M. histrio}. Similar growth relations probably exist in the other genera related to \textit{Metrocoris}.

In figure 140 the points representing the femora in \textit{Ventidius} fall close to the growth line for the femur of \textit{Ventidius henryi}. For the tibia all species, except for \textit{Ventidius malayensis}, conform very closely to the growth line for the same segment in \textit{V. henryi}. Due to a great deviation of the tibia in \textit{V. malayensis} the allomorphic line for the tibia is steeper than that for the femur. For the tarsus
V. malayensis also greatly deviates. It was found that the femur in two species of Esakia fall a little above the allomorphic slope for the femur in Ventidius; the other two segments in Esakia come close to the corresponding segments in Ventidius.

In Metrocorini the allomorphic slope for the femur is closest to the growth slope for the same segment. The allomorphic slope, however, tends to deviate more from the growth slope in the more distal segments, as is the case with some genera of Gerrinae. Because of this tendency the tibia is shorter in relation to the femur in the smaller species of some genera.

Rhagadotarsinae: In figure 141 the complete growth lines of leg segments in Rheumatobates rileyi palosi (female), and the incomplete growth lines in Rhagadotarsus (Caprivia) hutchinsoni (female) together with points representing the leg segments in all other species of the subfamily (female) are shown. In Rheumatobates the size of the body does not vary much among a majority of species, so that the points tend to cluster within a certain area, but the essential conformity of the points to the growth lines for the femur and tibia is evident from the fact that the points for both the smaller and larger species are roughly on the growth lines for the corresponding segments. The points for tarsi obviously deviate from the growth line for the same segment in Rheumatobates rileyi palosi.

As already found, there is a proximo-distal gradient of decreasing growth ratio (P<0.05) in R. rileyi palosi. The incomplete growth lines for the three segments in Rhagadotarsus (Caprivia) hutchinsoni also indicate the same order of decrease in growth ratio as in R. rileyi palosi. Hoffmann's data (1936) on the postembryonic development of the hind leg segments in Rhagadotarsus (Rhagadotarsus) kraepelini also indicate the same order of decrease in growth ratio, i.e., the femur at the fifth nymphal stage is five times as long as the same at the first nymphal stage; the tibia and tarsus at the fifth stage are 3.4 and 2.06 times as long as the same at the first nymphal stage. This ontogenetic evidence representing all major groups of this subfamily, in turn, indicates that the proximo-distal gradient of decreasing growth ratio for the hind leg segments is probably widely prevalent in this subfamily. There is a good possibility, however, that the growth ratio for the tarsus is considerably different at the specific level. It is important also to point out that the difference in growth lines for the femora between the two species (R. (C.) hutchinsoni and R. rileyi palosi) is less than the difference
in growth lines for the other two segments between the two species, suggesting that the growth pattern for the femur has been more well fixed than the other segments in this subfamily. The same tendency was already observed in the other subfamilies of the Gerridae. Another important matter is that most points representing the tibiae and femora fall above the growth line (regression line) for each segment. This is apparently due to an abrupt increase in growth ratio at the final stage of development for the segments, as evidently occurs in Rheumatobates rileyi palosi. Because of the proximo-distal gradient in growth ratio for the three segments there is no tendency for the tibia to be shorter in relation to the femur in the smaller species.

*Trepobatinae:* In figure 142 is shown the complete postembryonic development for the three segments in *Trepobates knighti*. It is immediately noted that in this species also the growth slope for the femur is steepest and that for the tarsus gentlest as in Rhagadotarsinae, although there is no statistically significant difference in growth ratio between the tibia and tarsus. The points representing the leg segments in other species within the genus also conform fairly well to the growth lines. Due to a small range in body sizes among species in this genus the points tend to aggregate within a certain area, but at least no conspicuous deviation is noted. As in the case with the femur and tibia in Rhagadotarsinae, all points representing the leg segments fall above the growth lines for the corresponding segments (here represented by regression lines). This is apparently due to an abrupt increase in growth ratio at the final stage of development, which evidently occurs at least in *T. knighti*. Because of the growth patterns noted above there is a tendency for the tibia to be relatively longer in the smaller species in this genus. *Trepobatoides boliviensis* and Telmatometra ujhelyi were also plotted on the same graph to show that in both species the lengths of femora and tibiae fall considerably above the growth lines for the corresponding leg segments in *T. knighti*.

In figure 143 the growth slope for the femur is steepest and gentlest for the tarsus in *Telmatometra indentata* (from a large nymph to an adult male). The allomorphic line for the femur closely conforms to the growth line for the same segment in *T. indentata*, with a slight deviation in *Telmatometra retusa*. The allomorphic slopes for the tibia and tarsus, however, are very much steeper than the growth slopes for the corresponding seg-
ments. In the same figure the growth slopes for the femur and tibia are nearly parallel, and steeper than the growth slope for the tarsus in *Halobatopsis spiniventris* (from a large male nymph to an adult male). While the points for the femur fall on the growth line in *H. spiniventris* the line connecting the tibiae and the one connecting tarsi in two species of *Halobatopsis* (allomorphic lines) are much more vertical than the growth lines for these segments in *H. spiniventris*, as in the genus *Telmatochroma*. The growth slopes for the femur is steeper than that for the tibia in *H. spiniventris*. In these two genera there is a tendency that the allomorphic slopes deviate from the growth slopes for the corresponding segments more in the more distal segments. In *Ovatametra* the femur and tarsus do not fall close to the allomorphic lines for these segments in *Telmatochroma* and *Halobatopsis*.

In figure 144 the incomplete growth lines for the femur and tibia are nearly parallel in *Metrobates denticornis*, although the growth slope for the femur is steeper than that for the tibia in another species, *Metrobates porcus*. While the points for the femora fall close to the growth lines for the femur in both species, the allomorphic slopes for the tibiae and tarsi are nearly vertical and deviate greatly from the growth lines for the corresponding segments. As will be noted from figure 144, the difference in the growth slopes for the femur between the two species is very slight, but the difference is much greater for the other two segments. This strongly suggests that the growth ratios for the tibia and tarsus may vary greatly at the species level in *Metrobates*. We have already observed a similar tendency for the second to fourth antennal segments in the same genus. As in *Telmatochroma* and *Halobatopsis*, the allomorphic slopes for the tibiae and tarsi are thus much steeper than that for the femur.

The proximo-distal gradient of decreasing growth ratios for the hind leg segments was found in *Hynesionella omercooperi* on the basis of incomplete data on the development (from a large male nymph to an adult male, fig. 145). In *Rheumatometra philarete* the growth slope (from a large female nymph to an adult female) for the tibia is steeper than that for the femur. This is the only trepobatine studied in which the tibial growth slope is steeper than the femoral (note that the data are incomplete and based on females instead of males). In figure 146 the allomorphic slopes for leg segments in *Stenobates biroi* and *Rheumatometroides browni* are much like typical growth lines in Trepobatinae. This suggests that
they possibly have similar growth patterns for the hind leg segments, assuming that the growth slopes coincide well with the allomorphic slopes for all segments. In fact these species are closely related. In the same figure, the allomorphic slopes for the leg segments in two species of Cryptobates are like typical allomorphic lines in Trepobatinae. In Metrobatopsis the data indicate that even the allomorphic slope for the femur does not reflect a probable growth slope for any one species of the genus, although no developmental data are available.

The mechanism of allomorphosis for the hind leg segments

It has become evident from the foregoing discussion that the allomorphic slope for the tibia is almost always steeper than that for the femur. It has become apparent further that the underlying growth mechanism by which the allomorphic slope is formed varies in different groups of the Gerridae. In figure 147 A is diagrammed the condition in which the allomorphic slope is identical with the growth slope for each segment (femur and tibia). To realize this condition all species (A, B, C) must have the same growth ratio and the same initial growth index for these two segments. A condition similar to this probably exists in some genera of Gerrini, etc. Type B is the condition in which the allomorphic slope is the same as the growth slope for the femur, but the growth ratio for the tibia is different at the specific level, i.e., higher growth ratios and lower initial growth indices in the larger species. The allomorphic line (secondary, a in the figure) thus obtained does not represent the growth line for the tibia in any one species, A, B, C. Type C is another condition by which the secondary allomorphic slope for the tibia is formed, i.e., by the lower growth ratios with higher initial growth indices in the larger species. The type B and C apparently occur in various groups of Gerridae. The type D is an exceptional condition in which the growth patterns for the femora are different with those for tibiae remaining much the same among species. This condition was observed in Platygerris. Types E and F are the conditions in which the initial growth indices are more or less greatly different while the growth ratios remain much the same among comparable species. If there is a tendency for the initial growth index to be smaller in larger species while the growth ratio remains the same, a nearly horizontal secondary allomorphic slope will be formed as shown in E. This is apparently the mechanism by which the nearly horizontal secondary allomorphic slopes are formed in Eurygerris. If, however, there is a tendency for the initial growth
index to be greater in larger species than in smaller species while
the same growth ratio is present among the comparable species, a
nearly vertical or very steep secondary allomorphic slope will be
formed (type F).

The middle leg

In figure 148 a majority of points representing the middle leg seg-
ments in adults of various species of both subgenera of Gerris
roughly fall on the growth lines for the corresponding segments.
Among the species of Gerris s. str. the segments of G. (G.)
gillettei deviate considerably from the growth lines for the corre-
spanding segments in G. (G.) marginatus. In the subgenus Limno-
porus of Gerris the points for femora and tibiae come below the
growth lines for the corresponding segments in G. (A.) remigis. In
Gigantometra, both the femur and tibia, especially the latter, fall
much above the growth lines for these segments in G. (A.) remigis,
and the tarsus falls roughly on the growth line for the same segment
in G. (A.) remigis. In Gerrisella the femur and tibia fall above the
regression lines (growth lines) for these segments in G. (G.) margi-
natus. Apparently, there are quite different growth patterns for
these segments in two genera (Gigantometra and Gerrisella) from
those in Gerris. In Gerriselloides all three segments fall close to
the growth lines for the three segments in G. (G.) marginatus, indi-
cating that this genus has the growth patterns for the middle leg
segments very similar to those in Gerris s. str. In Eurygerris (fig.
148) very gentle secondary allomorphic slope for the femur is
apparently formed by more or less great difference in initial growth
indices while the growth ratio remains practically the same among
species.

In the Limnometra-Tenagogonus s. str. complex (fig. 149) the
points representing femora and tibiae conform much more closely
to the incomplete growth lines for these segments in Tenagogonus
zambezinus than do the points for the hind leg segments in the
same species. Hoberlandt’s data on Tenagogonus madagascariensis
(1947) suggest that the femur grows a little more rapidly than the
tibia (femur in adult : femur in 2nd instar :: 181:103; tibia in
adult : tibia in 2nd instar :: 140:88), and the tarsus grows most
slowly (tarsus in adult : tarsus in 2nd instar :: 67:43). These
growth ratios appear to conform roughly to the differences in allo-
morphic slopes among segments. The nearly horizontal growth line
from a large nymph to an adult male in T. zambezinus is due possi-
bly to an abrupt decrease in growth ratio at the final stage of de-
velopment, so the difference in growth ratio for the tarsus between *T. zambezinus* and *T. madagascariensis* may be discounted. In three genera related to the *Limnometra-Tenagognus* complex, *Tenagometra*, *Tenagometrella*, and *Tenagogerris*, the three leg segments roughly fall on the allomorphic lines for the corresponding segments in the *Limnometra-Tenagogonus s. str.* complex. In *Tachygerris* (fig. 150) the allomorphic lines for all three segments conform to the growth lines of the corresponding segments much better than in the hind leg.

In figure 151 are plotted three middle leg segments in females of the *Limnogonus s. str.-Limnogonellus* complex. The allomorphic lines for all segments roughly reflect the growth lines for the corresponding segments in two species representing two subgenera of *Limnogonus* now under study. Note the deviation in *L. intermedius* (×).

**Charmatometrini:** In figure 152 the black points representing the femora in Charmatometrini fall along the incomplete growth line for the same segment in *Brachymetra unca*, the white points for the tibiae in the two smallest species deviate from the growth line for the same segment in *B. unca*. The growth slopes for the femora are evidently steeper than those for the tibiae in the two species studied. If this growth pattern persists among the species of this tribe, the relatively long femora in the larger species will be realized. This appears to be the case in this tribe. The femur is longer than the tibia in only two large species (*Charmatometra bakeri* which is the largest and *Eobates vittatus*); in all others the tibia is longer than the femur. The growth patterns for the femur and tibia in this tribe are essentially similar to those in *Gerris*, in which also the growth slope for the femur is steeper than that for the tibia (*P*<0.05 in *G. (A.) remigis*, *P*<0.1 in *G. (G.) marginatus*). Only because of the relatively small body size in this tribe is the relatively long femur (longer than the tibia) realized in the two large species. In *Gerris*, which is larger in body size than *Charmatometrini* generally, the femur is always longer than the tibia. The allomorphic slope for the tarsus deviates greatly from the growth lines for the same segments in the two species, and this deviation results probably from considerable difference in growth pattern for this segment among species.

**Cylindrostethini:** In the species of *Cylindrostethus* from the Eastern Hemisphere (fig. 154) the allomorphic slopes for all three segments conform fairly well to the incomplete growth slopes for
the corresponding segments in an unidentified species from the Philippines, suggesting that the growth patterns for all three segments are similar in all species. In the group of species of *Cylindrostethus* from the Western Hemisphere the allomorphic slopes, except that for the tarsus, are nearly parallel to those for the Eastern Hemisphere species of *Cylindrostethus*, and they always fall below those for the Eastern Hemisphere *Cylindrostethus*, indicating lower initial growth indices for them. We have already seen similar conditions for the antennal and the hind leg segments in this genus. In *Potamobates* (fig. 155), except for *P. thomasi*, the allomorphic slopes conform fairly well to the incomplete growth slopes in the two species of *Potamobates* studied. In *Platygerris* (fig. 156) the disconformity of the allomorphic line for the femur to the growth line for the same segment in *P. depressus* is conspicuous, although the allomorphic line for the tibia almost overlaps the growth line for the same segment. The middle femur is considerably longer than the body but a little shorter than the hind femur in this genus. This long middle femur appears to be realized by a relatively high growth ratio for the femur, as noted from figure 156. Also the growth pattern for the segments probably differs greatly in the largest species, *P. caeruleus*, as appears to be the case with the hind leg segments in this genus.

**Eotrechini**: The femur and tibia in *Eotrechus kalidasa* do not fall close to either one of the incomplete growth slopes for these segments in *Chimarrhometra orientalis* or *Onychotrechus rhexenor* (fig. 153). The allomorphic lines for the middle leg segments in all genera are not obtainable or difficult to obtain, due to few species of each genus available for study, or to a small range in body length when sufficient numbers of species are available for study (*Amembboa*, represented by triangles).

**Ptilomerinae**: In figure 157 the points for the femora and tibiae, except those in *P. wernerii*, conform fairly well to the incomplete growth line for each segment in the *Ptilomera* species studied. Deviation of the allomorphic slope for the tibia from the growth slope for the same segment is due partly to inaccuracy in measurement. The middle tibia in dried museum specimens of this genus is difficult to measure for the reasons mentioned previously. In *Potamometra berezowskii* the points for these two segments come above the allomorphic slopes for the corresponding segments in *Ptilomera*. In *Rhyacobates, Heterobates, Potamometroides*, and *Potamometropsis* the points for both segments come below the
slopes of the corresponding segments in *Ptilomera*. In *Rheumatomonus* the points for both segments, as might be expected, fall much below the growth lines for the two segments in the *Ptilomera* species from India. The growth slopes for the femur and tibia are apparently gentler than the equivalents in the Gerrinae, and the growth slope for the tibia is a little steeper than that for the femur in the species of *Ptilomera* studied.

*Halobatini*: In figure 159, while the points for the femora form a nearly straight slope, there is possibly no high correlation between the tibia and the length of body. This is due probably to the presence of a conspicuous mass of hairs on this segment. To carry a mass of hairs of varying degrees of development and density, different species probably have acquired different growth patterns for this segment. The points for the tarsi fall nearly parallel to the allomorphic slope for the femur. The conspicuous mass of hairs occur also on the first tarsal segment in the species of *Halobates*, but not in *Asclepios*. Miyamoto’s data (1937) on *Asclepios coreanus miyamotoi* indicate that the femur grows much more rapidly than the tibia or than the tarsus. The nearly parallel allomorphic slopes of the femur and tarsus do not reflect the growth slopes for these segments in *Asclepios coreanus miyamotoi*.

*Metrocorini*: In *Metrocoris histrio* (fig. 158) the points for all segments, except those for the femur and tibia in *Metrocoris stali(?)*, conform fairly well to the growth slopes in *M. histrio*. The points for all leg segments fall below growth lines (regression lines), although the decrease in growth ratio at the final stage of development is not as pronounced as it is for the hind femur and tibia. All three segments in *Eurymetra natalensis* fall roughly on the allomorphic slopes for the corresponding segments in *Metrocoris*. The femur in *Eurymetropsiella* and *Eurymetropsis* fall above the allomorphic line for the femur in *Metrocoris*.

In figure 160 the allomorphic lines for the femur and tibia, except for the femur of *Ventidius malayensis*, conform fairly well to the growth lines for these segments in *Ventidius henryi*. The points for the tarsi also form a slope nearly parallel to those for the preceding segments. Whether this allomorphic slope reflects the growth slope for this segment in *Ventidius* or not remains to be investigated (the tarsus is missing from the nymphal specimen of *V. henryi* available for study). In *Esakia* the points for femora and tibiae in the two species, especially those for the latter segments,
come considerably above the allomorphic slopes for these segments in Ventidius.

**Rhagadotarsinae:** In figure 161 the growth lines as well as the points representing leg segments are for the female in the two genera of *Rhagadotarsinae*. While the points for the femora in *Rheumatobates* conform fairly well to the growth line for this segment in *Rheumatobates rileyi palosi*, the tibia in three species (*Rheumatobates crassifemur esakii, Rheumatobates klagei, Rheumatobates bonariensis*) deviate conspicuously from the growth line for the tibia in *R. rileyi palosi*. A great majority of points for the tibiae and tarsi fall above the growth line for each segment in *R. rileyi palosi*. This is due probably to an abrupt increase in growth ratios at the final stage of development, as an abrupt increase in growth ratio at this stage in *R. rileyi palosi* suggests. The deviations of the tarsi in some species are greater than those in the other segments. The three segments in *Rhagadotarsus (Caprivia) hutchinsoni* considerably deviate from the growth lines for the corresponding segments in *R. rileyi palosi*. These deviations probably result from the gentler growth slopes for all segments in this species, as will be noted from figure 161. The growth ratios for the femora and tibae in both *Rheumatobates rileyi palosi* and *Rhagadotarsus kraepelini* (Hoffmann 1936) are about the same (no statistically significant difference between the two segments at the level of P. < 0.05 in *Rheumatobates rileyi palosi*).

**Trepobatinae:** In figure 162 the points for the tibiae fall nearly parallel to and above the growth line for the same segment (regression line) in *Trepobates knighti*, due probably to an abrupt increase in growth ratio for this segment at the final stage of development, as an abrupt increase in growth ratio at the final stage of development in *T. knighti* suggests. The points for femora fall considerably above the growth line for the same segment in *T. knighti* due probably to increase in growth ratio at the final stage of development. The points for tarsi (white points), however, fall roughly on the growth line for this segment in *T. knighti*, and the growth ratio for this segment does not increase abruptly at the final stage of development. In *Trepobatoides boliviensis* the points for the femur and tibia are above the allomorphic lines for the corresponding segments in *T. knighti*. In the same figure all segments in *Telmatometra ujhelyi* fall close to the growth lines for the corresponding segments in *T. knighti*.

In figure 163 the allomorphic slope for the femora in *Telmatometra*
deviates considerably from the growth line for the same segment in *Telmatometra indentata*; the slope for the tibias, in all species except for *Telmatometra retusa*, nearly conforms to the growth line for the tibia in *T. indentata*; for the tarsus the allomorphic slope for all species, except for *T. retusa*, cannot possibly be said to conform to the growth line for the tarsus in *T. indentata*. In the same figure the allomorphic slopes for the three segments in *Halobatopsis* may well be said to conform to the incomplete growth slopes for the corresponding segments in *Halobatopsis spiniventris*. In both species, for which incomplete data on the development of leg segments are available, the tibia apparently grows more than the femur. In the same figure the three segments in *Ovatametra minima* come below the growth lines for the corresponding segments in *Telmatometra indentata*.

In figure 164 the allomorphic slope for femora in the species of *Metrobates* conforms roughly to the incomplete growth line for the same segment in *Metrobates porcus*. The allomorphic lines for tibiae and tarsi, however, deviate greatly from the incomplete growth lines for the same segments in two species of *Metrobates* studied. The incomplete growth lines for the tibiae and femora are nearly parallel. In *Rheumatometra* (female) and *Hynesionella* the incomplete growth slopes for the tibiae are steeper than those for the femora.

The growth ratio for the tibia is greater than that for the femur in *Trepobates knighti* \( (P<0.05) \), and similar growth relations between the two segments probably exist in the other genera of Trepobatinae, as most of the incomplete data on the growth of these two segments indicate. The relatively short and robust femur (always shorter than the tibia) in Trepobatinae is probably realized from this peculiar growth relation between the two segments.

Throughout the major groups of Gerridae the allomorphic slopes for the middle leg segments usually conform much better to the growth slopes for the corresponding segments than do the allomorphic slopes for the hind leg segments to the growth slopes for their corresponding segments.

The front leg

**Gerrini:** There is no statistically significant difference in growth ratio between the femur and tibia in both species of *Gerris* studied. The growth ratios for both segments in *Gerris* (*Aquarius*) *remigis* are, however, considerably greater than those in *Gerris* (*Gerris*) *marginatus* \( (P<0.01) \). These differences in the growth ratio be-
tween the two species are well reflected by the allomorphic slopes for the corresponding segments in each subgenus (fig. 165). In the subgenus Limnoporus of Gerris the points for the femora and tibiae fall below the growth lines for the corresponding segments in G. (A.) remigis, and above those in G. (G.) marginatus, and the points for the tarsi fall below the growth line for the same segment in G. (A.) remigis. In Gerriselloides the points for the three segments fall roughly on the growth lines for the corresponding segments of Gerris (Gerris) marginatus. In Gerrisella the point for the femur falls a little above the growth line for the same segment in G. (G.) marginatus. In Gigantometra the three segments fall roughly on the growth lines for the corresponding segments in G. (A.) remigis. In Eurygerris the lengths of femora in different species are not well correlated with body sizes. This appears to have something to do with a high degree of modification of the inner margin of the femur in males of the smaller species. For example, in the smallest species, Eurygerris flavolineatus, the femur is unusually long in comparison with the tibia. In the Limnogonus s. str.-Limnogonellus complex also, the allomorphic slopes for femora and tibiae are nearly parallel, and this probably reflects the typical growth slopes for these two segments in the Limnogonus s. str.-Limnogonellus complex. In the Limnometra-Tenagogonus s. str. complex the front leg segments are considerably longer than in Gerris or Limnogonus, although the general size of the body is about as large as in the former genus. The points for the femora and tibiae form nearly straight parallel slopes; the slope for the tarsi is also about as steep as that for the two preceding segments. In the related genera, Tenagogerris, Tenagometra, and Tenagometrella (female), the points for all three segments fall roughly on the allomorphic slopes for the corresponding segments in the Limnometra-Tenagogonus s. str. complex. In Tachygerris the growth as well as allomorphic slopes are steeper than in the other genera, as in the other legs and the antenna.

Charmatometrini: The allomorphic slopes for the three segments are steeper than the incomplete growth slopes for these segments in the two species of Brachymetra studied.

Cylindrostethini: The points for three segments in the species of Cylindrostethus from the Eastern Hemisphere fall a little above the growth lines for the corresponding segments in a species of Cylindrostethus from the Philippines. The points for the three seg-
ments in the species of the Western Hemisphere *Cylindrostethus* fall nearly parallel to the allomorphic lines for the corresponding segments in the Eastern Hemisphere *Cylindrostethus* species, but they come definitely below the latter, as in all other leg and antennal segments. In *Potamobates* all three segments in all species including *P. thomasi*, which deviates otherwise, fall close to or on the growth lines for the corresponding segments in *P. woytkowskyi*. It was found that the incomplete growth lines for all three segments in *P. horváthi* are nearly parallel to those in *P. woytkowskyi*. The front leg segments are relatively short in *Platygerris*. In *Platygerris* the three segments in *P. asymmetricus* fall exactly on the extended growth lines for the corresponding segments in *P. depressus*, while the points for the segments in the largest species, *P. caeruleus*, fall considerably below the extended growth lines of *P. depressus*. We have already seen the deviations of the points for the middle and hind femora and the first antennal segment in this species. This largest species is apparently different in the growth patterns for most leg and antennal segments from those of the other two species of *Platygerris*.

*Eotrechini*: In *Amemboa* there is apparently no high correlation between the body length and the length of the front leg segments. For example, the femur and tibia are longest in one of the smallest species, *A. horváthi*. The absence of a high correlation has apparently something to do with more or less conspicuous modification on the inner margins of the femur and tibia in the smaller species (fig. 605). A very similar tendency for the front leg in *Eurygerris*, in which also more or less conspicuous modification occurs on the femur in the smaller species, was already noted. Since the number of species per genus is limited in the other genera, they are dismissed here.

*Ptilomerinae*: In figure 166 the allomorphic slopes for the three segments in *Ptilomera* conform fairly well to the growth lines for the corresponding segments of an unidentified species of *Ptilomera* from Southern India. Interestingly, the growth slope for the tarsus is steeper than slopes for the other two more proximal segments. This proximo-distal order of increasing growth ratio does not appear to be the case with the other legs, at least not with the hind leg. In *Potamometra berezowskii* the points for the femur and tibia fall on the allomorphic slopes for the corresponding segments in *Ptilomera*. In *Rhyacobates* all three segments fall below the growth slopes for the corresponding segments in the *Ptilomera*
species studied, as they do in *Heterobates* and *Potamometropsis*. In *Potamometroides* the points for the femora and tibia fall close to the growth lines for the corresponding segments of the *Ptilomera* species. In *Rheumatogonus* the points for all three segments fall much below the growth lines for the corresponding segments in the *Ptilomera* species from India, and this is probably the most primitive condition in this subfamily.

**Halobatinae:** In the *Asclepios-Halobates* complex (*Halobatini*) specific difference in the front leg segments is conspicuous as in the other legs. A rough allomorphic slope for tarsi is steeper than the slopes for the other two segments. Whether this reflects typical growth slopes in the *Asclepios-Halobates* complex or not is not known. Miyamoto (1937), in his study on *Asclepios coreanus miyamotoi*, did not give the data on the development of the front leg.

In *Metrocoris* (fig. 167) the allomorphic slopes for the three segments, except for *M. ståli(?)*, conform well to the growth lines for the corresponding segments in *Metrocoris histrio*. In *Eurymetra natalensis* the points for all three segments fall roughly on the allomorphic lines for the corresponding segments in *Metrocoris*. In *Eurymetropsis* and *Eurymetropsiella* the points for the tarsi fall much above the growth line for the same segment in *M. histrio*. In *Ventidius* the allomorphic slope for the tarsi is greater than that for the femur. Whether they reflect the typical growth patterns in *Ventidius* or not is not known, since the front leg in the nymphal specimen was not available for study. In *Esakia kuiteri* the points for the femora and tibia fall above the allomorphic slopes for these segments in *Ventidius*.

**Rhagadotarsinae:** In *Rheumatobates rileyi palosi* the growth slopes for the three segments from the female third developmental stage to the adult female follow the pattern of proximo-distal gradient of decreasing growth ratio (fig. 168). The points representing the leg segments in other species of the subfamily conform fairly well to the growth lines for the corresponding segments in *R. rileyi palosi*. A conspicuous deviation is noted for the tarsus in the smallest species, *Rheumatobates minutus*. The relatively short tarsus in the largest species, *Rhagadotarsus (Capricia) hutchinsoni*, is probably derived from a quite different growth pattern from that of *R. rileyi palosi*.

**Trepobatinae:** In the postembryonic development of *Trepobates knighti* (fig. 169) the growth ratio for the femur is greater than
incomplete ratios for the other two segments (P<0.05), and the growth lines for the tibia and tarsus are equally steep. The points representing the leg segments in adults of other species of Trepobates fall nearly in parallel with the growth lines for the corresponding segments in T. knighti. The relatively great distance of the points from the growth lines is presumably due to a rather abrupt increase in growth ratio at the final stage of development, especially for the femora and tibiae. In Trepobatooides the point for the tibia is considerably below the growth line for the same segment in Trepobates, and the tarsus falls above the growth line for the tarsus. In Telmatometra, Halobatopsis and Ovatametra the points for the femora and tibiae conform well to the growth slopes for the corresponding segments in Telmatometra indentata, although Telmatometra retusa makes a rather conspicuous deviation. The points for tarsi do not conform well to the growth slope for the same segment in T. indentata. In Metrobates, while the points for the femora fall rather close to the incomplete growth line for the same segment of Metrobates porcus, the allomorphic slopes for the tibiae and tarsi are almost vertical, deviating greatly from the growth lines for the corresponding segments in M. porcus. It was further found that the growth slopes for these segments in M. denticornis, a larger species, are considerably gentler than the equivalents in M. porcus. The deviations of the allomorphic slopes in the more distal segments from the growth slopes for the corresponding segments are thus consistently noted in antennal and all legs in this genus. A rather distinct proximo-distal gradient of decreasing growth ratio among the front tarsal segments appears to exist, as far as the incomplete data indicate. In Hynesionella and Rheumatometra (female) there appears to be no distinct proximo-distal gradient of decreasing growth ratios, as far as incomplete data indicate.

The tarsal segments

The tarsal segmentation becomes recognizable after the fourth or fifth nymphal stages of development in most genera, although it is distinct in considerably earlier stages in the middle and hind legs of some genera (e.g., Metrocoris). In spite of these difficulties in obtaining data, evidence indicates that the growth ratio for the first tarsal segment is greater than that for the second in most genera. There is thus a striking tendency for the first segment to be relatively longer in larger species within the same genus, as will be described below.
Gerrini: The length of the first tarsal segment relative to the second in Gigantometra is 1.22:1. This ratio is greater than the ratio for most species of Gerris. In Gerris the length of the first relative to the second is definitely greater in the subgenus Aquarius (0.67-1.3:1) than in Gerris s. str. (0.50-1.0:1), which is shorter in body size. Another subgenus of Gerris, Limnoporus, is about as large as Aquarius in body size except for G. (L.) canaliculatus, and the relative length of the first segment to the second ranges from 0.7:1 in the smallest species, G. (L.) canaliculatus, to 1.0:1. These ratios are similar to those in Aquarius, suggesting that all three subgenera have similar growth relations for these two segments. In Gerriselloides the length of the first relative to the second is as in a typical species of Gerris s. str.; the same ratio is much smaller in Gerrisella. In Eurygerris, in spite of relatively short body-size, the length of the first relative to the second is much greater (0.8-1.0:1) than in Gerris s. str., indicating the presence of growth patterns for both segments quite different from those of Gerris s. str. In the Limnogonus s. str. the length of the first relative to the second segment is 0.5-1.0:1, while it is 0.33-0.60 in Limnogonellus which is smaller in body size. This indicates that both subgenera presumably have similar growth patterns for these two segments. In the Limnometra-Tenagogonus s. str. complex there is a beautiful series of decrease in the relative length of the first to the second segment from the longer to the shorter species, as will be noted from the table 16. The relative lengths range from 0.84:1 to 1.9:1 in Limnometra, from 0.60:1 to 0.90:1 in Tenagogonus s. str. which is generally smaller in body size. Both subgenera appear to have similar growth patterns for the tarsal segments. In Tenagometrella the length of the first relative to the second segment, as well as the length of the body, are as in typical species of Limnometra. In Tenagometra and Tenagogerris the relative lengths of the first and second segments are as in a typical species of Tenagogonus s. str. In Tachygerris the first segment is nearly equal to the second in length as in Eurygerris, although they are not closely related.

Charmatometrini: The length of the first tarsal segment relative to the second is greatest in Charmatometra bakeri which is greatest in body length. In Brachymetra there is a clear tendency for the first segment to be relatively longer in the longer species.
Cylindrostethini: In *Cylindrostethus* the relative length of the first to the second segment varies relatively little (0.25-0.55:1), in spite of the fact that the body length varies considerably among species. In a nymph, apparently in the final stage of development, the tarsal segmentation is indistinct. In *Potamobates* the length of the first relative to the second segment also varies relatively little (0.29-0.38:1), in spite of a considerable range in body size among species. This is also the case with *Platygerris* (0.35-0.42:1). In all these genera there is thus no clear tendency for the first segment to be relatively longer in the larger species. In fact, in the last two genera there is evidence that the second segment grows more than, or about as much as, the first segment at the final stage of development (*Potamobates horváthi*, *Platygerris depressus*), and this tendency in growth pattern is presumably true of *Cylindrostethus*. This peculiar growth pattern is probably the mechanism by which the relatively short first tarsal segment occurs in this tribe.

Eotrechini: In *Eotrechus*, which is largest in body size, the length of the first tarsal segment relative to the second (1:1) is greater than in the other genera of Eotrechini. In *Onychotrechus* the length of the first segment in relation to the second (0.36-0.42:1) is small in comparison with other genera. This has presumably something to do with the presence of the conspicuous and more proximally located claws on the second tarsal segment. There is no conspicuous difference in the relative lengths of the two segments among species in *Amemboa* (0.54-0.75:1). The relative lengths in *Chimarrhometra* are similar to those in *Amemboa*.

Ptilomerinae: The first tarsal segment has apparently been greatly prolonged in evolution of this subfamily. It is always longer than the second segment, often two or three times as long as the second segment. *Rheumatogonus* is the only exception, in which the first segment is shorter than the second segment, and this is presumably the least specialized condition in this subfamily. In an unidentified species of *Ptilomera* from Southern India the first tarsal segment grows much more rapidly than the second at the final stage of development, and this is presumably the underlying mechanism by which the relatively long first tarsal segment is realized in this subfamily. In *Ptilomera* there is a tendency for the length of the first segment relative to the second to be greater in the larger species. That the lengths of the tarsal segments are allometrically derived in this subfamily is also evidenced by the fact that the relative length
of the first to the second segment is almost always greater in the females which are longer in body size.

Halobatinae: In the Asclepios-Halobates complex (Halobatini) the relative length of the first to the second segment is definitely greater in Halobates (0.37-1.15:1), which is longer in body length, than in Asclepios (0.15-0.28:1). In Metrocorini the first segment is greatly reduced, often one fourth to one fifth as long as the second segment. The only exception is Eurymetropsiella, in which the relative lengths of the first and second segments are as 0.58:1. The front leg tarsal segmentation becomes distinct only in adults of Metrocoris histrio, although tarsal segmentation is quite distinct in much earlier stages of development in the middle and hind legs in this species.

Rhagadotarsinae and Trepobatinae: In both subfamilies the first tarsal segment is greatly reduced, to about the same degree as in Halobatinae. How this highly reduced first tarsal segment is realized during the development remains to be elucidated.

(b) The middle tarsal segments

Gerrini: The data indicate that the first tarsal segment grows much more than the second segment at the final stage of development in both species of Gerris studied (G. (A.) remigis and G. (G.) marginatus). This difference in growth ratios between the two segments appear to have been inherited in all species of Gerris. In Aquarius the ratio of the first tarsal segment to the second is 2.9-8.0:1, while the same is 1.7-3.4:1 in Gerris s. str., which is shorter in body length. In another subgenus, Limnoporus, the ratio is 4.0-4.8:1 and the body length, except for G. (L.) canaliculatus, is as in typical species of Aquarius. All these facts indicate that the three subgenera have similar growth patterns in common. In Gigantometra the ratio of the first to the second is 9.5:1. Considering the gigantic size of the body in this genus, this extraordinarily long first tarsal segment is easily imaginable, assuming that this genus has similar growth ratios for the tarsal segments to those in Gerris. In Gerriselloides the ratio of the two segments are as in a typical species of Gerris s. str. In Gerrisella the relative lengths of the two segments are 3.1-3.3:1. This is much greater than the average ratio in the species of Gerris s. str. of equivalent body lengths. In Eurygerris the ratio of the first to the second is 4.6-6.0(?) :1. This is considerably greater than the ratios in Gerris s. str., although the body length in this genus is shorter than most species of Gerris s. str.,
indicating the presence of different growth patterns in the two genera.

In the *Limnogonus s. str.-Limnogonellus* complex the ratio of the first to the second is definitely greater in the former than in the latter group which is shorter in body length (3.3-5.4:1, 3.0-4.3:1, respectively). In the *Limnometra-Tenagogonus s. str.* complex there is a tendency, though not highly consistent, for the ratio of the first to the second segment to be greater in the longer species than in the shorter species (3.9-7.0:1, 3.4-4.6:1, respectively). Among the genera related to the *Limnometra-Tenagogonus s. str.* complex, the ratio of the first to the second is relatively great in *Tenagometra* (5.4:1) considering its body length. In *Tenagogometrella* the length of the first relative to the second is as in typical species of *Limnometra*. In spite of the difference in absolute lengths of the tarsus between the sexes, the relative lengths of the two segments are about the same in the two sexes, indicating the presence of similar growth ratios with different initial growth indices in different sexes. In *Tenagogogerris* the length of the first relative to the second is as in the shorter species of *Limnometra*, or of the longer species of *Tenagogonus s. str.* In *Tachygerris* the length of the first relative to the second ranges from 5.3:1 to 6.0:1; these ratios are similar to those in *Eurygerris*.

*Cylindrostethini*: In *Cylindrostethus* there is a striking tendency for the ratio of the first to the second to be greater in the longer species; it ranges from 3.1:1 to 6.0:1. In *Potamobates* also there is a striking tendency for the relative lengths of the first to the second to be greater in the longer species (4.0-3.2:1). An exception to this tendency is that the ratio is not greatest in *P. thomasi* which is much longer than the other species. In *Platygerris*, *P. caeruleus* is much longer than the other two species, but the relative length of the first to the second is smallest (absolute length of the tarsus is greater than the other two species). Unlike that of the front leg, the first segment grows much more rapidly than the second in *Platygerris depressus* and in an unidentified species of *Cylindrostethus* from the Philippines. This growth mechanism is presumably the one by which the relatively long first tarsal segment is realized in the middle leg of this tribe.

*Charmatometrini*: The ratio of the first to the second segment is greatest in the largest species, *Charmatometra bakeri*. There is a striking tendency in *Brachymetra* for the length of the first relative to the second to be greater in the larger species. In *Eobates* the
length of the first in relation to the second is the smallest (3.1-3.2:1) in the tribe, in spite of the fact that the body is longer than in most species of *Brachymetra*. This indicates that for these segments this genus has somewhat different growth patterns from those of the other two genera.

**Eotrechini**: In *Eotrechus*, according to Esaki (1928), the first tarsal segment is as long as the second. The ratio of the first to the second in *Amemboa* (1.9-2.27:1) is greater than in *Eotrechus*, which is much longer in body length. These two genera are so remotely related that it is hardly conceivable that both genera have similar growth patterns in common. In *Onychotrechus* the first segment is much shorter than the second (0.33-0.44:1). This unique ratio presumably has something to do with the occurrence of the conspicuous claws near the middle of the second tarsal segment. The underlying growth patterns for these two segments are unknown to me, since in an old nymph of *Onychotrechus rhexenor* the tarsal segmentation is not recognizable. In *Chimarrhometra* the length of the first relative to the second is 1.9:1, the ratio close to that of *Amemboa*.

**Ptilomerinae**: The tarsus is always greatly curved in the dried museum specimens, so that measurements are next to impossible. The first segment is usually five or six times as long as the second.

**Halobatinae**: In the *Asclepios-Halobates* complex (Halobatini) the length of the first relative to the second segment is greater in *Halobates* (2.7-6.7:1) than in *Asclepios* (2.2-2.3:1) which is shorter in body length. Presumably the greater ratios in *Halobates* are due partly to the presence of a dense mass of hairs of varying degrees of development in various species. The relative lengths of the two segments thus vary considerably at the specific level in *Halobates*. During the postembryonic development of *Metrocoris histrio* the first tarsal segment grows considerably faster than the second. In spite of the considerable difference in body length among species there is no tendency for the first segment to be relatively longer in the longer species, and the ratios of lengths of the two segments range from 8.0:1 to 4.6:1. In *Esakia* the relative lengths are greatest in the female of *E. usingeri* which has the longest body.

**Rhagadotarsinae**: In the females of this subfamily the ratio of the first to the second segment is greater in *Rheumatobates* than in the two subgenera of *Ragadotarsus* which are greater in body
length. The underlying growth patterns involved remain to be seen.

Trepobatinae: In Trepobates knighti the tarsal segmentation is not distinct even at the final nympha1 stage. The tendency for the relative length of the first to the second to be greater in the longer species of Trepobates is not clear, due primarily to a small range in body size among the species. In Metrobates the first segment is shorter than the second; this is unique in the subfamily.

The hind tarsal segments

Gerrini: In Aquarius the ratio of the first tarsal segment to the second (1.7-2.8:1) is greater than in Gerris s. str. (1.6-2.0:1), which is shorter in body length. In another subgenus, Limnoporus, the ratio ranges from 1.9:1 in the shortest species \([G. (L.) canaliculatus]\) to 2.6:1. The absolute body length as well as the length of the first tarsal segment relative to the second are as in typical species of Aquarius. In the late postembryonic developmental stages the first segment grows much faster than the second segment in the two species of Gerris studied. In Gigantometra the first tarsal segment is 3.75 times as long as the second, and this is considerably greater than the highest ratio in Aquarius. Considering the extraordinarily large body size of this genus, this ratio is conceivable if this genus has similar growth ratios for the two segments to those in Aquarius. In Gerriselloides the length of the first relative to the second is as in a typical species of Gerris s. str. In Gerrisella the length of the first relative to the second segment is much smaller (1.1:1) than in any species of Gerris s. str. In Eurygerris the ratio of the first to the second is as in Gerris s. str.

In the Limnogonus s. str.-Limnogonellus complex there is no significant difference in the relative length of the first to the second segment between the two genera (1.3-2.4:1, 1.66-2.2:1, respectively). Since the body length in the two subgenera is considerably different, the absence of a difference in the length of the first relative to the second segment denotes the presence of different growth patterns for the two segments in each subgenus. In the Limnometra-Tenagogonus s. str. complex there is a striking tendency that the length of the first relative to the second is greater in the longer species (1.8-3.3:1 in Limnometra, 1.1-1.8:1 in Tenagogonus s. str., respectively). In Tenagometra and Tenagogerris the ratio is as in a typical species of Tenagogonus s. str. In Tenagometrella it is as in a typical species of Limnometra. In Tachy-
gerris the length of the first relative to the second is as in Limnognus (1.6-2.5:1).

**Cylindrostethini:** The length of the first tarsal segment relative to the second is greatest in the largest species, *C. productus*. In *C. sumatranus* the ratio of the two segments is quite different from other species of *Cylindrostethus*. The ratio changes from 1.0:1 to 2.0:1 in *Cylindrostethus*. In *Potamobates* the length of the first relative to the second ranges from 1.3:1 to 2.3:1 in the longest species, *P. thomasi*. The relative length is smaller in the shorter species, as will be noted from the table 16. In *Platygerris* the length of the first relative to the second is greatest in the longest species, *P. caeruleus*. Developmental data indicate that the second segment becomes even a little shorter and the first segment grows to be considerably longer at the final stage of development. The above mentioned tendency toward reduction in the length of the first segment relative to the second in the shorter species appears to reflect this growth pattern.

**Charmatometrini:** The length of the first relative to the second segment is not greatest in the longest species, *Charmatometra bakeri*. In *Brachymetra* there is a tendency for the length of the first relative to the second to be greater in the longer species than in the shorter species. In *Eobates* the ratio, as in the middle leg, is the smallest in the tribe although the body is one of the longest. From the above it seems probable that each genus in this tribe has somewhat different growth patterns for these two segments.

**Eotrechini:** As in the middle leg the tarsal segments in *Eotrechus*, according to Esaki (1928), are nearly equal in length to each other. In *Amemboa*, which is shorter in body length, the length of the first relative to the second is greater than in *Eotrechus*, but the two genera are not closely related and it cannot possibly be conceived that both genera have, in common, similar growth patterns for these segments. The length of the first relative to the second in *Chimarrhometra*, however, is similar to that in *Amemboa*. In *Onychotrechus* the first segment is much shorter than the second. This unique proportion has presumably something to do with the conspicuous claws located near the middle of the second segment.

**Ptilomerinae:** In *Ptilomera* and *Potamometra* both tarsal segments are completely fused. In all other genera they are distinct from each other, and the first segment is shorter than or about as long as the second segment. Esaki (1930), however, says that the first segment is about twice as long as the second in *Plecio Bates*. 

Halobatinae: In Halobates the tarsal segments are completely fused. In Asclepios they are distinct from each other, and the first segment is shorter than, or about as long as, the second. In the postembryonic development of the hind leg the first segment grows more than the second in Metrocoris histrio. In all species of Metrocoris studied, however, the first segment is about as long as the second. There is thus no tendency that the first segment is longer in the longer species. In the related genera, Eurymetra, Eurymetopsis, and Eurymetopsisella, both segments are also nearly equal in length. In Ventidius there is a striking tendency for the first segment to be relatively longer in the larger species. The same tendency is seen in Esakia though less pronounced.

Rhagadotarsinae: In Rhagadotarsus the first segment is as long as, or a little shorter than the second; in Rheumatobates, which is shorter in body length, the first segment is considerably shorter than the second in a majority of species.

Trepobatinae: The tarsal segmentation is not distinct even at the fifth nymphal stage in Trepobates knighti. There is no great difference in relative lengths of the first and second segments among species of Trepobates, probably because the range in body size is rather small in this genus. In Rheumatometra and most species of Metrobatopsis both segments are completely fused. In many genera the first segment is a little shorter than the second, and this is especially pronounced in Metrobates in which the second segment is about two to three times as long as the first. These unique proportions have presumably something to do with the presence of conspicuous claws arising from near the middle of the second segment.

The coxa

The middle coxa: The coxa in the more primitive genera of the Gerridae is shorter than wide. It has apparently become elongate in evolution. In Gerrinae the coxa has apparently been prolonged in Onychotrechus and Amemboa. In Ptilomerinae the coxa has been greatly prolonged in the female of Potamometroides. In all genera of Halobatinae and Trepobatinae the coxa has remained short. In Rhagadotarsinae the coxa has become robust and long in some species of Rheumatobates.

The hind coxa: The degree of prolongation of the hind coxa is much more pronounced than in the middle coxa. In Gerrinae the prolongation of the coxa has arisen in Onychotrechus and Amemboa. In Ptilomerinae it has been apparently prolonged in Rhyacobates, Potamometra, Heterobates, and is very conspicuously prolonged in
the female of *Potamometroides*. In *Ptilomera* the coxa has remained short, but with a more or less conspicuous spinous process on the caudal margin in the subgenus *Ptilomera s. str.* In Halobatinae the coxa has apparently been prolonged in *Asclepios* and *Halobates*. In Rhagadotarsinae the coxa is wider than long in the subgenus *Caprita* of *Rhagadotarsus*; it is elongate and thickened in various degrees in *Rheumatobates*, which is more specialized.

Phylogenetic changes in relative lengths of the middle and hind legs

In the Gerridae there are only two genera (*Eotrechus* and *Gigantometra*), in which the hind leg is longer than the middle leg. Each genus, as repeatedly pointed out, is structurally very primitive and longest in its tribe. In all other genera the hind leg is shorter than the middle leg. A great contributing factor toward the reduction in length of the hind leg is the reduction of the hind tibia, apparently connected with changes of function of the hind leg [from locomotory organ(?) to steering organ] and with the reduction of the body length in phylogeny. In a great majority of species of Gerridae, except for Trepobatinae, the hind femur is about as long as the middle femur. The hind tarsus is also shorter than the middle tarsus in a great majority of species of Gerridae. It may thus safely be said that the condition in *Gigantometra* and *Eotrechus* is the most primitive, and the hind leg has become shorter in evolution, accompanied mainly by reduction of the tibia and the tarsus.

Shift of position of the claws

The primitive position of the claws is probably the apex of the second tarsal segment in all legs, as seen in *Eotrechus*. From this probable primitive position the claws have shifted their positions more and more basally. In the front leg the claws arise from beyond the middle of the second segment in the majority of genera of Gerrinae and Ptilomerinae. They arise from the middle, or even before the middle, of the second tarsal segment in the great majority of species of Halobatinae and Trepobatinae. Among Rhagadotarsinae the claws arise from the base of a deep cleft of the second segment in the genus *Rhagadotarsus*. In the middle and hind legs the claws are often lost in some genera of Ptilomerinae (*Rhyacobates, Heterobates, Potamometroides*) and Cylindrostethini of Gerrinae (except for *Cylindrostethus* from the Eastern Hemisphere). The claws of the middle leg in Metrocorini and
Trepobatinae are always inconspicuous and arise from near the apex. The claws of the hind leg in Halobatinae and Trepobatinae, however, are relatively well developed and slender, and arise more basally than the claws of the middle leg; sometimes they are conspicuous and located near the middle (Metrobates). Onychotrechus of Gerrinae is peculiar in that the conspicuous claws arise from near the apical third of the second segment of all tarsi, although the claws are less conspicuous and arise from the apex or near apex in all other genera of the Gerrinae. In Rhagadotarsus of Rhagadotarsinae the claws of the both middle and hind legs are inconspicuous, and the claws of the hind leg in Rheumatobates are relatively well developed and slender as in Trepobatinae. It is interesting to note that when the conspicuous claws occur on the middle or hind legs, the segment bearing them (second segment) is always unusually long (Onychotrechus, Metrobates).

(3) General Discussion
Ontogeny and phylogeny

De Beer (1951) has given an account of various relations between phylogeny and ontogeny. Some of them have bearing upon the present problem. For example, many groups showing phyletic increase in body size exhibit recapitulation; this is, by De Beer’s definition, hypermorphosis. In other groups showing phyletic decrease in body size, ontogeny often foreshadows phylogeny.

It has been found in this study that the body has apparently become shorter at all taxonomic levels in the evolution of the great majority of groups of Gerridae. It has also been found that similar allometric growth patterns appear to exist for certain antennal and leg segments within genera and subgenera. When both phenomena occur at the same time, ontogeny, as mentioned above, roughly foreshadows or anticipates phylogeny. The simplified relation of ontogeny to phylogeny in this case is diagrammatically shown in figure 170. In this figure the length of a certain leg or antennal segment in the more primitive and longer species A at its developmental stage B’ would roughly be equal to the length of the same segment in the adult of a derived, shorter species B, etc. Rensch (1948) has already discussed the overall tendency towards reduction in body size in evolution of insects in some detail. The case of Gerridae provides generally good support to Rensch’s view. If the reduction in body size is a wide spread phenomenon in insects, as Rensch contends and as the present study sub-
stantiates, and similar allometric growth mechanisms for certain structures among related species or genera persist generally in insects, the hypothesis diagrammed in figure 170 would generally hold true. It may, therefore, serve as a useful working hypothesis in the study of structural evolution of insects. Of course in the groups showing phyletic increase in body size, as has been observed in a few genera of Gerridae, ontogeny would recapitulate phylogeny if similar allometric growth patterns for certain structures persist among related species.

As already shown, there are many cases of deviation from the above mentioned simple picture. The formation of the consistent secondary allomorphic slope for the hind tibia in many genera of Gerridae is a case in point. Modification of the allomorphic growth pattern, either in growth ratio or initial growth index or both, for the hind tibia has apparently arisen at the specific level in most genera perhaps in adjustment to environmental changes. Many similar cases of alteration of allometric growth ratios in the same phyletic line are known in palaeontology (e.g., Reeve and Murray, evolution of the horse’s skull, 1942). Rensch’s (1947) studies on contemporaneous vertebrates also indicate that the growth ratios for certain structures shift with enlargement of the body size.

Indeed, the points for the hind tibiae fall roughly on an oblique straight line in many genera of Gerridae, so that there is a consistent tendency for the hind tibia to be relatively shorter in the shorter species of a genus. This fact may easily lead one to suspect that the line (allomorphic line) may reflect the ontogenetic growth line for the hind tibia in the group of species concerned, if ontogenetical evidence is not available. Whatever the underlying growth mechanism may be, the result is a steeper allomorphic slope than the equivalent for the femur in almost all genera of the Gerridae.

As is generally known, the hind leg in the Gerridae is of relatively secondary functional importance. It performs its function as a rudder, or steering organ in water; it is by no means as powerful a locomotory organ in water as the middle leg; on land the hind leg is merely dragged behind when walking and serves as a support to prevent retreat on a slope, as recorded by Miyamoto (1953) for Metrocoris histrio. Such being the function there has presumably been selection against powerful and long distal hind leg segments in the evolution of the Gerridae, and more and more relatively short
hind leg segments have been favored. If this interpretation is correct the case provides an example of orthoselection, and in this process of selection several different types of alteration in underlying growth patterns are involved.

**Taxonomic significance**

Taxonomists are agreed that mere body size differences may have no taxonomic significance, since they are often the direct effect of environmental conditions. But greater importance is sometimes attached to differences in proportional size. This tendency is pronounced in works with such groups of insects as Gerridae, in which the appendages and antennae are well developed, and the accounts of them occupy a large part of specific and generic descriptions.

The study of the allometric growth of the antennal and leg segments shows clearly that the proportional lengths of the segments are subject to change depending on different body lengths and the underlying growth patterns for these segments. It is obvious, therefore, that the underlying growth patterns, not the mere proportional lengths of segments in adults, are really of taxonomic importance. The indication obtained in this work in regard to the bearing of different growth patterns upon the taxonomy of Gerridae is not based on much ontogenetical evidence, so that the description of the growth patterns as taxonomic characters in the following lines is tentative. It is my serious intention to correct the mistakes, which will inevitably be made, by studying the development of more forms of the Gerridae in the future. The study of speciation or subspeciation is not the concern here, so that the taxonomic significance of the growth patterns at the levels above the subgenus is discussed below.

At the subfamilial level the Rhagadotarsinae is characterized by the much lower growth ratio for the second antennal segment than for the other segments, and probably by the proximo-distal order of decreasing growth ratios of the hind leg segments. Trepobatinae may be characterized by the relatively low growth ratio and initial growth index for the middle femur. The Ptilomerinae (at least *Ptilomera*) may be characterized by the relatively high initial growth index and the relatively low growth ratio for the proximal segments of the antenna and legs. The proximo-distal increase in growth ratio, which appears to exist at least in the front leg segments in *Ptilomera*, may occur in other genera of Ptilomerinae and thus may characterize this subfamily. In Gerrinae the growth ratio
for the femur is probably almost always greater than that for the tibia in the middle leg.

At the tribal level, Cylindrostethini appears to be characterized at least by a smaller growth ratio for the first tarsal segment than for the second in the front leg. Charmatometrini is probably similar in the growth patterns for the leg and antennal segments to the Gerrini.

At the generic or subgeneric level the growth pattern is of even greater taxonomic importance. The following factors were considered in the evaluation of the generic and subgeneric status of groups of Gerridae.

(1) It was a priori expected that all congeneric species would have more or less similar growth patterns for the antennal and leg segments, and the points for any segment were expected to fall on or close to the growth lines for the corresponding segments in the representative species of the same genus.

(2) As already observed, however, there is a tendency for certain segments, e.g., the hind tibiae, to form the nearly straight secondary phylogenetic allomorphic lines, due apparently to the differences in growth patterns for these segments at the specific level. In such cases the points for the segments are expected to fall on the same allomorphic line (or slope).

(3) Any striking deviation from (1) or (2) are thought to be probably indicative of marked phylogenetic difference and hence of probable generic or subgeneric rank.

In the three subgenera of Gerris the growth patterns for all leg and antennal segments appear to be more or less distinctly different. The growth ratios for at least many antennal and leg segments are probably greater in Aquarius than in Gerris s. str. Gerriselloides has essentially the same growth patterns for all antennal and leg segments as those in Gerris s. str., to which this genus was formerly assigned. Gerrisella, which was also formerly included in Gerris, presumably has quite different growth patterns for all antennal and leg segments from those of Gerris. In Gigantometra, which was formerly a part of Limnometra but is actually closer to Gerris, the growth patterns appear to be significantly different in many segments from those in Gerris. In Tenagogonus and related genera, Tenagogerris and Tenagometrella, the growth patterns for at least many antennal and leg segments are presumably similar, although the male in Tenagometrella appears to have unusually long initial sizes for all antennal and leg segments. In Tachygerris the growth
ratios for the first three antennal segments appear to be greater than those in the other genera of Gerrini occurring in the Western Hemisphere. The growth patterns for segments are probably similar in *Limnogonus s. str.* and *Limnogonellus* except that for the fourth antennal segment. *Eurygerris* is apparently characterized by formation of the secondary allomorphic lines for basal leg segments which are more nearly horizontal than in the other genera of Gerrini. Among the genera of Charmatometrini, the most distinctive generic differences appear to be in the proportional lengths of the tarsal segments of the middle and hind legs. The species of *Cylindrostethus* from the Western Hemisphere and those from the Eastern Hemisphere appear to be consistently different in the initial growth indices for all antennal and leg segments. The two groups may be described as distinct genera or subgenera by the future workers, since they differ from each other in some other characters. In *Potamobates* the allomorphic slopes are not continuous with those of *Cylindrostethus* from the Western Hemisphere, suggesting that these genera have significantly different growth patterns for the antennal and leg segments. In *Platygerris* the very long hind and middle femora appear to be realized by the very high growth ratio which apparently characterize this genus.

Among Ptilomerinae, *Rheumatogonus* is characterized by the unique proportional lengths of the antennal and leg segments which must be realized by quite different growth patterns from those of the rest of Ptilomerinae. In Halobatinae the proportional lengths of the front tarsal segments of the *Asclepios-Halobates* complex are presumably realized from a similar growth pattern in all species, although the relative lengths of the middle tibia and the first tarsal segment of the middle leg must be realized by quite different growth patterns at the specific level. In *Metrocoris, Eurymetra, Eurymetropsiella, Eurymetropsis* the growth patterns for the antennal and leg segments are presumably similar. *Ventidius* and *Esakia* are closely related, but the growth patterns at least for the first antennal segment and the middle tibia are presumably significantly different. *Trepobates* and *Telmatometra*, though related, are probably considerably different in the growth patterns at least for the more distal segments of the antenna and legs. *Stenobates* and *Rheumatometroides* are closely related and probably have similar growth patterns for many segments.

The last but by no means the least important thing that this study has revealed is a strong tendency for a species or a group of species,
which conspicuously deviates in one segment, to deviate also in all or many other segments. This tendency suggests that for the pro-
duction of the three legs and antennae, more or less the same physio-
genetical system is involved.* If this phenomenon is widely preva-
 lent in the other groups of insects or more widely in other arthropods
such as Crustacea, it would be of a considerable practical impor-
tance from the viewpoint of taxonomy, since deviations in growth
patterns for the other segments would become more or less pre-
dictable by the deviation of a single segment. *Potamobates thomasi
Hungerford, *Platygerris caeruleus* Champion, *Cylindrostethus suma-
tranus* Lundblad, *Limnogonus intermedius* Poisson, etc., are ex-
amples. I have noticed deviations in the other structures also at
least in a few of these species. Upon more careful study of such
structures as the male genitalia and with discovery of related species
they may eventually be described as distinct genera or subgenera.

Another tendency to be recalled, in this connection, is that the
growth patterns for the proximal segments with higher growth ratios (e.
g., the femur, the first antennal segment) often appear to be more similar among related species than those for the more
distal segments. This tendency, in turn, indicates that the growth
patterns for the first antennal segment and the femur, for instance,
are often generically constant. The growth patterns for more distal
segments, e.
g., for the tarsus and the fourth antennal segment, are
often variable at the specific level. Of course the growth patterns
for the proximal segments also must differ considerably at the spe-
cific level when the segments are more or less greatly modified
(e.
g., the front femur in *Amemboa* and *Eurygerris*).

(4) Parallelism

Parallelism of structures, which has been observed in the fore-
going pages, results from divergence of groups in adjustment to
similar environmental factors, combined with genetic potentialities
intrinsic to the groups concerned. The apparent cases of parallel-
ism in the Gerridae are summarized below (Table 4).

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*Wigglesworth (1954) suggests a single inductor for the development of legs and antennae in insects in discussing the aristopedia.*
Table 4.—Table of the cases of parallelism.*

<table>
<thead>
<tr>
<th>Characters</th>
<th>Names of Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Reduction in length of third relative to fourth rostral segment.</td>
<td>Eotrechini (Gerrinae), Cylindrostethini (Gerrinae), Charmatometrini (Gerrinae), and Ventidius-Esakia complex (Halobatinae).</td>
</tr>
<tr>
<td>2. Reduction in length of second relative to third antennal segment in more specialized shorter forms.</td>
<td>Aquarius, Gerris s. str. (Gerrini, Gerrinae), Limnogonus s. str.-Limnogonellus complex (Gerrini, Gerrinae), and Ventidius-Esakia complex (Halobatinae).</td>
</tr>
<tr>
<td>3. Reduction of pronotum in wingless forms.</td>
<td>Limnogonus s. str.-Limnogonellus complex, Limnometra-Tenagogonus s. str. complex, and Eurygerris (Gerrini, Gerrinae).</td>
</tr>
<tr>
<td>4. Shift of position of abdominal spiracles caudad in more specialized shorter species.</td>
<td>Aquarius, Gerriss. str., and Limnometra-Tenagogonellus complex (Cylindrostethini, Gerrinae), Charmatometrini (Gerrinae), and Rhagadotarsinae.</td>
</tr>
<tr>
<td>5. Reduction of connexival spine in more specialized and shorter forms.</td>
<td>Gerrini (Gerrinae), and Cylindrostethini (Gerrinae).</td>
</tr>
<tr>
<td>6. Production of secondary connexival spine.</td>
<td>Ptilomerinae except Ptilomera (Proptilomerinae), Rheumatogonus, and Potamometropsis; Eurygerris and Tenagogonus (Gerrini, Gerrinae), and Trepobates (Trepobatinae).</td>
</tr>
<tr>
<td>7. Median emargination of ventral apical margin of seventh abdominal segment in males of more specialized forms.</td>
<td>Aquarius, and Gerris s. str. (Gerrini, Gerrinae); Cylindrostethini (Gerrinae).</td>
</tr>
<tr>
<td>8. Ventral apical margin of seventh abdominal segment in female lobately produced.</td>
<td>Tachygerris (Gerrini, Gerrinae), Platygerris (Cylindrostethini, Gerrinae), Metrocoris (Halobatinae), Rheumatometroides and Metrobatopsis (Trepobatinae).</td>
</tr>
<tr>
<td>9. Ventral basal area of eighth abdominal segment depressed.</td>
<td>Rhyacobates and Ptilomera (Ptilomerinae); Potamobates and Platygerris (Cylindrostethini, Gerrinae).</td>
</tr>
<tr>
<td>10. Formation of median longitudinal ridge in eighth abdominal segments in males.</td>
<td>Heterobates and Rhyacobates (Ptilomerinae); Aquarius and Gerris s. str. (Gerrini, Gerrinae).</td>
</tr>
<tr>
<td>11. Modification of apical margin of eighth abdominal segments in males.</td>
<td>Cylindrostethini (Gerrinae), and Halobatini (Halobatinae).</td>
</tr>
<tr>
<td>12. Rotation of pygophore.</td>
<td>Potamobates and Platygerris (Cylindrostethini, Gerrinae); Halobates (Halobatinae), and Metrobatopsis (Trepobatinae).</td>
</tr>
<tr>
<td>Characters</td>
<td>Names of Groups</td>
</tr>
<tr>
<td>---------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>13. Modification of apical margin of pygophore.</td>
<td>Amemboa and Chimarrhometra (Eotrechini, Gerrinae); Metrocoris and Eurymetropolis (Halobatinae).</td>
</tr>
<tr>
<td>14. Modification of front femur.</td>
<td>Conspicuously in Eurygerris and Amemboa (Gerrini, Gerrinae); less conspicuously in Metrocoris and Ventidius (Ventidioides) (Halobatinae), and Ptilomera (Ptilomerinae).</td>
</tr>
<tr>
<td>15. Prolongation of middle and hind coxae.</td>
<td>Onychotrechus and Amemboa (Eotrechini, Gerrinae); Eurygerris (Gerrini, Gerrinae); Potamometroides, Rhagadobates and Heterobates (Ptilomerinae); Rhagadotarsinae.</td>
</tr>
<tr>
<td>16. Reduction of hind tibia.</td>
<td>All groups except Trepobates (Trepobatinae) and Rhagadotarsinae.</td>
</tr>
<tr>
<td>17. Prolongation of femora of all legs and first antennal segment.</td>
<td>Platygerris (Cylindrostethini, Gerrinae) and Ptilomerinae except for Rheumatogonus.</td>
</tr>
<tr>
<td>18. Fusion of hind tarsal segments.</td>
<td>Ptilomera and Potamomera (Ptilomerinae); Halobates (Halobatinae); Rheumatometroides and Metrobatopsis (Trepobatinae).</td>
</tr>
<tr>
<td>19. Loss of claws.</td>
<td>Western Hemisphere Cylindrostethus (Gerrinae); Heterobates, Rhyacobates, and Potamometroides (Ptilomerinae).</td>
</tr>
<tr>
<td>20. More distal separation of R + M into R and M in specialized genera.</td>
<td>Gerrini (Gerrinae), Cylindrostethini (Gerrinae) and Eotrechini (Gerrinae).</td>
</tr>
<tr>
<td>21. Concomittal prolongation of apical abdominal segments with reduction of preceding segments.</td>
<td>All groups. Very conspicuously in Cylindrostethus-Potamobates-Platygerris series (Cylindrostethini, Gerrinae), Limnometroides-Tenagonous s. str. complex and Amemboa (Gerrini, Gerrinae), Asclepios-Halobates complex (Halobatinae), and Proptilomera-Ptilomera complex (Ptilomerinae).</td>
</tr>
<tr>
<td>22. Loss of indentation of eyes.</td>
<td>Amemboa (Eotrechini, Gerrinae), Platygerris (Cylindrostethini, Gerrinae).</td>
</tr>
<tr>
<td>23. Modification of suranal plate on lateral margin.</td>
<td>Amemboa (Eotrechini, Gerrinae), Gerrisella (Gerrini, Gerrinae), Cylindrostethini (Gerrinae), Ptilomera s. str. (Ptilomerinae), Metrobatopsis, Hynesionella, Rheumatometroides and Stenobates (Trepobatinae).</td>
</tr>
<tr>
<td>24. Loss of parameres.</td>
<td>All subfamilies except for Ptilomerinae.</td>
</tr>
<tr>
<td>25. Mutual functional replacement between parameres and lateral projection of suranal plate.</td>
<td>Amemboa (Eotrechini, Gerrinae), Gerrisella (Gerrini, Gerrinae), Metrobatopsis and Hynesionella (Trepobatinae).</td>
</tr>
</tbody>
</table>
STUDY OF THE GERRIDAE OF THE WORLD

Table 4.—Table of the cases of parallelism—Concluded

<table>
<thead>
<tr>
<th>Characters</th>
<th>Names of Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>27. Metacetabular suture connected with posterior margin of metathoracic postnotum in wingless forms.</td>
<td>Rhagadotarsinae and Trepobatinae.</td>
</tr>
</tbody>
</table>

* The cases, in which certain primitive structures are retained only in certain genera of primitive subfamilies and are lost completely in all other more specialized (but not necessarily directly derived) subfamilies, are not enumerated.
Table 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters.

<table>
<thead>
<tr>
<th>PRIMITIVE</th>
<th>SPECIALIZED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1  Freshwater habitat.</td>
<td>Marine habitat.</td>
</tr>
<tr>
<td>2  Body long and slender (in most cases).</td>
<td>Body short and wide (in most cases).</td>
</tr>
<tr>
<td>3A  Ventral surface of body without modification in female.</td>
<td>Ventral surface of body medially with a well defined area extending from mesosternum to apical abdominal segments in female.</td>
</tr>
<tr>
<td>4  Anterior margin of head produced medially (clypeal region) and directed forward.</td>
<td>Anterior margin of head rounded and bent ventrally.</td>
</tr>
<tr>
<td>5*  Antenniferous tubereles well developed.</td>
<td>Antenniferous tubereles greatly reduced.</td>
</tr>
<tr>
<td>6  Rostrum free from ventral surface of body when at rest.</td>
<td>Rostrum on ventral surface of body when at rest.</td>
</tr>
<tr>
<td>7*  Rostrum slender.</td>
<td>Rostrum incrassate.</td>
</tr>
<tr>
<td>8*  Antennal cavity open anteriorly and dorsally.</td>
<td>Antennal cavity open more posteriorly and more ventrally.</td>
</tr>
<tr>
<td>9  Basal margin of clypeus distinct.</td>
<td>Basal margin of clypeus lost.</td>
</tr>
<tr>
<td>10  Anterior margin of clypeus in contact with labrum.</td>
<td>Anterior margin of clypeus separated from labrum by a membranous area.</td>
</tr>
<tr>
<td>11  Mandibular and maxillary plates separated from each other.</td>
<td>Mandibular and maxillary plates fused together.</td>
</tr>
<tr>
<td>12* Buccelese formed.</td>
<td>Buccelese not formed.</td>
</tr>
<tr>
<td>13* Eyes globular in shape and small.</td>
<td>Eyes elongate and large.</td>
</tr>
<tr>
<td>14* Eyes with indentation.</td>
<td>Eyes without indentation.</td>
</tr>
<tr>
<td>15A Eyes not covering anterolateral angles of pronotum.</td>
<td>Eyes covering anterolateral angles of pronotum.</td>
</tr>
<tr>
<td>15B Eyes not completely covering lateral margins of pronotum.</td>
<td>Eyes completely covering lateral margins of pronotum.</td>
</tr>
<tr>
<td>16  Antennal segments subequal in length to each other.</td>
<td>Antennal segments not subequal to each other.</td>
</tr>
<tr>
<td>17  First antennal segment shorter than or equal to second and third segments together.</td>
<td>First antennal segment longer than two following segments together.</td>
</tr>
<tr>
<td>18  First antennal segment shorter than three following segments together.</td>
<td>First antennal segment longer than three following segments together.</td>
</tr>
<tr>
<td>19  First antennal segment not incrassate in male.</td>
<td>First antennal segment strongly incrassate in male.</td>
</tr>
<tr>
<td>20  Relative lengths of first and second antennal segments without sexual difference.</td>
<td>Relative lengths of first and second antennal segments sexually different.</td>
</tr>
<tr>
<td>21A Third antennal segment not modified in male.</td>
<td>Third antennal segment modified in male.</td>
</tr>
<tr>
<td>21B Third antennal segment with simple basal accessory segment.</td>
<td>Third antennal segment with ear-shaped basal accessory segment.</td>
</tr>
<tr>
<td>22A Relative lengths of second and third antennal segments without significant sexual difference.</td>
<td>Relative lengths of second and third segments sexually different.</td>
</tr>
<tr>
<td>22B Second and third antennal segments not modified.</td>
<td>Second and third antennal segments modified distally.</td>
</tr>
<tr>
<td>23  Fourth antennal segment straight.</td>
<td>Fourth antennal segment curved.</td>
</tr>
<tr>
<td>24* Pronotum prolonged in wingless form.</td>
<td>Pronotum not prolonged in wingless form.</td>
</tr>
<tr>
<td>Primitive</td>
<td>Specialized</td>
</tr>
<tr>
<td>--------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>25 Pronotum simply rounded on apical margin in wingless form.</td>
<td>Pronotum greatly modified apically.</td>
</tr>
<tr>
<td>26 Lateral longitudinal suture of mesothorax separating mesonotum from mesopleuron present.</td>
<td>Lateral longitudinal suture of mesothorax separating mesonotum from mesopleuron lost.</td>
</tr>
<tr>
<td>27 Longitudinal suture separating mesosternum from mesopleuron present.</td>
<td>Longitudinal suture separating mesosternum from mesopleuron lost.</td>
</tr>
<tr>
<td>28 Mesosternum without median longitudinal suture</td>
<td>Mesosternum with median longitudinal suture anteriorly.</td>
</tr>
<tr>
<td>29 Anterior margin of mesosternum simply rounded.</td>
<td>Anterior margin of mesosternum more or less greatly produced medially.</td>
</tr>
<tr>
<td>30 Mesonotum without depressions near anterior margin.</td>
<td>Mesonotum with well marked paired depressions near anterior margin.</td>
</tr>
<tr>
<td>31 Mesonotum without conspicuous median longitudinal impression.</td>
<td>Mesonotum with a very conspicuous median longitudinal impression.</td>
</tr>
<tr>
<td>32A Intersegmental suture between meso- and metanota retained dorsally.</td>
<td>Intersegmental suture between meso- and metanota lost dorsally.</td>
</tr>
<tr>
<td>32B Intersegmental suture between meso- and metanota dorsally not carinate.</td>
<td>Intersegmental suture between meso- and metanota carinate dorsally.</td>
</tr>
<tr>
<td>33 Intersegmental suture between meso- and metanota retained laterally.</td>
<td>Intersegmental suture between meso- and metanota lost laterally.</td>
</tr>
<tr>
<td>34A Metacetabular suture poorly developed dorsally.</td>
<td>Metacetabular suture connected with primary intersegmental suture dorsally.</td>
</tr>
<tr>
<td>34B Metacetabular suture poorly developed dorsally.</td>
<td>Metacetabular suture connected with anterolateral angle of first tergite.</td>
</tr>
<tr>
<td>35 Metanotum without lateral longitudinal elevation.</td>
<td>Metanotum with well developed lateral longitudinal elevation.</td>
</tr>
<tr>
<td>36 Metactabulum simple on posterolateral angle.</td>
<td>Metactabulum flattened and broad posterolaterally, and often acute at tip.</td>
</tr>
<tr>
<td>37 Metactabulum simple on posterolateral angle in female.</td>
<td>Metactabulum with a conspicuous apical process in female.</td>
</tr>
<tr>
<td>38 Elevated metactabular regions nearly parallel-sided.</td>
<td>Elevated metactabular regions strongly convergent anteriorly.</td>
</tr>
<tr>
<td>39B Metasternum relatively short, not greatly produced anteriorly.</td>
<td>Metasternum relatively short, and greatly produced anteriorly.</td>
</tr>
<tr>
<td>40 Metasternum represented by a narrow plate reaching metactabular region.</td>
<td>Metasternum represented merely by a small median subtriangular plate.</td>
</tr>
<tr>
<td>41 Omphalium present.</td>
<td>Omphalium absent.</td>
</tr>
<tr>
<td>42 Omphalial groove present.</td>
<td>Omphalial groove absent.</td>
</tr>
<tr>
<td>44 Abdomen normally exposed in female.</td>
<td>Abdomen withdrawn into thoracic cavity in female.</td>
</tr>
<tr>
<td>45A Pregenital abdominal segments more or less uniform and long.</td>
<td>Pregenital abdominal segments not uniform and short.</td>
</tr>
<tr>
<td>45B Pregenital segments without depression centrally in male.</td>
<td>Pregenital segments with a depression in male.</td>
</tr>
<tr>
<td>46* Abdominal spiracles placed anterior to middle of each segment.</td>
<td>Abdominal spiracles placed at middle of each segment.</td>
</tr>
<tr>
<td>PRIMITIVE</td>
<td>SPECIALIZED</td>
</tr>
<tr>
<td>---------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>47  First abdominal segment well retained ventrally.</td>
<td>First abdominal segment completely lost ventrally.</td>
</tr>
<tr>
<td>48  Anterior margin of first tergite nearly straight.</td>
<td>Anterior margin of first tergite flattened W-shaped.</td>
</tr>
<tr>
<td>49  Anterior margin of first tergite retained.</td>
<td>Anterior margin of first tergite lost.</td>
</tr>
<tr>
<td>50  Anterior margin of first tergite without modification in female.</td>
<td>Anterior margin of first tergite with a process, elevation, etc. in female.</td>
</tr>
<tr>
<td>51  First connexival segment well defined posteriorly.</td>
<td>First connexival segment with posterior margin lost.</td>
</tr>
<tr>
<td>52  Ventrolateral longitudinal suture of pregenital abdominal segments present.</td>
<td>Ventrolateral longitudinal suture of pregenital segments absent.</td>
</tr>
<tr>
<td>53  Connexivum more or less horizontal or slightly reflexed in female.</td>
<td>Connexivum greatly reflexed and folded onto dorsum in female.</td>
</tr>
<tr>
<td>54  Anterior margin of second tergite retained.</td>
<td>Anterior margin of second tergite lost at least medially.</td>
</tr>
<tr>
<td>55  Second and third connexival segments not fused.</td>
<td>Second and third connexival segments fused.</td>
</tr>
<tr>
<td>56  Anterior margin of third tergite retained.</td>
<td>Anterior margin of third tergite lost.</td>
</tr>
<tr>
<td>57  Sixth tergite not modified in female.</td>
<td>Sixth tergite with more or less conspicuous modification (round elevation, etc.) in female.</td>
</tr>
<tr>
<td>58  Seventh abdominal segment shorter than sixth on ventral longitudinal axis.</td>
<td>Seventh abdominal segment longer than sixth on ventral median longitudinal axis.</td>
</tr>
<tr>
<td>59* Connexival spine conspicuous, especially in female (in some groups).</td>
<td>Connexival spine absent (in some groups).</td>
</tr>
<tr>
<td>60  Posterolateral angle of seventh abdominal segment simple in female.</td>
<td>Posterolateral angle of seventh abdominal segment conspicuously modified (spinous process, lateral projection etc.) in female.</td>
</tr>
<tr>
<td>61A Ventral apical margin of seventh abdominal segment not modified in male.</td>
<td>Ventral apical margin of seventh abdominal segment greatly modified in male.</td>
</tr>
<tr>
<td>61B Ventral apical margin of seventh abdominal segment simply concave in male.</td>
<td>Ventral apical margin of seventh abdominal segment with a median emargination in male.</td>
</tr>
<tr>
<td>61C Ventral apical margin of seventh abdominal segment simply concave in male.</td>
<td>Ventral apical margin of seventh abdominal segment with conspicuous paired processes in male.</td>
</tr>
<tr>
<td>61D Ventral apical margin and surface of seventh abdominal segment unmodified in male.</td>
<td>Ventral surface of seventh abdominal segment modified (depression etc.) in male.</td>
</tr>
<tr>
<td>62A Ventral apical margin of seventh abdominal segment simply concave or nearly horizontal in female.</td>
<td>Ventral apical margin of seventh abdominal segment with large lobate projection in female.</td>
</tr>
<tr>
<td>62B Ventral basal margin of seventh abdominal segment not strongly produced anteriorly in female.</td>
<td>Eighth abdominal segment produced anteriorly in female.</td>
</tr>
<tr>
<td>63A Eighth abdominal segment not prolonged in male.</td>
<td>Eighth abdominal segment greatly prolonged in male.</td>
</tr>
<tr>
<td>63B Eighth abdominal segment not modified besides prolongation in male.</td>
<td>Eighth abdominal segment greatly modified besides prolongation in male.</td>
</tr>
<tr>
<td>64A Ventral surface of eighth abdominal segment smooth in male.</td>
<td>Ventral surface of eighth abdominal segment depressed basally in male.</td>
</tr>
<tr>
<td>64B Ventral surface of eighth abdominal segment smooth in male.</td>
<td>Ventral surface of eighth abdominal segment with a median longitudinal ridge in male.</td>
</tr>
</tbody>
</table>
Table 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters.—

Continued.

<table>
<thead>
<tr>
<th>Primitive</th>
<th>Specialized</th>
</tr>
</thead>
<tbody>
<tr>
<td>64C</td>
<td>Ventral surface of eighth abdominal segment smooth in male.</td>
</tr>
<tr>
<td>65</td>
<td>Ventral apical margin of eighth abdominal segment not symmetrical in male.</td>
</tr>
<tr>
<td>66A</td>
<td>Basal lateral process on ninth tergite small and inconspicuous in male.</td>
</tr>
<tr>
<td>66B</td>
<td>Basal lateral process on ninth tergite small and inconspicuous in male.</td>
</tr>
<tr>
<td>67</td>
<td>Basal region of ninth tergite without internal hook.</td>
</tr>
<tr>
<td>68A</td>
<td>Ninth tergite simple in male.</td>
</tr>
<tr>
<td>68B</td>
<td>Ninth tergite simple in male.</td>
</tr>
<tr>
<td>69A</td>
<td>Parameres present and simple.</td>
</tr>
<tr>
<td>69B</td>
<td>Parameres simple.</td>
</tr>
<tr>
<td>70</td>
<td>Parameres symmetrical.</td>
</tr>
<tr>
<td>71</td>
<td>Pygophore not prolonged.</td>
</tr>
<tr>
<td>72A</td>
<td>Pygophore not rotated.</td>
</tr>
<tr>
<td>72B</td>
<td>Pygophore not rotated.</td>
</tr>
<tr>
<td>73</td>
<td>Pygophore without conspicuous projection on lateral margin.</td>
</tr>
<tr>
<td>74</td>
<td>Pygophore simply rounded on apical margin.</td>
</tr>
<tr>
<td>75A</td>
<td>Pygophore without modification on ventral surface.</td>
</tr>
<tr>
<td>75B</td>
<td>Pygophore without modification on ventral surface.</td>
</tr>
<tr>
<td>76</td>
<td>Styloide present.</td>
</tr>
<tr>
<td>77</td>
<td>Apical, dorsal, basal and ventral plates of endosoma incompletely fused, not forming a ring.</td>
</tr>
<tr>
<td>78</td>
<td>Apical plate of endosoma clearly separated from dorsal plate.</td>
</tr>
<tr>
<td>79</td>
<td>Ventral plate of endosoma distinctly paired and membranous.</td>
</tr>
<tr>
<td>80</td>
<td>Basal plate of endosoma separated from ventral plate or from dorsal plate.</td>
</tr>
<tr>
<td>81</td>
<td>Apical plate of endosoma present.</td>
</tr>
<tr>
<td>82</td>
<td>Apical segment of endosoma simply rounded apically.</td>
</tr>
<tr>
<td>83</td>
<td>Third valvulae present.</td>
</tr>
<tr>
<td>84</td>
<td>Rami of first valvulae distinguishable from process of ninth tergite.</td>
</tr>
<tr>
<td>85</td>
<td>Apical margin of intervalvular membrane not sclerotized.</td>
</tr>
</tbody>
</table>
Table 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—Continued

<table>
<thead>
<tr>
<th>Number</th>
<th>Primitive</th>
<th>Specialized</th>
</tr>
</thead>
<tbody>
<tr>
<td>86</td>
<td>Valvulae normally developed.</td>
<td>Valvulae greatly reduced.</td>
</tr>
<tr>
<td>87</td>
<td>Winged.</td>
<td>Wingless.</td>
</tr>
<tr>
<td>88</td>
<td>Embolium is not formed.</td>
<td>Embolium is formed.</td>
</tr>
<tr>
<td>89</td>
<td>Basal part of forewing membranous.</td>
<td>Basal part of forewing coriaceous.</td>
</tr>
<tr>
<td>90</td>
<td>Coriaceous region of forewing occupies basal half.</td>
<td>Coriaceous region of forewing occupies basal one fourth to one third.</td>
</tr>
<tr>
<td>91</td>
<td>R+M and Cu arise independently from near base of forewing.</td>
<td>R+M and Cu basally fused.</td>
</tr>
<tr>
<td>92</td>
<td>Se2 united with R+M at point of separation of the latter into R and M.</td>
<td>Se2 united with R+M at the point basal to point of separation of the latter into R and M.</td>
</tr>
<tr>
<td>93</td>
<td>Se2 present.</td>
<td>Se2 lost.</td>
</tr>
<tr>
<td>94</td>
<td>R+M branches into R and M apically.</td>
<td>R+M not branching into R and M apically.</td>
</tr>
<tr>
<td>95</td>
<td>Cu and A joined apically.</td>
<td>Cu and A not joined apically.</td>
</tr>
<tr>
<td>96</td>
<td>Line of weakness on forewing absent.</td>
<td>Line of weakness on forewing present.</td>
</tr>
<tr>
<td>97</td>
<td>Hind leg longer than middle leg.</td>
<td>Hind leg shorter than middle leg.</td>
</tr>
<tr>
<td>98</td>
<td>Front trochanter without a tubercle.</td>
<td>Front trochanter with a tubercle.</td>
</tr>
<tr>
<td>99</td>
<td>Claws arise from apex of second tarsal segment of front leg.</td>
<td>Claws arise from near middle of second tarsal segment of front leg.</td>
</tr>
<tr>
<td>100</td>
<td>Front trochanter without a tubercle.</td>
<td>Front trochanter with a tubercle.</td>
</tr>
<tr>
<td>101</td>
<td>Front femur not modified in male.</td>
<td>Front femur greatly modified (dilated, strongly curved, with tubercle etc.) in male.</td>
</tr>
<tr>
<td>102</td>
<td>Front tibia without apical conspicuous process.</td>
<td>Front tibia with conspicuous apical process.</td>
</tr>
<tr>
<td>103A</td>
<td>Front tibia without denticles on inner margin.</td>
<td>Front tibia with a series of denticles on inner margin.</td>
</tr>
<tr>
<td>103B</td>
<td>Front tibia without tuberculoseous process on inner margin in male.</td>
<td>Front tibia with tuberculoseous process on inner margin in male.</td>
</tr>
<tr>
<td>104</td>
<td>Apical region of femur and basal region of tibia of front leg without conspicuous tubercles.</td>
<td>Apical region of femur and basal region of tibia of front leg with conspicuous tubercles.</td>
</tr>
<tr>
<td>105</td>
<td>First tarsal segment of front leg long.</td>
<td>First tarsal segment of front leg greatly reduced.</td>
</tr>
<tr>
<td>106</td>
<td>Middle femur lacks a fringe of long hairs.</td>
<td>Middle femur provided with a fringe of long hairs.</td>
</tr>
<tr>
<td>107</td>
<td>Middle tibia lacks a row of long hairs on inner margin.</td>
<td>Middle tibia bears a row of long hairs on inner margin.</td>
</tr>
<tr>
<td>108</td>
<td>Middle tarsus has claws.</td>
<td>Middle tarsus without claws.</td>
</tr>
<tr>
<td>109</td>
<td>Middle first tarsal segment without a row of long hairs.</td>
<td>Middle first tarsal segment with a row of long hairs.</td>
</tr>
<tr>
<td>110</td>
<td>Middle tibia and hind femur as long as or shorter than length of body.</td>
<td>Middle tibia and hind femur considerably longer than length of body.</td>
</tr>
<tr>
<td>111A</td>
<td>Claws arise apically or from near apex of second tarsal segment in middle and hind legs.</td>
<td>Claws arise from near middle of second tarsal segment in middle and hind legs.</td>
</tr>
<tr>
<td>111B</td>
<td>Claws present in middle leg.</td>
<td>Claws absent in middle leg.</td>
</tr>
<tr>
<td>112</td>
<td>Hind coxa wide : than or as wide as long.</td>
<td>Hind coxa longer than wide.</td>
</tr>
</tbody>
</table>
Table 5.—List Indicating Primitive and Specialized Alternatives for Certain Characters—

<table>
<thead>
<tr>
<th>PRIMITIVE</th>
<th>SPECIALIZED</th>
</tr>
</thead>
<tbody>
<tr>
<td>113</td>
<td>Hind coxa without spinous process on apical margin.</td>
</tr>
<tr>
<td>114</td>
<td>Hind first and second tarsal segments not fused.</td>
</tr>
<tr>
<td>115</td>
<td>Hind tarsal claws normal in size.</td>
</tr>
<tr>
<td>116</td>
<td>Hind tarsal claws present.</td>
</tr>
</tbody>
</table>

*Primitive or specialized alternative is based on association. See p. 47.

Characters Whose Primitive or Specialized Alternatives Were Not Determined.

<table>
<thead>
<tr>
<th>O</th>
<th>X</th>
</tr>
</thead>
<tbody>
<tr>
<td>117 Pronotum with yellow median longitudinal and marginal stripes.</td>
<td>Pronotum with median and marginal black stripes.</td>
</tr>
<tr>
<td>118** Dorsal surface without median longitudinal sulcus.</td>
<td>Dorsal surface of head with a median longitudinal sulcus.</td>
</tr>
<tr>
<td>119** Mesonotum with an inconspicuous median longitudinal impression.</td>
<td>Mesonotum without a median longitudinal impression.</td>
</tr>
<tr>
<td>120** Metanotum with a median longitudinal sulcus.</td>
<td>Metanotum without a median longitudinal sulcus.</td>
</tr>
<tr>
<td>121 Metathoracic spiracle located at some distance from pronotum in wingless forms.</td>
<td>Metathoracic spiracle located very close to lateral margin of pronotum in wingless forms.</td>
</tr>
<tr>
<td>122 Ovipositor formed.</td>
<td>Ovipositor not formed.</td>
</tr>
<tr>
<td>123 Middle femur longer than middle tibia.</td>
<td>Middle femur shorter than middle tibia.</td>
</tr>
</tbody>
</table>

** Nymphal characters.

124† Relative lengths of mesosternum and metasternum.
125 Relative lengths of first and second tarsal segment of front leg.
126 Relative lengths of tibia and femur of middle leg.
127 Relative lengths of first and second tarsal segments of middle leg.
128 Relative lengths of tibia and femur of hind leg.
129 Relative lengths of first and second tarsal segments of hind leg.

† The smaller the length of mesosternum relative to metasternum, the more primitive.
CLASSIFICATION

Earlier Classifications

It seems worth-while to review some previous works that have contributed to the current concept of the classification of the Gerridae before discussing a new interpretation. Dufour (1834) included the Hydrometridae, Veliidae and Gerridae within the family Amphibicorises based primarily on the habitat. Amyot and Serville (1843) and other workers in the nineteenth century treated the Gerridae as a tribe or subfamily (group by Amyot and Serville, 1843) of the Amphibicorises of Dufour, or of the Gerridae s. lat. Bianchi (1896) subdivided the family Gerridae into two subfamilies based on the ratio of the length of the body to the width. His division is as follows:


2. Subfamily Gerrinae

A. Gerrids, with the genera Hydrobates Erichson, 1848 (Cylindrostethus Fieber, 1861), Gerris Fabricius, 1794, Limnotrechus Stål, Hygrotrechus Stål, Limnoporus Stål, 1868, Limnogonus Stål, 1868 (Lamprotrechtis Reuter, 1883), Limnometra Mayr, 1865, Tenagogonus Stål, 1853.

B. Ptilomerae, with genera Ptilomera Amyot et Serville, 1843, and Heterobates Bianchi, 1896.

Bergroth (1908) employed the shape of eyes for the recognition of the two subfamilies (tribes), i.e., those genera with indented eyes belong to the Gerrinae and those without indentation are the Halobatinae. This character has been used widely until the present time. Meanwhile, Esaki (1929) raised Bianchi's Ptilomerae to the subfamily rank with Rheumatogonus, Ptilomera, Potamometra, Rhyacobates, Teratobates, Heterobates as members. Another significant contribution of Esaki (1928c) was his establishment of synonymy for invalid genera of Distant. Esaki (1928a) further maintains that the Haloveliiinae should be included within the Gerridae on the basis of the four-jointed rostrum, the unusually long distance between the bases of the anterior and posterior legs, and the long posterior femur which extends beyond the end of the abdomen, and included Strongylovelia, Xenobates, Halovelia, and


Entomovelia within the Haloveliiinae. The Haloveliiinae was later transferred to the Veliidae by China and Usinger (1949), and further raised to the familial rank by Poisson (1956). Lundblad (1933) established the subfamily Rhagadotarsinae for the genus Rhagadotarsus on the basis of some good morphological characters, such as the well-developed genae, the absence of the accessory segment in the third antennal segment, the mesonotum and metanotum being laterally well defined by a longitudinal line, etc. Meanwhile, the Hermatobatinae was established by Coutière and Martin (1901) for the genus Hermatobates. Since then this subfamily has been treated as a part of the Gerridae in various works including the recent monographic work on this group by China (1957). According to Kenaga (1941) and Kuitert (1942) who last worked out the key to genera of the Gerridae of the world, the breakdown of genera of the Gerridae is as follows:

The Gerrinae.—Onychotrechus Kirkaldy, Cylindrostethus Fieber, Rheumatotrechus Kirkaldy, Potamobates Champion, Limnogonous Stål, Eotrechus Kirkaldy, Gerris Fabricius, Tenagogonus Stål, Potamometropsis Lundblad.


The Hermatobatinae.—Hermatobates Coutière et Martin.

After Kenaga and Kuitert, China (1943) described Hynesia. Hungerford (1954) reduced Hynesia to a subgenus of Rheumatobates, and transferred Rheumatobates to Rhagadotarsinae. Hungerford (1951) also described Potamometroides from Madagascar. Poisson described Gerrisella (1940) as a subgenus of Gerris. He also described Tenagometra and Tenagogonellus (1948) as subgenera of Tenagogonus, Eurymetropsis (1948), Hynesionella (1949), Eurymetropsiella (1950), Eurymetropsielloides (1956), and Tenagometrella (1957) as independent genera and subgenus. Drake (1957 described Tachygerris for the groups of species of Tenagogonus from the Western Hemisphere. In their recent
studies (1958-1959) Hungerford and Matsuda have described *Gigantometra, Eurygerris, Tenagogerris, Gerriselloides, Rheumatometroides, Trepobatoides* as new genera, *Limnogonellus, Ventidioides, Proptilomera* as new subgenera, raised *Gerrisella* to the generic rank, and reduced *Teratobates* and *Esakobates* to the synonyms of *Heterobates* and *Rhijacobates* respectively.

**A New Classification**

As Matsuda (1957) pointed out, and more detailed morphological and evolutionary studies of structures in the foregoing sections of this work have verified, the primary characters in the subfamily classification of the Gerridae thus far used, such as the shape of eyes, and the length of the body relative to width, are by no means well stabilized at the level of higher taxonomic units. One of the most important higher taxonomic characters appears to be the intersegmental suture between the mesonotum and metanotum. The morphological origin of this suture (either primary or secondary definitive) varies in various groups of Gerridae, indicating various stages of evolution. Correlated with this the forewing venation was found to be fairly well stabilized within each group, indicating also various stages of evolution. In addition to these fundamental characters the following five characters were found to be significant diagnostic features in separating the subfamilies. So altogether seven characters are used in describing each subfamily. The five additional characters are 12, 27, 41, 47, and 122 on table 5.

**Subfamily Gerrinae Amyot and Serville**

Forewing with veins $R + M$ connected with $Sc$ by $Sc_2$; $R + M$ and $Cu$ fused basally. Primary intersegmental suture between mesonotum and metanotum either distinct or obliterated laterally. Lateral longitudinal suture separating mesonotum and mesopleuron absent in most genera. Genae not lobately developed. Omphalium always present. First abdominal segment ventrally lost. Well formed ovipositor absent.

In the Gerrinae the characters 23, 24, 33, 34A, 42, 48, 59, 105 are diagnostic characters separating the four tribes.

(a) Tribe Gerrini Amyot and Serville

Fourth antennal segment straight and slender. Pronotum in wingless forms fully developed in most species. Intersegmental suture between meso- and metanota obliterated laterally in some genera. Metacetabular suture never united with posterior margin

The following genera belong to this tribe:


(b) _Cylindrostethini_ Matsuda, new tribe


The following genera belong to this tribe:

_Cylindrostethus_ Fieber, _Potamobates_ Champion, _Platygerris_ Buchanan-White.

(c) _Charmatometrini_ Matsuda, new tribe


The following genera belong to this tribe:

_Charmatometra_ Kirkaldy, _Eobates_ Drake and Harris, _Brachy- metra_ Mayr.

(d) _Eotrechini_ Matsuda, new tribe

Fourth antennal segment straight. Pronotum in wingless forms not prolonged. Intersegmental suture between meso- and metanota distinct laterally except for _Amemboa_. Metacetabular suture not reaching posterior margin of mesonotum. Omphalial groove ab-
sent. Anterior margin of first abdominal tergite flattened W-shaped. Connexival spine absent. First front tarsal segment not reduced.

The following genera belong to this tribe:


**Subfamily Ptilomerinae Bianchi**

Forewing with veins $R + M$ and $Cu$ basally either distinct or fused. Sc not connected to $R + M$ by an oblique vein. Primary intersegmental suture always distinct laterally. *Metacetabular suture dorsally connected with anterolateral angle of first abdominal tergite.* Lateral longitudinal suture separating mesonotum from mesopleuron absent in most genera (present only in *Potamometra*). Genae not lobately developed. Omphalium present. First abdominal segment ventrally absent. Ovipositor not formed.

The following genera belong to this subfamily:


**Subfamily Halobatine Bianchi**


The two tribes belonging to this subfamily can be divided by characters 1, 3B, 9, 87, 107, 109, 113.

(a) Tribe Halobatini Bianchi

Marine habitat. Body surface clothed with short velvety hairs. Clypeus with basal margin distinct. Middle tibia and first middle tarsal segment (or middle tibia alone) clothed with conspicuous rows of long hairs. Hind coxa longer than wide. Winged forms unknown.

The following two genera belong to this tribe:

*Asclepios* Distant, *Halobates* Eschscholtz.
(b) Metrocorini Matsuda, new tribe

Fresh water habitat. Body surface smooth. Clypeus with basal margin lost. Middle tibia and first tarsal segment without conspicuous mass of hairs. Hind coxa wider than long. Winged forms occur.

The following genera belong to this tribe:
Metrocoris Mayr, Eurymetra Esaki, Eurymetropsis Poisson, Eurymetropsiella Poisson, Eurymetropsielloides Poisson, Ventidius Distant including two subgenera (Ventidius Distant s. str. and Ventidioides Hungerford and Matsuda), Esakia Lundblad.

Subfamily Rhagadotarsinae Lundblad

Forewing with $R + M + Cu$ simply branched into two apical veins beyond middle of wing, always with pale line of weakness horizontally at middle of wing. Definitive intersegmental suture represented by posterior margin of mesothoracic postnotum and metacetabular suture. Lateral suture separating mesonotum from mesopleuron always present. Genae well developed (lobate). Omphalium absent. First abdominal segment ventrally well retained. Ovipositor well formed.

The following genera belong to this subfamily:
Rhagadotarsus Breddin including two subgenera (Rhagadotarsus Breddin s. str., Caprivia China), Rheumatobates Bergroth including two subgenera (Rheumatobates Bergroth s. str., Hynesia China).

Subfamily Trepobatinae Matsuda, new subfamily

Forewing with $R + M + Cu$ simply branched into two apical veins, always with horizontal line of weakness at middle of wing. Definitive intersegmental suture dorsally represented by posterior margin of mesothoracic postnotum and laterally by metacetabular suture. Lateral longitudinal suture separating mesonotum from mesopleuron absent. Genae not lobately developed. Omphalium absent in most species. First abdominal segment ventrally absent. Ovipositor not formed.

The following genera belong to this subfamily:

In the above new classification Amemboa, Platygerris, Charmatometra, and Brachymetra have been transferred from the Halobatinae
to the Gerrinae. *Amemboa* and *Platygerris*, in spite of their relatively short size and round inner margin of the eye, are nothing but highly specialized genera of Eotrechini and Cylindrostethini respectively. They are closer to *Onychotrechus* and *Potamobates* of the Gerrinae respectively than to any genera of Halobatinae. *Charmatometra* and *Brachymetra* are also structurally much closer to Gerrinae than to any genus of Halobatinae. They are, therefore, transferred to the Gerrinae in spite of relatively short body size and round eyes, and a new tribe Charmatometrini is erected to receive these two genera and *Eobates*. Halobatinae, after removal of the above genera, is further divided into two subfamilies, i.e., Halobatinae and Trepobatinae. The subfamilies are quite distinct in some fundamental characters as noted from the foregoing diagnoses. The two subfamilies are, in fact, not closely related. The Hermatobatinae is excluded from the Gerridae in this new classification, since this group is obviously very different from the rest in the basic structural plan, as will be discussed more fully elsewhere. No further taxonomic treatment of this group other than the exclusion from the Gerridae is attempted here.

Relationships of subfamilies

Since the known fossils of the Gerridae are members of modern genera (*Metrobates, Gerris*) they do not contribute information to phylogeny or relationships of groups of Gerridae. The understanding of relationships of subfamilies thus can be made only on the basis of the information presented in the section of the structural evolution in this work.

The subfamilies of the Gerridae are well defined and the family Gerridae appears to be considerably heterogeneous. No one subfamily is a direct ancestor nor do they seem to be derivatives one from another. In spite of this heterogeneity there appears to be definitely two main groups in the Gerridae, i.e., the group including the Rhagadotarsinae and Trepobatinae on one hand and another group including the three other subfamilies on the other. The Rhagadotarsinae and Trepobatinae share two very fundamental characters in common, i.e., the definitive intersegmental suture between the mesonotum and metanotum of the same morphological nature, and the occurrence of a line of weakness on the hemelytra. The sharp increase of growth ratios for the antennal and leg segments, which were found in a representative species of each subfamily, also indicates their close relationship. In spite of these
similarities the two subfamilies are well differentiated from each other by certain characters, such as the retention of the first abdominal segment ventrally, formation of the well-developed ovipositor in Rhagadotarsinae. The other group comprising three subfamilies is more heterogeneous than the first group. The Gerrinae and Ptilomerinae are apparently closer to each other than they are to the Halobatinae. The primary intersegmental suture between the mesonotum and metanotum is retained in all species of Ptilomerinae, while it has been lost laterally in varying degrees in various tribes in the Gerrinae. The forewing venation is also definitely more primitive than in the Gerrinae. In spite of retention of these two highly primitive characters, the Ptilomerinae has evolved to become a distinct subfamily by acquiring some peculiar characters in the legs and antennae, obviously in adaptation to the peculiar habitat (swift and turbulent currents). Due probably to a strong predilection for this peculiar habitat, wider distribution of this subfamily must have been prevented. It occurs only in the tropical oriental region and Madagascar. The Halobatinae, though closer to the Gerrinae than to the others, is still remotely related. Important characters such as the different morphological origin of the intersegmental suture between the mesonotum and metanotum distinguish it from any other subfamily of the Gerridae; its extremely reduced metasternum cannot directly be derivable from any form of the Gerrinae known, but the proportional lengths of leg segments as well as the growth pattern for the antennal and leg segments (especially the fact that the growth ratios for the segments rather abruptly decrease at the

Diagram 1.—Diagram showing the relationships of subfamilies of the Gerridae.
The final stage of development in *Metrocoris histrio*), the fact that the metacetabular suture is not well developed dorsally, etc., lead one to suppose that this subfamily is at least closer to the Gerrinae than either to the Rhagadotarsinae or to the Trepobatinae.

The above discussion on the relationships of subfamilies of the Gerridae can be summarized in diagram 1.

**Subfamily Gerrinae Amyot and Serville**

Gerrinae Lundblad, Arch. Hydrobiol. Suppl. 12:374 (1933)

Structures in wingless forms: Body large and elongate. Head with clypeal region always produced, basal margin of clypeus distinct or lost. Eye indented, not covering anterolateral angle of pronotum in most genera. Antenniferous tubercle well developed in most genera; antennal cavity open anterior to eyes. Antenna slender in most genera; first segment longest in most genera; second segment about as long as or longer than third except for Charmatometrini in which third always longer than second; third segment always with small but distinct accessory segment (basal peduncle); fourth segment simple and long, or short and curved (Cylindrostethini). Mandibular and maxillary plates more or less distinct from each other in most genera. Rostrum either extending or not extending beyond prosternum.

Pronotum prolonged or not prolonged. Intersegmental suture between mesonotum and metanotum dorsally represented by true posterior margin of mesonotum, laterally absent or continuous with conspicuous metathoracic spiracle, which is nearly cephalocaudally placed. Longitudinal mesopleural suture separating mesonotum from mesopleuron completely absent in most genera. Mesosternum with paired longitudinal sutures separating mesosternum from mesopleuron present in some species of some genera. Metanotum with median longitudinal sulcus present in most genera. Metacetabular suture connected with intersegmental suture between mesonotum and metanotum dorsally in Cylindrostethini or not much extending dorsally in other tribes. Metasternum at least longer than first definitive abdominal ventrite (second abdominal ventrite). Omphalium present in all genera; omphalial groove leading onto metacetabulum present in some genera. Front leg with femur simple in
most genera, always a little longer than tibia; tibia with or without conspicuous process at inner apical angle; tarsus with first segment greatly reduced only in Cylindrostethini; claws arising preapically in most genera. Middle leg longer than hind leg in great majority of species; femur longer than tibia in most genera; first tarsal segment longer than second except in Onychotrechus. Hind leg with femur longer than tibia in great majority of species; first tarsal segment longer than second in great majority of species.

Abdomen elongate. First tergite with anterior margin either straight or flattened W-shaped; first ventrite absent. Connexivum nearly horizontal or reflexed, with or without connexival spine, ventral margin of connexivum distinct in many genera. Definitive first connexival segment is the fused first and second connexival segments.

Male: Seventh segment longer than sixth segment in many species, variously modified in some species. Eighth segment often greatly prolonged. Ninth segment with suranal plate simple on lateral margin in most species; pygophore with apical margin simply rounded in majority of species; parameres simple and well developed or greatly reduced. Endosoma variable in various groups.

Female: Seventh segment longer than sixth in most species, ventral apical margin greatly modified in some genera. First valvula split into two lobes. Second valvulae convergent apically; intervalvular membrane with apical margin strongly sclerotized in Cylindrostethini.

Winged forms: Hemelytra with Sc connected with R + M by oblique vein Sc₂ at the point of separation into R and M, or connected with R + M; Vein A connected with posterior margin of hemelytra by a short, obscure cross vein. Line of weakness absent.

Distribution: World-wide.

Relationships of tribes.

The Cylindrostethini shares 15 characters * in common with the Gerrini, more characters than with any other tribe, indicating a closer relationship. Primitive genera of both tribes have highly elongate bodies. The Cylindrostethini, as will be noted from the table, has the smallest number of primitive characters although this tribe retains such obviously primitive features as the omphalial

*(+-)* sign is here regarded as (+), since (-) alternatives are shared only by some specialized forms of each tribe.

6—3883
Table 6.—Table of significant tribal characters in Gerrinae.

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<tr>
<th></th>
<th>Gerrini</th>
<th>Cylindrostethini</th>
<th>Estrechini</th>
<th>Charmatometrini</th>
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For explanations of symbols see introduction and table 5.

groove in many species. Many more specialized characters peculiar to this tribe, such as the curved fourth antennal segment, the greatly reduced first tarsal segment of the front leg, the peculiar way of connection of the clypeus with the labrum, and the well developed metacetabular suture which is dorsally connected with the primary intersegmental suture between the mesonotum and metanotum make this tribe quite distinct from the others.

The Gerrini also shares 15 characters with the Charomatometrini and with the Eotrechini. The tribe thus shares the highest total number of characters with the other tribes (45), suggesting that it is probably the closest to the ancestral gerrine.

The Charomatometrini has the largest number of primitive characters (16), but this is due partly to the fact that this tribe has never diversified as much as in the other tribes, thus remaining relatively primitive as a whole. In fact the number of primitive characters in Charomatometra, the most primitive genus in this tribe,
is about the same as in the primitive genera of the other tribes, such as *Eotrechus* and *Gigantometra*. The tribe Charmatometrini shares 14 characters with the Eotrechini, 10 with the Cylindrostethini, and 15 with the Gerrini. This indicates that this tribe, while it has evolved from near the base of gerrine phylogeny, is related to the Eotrechini. Both tribes are relatively small in body size and the spine of the seventh connexival segment has not arisen in either.

Based on the above discussion the relationships of the tribes are indicated in diagram 2.

![Diagram 2](image)

**Diagram 2.—Diagram showing the relationships of tribes of the Gerrinae.**

**Tribe Gerrini Amyot and Serville**

*Color pattern:* Pronotum with either yellow or black median longitudinal and marginal stripes. Mesonotal and metanotal regions normally with silvery areas.

*Structures in wingless forms:* Head between eyes widened posteriorly. Clypeal region well produced anteriorly, basal margin of clypeus either distinct or indistinct, apical margin directly connected with base of labrum. Antennae shorter than body; first segment longest in most genera; third segment a little longer than second in most genera and with a small but distinct basal peduncle; fourth segment longer than third. Antenniferous tubercles well developed and somewhat divergent apically. Eye exserted, globular, inner margin more or less emarginated. Mandibular and maxillary plates usually distinct from each other. Rostrum extending beyond base of prosternum, third segment over two and a half times as long as fourth segment.

Pronotum prolonged in most genera. Mesosternum with median longitudinal sulcus distinct anteriorly; paired longitudinal sutures present in some species of some genera. Intersegmental suture be-
between mesonotum and metanotum laterally retained, or directly continuous to conspicuous metathoracic spiracle, or obliterated. Metanotum with distinct medial longitudinal sulcus in most species; lateral longitudinal elevation well developed, reaching anteriorly nearly to mesonotum; metacetabular suture well impressed behind spiracle and dorsally meeting lateral longitudinal elevation. Meta-
sternum with omphalium distinct; omphalial groove lost except in Gigantometra and Gerriselloides. Front leg with femur simple, a little longer than tibia; tibia simple, without conspicuous inner apical process; tarsus with first segment not strongly reduced in most species; claws arising preapically. Middle leg longer than hind leg except in Gigantometra; tibia 0.7 to 1.08 times as long as femur; tarsus with first segment 2.2 to 9.5 times as long as second segment. Hind leg with tibia 0.23 to 1.6 times as long as femur; first tarsal segment 1.1 to 3.25 times as long as second.

Abdomen elongate. First tergite with anterior margin flattened W-shaped; anterior limit of connexivum extending beyond anterior margin of first tergite; ventral margin of connexivum recognizable either as broken longitudinal suture or as depressions on each segment.

**Male:** Seventh segment with ventral apical margin either simply concave or with a small median emargination, or with a median process; ventral surface longitudinally elevated medially in some species. Eighth segment prolonged and modified on ventral surface in some species. Ninth segment with suranal plate simple in great majority of species; pygophore not rotated, simply rounded on apical margin; parameres greatly reduced. Endosoma strongly sclerotized and produced apically in some genera; definitive dorsal plate bent along apical margin of endosoma; ventral plate more or less membranous, bilobed or not bilobed.

**Female:** Seventh segment with ventral apical margin simply concave or produced medially, or more or less greatly produced and modified. First valvula rather thinly sclerotized, apex membranous and rounded, inner lobe well differentiated from outer lobe in most species. Second valvulae membranous apically and convergent (in Tachygerris both valvulae are greatly reduced); intervalvular membrane with apical margin not heavily sclerotized. Vulva membranous, simply rounded or with median apical projection.

**Winged forms:** Vein Sc2 connected with R + M at point of separation into R and M, or joining R + M basal to that point. Vein A connected by a short cross vein with posterior margin of hemelytron.

**Distribution:** World wide.
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</table>

Table 7.—Table of significant generic characters in Gerrini.
| Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | 3.5-1 |
| Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | Tenebromyidae | ? |
| Limonoptera | Limonoptera | Limonoptera | 3.1-5.7 |
| Limonoptera | Limonoptera | Limonoptera | 3.0-3.9 |
| Limonoptera | Limonoptera | Limonoptera | 3.5-4.1 |
| Limonoptera | Limonoptera | Limonoptera | 3.7-4.8 |
| Limonoptera | Limonoptera | Limonoptera | 2.8-4.4 |
| Limonoptera | Limonoptera | Limonoptera | 2.3-3.5 |
| Limonoptera | Limonoptera | Limonoptera | 2.1-2.5 |
| Limonoptera | Limonoptera | Limonoptera | 2.1-2.9 |
| Limonoptera | Limonoptera | Limonoptera | 2.1-2.9 |
| Limonoptera | Limonoptera | Limonoptera | 2.1-2.9 |
| Limonoptera | Limonoptera | Limonoptera | 2.1-2.9 |
| 63A, B | 68A | 72 | 86 | 92 | 97 | 101 | 117 | 120 | 121 | 124 | 127 |
Table 7.—Table of significant generic characters in Gerrini.—concluded.

<table>
<thead>
<tr>
<th>Character</th>
<th>Gigantometra</th>
<th>Aquarius</th>
<th>Gerris s. str.</th>
<th>Linnomorus</th>
<th>Gerriella</th>
<th>Gerriellodes</th>
<th>Eurygerris</th>
<th>Limnogonus s. str.</th>
<th>Limnogonius</th>
<th>Taicygerris</th>
<th>Linnometra</th>
<th>Tenagogonus</th>
<th>Tenagogerris</th>
<th>Tenagometra</th>
<th>Tenagometrella</th>
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<tr>
<td>125</td>
<td>1.2:1</td>
<td>0.67-1.26</td>
<td>0.5-1.0</td>
<td>0.7-1</td>
<td>0.25-0.35</td>
<td>0.67:1</td>
<td>0.8-1</td>
<td>0.5-1.0</td>
<td>0.33-0.6</td>
<td>0.83-1</td>
<td>0.84-1.4</td>
<td>0.6-0.9</td>
<td>0.5:1</td>
<td>0.75:1</td>
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<td>0.76-0.92</td>
<td>0.76-0.86</td>
<td>0.93:1</td>
<td>0.70:1</td>
<td>0.78-0.97</td>
<td>0.82-0.96</td>
<td>0.88-0.97</td>
<td>0.70-0.78</td>
<td>0.78-1.08</td>
<td>0.71-0.80</td>
<td>0.94:1</td>
<td>0.93:1</td>
<td>0.99:1</td>
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<td>4.0-4.8</td>
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<td>4.6-6</td>
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<td>5.3-6.1</td>
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* Limnogonus intermedius* Poisson, a deviated species.

For explanations of symbols see introduction and table 5.
Relationships of Genera

On the basis of the difference in location of the metathoracic spiracle, the tribe can be divided into two major groups, one with the spiracle anteriorly approximated to the pronotum (*Gigantometra*, *Aquarius*, *Gerris* s. *str.*, *Limnoporus* and *Gerriselloides*); the other with the metathoracic spiracle located at some distance from the pronotum (other genera). In the first group, *Gigantometra* retains the largest number of primitive characters, such as the omphalial groove, enormously large body size, etc., and this genus is probably closest to the ancestor of the first group of the Gerrini. *Aquarius* and *Gerris* s. *str.* are closely related to *Gigantometra*, although they are structurally more specialized and the growth patterns for the antennal and leg segments are probably considerably different from those in *Gigantometra*. *Gerriselloides*, though related to *Gerris* s. *str.*, is an aberrant and more primitive group represented by a single species. It retains the omphalial groove which is laterally obliterated on the metacetabula, has a short pronotum and the relatively long metasternum. *Limnoporus* is closely related to *Aquarius* but distinct from it by a few minor structural differences and apparently different growth patterns for many leg and antennal segments.

Among the genera of the second group, Australian *Tenagogerris* shares the largest number of characters with other genera. This genus is structurally relatively primitive and similar to the *Limnometra-Tenagogonus* complex in color pattern, but similar also to *Gerris* in certain features, such as the short rostrum, similar proportional lengths of the first three antennal segments. This genus may possibly be the closest to the ancestral group of the Gerrini. *Tenagogonella* is nothing but a specialized group of *Limnometra*. *Tenagometra* has apparently become distinct from *Tenagogonus* with reduction of the pronotum in the wingless forms, etc., *Tenagometrella* is related to *Limnometra*. *Gerrisella* appears to be related to *Gerris* s. *str.*, but the difference in location of the metathoracic spiracle, the relatively short middle and hind tibiae, etc., which must have resulted from a considerably different growth pattern, the completely reduced pronotum in wingless forms, etc., make this genus quite peculiar and distinct. As will be noted from table 7, *Gerrisella* does not share large enough number of characters with any other genera to suggest any close relationship. *Limnometra* s. *str.* is similar to *Gerris* in color pattern, but is different in the location of the metathoracic spiracle, etc. *Limnogonellus*, though closely related to *Limnogonus* s. *str.*, has apparently be-
come distinct from it by minor alteration in the growth patterns for the antennal segments and by a different process of evolution of the male eighth abdominal segment, etc.

The last two genera occurring in the Western Hemisphere, *Eurygerris* and *Tachygerris*, are divergent in many respects. *Eurygerris*, though formerly included in *Gerris*, is quite distinct by the different location of the metathoracic spiracle, retention of the primary intersegmental suture between the mesonotum and metanotum laterally, the different lengths of the antennal and leg segments in relation to the body size, a strong tendency towards reduction of the pronotum, etc. As will be noted from table 7, *Eurygerris* does not have a large enough number of characters in common with any group to show any close phylogenetic relationship, and the total number of characters it shares with other genera is one of the smallest. *Tachygerris*, although unique in the modification of the female seventh abdominal segment and in the female and male genitalia, etc., is more closely related to the *Limnometra-Tenagogonus* complex than to the other genera.

The relationships of genera in the Gerrini discussed above can be summarized in the following diagram 3.

![Diagram 3](image-url)

Diagram 3.—Diagram showing the relationships of genera of the Gerrini.
The evolutionary tendencies and characters more or less peculiar to the Gerrini

(1) The pronotum is always prolonged in primitive wingless forms, but it has become reduced in the more specialized genera.

(2) The venter of the mesothorax has the paired longitudinal sutures separating the mesosternum from the mesopleural regions retained in the more primitive species of more primitive genera; they have become lost in more specialized forms.

(3) The primary intersegmental suture between the mesonotum and metanotum is laterally retained only in Eurygerris, Onychotrichus, and Chimarrhometra. In other genera it is laterally either occupied by the metathoracic spiracle which is anteriorly approximated to the pronotum, or has become lost.

(4) The omphalial groove and its lateral opening on the metacetabula are retained in Gigantometra; the groove is retained but its lateral openings are lost in Gerriselloides; both the groove and the lateral opening are completely lost in the other genera.

(5) The connexival spine is retained in the more primitive genera or more primitive species of some genera. It has become highly reduced or lost in the more specialized forms.

(6) The second to seventh abdominal spiracles are located closer to the anterior margin than to the posterior margin of each segment in the more primitive species of the more primitive genera. They have become placed at the middle between the anterior and posterior margins of each segment in the more specialized forms.

(7) The vein Sc has become connected with R + M basal to the point of separation into R and M in more specialized forms.

(8) In the middle leg, there is evidence that the allometric growth slope for the tibia is about as steep as or gentler than that for the femur, and this growth pattern appears to have persisted in phylogeny of at least a great majority of genera.

(9) In the hind leg, the tibia has become shorter in relation to the femur in more specialized forms.
Genus *Gigantometra* Hungerford and Matsuda (Figs. 3, 171-178)


Type species: *Linnometra gigas* China, by original designation.

Species examined: *Gigantometra gigas* (China).

**Color pattern:** Predominantly black. Head with pale, crescent shaped mark at base, a pair of lateral and median black stripes confluent anteriorly. Pronotum with median pale longitudinal stripe extending onto posterior lobe, lateral margin with pale stripe. Mesopleural region with longitudinal stripe of silvery pubescence.

**Structures in wingless forms:** Largest gerrid known. Head including eyes wider than long. Eye exserted, strongly indented, rather small and globular. Antenna slender, considerably shorter than length of body; first segment much shorter than second and third segments together; second segment short, third segment longer than second and than fourth; fourth segment about half as long as first. Antenniferous tubercles subparallel, about as long as eye. Clypeus with basal margin indistinct. Mandibular and maxillary plates distinct from each other. Rostrum extending beyond prosternum; first segment about one third as long as head, third segment over four times as long as fourth segment.

Pronotum fully prolonged, apical margin rounded. Mesothorax strongly widened posteriorly. Intersegmental suture between mesonotum and metanotum laterally continuous to conspicuous metathoracic spiracle. Mesosternum a little less than twice as long as metasternum; median longitudinal sulcus distinct in anterior third; paired longitudinal sutures distinct in anterior two thirds of mesosternum. Metathoracic spiracle very conspicuous, obliquely placed. Metanotum with lateral longitudinal elevation distinct, median longitudinal sulcus shallowly impressed. Metasternum with distinct omphalium located at apical one sixth of metasternum, omphalial groove leading onto metacetabula well impressed, lateral opening clothed with tuft of straight hairs. Front leg with femur slender, subequal in breadth throughout, a little longer than tibia; tibia slender, a little thickened apically, with a slight constriction near apex, and with obscure, bare and shallow depression on inner surface near apex. Middle leg a
little less than three times as long as body, femur only slightly longer than tibia; tibia a little less than four and a half times as long as first tarsal segment; first tarsal segment almost ten times as long as second. Hind leg much longer than middle leg; femur about as long as middle femur; tibia over one and a half times as long as femur, over twenty-five times as long as first tarsal segment; first tarsal segment a little less than four times as long as second.

Abdomen long. First abdominal tergite with flattened W-shaped anterior margin; second to seventh tergites subequal in length, each a little longer than wide; first to sixth ventrites subequal in length; seventh segment with connexival spines conspicuous in both sexes. Abdominal spiracles placed much closer to anterior margin than to posterior margin of each segment. Ventral longitudinal margin of connexivum distinct, broken at anterior one third and not reaching posterior margin of each segment. Ventral median longitudinal impression distinct throughout.

Male: Seventh segment with ventral apical margin simply concave. Eighth segment slightly exposed ventrally, simple on ventral surface. Ninth segment with suranal plate simply narrowed near apex, with a fine foot-shaped process on basal region of each side; pygophore rather small, feebly notched at middle of apical margin; parameres robust and simple, relatively short. Endosoma with dorsal plate slender, forked basally (the part of basal plate); apical plate not fused with dorsal plate; ventral plate membranous; lateral plates slender.

Female: Not available for study.

Winged forms: Metathoracic spiracle approaching nearly to wing base. Pronotum elongate, humeri located behind middle of pronotum. Hemelytra with Sc connected with R + M at the point of separation into R and M.

(The description of the dorsal surface of the body is based on the illustration of the wingless form given by Hoffmann, 1936.)

Distribution: The oriental region (Hainan Island, Tonking).

This monotypic genus is more primitive than any other genera of the Gerrini in the following points:

1. The omphalium and the omphalial groove are clearly retained.
2. The mesosternum is only a little less than twice as long as the metasternum.
3. The hind leg is longer than the middle leg.
(4) The parameres are better developed than in any other species of the tribe examined.

Besides the above mentioned characters peculiar to this genus, the extraordinarily long body and legs separate this genus readily from the other genera of the tribe.

Genus *Gerris* Fabricius

*Gerris* Fabricius, Ent. Syst., 4:187 (1794)
*Gerris* Latreille, Consid. Génl., pp. 259, 434 (1810)
*Gerris* Van Duzee, Cat. Hemip., 1:426 (1917)

Type species: *Cimex lacustris* Linnaeus, by subsequent designation (Latreille 1810, in the above reference).

**Color pattern:** Head with a crescent shaped yellow marking at base. Pronotum with yellowish median longitudinal stripe either extending onto or not extending onto posterior lobe. Mesopleural and metapleural regions silvery pubescent.

**Structures in wingless forms:** Head including eyes wider than long. Vertical region strongly widened. Eye with inner margin strongly emarginated. Antenna slender, definitely shorter than length of body; first segment a little longer than or shorter than two following segments together; second segment as long as or longer than third; fourth segment always longer than third segment. Antenniferous tubercles either as long as or shorter than eye. Clypeus with basal margin indistinct. Mandibular and maxillary plates distinct from each other. Rostrum extends beyond prosternum; third segment over two and a half times to a little over four times as long as fourth segment.

Pronotum prolonged, lateral margin slightly concave at middle, posterior margin broadly rounded. Intersegmental suture between mesonotum and metanotum laterally occupied by metathoracic spiracle which reaches anterodorsally nearly to pronotum. Meso-sternum twice to three times as long as metasternum, with a distinct median longitudinal sulcus anteriorly; paired longitudinal sutures distinct anteriorly in some species. Metanotum with lateral longitudinal elevation distinct, median longitudinal sulcus distinct. Metasternum with omphalium reduced but distinct; lateral omphalial groove absent. Front leg with femur simple, a little longer than tibia; tibia with inner apical process inconspicuous; tarsus with
first segment one and one fourth to one half as long as second segment; second segment with claws arising preapically. Middle leg with femur about as long as to one and one fourth times as long as tibia; tibia over four times to a little over one and a half times as long as first tarsal segment; first tarsal segment a little less than twice to almost eight times as long as second tarsal segment. Hind leg shorter than middle leg, femur over twice to a little longer than tibia; tibia a little less than three times to about five times as long as first tarsal segment in most species. (In *ventralis* seven times as long as first tarsal); first tarsal segment a little over one and one half to almost three times as long as second tarsal segment.

Abdomen elongate. First tergite with anterior margin W-shaped (or bisinuate); second to seventh tergites nearly equal in length in most species; first to sixth ventrites subequal in lengths in most species. Seventh segment with connexival spine present in both sexes of many species. Abdominal spiracle placed either closer to anterior margin than to posterior margin, or at middle of each segment; ventral connexival suture present; ventral median longitudinal impression distinct throughout.

**Male:** Seventh segment with ventral apical margin simply concave or with a median small emargination on concave ventral apical margin. Eighth segment with more or less conspicuous median longitudinal elevation on ventral surface in most species. Ninth segment with suranal plate simple; pygophore well exposed, with simple apical margin; parameres highly reduced but recognizable. Endosoma more or less strongly sclerotized and produced apically in many species; definitive dorsal plate extends apically along apical margin of endosoma; ventral plate more or less membranous, bifurcate or not bifurcate apically.

**Female:** Seventh segment with ventral apical margin simply concave or feebly produced medially. Eighth segment ventrally always well exposed. First valvula with well differentiated inner lobe of varying lengths, apex of outer lobe either acute or rounded. Second valvulae lobate or simply narrowed apically, directed mesad beyond apical margin of intervaginal membrane.

**Winged forms:** Sex normally connected with R + M at the point of branching into R and M. Pronotum with humeri located behind middle.

**Distribution:** World-wide. The study of more material is necessary before clear distributional pattern for each subgenus can be obtained.
Subgenus Aquarius Schellenberg


Aquarius Van Duzee, Cat. Het., 1:426-427(1917).
Aquarius Kiritschenko, Heteroptera of the European part of the Soviet Union (in Russian) (1951) (as genus).

Type species: Gerris paludum Schellenberg 1800 nec Fabricius 1794 = Cimex najas De Geer, by subsequent designation (Kirkaldy 1906).


Color pattern: Pronotum with a median longitudinal stripe only in anterior half, with yellow lateral margin usually between humeri and anterior lobe (total posterior margin in spinolae) in winged forms. Thorax ventrally with adpressed silvery hairs.

Structures in wingless forms: Antenniferous tubercles subparallel, about as long as eyes. Antenna with first segment always longer than second and third segments together; second segment a little longer than or equal to third. Clypeus with basal margin more or less obliterated. Mandibular and maxillary plates distinct from each other although usually densely clothed with long hairs; the former overlaps basal upper part of the latter. Rostrum thick; third segment between three and four times as long as fourth segment. Ventral surface of head densely clothed with long silvery hairs.

Pronotum with anterior margin straightly elevated between eyes; anterior lobe distinct from posterior lobe by an obscure transverse depression; posterior lobe entirely covering mesonotum, broadly rounded on apical margin; lateral margin slightly sinuate; upper surface usually with a median longitudinal carina of the same
color as ground color, or of darker color. Mesosternum about two and a half times as long as metasternum in most species, never more than three times as long as metasternum; median longitudinal sulcus distinct anteriorly; paired longitudinal sutures divergent posteriorly, more or less distinct in all species. Metanotum with median longitudinal sulcus distinct in most species; metacetabular suture meets dorsally with lateral longitudinal elevation. Metasternum with posterior margin concave; omphalium placed close to posterior margin of metasternum. Front leg with femur straight, occasionally dorsoventrally flattened in male (e.g., chilensis); tibia straight, slightly thickened apically, with a faint longitudinal depression on inner surface near apex; second tarsal segment not more than one and a half times as long as first segment. Middle leg with femur only slightly longer than tibia in most species; tibia about three and a half times as long as first tarsal segment in most species; first tarsal segment three to eight times as long as second segment. Hind leg with femur less than one and a half times as long as tibia in most species; tibia about five times as long as first tarsal segment in most species; first tarsal segment less than three times as long as second tarsal segment; second segment with distinct claws.

Abdomen narrow, with connexival spine conspicuous in most species, surpassing apical margin of eighth segment. First tergite shorter than second tergite, each abdominal tergite relatively long. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment; ventral longitudinal margin of connexivum distinct; ventral median longitudinal carina distinct at least in anterior segments in female.

Male: Seventh segment with ventral apical margin simply concave in some species, with an additional median emargination in many species; ventral surface simple. Eighth segment ventrally emarginated on apical margin in some species or produced medially in some species, with a conspicuous elevation of various shapes and degrees of development on ventral surface in most species; dorsal apical margin nearly straight or feebly concave. Ninth segment with suranal plate simple; pygophore rounded on apical margin; parameres reduced but distinctly recognizable. Endosoma with apical margin prolonged and more strongly sclerotized in many species; definitive dorsal plate curved ventrad along apical margin of endosoma, fused with robust bifurcate apical plate in many species; ventral plate membranous, bilobed in some species, the
lobes fused together in some species. (Description of the genitalia is based on *najas, elongatus, cinereus, conformis, antigone, ventralis, amplus, nyctalis, remigis.*)

**Female:** Seventh segment ventrally broadly concave on apical margin in some species, slightly produced in some species. Eighth segment with valvifers together more or less produced at middle; surface smooth, or with oblique suture, or elevated along inner margin of each valvifer. First valvula with well differentiated inner lobe, apex of outer lobe rounded and membranous, with a spinous process in all species examined except for *chilensis.* Second valvula lobate apically, slightly extending beyond apical margin of inter-valvular membrane, directed mesad and broadly rounded apically; inter-valvular membrane with a pair of oblique sclerotized areas; ramus of second valvula fine. Vulva membranous and simply narrowed apically in most species. (Description of genitalia is based on *elongatus, cinereus, conformis, ventralis, remigis, amplus, and chilensis.*)

**Modifications of the abdomen**

*The male seventh segment* (figs. 193-196). In *elongatus, conformis, cinereus, chilensis, ventralis* the ventral apical margin is simply concave, and the segment is a little shorter than the sixth segment on the median longitudinal axis. The connexival spine is very conspicuous especially in the first two species. In *najas and antigone* the seventh segment is a little longer than the sixth ventrally and ventral apical margin is also concave; in *najas, remigator* and *uhleri* an incipient stage of modification of the segment is noted, *i.e.*, the ventral apical margin has become triangularly incised, and the seventh segment is distinctly longer than the sixth on the ventral longitudinal axis (7th:6th :: 10:9 in *remigator, 12:10 in najas*), or a little shorter than sixth (*uhleri, 11:12*). In *nyctalis, remigis, nebularis, amplus,* and *stappersi,* the ventral apical margin of the seventh segment has a median emargination, the seventh segment is definitely longer than the sixth ventrally, and the connexival spine is definitely less conspicuous than in other more primitive species. The relative lengths of the seventh and sixth segments range 13:12 in *nebularis* to 16:12 in *ampius* and 12:7 in *remigis* and *stappersi.*

*The eighth abdominal segments* (figs. 193-196): The eighth segment is simple on the ventral surface in *elongatus, cinereus, conformis, ventralis,* etc., in which the seventh segment is also primitive; the eighth segment has a basal elevated area in *najas, remigator* and *uhleri;* in *nyctalis, remigis, amplus,* and *stappersi* the eighth segment
is more or less greatly prolonged and the ventral surface is provided with a strong, longitudinal elevation throughout its entire length.

The ninth segment: The suranal plate as well as pygophore have remained relatively unmodified. The parameres are greatly reduced but distinctly recognizable in all species. The endosoma with its apical region is simple in the more primitive species like elongatus but the apical region has become greatly prolonged and more strongly sclerotized in more specialized species such as remigis, etc., as will be noted from the figures, 212-219.

The female seventh segment (figs. 204, 206, 208): In the female the degree of modification of the seventh segment is less than in the male. In elongatus the seventh ventrite is a little shorter than the sixth on the median longitudinal axis, the connexival spine surpasses the tip of the abdomen and the ventral apical margin is simply concave. This is the most primitive condition in this genus. In uhleri, najas, cinereus, etc., the segment is more or less similar to elongatus. In remigis, amplus, nyctalis, conformis the seventh ventrite is definitely longer than the sixth and the connexival spine has become considerably reduced.

The female eighth segment (figs. 204, 206, 208): In elongatus and a few other species (nebularis, ventralis, najas), in which the seventh segment is not much prolonged, the inner margin of each valvifer is elevated only apically. In antigone, cinereus, and chilenesis, in which the seventh segment is equal to or only slightly longer than the sixth ventrite, the valvifer is not elevated along the inner margin and this condition appears to be the primitive one in this genus. In some other species such as remigis, conformis, nyctalis and amplus, in which the seventh segment is more or less greatly prolonged, the elevation is narrower than in elongatus but much more well marked, and this condition is the most specialized one in this genus.

Modification of the other structures

The antennae: The length of the second segment in relation to the third is greatest in the largest species, elongatus, and there is a striking tendency for the relative length of the second to the third to become smaller with reduction in the body size. The relative length of the second segment is smallest in the smallest species, cinereus. Slight deviation from the above tendency is, however, noted in three species, remigis, amplus, and nyctalis, all from the Western Hemisphere. In these species the relative length of the
second segment is nearly the smallest in spite of the fact that they are relatively large sized species. The above noted tendency has apparently resulted, as we already observed, from a greater growth ratio for the second segment than for the third segment in this subgenus.

Deviations in some species

G. (A.) remigis, amplus, and nyctalis, all from the Western Hemisphere, are included in the subgenus Aquarius but they differ in certain structures from the rest of the species as follow:

(1) The lengths of middle and hind leg segments slightly deviate from the allomorphic slopes for these leg segments in this subgenus.

(2) In spite of the fact that they are relatively large in size, the male apical abdominal segments are highly specialized; among other species the abdomen is more primitive in the larger species and more specialized in the smaller species.

(3) The metasternum is relatively long, or relatively less reduced in comparison to other species although the abdomen is highly specialized.

(4) The first antennal segment is only slightly longer than the second and third segments together; while in all others the first segment is distinctly longer than the second and third segments together.

(5) The second and third segments are nearly equal in length; in other species the second segment is definitely longer than the third segment.

(6) The ventral side of the abdomen of the male is longitudinally impressed, instead of longitudinally carinated in the other species.

G. (A.) stappersi Poisson from Africa also has somewhat different lengths of antennal and leg segments and the more conspicuous connexival spine compared to the other species with equivalent body sizes.

Subgenus Gerris Fabricius s. str.

(Figs. 13, 111, 127, 129, 148, 165, 187-192, 194, 197-203, 205, 207, 209, 210, 221, 222)


Color pattern: Dark fuscous to black in ground color. Pronotum with a yellow median longitudinal stripe only on anterior lobe and often with yellow lateral margin. Front femur dark yellow, always with a black spot spreading usually almost entire length on outer surface. Connexivum always yellowish or red at least laterally.

Structures in wingless forms: Antenniferous tubercles as long as or a little shorter than length of eyes. Antenna relatively thick; first segment about as long as or a little shorter than second and third segments together; second and third subequal in length to each other. Basal margin of clypeus indistinct, widened apically. Mandibular and maxillary plates distinct from each other; the former apically covering upper basal region of the latter. Rostrum rather short; third segment always less than three times as long as last segment.

Pronotum with anterior margin broadly rounded, without conspicuous straight elevation as in Aquarius; anterior lobe distinct from posterior lobe by transverse obscure suture, lateral margin not or feebly sinuate behind anterior lobe, posterior lobe with broadly rounded apical margin; upper surface with narrow median longitudinal elevation. Mesosternum a little over twice to three times as long as metasternum, convex, median longitudinal sulcus distinct in anterior half; paired lateral sutures distinct in many species. Metanotum with median longitudinal sulcus distinct; lateral longitudinal elevation extend forward to meet metacacetabular suture. Metasternum much longer than second ventrite. Omphalium highly reduced but distinct, located at about posterior one fifth of metasternum. Front leg with femur rather incrassate
basally; tibia slightly thickened at apex, with shallow longitudinal depression on inner surface near apex. Second tarsal segment from one and a half to twice as long as first segment, claws arising from near apex. Middle leg with femur about one and two sevenths times as long as tibia except for argentatus, in which femur is just a little longer than tibia; tibia about twice as long as first tarsal segment in most species; first tarsal segment about three times as long as second tarsal segment in most species, less than twice as long as second segment in some species. Hind leg with femur about as long as or a little shorter than middle femur, usually about twice as long as tibia; tibia about three times as long as first tarsal segment in most species; first tarsal segment between one and a half to twice as long as second tarsal segment; apical claws recognizable as in middle leg.

Abdomen narrowed posteriorly. Connexivum with spine on seventh segment more or less greatly reduced, directed dorsad apically in some species. Abdominal spiracles placed closer to anterior than to posterior margin of each segment in most species, placed at middle between both margins in some species. Median ventral longitudinal carina distinct in most species; ventral longitudinal suture of connexivum interrupted at anterior third of each segment, the suture obscure and represented by shallow dot like depressions in some species.

Male: Seventh segment without connixival spine, ventral apical margin with double emargination in most species, with longitudinal depression on either side of median longitudinal axis in some species, with a pair of conspicuous tubercles near posterior margin at middle in odontogaster. Eighth segment with a conspicuous median longitudinal elevation on ventral surface in some species. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded; parameres vestigial. Endosoma prolonged but not as much as in some species of Aquarius and not strongly sclerotized. Definitive dorsal and lateral plates as in Aquarius; ventral lobe long and slender, at least reaching apex of endosoma. (Description of the genitalia is based on thoracicus, marginatus, firmus, odontogaster.)

Female: Ventral apical margin of the seventh segment concave. Eighth segment with both valvifers together produced at middle in some species, upper surface with more or less distinct oblique sutures in some species. First valvula with well differentiated inner lobe of varying lengths in various species; apex of outer lobe simply
narrowed apically, often acute at tip. Second valvula swollen and rounded at apex, slightly extending beyond apical margin of intervalvular membrane which is straight or straight with a small median notch. (Description of the female genitalia is based on *gillettei*.)

**Modifications of the abdomen**

(Figs. 197-203, 205, 207)

The process of modification of the abdomen can be traced, to a large extent, directly back to the abdomen of *Aquarius*.

The male seventh segment: In no species of *Gerris s. str.* is the seventh segment ventrally shorter than the sixth although this situation occurs in some species of *Aquarius*. In *thoracicus* (fig. 197) *costae*, *gibbifer* (fig. 194), *marginatus* and *lacustris* the seventh segment is as long as the sixth and this condition is the shortest or the least prolonged found in *Gerris s. str.* The ventral apical margin in these species is simply concave and without a distinct median notch, the connexival spine is clearly retained, and the ventral surface is unmodified. In *argentatus*, *buenoi*, and *inseparatus* the seventh segment is considerably longer than the sixth (6th:7th :: 8:9-10:13) but otherwise much as in the first group. In *argenticolis* (fig. 199), *incurvatus*, *comatus*, *incognitus*, and *alacris* the seventh segment is also considerably longer than the sixth, the ventral apical margin has a distinct median emargination and the connexival spine is more reduced, but the ventral surface is not conspicuously modified. In *gillettei* (fig. 201) and *pingreensis* (fig. 202) the seventh segment is also longer than the sixth segment, especially in *gillettei*, and the ventral surface is provided with well marked impressions along the median longitudinal elevation which extends the entire segment. In the last two species, *firmus* (fig. 200, 203) and *odontogaster* (fig. 198), the seventh segment is twice or almost twice as long as the sixth, and the ventral surface is greatly modified; the connexival spine in these species is absent.

The male eighth segment: In *thoracicus* (fig. 197), *marginatus*, *lacustris*, *gibbifer* (fig. 194), *costae*, and *inseparatus* the eighth segment has remained short and the ventral surface is relatively less modified. It has become more or less prolonged and with a more or less conspicuous longitudinal elevation in *gillettei* (fig. 201) and *pingreensis* (fig. 202). It is more strongly prolonged and the ventral surface is strongly longitudinally carinated and densely clothed with long adpressed hairs on either side of the median longitudinal elevation in *argenticolis* (fig. 199), *incurvatus*, mar-
ginatus, comatus, incognitus and alacris. The eighth segment is
dorsally prolonged but ventrally relatively short and the ventral
surface is not or only slightly modified in firmus (fig. 200) and
odontogaster (fig. 198), although the seventh segment in these
forms is highly modified. It should be noted that the trend in
modification of the ventral surface of the eighth segment is similar
to that of Aquarius, in which the median longitudinal elevation with
adpressed long hairs on either side occur in somewhat divergent
and specialized group including G. (A.) remigis, G. (A.) amplus,
G. (A.) nyctalis. It is noted from the above description that the
species with relatively long body are more primitive in the seventh
and eighth abdominal segments than the species with shorter body.

The male ninth segment: As in Aquarius the ninth segment has
remained simple. The apical segment of the endosoma has not
become prolonged as in some species of Aquarius.

The female seventh and eighth segments: In all species examined
the ventral apical margin of the seventh segment is more or less
concave. The eighth segment, both valvifers together, more or
less produced at the middle in marginatus (fig. 205), incognitus,
alacris, thoracicus, inseparatus, costae, gillettei, incurvatus, gibbifer
and comatus. In the last two species the surface of each valvifer
has an oblique suture. It should be noticed that in all these species
the sixth and seventh ventrites are more or less subequal in length.
In all other species the posterior margin of each valvifer is emar-
ginate laterally, and in some of these species the basal region of
the valvifer is strongly depressed. In all these species the seventh
ventrite is at least a little longer than the sixth; in firma it is much
longer than the sixth.

The second to sixth ventrites: Compared with species of Aquarius,
the abdominal segments have become generally considerably shorter. In some species (buenoi, argenticollis, firmus, odonto-
gaster) this tendency is especially pronounced and the abdominal
spiracles in these forms have shifted their positions to the middle
of each segment. The ventral connexival sutures are reduced to
two punctiform depressions in some species with more shortened
abdominal segments. It should be noted that the abdominal spiracles
are placed at the middle of each segment in two species of
Aquarius with reduced abdominal segments (G. (A.) remigis, G.
(A.) ampla).
Modifications of the other structures

The antennae: As noted under Aquarius, the length of the second segment in relation to the third has apparently become progressively smaller. In all species of Gerris s. str., in which many structures especially the abdominal segments are more specialized, the second and third segments are subequal to each other as in some specialized species of Aquarius.

The rostrum: The third segment is less than three times as long as the last segment in all species and the proportional lengths of the two segments are quite constant in this subgenus. In Aquarius the relative length of the third to the fourth is evidently greater than in Gerris s. str. The relative length of the third to the fourth has apparently become smaller in the more specialized subgenus, Gerris s. str.

The subgenus Gerris s. str. is separated from Aquarius by the following characteristics:

1. Different proportional lengths of the antennal segments.
2. The hind tibia is about three times as long as its first tarsal segment, while it is over five times as long as its first tarsal segment in most species of Aquarius.
3. The pronotum is without straight and carinated anterior margin in Gerris s. str.
4. The connexival spine is much reduced or completely lost in Gerris s. str.
5. The front leg has black mark instead of being wholly black as in Aquarius.
6. There is evidence that the growth ratios for practically all antennal and leg segments are smaller than in Aquarius.

Subgenus Limnoporus Stål

 type species: Gerris rufoscutellatus Latreille, monobasic.

Species examined: G. (L.) canaliculatus Say, G. (L.) dissortis
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Drake and Harris, G. (L.) notabilis Drake and Hottes, G. (L.) rufoscutellatus Latreille.

Color pattern: Pronotum with median longitudinal yellowish stripe extending onto posterior lobe.

Structures in wingless forms: Antenniferous tubercles long. Antenna slender, first segment always longest, but distinctly shorter than second and third ones together; third one shortest. Clypeus with basal margin distinct. Mandibular and maxillary plates clearly defined from each other. Rostrum long and slender, extending far beyond prosternum; third segment always over four times as long as last segment.

Pronotum slender, extending beyond posterior margin of mesonotum, anterior margin straight and carinated except for canaliculatus, posterior margin broadly rounded; uppersurface with a narrow, pale longitudinal carina throughout. Mesosternum a little over twice to two and a half times as long as metasternum; median longitudinal sulcus distinct in anterior half; paired longitudinal sutures distinct in anterior three fourths except for canaliculatus in which they are absent. Metanotum with median longitudinal sulcus distinct; metacetabular suture reaching well carinated lateral longitudinal suture of metanotum. Metasternum with omphalium located at about apical fifth of metasternum. Front leg slender; femur slightly dilated at apical third; tibia slightly swollen apically, without conspicuous process at inner apical angle; tarsus with first segment a little shorter than or subequal to second segment; claws arising from apical one fourth. Middle leg with femur considerably shorter than hind femur, about one and one fourth times as long as tibia; tibia a little less than twice as long as first tarsal segment; first tarsal segment under four times as long as second segment. Hind leg about as long as middle leg (only slightly shorter than middle leg); femur over one and a half times as long as tibia; tibia a little less than four times as long as first tarsal segment; first tarsal segment over twice as long as second tarsal segment.

Abdomen long, slightly dilated at middle. First tergite much shorter than second tergite, second to sixth tergite about as long as wide; seventh connexival segment always with conspicuous spine; second to seventh ventrites subequal in length to each other. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment. Ventral median longitudinal carina distinct; ventral connexival suture distinct, represented by discontinuous well impressed sutures on each segment.
Male: Seventh segment with ventral apical margin broadly concave. Eighth segment with ventral apical margin bisinuate or feebly produced at middle; ventral surface with or without median longitudinal elevation. Ninth segment with suranal plate simple; pygophore relatively small, rounded on apical margin; parameres reduced but distinctly recognizable. Endosoma with definitive dorsal plate roundly dilated on apical margin (part of apical plate), basally extends ventrad (fused basal plate); lateral plates rounded in apical regions; ventral lobe totally membranous and apically bifurcate in _dissortis_, more sclerotized and not bilobed in _canaliculatus_; apical region of endosoma not prolonged. (Description of the genitalia is based on _dissortis_ and _canaliculatus_).

Female: Seventh segment ventrally slightly concave or feebly produced at middle on ventral apical margin. Eighth segment well exposed both dorsally and ventrally, both valvifers together narrowed apically and produced at middle or sinuate on apical margin, slightly elevated along inner margin of each valvifer (_canaliculatus_). First valvula with inner lobe split apically into two lobes, inner one of them membranous; outer lobe apically dilated, membranous and obtusely rounded. Second valvula with apex simply narrowed, folded on broadly rounded apical margin of intervalvular membrane; ramus slender but long. Vulva membranous, simply narrowed apically. (Description of the genitalia is based on _canaliculatus_, _dissortis_, and _notabilis_).

Modifications of the abdomen
(Figs. 317-320)

The male seventh segment: In _dissortis_ and _notabilis_ the seventh segment is considerably shorter than the sixth ventrally and has a more conspicuous connexival spine; in the other two species (figs. 317, 318) the seventh segment has become as long as sixth ventrally, accompanied by slight reduction of the connexival spine.

The male eighth segment: In _rufoscutellatus_ (fig. 317) the apical half of the eighth ventrite is carinate on the median longitudinal axis and the apical margin is strongly produced. In _canaliculatus_ (fig. 318) the eighth segment is elevated basally on the median longitudinal axis. In the other two more primitive species no conspicuous modification is apparent on the ventral surface.

The female seventh segment: The ventral apical margin of the seventh segment is simple and concave in all species except for _canaliculatus_ (fig. 320) in which it is strongly produced at the middle. The degree of specialization as indicated by the relative
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lengths of the seventh and sixth segments is roughly in the following order from more primitive to more specialized: *notabilis, dissortis, rufoscutellatus, canaliculatus*. This order conforms well with that based on characters of the males. It should be also noted that in this genus, as in many other genera, the largest species is most primitive and the smallest one is most specialized as indicated by abdominal characters.

The subgenus *Limnoporus* is structurally close to *Aquarius* but can be distinguished by the following characteristics:

1. Distinctly different proportional lengths of the antennal segments, *i.e.*, the first segment is shorter than the second and third together.
2. The median longitudinal yellow stripe on the pronotum extends well onto the posterior lobe.
3. The clypeus is more clearly defined basally.
4. The hind femur is distinctly longer than middle femur; it is about as long as middle femur in *Aquarius* and also in *Gerris s. str*.
5. The hind leg is only slightly shorter than the middle leg, while it is considerably shorter than middle leg in *Aquarius* and *Gerris s. str*.
6. There is evidence that the growth patterns for at least the fourth antennal segments, the front and middle leg segments are probably significantly different from those in *Aquarius* and *Gerris s. str*.

Genus *Gerriselloides* Hungerford and Matsuda

(Figs. 9, 234-242)


Type species: *Gerris brachynotus* Horváth, by original designation.

Species examined: *G. brachynotus* (Horváth).

Color pattern: Predominantly black dorsally. Head with a yellow crescent shaped spot at vertex. Pronotum with a median yellow stripe confined to anterior lobe; posterior lobe reddish brown. Meso- and metapleural regions with silvery pubescence. Abdominal tergites with a median elongate silvery spot on each segment.

Structures in wingless forms: Spindle shaped gerrids. Head wider than long including eyes. Eye with inner margin emarginated posteriorly, small, reaching posteriorly to anterolateral angle of pronotum, antenna short; first segment longest but shorter than
second and third segments together; second and third segments sub-
equal in length to each other; fourth segment much longer than
third. Antenniferous tubercles well developed, about as long as
eyes in dorsal view. Clypeus with basal margin well defined.
Mandibular and maxillary plates distinct from each other. Rostrum
short; third segment not extending beyond prosternum, about three
times as long as last segment.

Pronotum fully prolonged, entirely covering mesonotum, but rela-
tively short, a little over twice as long as head; anterior lobe with
anterior margin nearly straight; posterior lobe a little longer than
anterior lobe, defined from the latter by oblique suture coming from
each side, slightly widened posteriorly and with a broadly rounded
caudal margin, with a dark sublateral longitudinal elevation; upper-
surface with a fine median longitudinal elevation tapering apically.
Intersegmental suture between mesonotum and metanotum later-
ally continuous with metathoracic spiracle. Mesosternum relatively
short, about twice as long as metasternum; median longitudinal
sulcus distinct anteriorly; paired longitudinal sutures divergent
posteriorly, distinct in anterior half of mesosternum. Metathoracic
spiracle conspicuous. Metasternum with omphalium highly re-
duced; omphalial groove retained though lateral openings on met-
acetabula lost. Metanotum with lateral longitudinal elevations con-
vergent anteriorly behind posterolateral angles of pronotum,
without median longitudinal sulcus. Front leg with femur robust;
tibia without apical thickening; tarsus with second segment longer
than first segment and claws arising from near apex. Middle leg
relatively stout; femur a little less than one and a half times as long
as tibia; tibia twice as long as first tarsal segment; first tarsal segment
a little over twice as long as second segment. Hind leg shorter than
middle leg; femur a little less than twice as long as tibia; tibia over
twice as long as first tarsal segment; tarsus relatively long, first
segment twice as long as second segment.

Abdomen long, narrowed apically. First tergite with flattened
W-shaped anterior margin, posterior margin elevated medially in
male; second to fifth tergites subequal in length; sixth to seventh
longer and narrower than the preceding segments; second to sixth
ventrites subequal in length. Connexivum slightly reflexed; seventh
segment without connexival spine in male, or slightly developed in
female. Abdominal spiracles located closer to anterior margin
than to posterior margin of each segment; ventral longitudinal su-
ture of connexivum distinct throughout the entire length of each
segment. Ventral median longitudinal elevation indistinct.
Male: Seventh segment longer than sixth ventrally, ventral apical margin simply concave. Eighth segment with ventral apical margin feebly concave. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded. (Male genitalia were not dissected for study).

Female: Seventh segment longer than sixth ventrally; ventral apical margin slightly produced medially. Eighth segment with each valvifer depressed on surface. (Female genitalia were not studied).

Distribution: Eastern Siberia.

The genus Gerriselloides was originally assigned to Gerris s. str., but it is different from the latter as follows:

1. The clypeus has the basal margin distinct.
2. The pronotum is short and with a sublateral longitudinal elevation.
3. The mesosternum is relatively short. In a majority of species of Gerris s. str. the mesosternum is over two and a half times as long as the metasternum, while in this genus the mesosternum is only twice as long as the metasternum.
4. The metasternum has retained the omphalial groove, although its lateral opening on the metacetabulum is lost.
5. The metanotum is without median longitudinal sulcus.
6. The ventral apical margin of the seventh abdominal segment of the male is simply concave; in a majority of species of Gerris s. str. the concave ventral apical margin of the same segment has a median smaller emargination.
7. The ventral longitudinal suture of the connexivum is distinct as in Aquarius.

In spite of the above-mentioned differences, this genus is close to Gerris s. str. The lengths of the antennal and leg segments in relation to the body size are much as in Gerris s. str., and roughly fall on the allometric growth slopes for those segments in Gerris (Gerris) marginatus Say.

Genus Gerrisella Poisson

(Figs. 10-11, 243-251)

Gerrisella Hungerford and Matsuda, Florida Ent., 41(4); 165-168 (1958) (as genus).

Type species: Gerris settembrinioi Poisson, by original designation.
Species examined: *Gerrisella settembrinoi* (Poisson).

**Color pattern:** Predominantly black. Eye reddish brown. Head with basal yellow mark. Pronotum with a broad median yellow stripe. Meso- and metapleural regions continuously grayish on either side of mesonotum and metanotum. Abdomen black. Basal half of legs yellow.

**Structures in wingless forms:** Female considerably larger than male. Head including eyes much wider than long, vertical region widened. Eye large, kidney-shaped, basal half of inner margin concave. Antenna slender. First segment strongly outcurved in apical half, about as long as second and third segments together, second to fourth segments subequal in length. Antenniferous tubercles slightly convergent anteriorly. Clypeus narrow, well defined at base. Mandibular and maxillary plates distinct from each other. Rostrum relatively long; third segment about three times as long as last segment.

Pronotum only feebly prolonged, its apical margin rounded, uppersurface longitudinally depressed in the middle. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesothorax strongly widened posteriorly. Mesosternum about four times as long as metasternum in male; median longitudinal sulcus recognizable only anteriorly. Metathoracic lateral longitudinal suture distinct, nearly reaching posterolateral margin of mesonotum, median longitudinal sulcus absent. Metasternum with distinct omphalium near posterior margin, without lateral groove of omphalium. Front leg without sexual difference in shape. Femur distinctly longer than tibia, somewhat curved and flattened at middle; tibia simply thickened apically; first tarsal segment greatly reduced; second segment with claws arising from apical fourth of second segment. Middle leg much longer than hind leg; femur a little longer and much more robust than tibia; first tarsal segment about three times as long as second tarsal segment, claws not recognized in the specimens examined. Hind leg with femur slender, a little longer than middle femur, about four times as long as tibia; first and second tarsal segment nearly equal in length.

Abdomen somewhat reduced in length. First segment (tergite) with flattened W-shaped anterior margin; second to seventh tergites with anterior margins feebly produced; first to sixth ventrites somewhat reduced in length; seventh segment with connexival spines absent. Abdominal spiracles from second to seventh located
a little closer to anterior margin than to posterior margin of each segment; ventral margin of connexivum obscure.

**Male:** Seventh segment without median emargination on ventral apical margin. Eighth tergite greatly prolonged and broadly rounded on apical margin. Ninth segment with suranal plate provided with a ventrally directed process arising from apical region of each lateral margin; pygophore simply rounded on apical margin, elongate; parameres present.

**Female:** Not available for study.

**Winged forms:** Pronotum with anterior lobe well defined from posterior lobe, humeri located behind middle of pronotum. Hemelytra with Sc joined to R + M by oblique Sc₂ vein at the point of separation of R and M from basal R + M.

**Distribution:** Africa (Belgian Congo, Ivory Coast, Guinea).

This genus was formerly included in *Gerris*, but apparently is not closely related to it. This genus is more specialized than *Gerris s. str.* in the presence of the process on the lateral margin of the suranal plate, complete loss of the connexival spine of the seventh abdominal segment, great reduction of the pronotum in the wingless forms, etc. This genus, however, is more primitive than *Gerris s. str.* in the presence of the distinct basal margin of the clypeus, and distinctly differentiated mandibular and maxillary plates. As already found, the growth patterns for the antennal and leg segments are presumably considerably different from those in *Gerris s. str.* The location of the metathoracic spiracle is also different from that in *Gerris s. str.*

The phylogenetic position of this genus is obscure. It has possibly arisen as a distinct genus as a result of an independent specialization from a group ancestral to *Gerris* or *Limnogonus*.

**Genus Tenagogerris** Hungerford and Matsuda

(Figs. 12, 252-262)


**Type species:** *Gerris euphrosyne* Kirkaldy, by original designation.

**Species examined:** *T. euphrosyne* (Kirkaldy).

**Color pattern:** Head and pronotum ferrugineous brown in ground color. Head with a broad black median longitudinal stripe and
sublateral black stripes. Pronotum with a median longitudinal stripe which reaches posterior margin and with marginal black stripe, also with a pair of elongate black spots at anterolateral angles of pronotum which are continuous with marginal black stripe; pleural region with a broad black longitudinal stripe. The rest of body with dorsal surface black in ground color; mesopleural region largely clothed with short white pubescence on black ground color, thus giving a bluish tinge in certain lights, with a yellowish brown longitudinal stripe more ventrally. Body beneath paler.

Structures in wingless forms: Female much larger than male. Head including eyes wider than long. Eye strongly emarginated on inner margin. Antenna with first segment longest, but shorter than second and third segments together; second and third segments subequal in length, fourth a little longer than second and than third. Antenniferous tubercles shorter than eyes. Clypeus with basal margin indistinct but traceable. Mandibular and maxillary plates distinct from each other. Rostrum robust; third segment not extending beyond prosternum, about three times as long as fourth segment.

Pronotum fully prolonged, reaching a little beyond posterior margin of mesonotum, posterior margin broadly rounded; anterior and posterior lobes ill defined. Mesosternum a little over four times as long as metasternum, median longitudinal sulcus distinct only anteriorly; paired longitudinal sutures sometimes distinct in anterior third or half of mesosternum. Intersegmental suture between mesonotum and metanotum obliterated laterally. Metathoracic spiracle placed remotely from lateral margin of pronotum. Metanotum with lateral longitudinal suture well carinated, convergent anteriorly; median longitudinal sulcus of metanotum distinct. Metasternum with omphalium located near posterior margin; omphalial groove absent. Front leg slender; femur simple, without sexual difference; tibia simple, not dilated apically; tarsus with first segment shorter than second segment, claws arising from near apex of second segment. Middle leg slender; femur only slightly longer than tibia; tibia a little less than three times as long as first tarsal segment; first tarsal segment over four times as long as second. Hind leg shorter than middle leg; femur a little less than twice as long as tibia; tibia five times as long as first tarsal segment; first tarsal segment about twice as long as second segment.

Abdomen strongly narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin, longer than second tergite;
second to fifth tergites subequal in length; seventh segment without connexival spine; ventrites more reduced than tergites. Abdominal spiracles placed a little closer to anterior margin than to posterior margin of each segment; ventral longitudinal margin of connexivum obliterated or represented by a shallow and obscure depression; ventral median longitudinal elevation distinct in female.

Male: Seventh segment much longer than sixth segment both dorsally and ventrally; ventral apical margin simply concave. Eighth segment with ventral apical margin concave. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded; parameres vestigial. Endosoma with definitive dorsal plate with small apically rounded area; basal plate detached from base of dorsal plate, bearing largely membranous ventral plate apically; lateral plates slender and long, placed parallel to dorsal plate.

Female: Seventh segment about twice as long as sixth segment ventrally, ventral apical margin concave. Eighth segment with inner lobe of first valvula highly membranous and short; outer lobe sclerotized along both inner and outer margins except apex where is membranous and rather acutely narrowed apically. Second valvula sclerotized along outer margin, with membranous apical processes extending beyond apical margin of intervalvular membrane, which is with U-shaped dark area reaching apical margin; ramus slender. Vulva with broadly rounded apex and attached laterally to inner membranous lobe of first valvula.

Winged forms: Pronotum with humeri located behind middle, apical margin broadly rounded. Hemelytra with Sc joined to R + M near the point of branching into R and M.

Distribution: Australia.

This genus, at first glance, appears to be nothing but a Tenagogonus. Its general color pattern, the remote position of the metathoracic spiracle from the lateral margin of the pronotum, etc., suggest that this genus is a close relative of the Limnometra-Tenagogonus complex, but the relatively short and robust rostrum is exactly like Gerris, and the proportional lengths of the first three antennal segments are also more like Gerris s. str. than in Tenagogonus. In the species of the Limnometra-Tenagogonus complex of this size (8 to 10 mm.), the male is definitely longer than the female and the male apical abdominal segments are more or less conspicuously modified; while in this genus, which is represented by a single species, the female is definitely longer than the male,
and the male apical abdominal segments are unmodified. This genus may possibly be the closest to the ancestral group of the Gerrini.

Genus *Eurygerris* Hungerford and Matsuda
(Figs. 5, 129, 263-287)


Type species: *Brachymetra fuscinervis* Berg, by original designation.

Species examined: *E. cariniventris* (Champion), *E. carmelus* (Drake and Harris), *E. flavolineatus* (Champion), *E. fuscinervis* (Berg), *E. kahli* (Drake and Harris), *E. mexicanus* (Champion), *E. summatus* (Drake and Harris).

Color pattern: Reddish brown in ground color in all species except for *flavolineatus*, in which it is nearly black. Head with a large black marking, basal pale yellow crescent-shaped marking well impressed. Pronotum in anterior lobe with pale yellow median longitudinal stripe. Silvery pubescent on the thorax. Abdomen and pronotum with at least anterior lobe black and with greenish tinge.

Structures in wingless forms: Male much smaller than female. Head including eyes about as long as wide. Eye elongate, inner margin strongly emarginated in posterior half. Antenna without conspicuous difference in lengths among segments. First segment always a little longer than second. Antenniferous tubercles feebly rounded on lateral margins. Clypeus with basal margin obliterated. Mandibular and maxillary plates sometimes indistinctly separated. Rostrum rather slender, slightly extending beyond prosternum; third segment from a little over three times to four times as long as last segment.

Pronotum prolonged in varying degrees in various species, reaching posterior margin of mesonotum in *mexicanus*; transverse suture separating anterior lobe from posterior lobe well marked. Intersegmental suture between mesonotum and metanotum distinct laterally. Mesonotal region laterally more or less well carinated longitudinally and defined from mesopleural region. Mesosternum with posterior margin feebly concave, about twice to a little over three times as long as metasternum in male; median longitudinal sulcus shallow or obscure; paired longitudinal sutures sometimes recogniz-
able. Metathoracic spiracle located remotely from lateral margin of pronotum or of mesanotum. Metanotum with median longitudinal sulcus obliterated posteriorly; lateral longitudinal elevation not reaching mesonotum. Metasternum more or less conspicuously elevated on longitudinal axis in all species except for *flavolineatus* and *mexicanus*; omphalium highly vestigial, omphalial groove completely lost. Front leg with femur strongly curved and depressed on inner margin and with a protuberance at the apical end of depression in male; tibia slightly swollen apically, with a shallow longitudinal depression on inner margin near apex; first tarsal segment about as long as second segment; claws arising from near apex of second segment. Middle leg with femur a little longer than tibia; tibia apically curved in dried specimens, a little less than twice as long as first tarsal segment; first tarsal segment over five times as long as second in most species. Hind leg shorter than middle leg; femur a little longer than middle femur in most species; about twice as long as tibia in all species except for *mexicanus*, in which femur much less than twice as long as tibia; tibia about twice to three times as long as first tarsal segment; first tarsal segment twice to almost three times as long as second.

Abdomen more or less strongly narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin, longer than second; second to sixth tergites and second to fifth ventrites subequal in length. Connexivum more or less strongly reflexed; connexival spine absent. Abdominal spiracles from second to sixth segments placed at middle of each segment except for female of *mexicanus*, in which they are placed closer to anterior margin than to posterior margin of each segment; those of seventh segment in female placed closer to anterior margin than to posterior margin. Median longitudinal carina present except for male of *mexicanus* and male and female of *flavolineatus*. Ventral longitudinal suture of connexivum represented by a dot-like depression on each segment in most species.

**Male:** Seventh segment with ventral apical margin with a shallow median emargination, longer than the preceding segment both dorsally and ventrally. Eighth segment strongly prolonged and cylindrical in some species; ventral apical margin emarginated. Ninth segment with suranal plate simply narrowed apically; pygophore rounded on apical margin; parameres vestigial. Endosoma with apical margin always strongly sclerotized, flat and broad; dorsal plate as in *Aquarius* and *Gerris s. str.*, basally appears to be fused with basal plate; ventral lobe membranous, broad and short; lateral
plates short, almost indistinguishably fused with well sclerotized ventral basal region of endosoma in *mexicanus*. (Description of the genitalia is based on *mexicanus*, *fuscinervis*, and *carmelus*.)

**Female:** Seventh segment much longer than sixth in most species, telescoping eighth segment. Eighth segment apically exposed ventrally in most species. First valvula with well sclerotized inner lobe reaching middle of outer lobe; outer lobe thick, largely sclerotized, apex membranous and rounded, with a small spinous projection on inner apical angle. Second valvula with apex membranous, folded mesad, thus presenting a round apex; intervalvalar membrane with apical margin membranous, broadly rounded, feebly notched at middle. Vulva membranous, with a median apical production (Description of the genitalia is based on *fuscinervis*, *mexicanus*, and *cariniventris*).

**Winged forms:** Pronotum with humeri located at apical third, posterior margin broadly rounded. Hemelytra with Sc connected by Sc₂ with R + M basal to the point of separation of R and M from basal R + M, or with R near the point of separation.

**Modifications of the abdomen**

The male abdomen: The degree of specialization is seen in varying degrees of prolongation of the seventh to ninth segments. Six species, for which male specimens are available for study, can be arranged roughly in the following order from more primitive to more specialized on the basis of this feature.

- *mexicanus*  
  - The seventh segment is a little longer than either the sixth or the eighth ventrally.
- *fiavolineatus*  
  - The eighth segment is longer than the seventh segment ventrally. In *carmelus* the seventh is about twice as long as sixth and the eighth is also about twice as long as the seventh and tubular in shape.
- *cariniventris*  
  - *kahl*  
- *fuscinervis*  
- *carmelus*  

The female abdomen: In *mexicanus* and *fiavolineatus* the seventh ventricle is a little less than twice as long as the sixth, but in *carmelus* the seventh is a little over twice as long as sixth at the middle, and laterally almost three times as long as the sixth due to prolongation of the posterolateral angle of the seventh connexival region. In the other four species the seventh segment is over twice as long as sixth. The spiracles of the third to fifth segments are located midway between the anterior and posterior margins of the segments except for *mexicanus* and *fiavolineatus*, in which the pregenital abdominal segments are relatively long and the spiracles of the third, fourth and
fifth segments are placed closer to the anterior margin than to posterior margin of each segment.

Modifications of the other structures

The pronotum: The pronotum in wingless forms is almost fully prolonged, reaching close to the posterior margin of the mesonotum in *mexicanus* (fig. 263); it reaches about the middle of the mesonotum in *carmelus*, *cariniventris*, *summatus*, *kahli*, and *fuscinervis* (fig. 264); it is only slightly prolonged and with a broad round margin in *flavolineatus* (fig. 265). The degree of reduction of the pronotum in wingless forms is thus least in *mexicanus* and highest in *flavolineatus*, although other structures have remained primitive in the latter species.

The front femur: In all species the front femur is more or less greatly depressed on the inner surface and the femur is greatly arched. In *mexicanus* and *flavolineatus* the inner surface is least depressed (figs. 282, 283), but in all others the inner surface is more strongly depressed and a low black protuberance exists near the apical end of the depression (figs. 284-287).

The hemelytra: The hemelytra with the vein Sc occasionally connected with R near the point of separation of R and M from the basal R + M by Sc in *mexicanus*; in all other species the vein Sc is connected with R + M at various points basal to the point of separation of R and M, due to more distal separation of R and M.

This genus, though formerly included within the genus *Gerris*, cannot be the direct derivative of any one of more primitive subgenera of *Gerris*.

Genus *Limnogonus* Stål

(Figs. 7-8, 131, 151, 288-316, 321-334)

*Tenagogonus* Van Duzee, Cat. Hemip., 249 (1917) (misidentification).
Type species: *Hydrometra hyalina* Fabricius, by subsequent designation (Drake and Harris 1934, in the above reference).


Color pattern: Uppersurface predominantly black, lustrous in most species. Head typically with a pair of yellow sublateral longitudinal stripes. Pronotum typically with a median longitudinal yellow stripe either reaching or not reaching posterior margin, and with a pair of elongate yellowish spots on either side of the median longitudinal yellow stripe; in *Limnogonellus* the yellow longitudinal stripe is replaced by a yellow spot. Mesothorax typically with a silvery longitudinal stripe. Tergites with a continuous yellow longitudinal stripe in many species.

Structures in wingless forms: Head including eyes wider than long. Eye with inner margin strongly emarginated. Antenna slender, much shorter than length of body. First segment two thirds to three fourths as long as second and third together in most species; third segment as long as or a little shorter than second; fourth segment much longer than third in most species. Antenniferous tubercles shorter than eyes. Clypeus with basal margin not very distinct. Mandibular and maxillary plates indistinctly separated. Rostrum rather slender and long; third segment about two and a half times to about four times as long as last segment.

Pronotum fully prolonged and covering mesonotum in most species; anterior lobe with a pair of obscure depressions; posterior lobe occasionally faintly longitudinally carinate in the middle. Intersegmental suture between mesonotum and metanotum lost laterally. Mesosternum three to five times as long as metasternum;
median longitudinal sulcus distinct anteriorly; paired longitudinal sutures distinct in some species. Metathoracic spiracle placed at some distance from pronotum. Metanotum with lateral elevations well marked and convergent anteriorly; median longitudinal sulcus distinct in some species. Metasternum with omphalium present; omphalial groove absent. Front leg with femur a little longer than tibia, curved in basal third in some species; tibia slender, without conspicuous process; tarsus with first segment about as long as second to less than half as long as second. Middle leg with femur always a little longer than tibia; tibia about twice to three times as long as first tarsal segment; first tarsal three to five and one third times as long as second segment. Hind leg shorter than middle leg; femur two and a half times to a little less than one and a half times as long as tibia; tibia three to six times as long as first tarsal segment; first tarsal segment one and a half to a little less than two and a half times as long as second.

Abdomen narrowed posteriorly. First tergite with anterior margin W-shaped, as long as second tergite in most species; second to fifth tergites subequal in lengths; ventrites more reduced. Connexivum with or without connexival spine. Abdominal spiracles placed at middle between anterior and posterior margins of each segment; ventral margin of connexivum represented by two dot like depressions on each segment; ventral median longitudinal elevation or suture obscure or lost.

Male: Seventh segment simply concave and without smaller median emargination on ventral apical margin. Eighth segment with ventral apical margin simply concave or with a median production of various shapes in some species. Ninth segment with suranal plate narrowed apically in distal half; pygphore broadly rounded on apical margin; parameres vestigial or absent. Endosoma in species from the Western Hemisphere highly uniform (aduncus, guerini, recens, profugus, hyalinus, ignotus, recurvus), always well developed and sclerotized apically; definitive dorsal plate on apical margin bifurcate and directed cephalad apically; ventral lobe always slender and relatively long, sclerotized at least basally. In species from the Eastern Hemisphere (fossarum, cereventris, hypoleucus, australis, nitidus) structural patterns are widely different from each other; basal plate fused to dorsal plate in most species. In Limnogonellus (lubricus, visendus, hesione) endosoma is also widely different in shape. In lubricus endosoma is without apical prolongation and ventral plate totally membranous; in visendus endosoma abnormally prolonged and well
sclerotized apically; in *hesione* lateral plate long etc. (Description of the genitalia is based on the species mentioned in the above description).

**Female:** Seventh segment always longer than sixth ventrally; connexivum with spine rather conspicuous in some species, or strongly reduced in some species; ventral apical margin simply concave or produced medially in some species. Eighth segment basally telescoped within tubular seventh segment. First valvula not well sclerotized, with well differentiated inner lobe reaching middle of outer lobe, or inner lobe lacking; outer lobe narrowed apically, with short dark hairs scattered over surface of apical half. Second valvulae membranous, with short dark hairs scattered in apical half, apex acute or broadly rounded, directed mesad beyond apical margin of intervalvular membrane. (Description of the genitalia is based on *aduncus, recurvus, guerini, hyalinus, hesione,* and *visendus*).

**Winged form:** Pronotum with humeri located behind middle, apex subacute in most species. Hemelytra as in *Gerris*. Sc is connected with R + M at the point of separation into R and M.

**Distribution:** World-wide. The subgenus *Limnogonellus* occurs both in the Eastern and Western Hemispheres.

Subgenus *Limnogonellus* Stål, *s. str.*

For type designation and citations see generic bibliography.

**Color pattern:** Pronotum with a median longitudinal yellow stripe either reaching or not reaching posterior margin, and with a pair of elongate yellow spots or short stripes on either side of median longitudinal stripe.

**Structures in wingless forms:** Fourth antennal segment much longer than third segment. Pronotum fully prolonged. Middle tibia a little over twice as long as first tarsal segment in most species; first tarsal segment a little over four times as long as second. Hind leg with tibia over half as long as femur. Abdomen with male eighth abdominal segment prolonged and modified on ventral apical margin in many species.

Subgenus *Limnogonellus* Hungerford and Matsuda


**Type species:** *Gerris parvula* Stål, by original designation.

**Structures in wingless forms:** Fourth antennal segment about as long as or shorter than third in majority of species. Pronotum not
fully prolonged in most species. Middle tibia much over twice as long as first tarsal segment in majority of species. Hind leg with tibia about half or less than half as long as first tarsal segment. Abdomen with male eighth abdominal segment neither prolonged nor modified ventrally.

Besides the above mentioned distinctions between the two subgenera we have already observed indications that the growth patterns at least for the fourth antennal segment in *Limnogonellus* are significantly different from those in *Limnogonus s. str.*

In an African species, *Limnogonus intermedius* Poisson, there is strong indication that the growth patterns for all antennal and leg segments are presumably greatly different from those in any subgenus of *Limnogonus*. In this species the color patterns of the head, pronotum, mesopleuron, and abdomen are also considerably different from those in typical *Limnogonus* species. This species, together with a few other African species, probably represent a distinct genus.

**Modifications of the abdomen**

(Figs. 302-316)

*The male seventh segment:* The degree of specialization of the segment as indicated by the relative lengths of the seventh and sixth can be roughly arranged in the following order: *nitidus, cereiventris leptocerus, darthulus, guerini, australis, ignotus, aduncus, luctuosus, recens, profugus, buxtoni, hyalinus, recurvus, visendus, lotus, lubricus, celeris, parvulus, hesione, lundbladi.* It can well be said that *Limnogonellus*, which is shorter in body length, is more specialized than *Limnogonus s. str.* in this respect. The relative lengths of the seventh to the sixth ranges from 10:9 in *nitidus* to 3:10 in *lundbladi*. A conspicuous connexival spine occurs only in *nitidus* and *hypoleucus*; in all other species the spine has been more or less greatly reduced or is completely lost.

*The male eighth segment:* The specialization of the eighth segment is indicated by the prolongation of the segment itself and the modification of the ventral apical margin. In *nitidus, hypoleucus, ignotus, cereiventris, guerini, leptocerus, buxtoni, darthulus and profugus* the eighth segment is relatively short (exception *profugus*) and the ventral apical margin is simply concave. In *fossarum* and *luctuosus* the eighth segment is more or less prolonged and the ventral apical margin is produced at the middle but not modified into conspicuous process. In *aduncus, hyalinus, recens* and *lundbladi* the eighth segment is prolonged and the ventral apical mar-
gin is provided with a conspicuous process of various shapes at the middle. In *parvulus, celeris, visendus, hesione, lotus*, which belong to the subgenus *Limnogonellus*, the segment is not prolonged and the ventral apical margin is simply concave although the seventh segment in this subgenus is greatly prolonged.

The male ninth segment: The ninth segment has remained relatively simple in this genus. The pygophore is always simply rounded on the apical margin. In some species, in which the seventh and eighth segments are specialized, the pygophore is also somewhat prolonged. In *hyalinus* the pygophore is covered with a mass of long hairs laterally and in *lundbladi* it is large and with a lateral depression on each side. The suranal plate is simple in all species except for *visendus*, in which the middle area is strongly dilated and clothed with a conspicuous tuft of hairs.

The female seventh segment: The relative lengths of the sixth and the seventh ventrites are from 18:21 in *cereiventris leptocerus*, 17:21 in *nitidus*, 14:28 in *recens*, 15:33 in *hyalinus* to 3:10 in *lundbladi*. In the more primitive species such as *nitidus, hypoleucus* and *cereiventris leptocerus* the connexival spine is conspicuous or at least clearly recognizable and the ventral apical margin of the seventh ventrite is simply broadly concave. In *fossarum, buxtoni, australis, recens, recurvus, hyalinus*, etc., the segment is prolonged and the ventral apical margin is more or less bisinuate with a median projection and the connexival spine is rather inconspicuous or nearly absent. The highest degree of prolongation of the seventh ventrite is noted in *lundbladi* as seen from figure 316. In *Limnogonellus* including *visendus, hibricus, parvulus, hesione, celeris* and *lotus*, the relative lengths of the sixth and seventh segments are about as 1:2, the connexival spine is obsolete except for *visendus*, and the apical margin of the ventrite is slightly produced at the middle except for *lotus*, in which it is simply concave.

It is noted from the foregoing discussion that the subgenus *Limnogonellus* appears to exhibit a trend in the eighth (male) and seventh (female) segments somewhat different from *Limnogonus s. str.*

Genus *Tachygerris* Drake

(Figs. 2, 112, 132, 150, 335-358)

Study of the Gerridae of the World


Type species: Tenaggonus adamsoni Drake, by original designation.

Species examined: T. celocis (Drake and Harris), T. adamsoni (Drake), T. opacus (Champion), T. quadrilineatus (Champion), T. spinulatus (Kuitert), T. surinamensis Hungerford and Matsuda.

Color pattern: Predominantly reddish brown. Head with a median pair of black stripes confluent posteriorly, lateral pair of black to fuscous stripes are along inner margin of eyes. Pronotum with a median and lateral pair of black stripes which together tend to be confluent in posterior half of pronotum. Mesopleural region usually with two rather faint fuscous stripes, and white between them. Hemelytra dark fuscous, scattered with short golden hairs. Body beneath paler. Silvery pubescent on mesocoxa and metacoxa. General color pattern somewhat similar to that in Onychotrechus and Amemboa.

Structures in winged forms: Always winged. Head including eyes wider than long. Eye elongate but large, inner margin strongly emarginated posteriorly. Antenna slender but shorter than body; first segment curved, thicker than the rest, apex truncate, shorter than third; second segment always shortest; third segment twice or little less than twice as long as second; fourth segment longest. Antenniferous tubercle acute at tip, rounded on lateral margin. Clypeus with basal margin indistinct. Mandibular and maxillary plates clearly separated. Rostrum long, reaching mesosternum; first segment well developed, about half as long as head; third segment three to four times as long as fourth.

Pronotum long, simply gradually widened in anterior two thirds, then narrowed posteriorly ending in rather narrowly rounded apical margin. Hemelytra with Sc connected with R + M by Sc₂ before the point of separation of R and M from basal R + M. Primary intersegmental suture between mesonotum and metanotum distinct laterally between metathoracic spiracle and wing base. Mesosternum three and a half to four times as long as metasternum; paired longitudinal sutures absent; median longitudinal sulcus distinct anteriorly. Metanotum with median longitudinal sulcus distinct, lateral longitudinal elevation extending anteriorly nearly to hind wing base; metacetabular suture obliterated dorsally. Metasternum about twice as long as definitive first abdominal ventrite; omphalium located on median longitudinal elevation at apical third, posterior margin feebly concave. Front leg long. Femur longer
than tibia, more curved and slightly dorsoventrally flattened basally; tarsus with first segment subequal to second in length, claws small, arising preapically. Middle leg with femur one and one third as long as tibia in most species; tibia about one and a half times as long as tarsus; first tarsal segment about six times as long as second, claws arising from near apex. Hind leg shorter than middle leg; femur over twice as long as tibia in most species; tibia about one and a half times as long as tarsus; first tarsal segment about six times as long as second, claws slender, arising from near apex.

Abdomen long. First tergite with flattened W-shaped anterior margin. Pregenital ventrites subequal in length; seventh segment with connexival spines inconspicuous or absent. Abdominal spiracles placed at middle of segments. Ventral longitudinal margin of connexivum clearly recognizable, especially in females. Ventral median longitudinal elevation present in some species.

Male: Seventh segment with ventral apical margin simply concave, without distinct connexival spines. Eighth segment with ventral apical margin shallowly concave. Ninth segment with suranal plate widen at middle; pygophore ventrally well exposed, simply rounded on apical margin; parameres vestigial. Endosoma with definitive dorsal plate (dorsal plate + basal plate) reaching basal half of dorsal margin of endosoma, extending posteriorly along basal margin; membranous ventral plate reaching apex of endosoma; apical plate apparently lost; lateral plates slender and simple. (Description of male genitalia is based on spinulatus, celocis, quadrilineatus.)

Female: Seventh segment ventrally well developed, variously modified in various species, connexival spines inconspicuous. Eighth segment ventrally completely concealed by seventh ventrite; first valvula highly reduced, inner lobe short and acutely pointed, lateral lobe short and connected by ramus with outer margin of process of ninth tergite (in figure 352 the ramus appears to be attached on inner margin, but this is actually outer margin. The lobe is twisted around laterally in the figure). Second valvula with lateral lobe far extending beyond apical margin of intervalvular membrane which is broadly rounded. (Description of female genitalia is based on opacus.)

Distribution: Central and South America (Bolivia, Brazil, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Surinam).
The genus *Tachygerris* is peculiar in the following characteristics:

1. The wingless form has never been found.
2. The omphalium is located on the longitudinal elevation.
3. The vein Sc is connected with R + M at a point basal to the point of separation of R and M from R+M.
4. The second antennal segment is shortest.
5. The seventh abdominal segment of the female has the ventral apical margin more or less greatly modified in various shapes in different species.
6. The female genitalia have the first and second valvu'ae greatly reduced.
7. The apical segment of the endosoma has the dorsal plate reaching only to the middle of dorsal margin of endosoma.
8. The growth slopes for the first three antennal segments are probably very steep.
9. The growth slopes for the leg segments are also probably steeper than in other genera of the tribe.

Modifications of the abdomen in *Tachygerris*

**The male:** The degree of specialization of the seventh segment, as indicated by its length in relation to the sixth, indicates an order, from more primitive to specialized as follows: *quadrilineatus, spinilatus, celocis, adamsoni, opacus*. There is no conspicuous modification on the ventral surface of the eighth segment in any species of the genus. In *quadrilineatus* and *duilineatus* the eighth segment is quite short, thus presumably most primitive; in the other species the segment is considerably more prolonged.

**The female:** The connexival spine is more developed in *duilineatus* than in the other species. The ventral apical margin is variously modified in the species and is of taxonomic importance at the species level (figs. 346-351).

Genus *Tenagogonus* Stål

(Figs. 4, 6, 16, 127, 130, 149, 399-415)

As has been revealed in the study by Hungerford and Matsuda (1858), *Limnometra* and *Tenagogonus*, though treated as distinct genera, actually constitute a large natural group. To express this relationship and yet maintain *Tenagogonus* and *Limnometra* as entities, Doctor Hungerford and I now think that these groups can be best regarded as subgenera. *Tenagometra* Poisson also belongs to this genus.
Type species: *Tenagogonus albovittatus* Stål, first included species.


*Color pattern:* Reddish brown to yellowish brown in general coloration. Head always with a pair of lateral and a pair of median black longitudinal stripes which are confluent anteriorly, median pair often represented by a single median black longitudinal stripe. Pronotum always with black marginal stripe and a median longitudinal stripe which usually extends entire longitudinal axis of pronotum, anterior lobe occasionally provided with a pair of black markings on either side of middle. Mesothorax with two black longitudinal stripes which may or may not be confluent posteriorly. Undersurface paler.

*Structures in wingless forms:* Head including eyes wider than long. Eye strongly emarginated in posterior half of inner margin. Antenna slender, often as long as or longer than length of body; proportional length of second segment to first greater in male than in female; first segment longer than or at least as long as second; second segment more often longer than third segment than vice versa; fourth segment longest except for *ciliatus*, *cursitans* and *Tenagometra*. Antenniferous tubercles short. Clypeus with basal margin distinct in most species, widened posteriorly. Mandibular and maxillary plates at least distinguishable from each other in most species. Rostrum reaching anterior third of mesosternum in most species; first segment relatively long, about half as long as head; third segment three to five times as long as last segment.

Pronotum fully prolonged to cover mesonotum except for *mada-
gascariensis and Tenagometra, slightly dilated in apical fourth, occasionally apical region modified into a narrow process (fijiensis). Intersegmental suture between mesonotum and metanotum indistinct laterally. Mesosternum three to six and a half times as long as metasternum; median longitudinal sulcus present at least in anterior half; paired longitudinal sutures retained in more primitive species of Limnometra (femoratus, etc.). Mesonotum with median longitudinal sulcus distinct throughout; lateral longitudinal elevation distinct. Metathoracic spiracle located at some distance from lateral margin of pronotum. Metasternum with omphalium represented by small tubercle placed close to apical margin of metasternum (position of omphalium somewhat varies in various species); omphalial groove absent. Front leg relatively long, longer than length of body in some specialized species of Tenagogonus s. str.; femur subequal in thickness throughout; tibia slightly thickened at apex, distinctively constricted near apex, with a shallow longitudinal depression on inner margin near apex, without conspicuous process at inner apical angle; proportional length of first tarsal segment to second segment varies in various species, but never less than half as long as second; claws arising from near apex, with a short membranous arolium. Middle leg with femur a little longer than tibia in some species, less than one and one fourth as long as tibia in most species; tibia twice to four times as long as first tarsal segment in most species, seldom over four times as long as first tarsal segment (nigripennis); first tarsal segment three and one fourth to seven times as long as second tarsal segment; second segment with claws arising from near apex; middle femur and tibia ventrally ciliated in some species (ciliatus, femoratus). Hind leg shorter than middle leg; femur as long as to a little over twice as long as tibia; tibia always about five times as long as first tarsal segment; first tarsal segment a little over three times to one and two seventh times as long as second segment; second segment with small claws arising from near apex.

Abdomen varies greatly in length. In some more primitive species of Limnometra pregenital segments are subequal in length to each other; in some more specialized species of Tenagogonus pregenital segments are highly reduced. First tergite with usual flattened W-shaped anterior margin. Abdominal spiracles placed closer to anterior margin than to posterior margin in majority of species of Limnometra and Tenagometra, or placed at middle of each segment in all species of Tenagogonus; ventral connexival suture not very distinct, represented by a dot like depression or
obscure in specialized species; ventral median longitudinal carina distinct in most species of *Limnometra*.

**Male:** Seventh segment with connexival spine in more primitive species, absent in more specialized species; ventral apical margin simply concave, or with paired processes of various shapes, ventral surface also modified in some species. Eighth segment with ventral apical margin simply concave in most species, modified in some species (*madagascariensis, robustus*). Ninth segment with suranal plate simple in all species; pygophore simply concave, or with paired processes of various shapes, ventral surface also modified in some species. Eighth segment with ventral apical margin simply concave in most species, modified in some species (*madagascariensis, robu**tus*). Ninth segment with anal plate simple in all species; pygophore simply narrowed apically, surface modified and lateral margin with a conspicuous mass of black hairs in *madagascariensis*; parameres highly reduced. Endosoma without apical prolongation in more specialized species; dorsal plate bifurcate apically, basally articulated with basal plate; ventral lobes always bilobed and more sclerotized in some species, supported basally by basal plate; lateral plates simple and long; proximal segment of endosoma strongly sclerotized (*albovittatus*) or with paired ventral processes and smaller lateral processes arising from lateral apical margin (*madagascariensis*). (Description of the genitalia is based on *ciliatus, cursitans, femorata, madagascariensis, albovittatus*.)

**Female:** Seventh segment with or without conspicuous connexival spine; ventral apical margin concave or prolonged medially covering eighth segment above in some species. Eighth segment ventrally exposed in some species; first valvula with inner lobe loosely attached to outer lobe; outer lobe simply narrowed, or shorter and rounded apically. Second valvula apically directed mesad from each side, far extending beyond apical margin of inter-valvular membrane which is straight (in *albovittatus* inner apical margin subhorizontally continuous); ramus short in more specialized species. (Description of the genitalia is based on *ciliatus, femoratus, pravipes bergrothi, madagascariensis and albovittatus*.)

**Winged forms:** Sc connected with R + M at the point of separation into R and M. Pronotum with humeri located at apical third or a little behind middle.

**Distribution:** Oriental region (Borneo, Burma, Ceylon, India, Java, Malaya, Philippines, Sumatra, Thailand), Australian region (Australia, Fiji, Moluccas, New Guinea, Palau Island, Solomon Islands), and Ethiopian region (Belgian Congo, Gabon, Madagascar, Natal, Rhodesia, South Africa, Tanganyika, West Africa, Zululand). Only one species included in the subgenus *Limnometra* is known from Africa.
Subgenus Limnometra Mayr


Type species: Limnometra femorata Mayr, by original designation.

Body relatively long. Length of second relative to first antennal segment greater in male than in female. Pronotum fully prolonged in wingless forms. Abdomen long. Connexival spine present. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment in most species. Male seventh and eighth segments not greatly modified.

Subgenus Tenagogonus Stål s. str.


Type species: Tenagogonus albovittatus Stål, first included species.

Body relatively short. Length of second relative to first antennal segment greater in male than in female. Pronotum fully prolonged in wingless forms of most species. Abdomen relatively short. Connexival spine absent in most species. Abdominal spiracles placed at middle of abdominal segments. Male seventh and eighth abdominal segments more or less greatly modified.

Modification of the abdomen
(Figs. 388-406)

The male seventh segment: In T. (L.) ciliatus, T. (L.) cursitans, T. (L.) femoratus, T. (L.) nigripennis, T. (L.) pulchrus, T. (L.) annulicornis, T. (L.) kallisto, T. (L.) lipovskyi, T. (L.) fluviorum, T. (L.) borneensis, T. (L.) rossi the seventh segment is shorter than or nearly equal to the sixth and the connexival spine is more or less
conspicuous, surpassing the tip of the abdomen in many species; 
*T. (L.) lipovskyi* (fig. 398) is the only exception, and in this species 
the connexival spine is almost completely lost. In these species the 
second to sixth ventrites are long, more or less subequal in length, 
and the mesosternum is never more than four times as long as 
metasternum.

In *T. (L.) anadyomene* (fig. 389), *T. (L.) palauanus*, *T. (L.)
octopunctatus* (fig. 397), *T. (T.) kuiterti* (fig. 399) the seventh 
ventrite is longer than the sixth, and the connexival spine has be-
come less conspicuous, never surpassing the tip of the abdomen; 
in *T. (T.) kuiterti* the connexival spine is completely lost. In these 
species the mesosternum is about four times as long as the meta-
sternum or even much over four times as long as metasternum in *T. (T.)
kuiterti*; the first to sixth segments are shorter than in the preceding 
groups of species and the segments have become increasingly 
unequal in length to each other. The abdominal spiracles have shifted 
their positions to the middle of each segment in *T. (L.) anadyomene*
and *T. (T.) kuiterti*.

Accompanied by further reduction of the metasternum and the 
first to sixth abdominal segments, *T. (T.) kampaspe* (fig. 395), 
*T. (T.) robustus* (fig. 402), *T. (T.) divergens* (fig. 392), *T. (T.)
fiijensis*, *T. (T.) pravipes bergrothi*, *T. (T.) madagascariensis* (fig. 
393, 401), *T. (T.) albovittatus* (fig. 400), *T. (T.) zambezinus* 
(fig. 391) exhibit paired processes on the ventral apical margin 
of the seventh segment except for *T. (T.) robustus*, *T. (T.) pravipes 
bergrothi*, and *T. (T.) fiijensis*. The processes arise on different parts 
of the ventrolateral margin in different species, from near the 
posterolateral angle of the seventh connexival segment almost to 
the ventral longitudinal axis of the abdomen. It is interesting to 
observe the sequence of reduction of the connexival spine and the 
concomittal development of the processes on the ventrolateral mar-
gin (figs. 391-395). In the last group of species the abdominal 
spiracles of the second to sixth segments are in the middle of each 
segment.

The male eighth abdominal segment: The modification of 
the eighth segment is also correlated with reduction of the first to sixth 
abdominal segments. Among the species with more primitive pre-
genital segments (first to sixth) the eighth ventrite has remained 
unmodified in most species. In *T. (L.) ciliatus* and *T. (L.) octo-
punctatus* (fig. 397), however, a small projection has arisen on the 
posterior margin laterally, and in *T. (L.) lipovskyi* (fig. 398) paired
processes have arisen on the basal lateral area of the eighth ventrite. Among the species with more specialized abdomens a triangular notch occurs at the middle of apical margin of the eighth ventrite in *robustus* (fig. 402) and a pair of slender processes occurs on the apical margin in *T. (T.) madagascariensis* (fig. 401).

The male ninth segment: The suranal plate has remained simple except in *T. (T.) albovittatus*, in which a pair of slender, black processes arises from the middle of lower margin. The pygophore is modified in a highly specialized species, *T. (T.) madagascariensis* (fig. 401), in which it is strongly widened medially and provided with a conspicuous tuft of thick, black hairs on the upper margin at the middle. The endosoma has the proximal segment simply membranous in primitive species, but in *T. madagascariensis* the proximal segment is provided with ventral apical processes and with a lateral subtriangular process; in *T. (T.) albovittatus* the proximal segment is strongly sclerotized.

The female abdomen: The degree of specialization of the female in this group of gerrids is also indicated by loss of uniformity in the lengths of abdominal segments, accompanied by prolongation, especially of the sixth and seventh segments. In most species with more primitive abdomens, such as *T. (L.) ciliatus* (fig. 403), *T. (L.) femoratus*, *T. (L.) palauanus*, *T. (L.) borneensis*, *T. (L.) nigripennis*, *T. (L.) pulchrus*, *T. (L.) cursitans*, *T. (L.) annulicornis*, and *T. (L.) callisto*, the seventh segment is shorter than the sixth, its apical margin is simply concave, and the connexival spine is always conspicuous. In *T. (L.) octopunctatus* (fig. 404), *T. (L.) rossi*, *T. (L.) lipovskyi*, and *T. (L.) anadyomene* the seventh segment is considerably longer than the sixth except for *T. (L.) lipovskyi*; the connexival spine is less conspicuous and never surpasses the tip of the abdomen. In the rest of the species the seventh segment is much longer than the sixth, and the connexival spine has become inconspicuous or is totally lost as noted in *T. (T.) kampaspe* and *T. (T.) fijiensis* (fig. 406), in which the apical margin of the seventh ventrite is produced medially. The highest degree of prolongation of the seventh segment is attained also in *T. (T.) fijiensis*, in which the seventh segment is over three times as long as the sixth ventrally. In one undescribed species of *Tenagogonus s. str.* from the Fiji Islands the posterolateral angle of the seventh segment is produced as a spinous process, a condition that occurs also in a species of *Eurygerris*. 
Modifications of the other structures.

The size of body: As will be noted from table 8, the length of the body ranges from 19.5 mm. in *T. (L.) inermis* to 5.0 mm. in *T. (T.) pravipes bergrothi*. It has been observed that the reduction of the metasternum and pregenital segments are to a large extent responsible for the reduction in body size. In the larger species listed in the upper part of the table, the abdomen is more primitive and the metasternum is less reduced; in the smaller species listed in the lower part of the table, both the metasternum and the pregenital segments are more or less greatly reduced. It is interesting to note that there is a striking tendency among the larger species for the male to be larger than female and that this relation is reversed among the smaller species.

**Table 8.—Length of body in species of *Tenagogonus.***

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
<th>Rostrum 3rd:4th</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. (L.) femoratus</em></td>
<td>19 mm. (wgd.)</td>
<td>17.6 mm. (wgd.)</td>
<td>5.0 :1</td>
</tr>
<tr>
<td><em>T. (L.) cursitans</em></td>
<td>19 mm. (wgd.)</td>
<td>16.4 mm. (wgd.)</td>
<td>5.0 :1</td>
</tr>
<tr>
<td><em>T. (L.) inermis</em></td>
<td>19.5 mm. (wgd.)</td>
<td>13.6 mm. (wgd.)</td>
<td>4.75:1</td>
</tr>
<tr>
<td><em>T. (L.) ciliatus</em></td>
<td>13–19.5 mm. (wgd.)</td>
<td>14.2 mm. (largest wgd.)</td>
<td>4.11:1</td>
</tr>
<tr>
<td><em>T. (L.) lipovskyi</em></td>
<td>13.4 mm. (wgd.)</td>
<td>10.9 mm. (wgd.)</td>
<td>3.91:1</td>
</tr>
<tr>
<td><em>T. (L.) insularis</em></td>
<td>11.8 mm. (wgd.)</td>
<td>9.8 mm.</td>
<td></td>
</tr>
<tr>
<td><em>T. (L.) palawanus</em></td>
<td>9.0 mm. (wl.)</td>
<td>11.0 mm. (wl.)</td>
<td>3.85:1</td>
</tr>
<tr>
<td><em>T. (L.) borneensis</em></td>
<td>10.0 mm. (wgd.)</td>
<td>9.8 mm. (wgd.)</td>
<td>4.37:1</td>
</tr>
<tr>
<td><em>T. (L.) anadyomene</em></td>
<td>9.8 mm. (wl.)</td>
<td>12.0 mm. (wl.)</td>
<td>4.11:1</td>
</tr>
<tr>
<td><em>T. (L.) octopunctatus</em></td>
<td>9.2 mm. (wl.)</td>
<td>11.3 mm. (wl.)</td>
<td>4.11:1</td>
</tr>
<tr>
<td><em>T. (L.) rossi</em></td>
<td>6.9 mm. (wgd.)</td>
<td>7.6 mm. (wgd.)</td>
<td>3.91:1</td>
</tr>
<tr>
<td><em>T. (L.) minutus</em></td>
<td>8.6 mm. (wgd.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. (T.) kuiteri</em></td>
<td>8.7 mm. (wl.)</td>
<td>8.0 mm. (wl.)</td>
<td>3.70:1</td>
</tr>
<tr>
<td><em>T. (T.) zambezinus</em></td>
<td>8.5 mm. (wl.)</td>
<td>9.9 mm. (wl.)</td>
<td></td>
</tr>
<tr>
<td><em>T. (T.) divergens</em></td>
<td>7.6 mm. (wl.)</td>
<td></td>
<td>4.27:1</td>
</tr>
<tr>
<td><em>T. (T.) robustus</em></td>
<td>7.6 mm. (wl.)</td>
<td>7.4 mm. (wl.)</td>
<td>3.88:1</td>
</tr>
<tr>
<td><em>T. (T.) madagascariensis</em></td>
<td>7.3 mm. (wl.)</td>
<td>8.3–8.9 mm. (wl.)</td>
<td>4.00:1</td>
</tr>
<tr>
<td><em>T. (T.) alborivittatus</em></td>
<td>6.7–7.4 mm. (wl.)</td>
<td>7.3–7.6 mm. (wl.)</td>
<td>3.50:1</td>
</tr>
<tr>
<td><em>T. (T.) kampaspe</em></td>
<td>5.3 mm. (wl.)</td>
<td>6.3 mm. (wl.)</td>
<td>3.17:1</td>
</tr>
<tr>
<td><em>T. (T.) pravipes bergrothi</em></td>
<td>5.0 mm. (wl.)</td>
<td>6.6 mm. (wl.)</td>
<td>3.84:1</td>
</tr>
<tr>
<td><em>T. (T.) fijiensis</em></td>
<td>5.3 mm. (wl.)</td>
<td>6.7 mm. (wl.)</td>
<td>3.17:1</td>
</tr>
</tbody>
</table>

wgd.=winged, wl.=wingless.
Rostrum: As noted from table 8, the length of the third segment in relation to the fourth segment has apparently decreased with reduction in size of the body accompanied by specialization of structures.

Subgenus Tenagometra Poisson
(Figures 407-415.)


Type species: Tenagogonus lanuginus Poisson, monobasic.

Structures in wingless forms: Body relatively small. Male much smaller than female. Antenna without conspicuous sexual difference in length of first segment in relation to second. Pronotum not at all or feebly prolonged. Mesonotum wholly exposed, posterior margin broadly rounded, lateral longitudinal margin defining mesonotum from mesopleuron distinct. Front leg with femur strongly arched and with a dark stripe on inner margin in male; tibia curved in male; tarsus with first segment a little shorter than second. Abdomen relatively short, without connexival spine in both sexes. Abdominal spiracles on second to seventh placed closer to anterior margin than to posterior margin of each segment.

Male: Seventh segment with ventral apical margin broadly concave. Eighth segment with ventral apical margin feebly sinuate, broadly rounded on dorsal apical margin. Ninth segment with suranal plate simply narrowed near apex; pygophore rounded on apical margin; parameres vestigial. Endosoma with definitive dorsal plate thick, bifurcate apically, strongly thickened at base; ventral lobe short and lobate; lateral plates long and simple; basal segment of endosoma with a pair of two black processes near ventral apical margin on each side. (Description of the genitalia is based on an unidentified species of this subgenus.)

Female: Eighth segment ventrally largely covered by seventh ventrite, which is longer than the preceding segment. (The female genitalia were not examined.)

Distribution: Africa (Madagascar, East Africa).

The subgenus Tenagometra is distinguishable from the Limnometra-Tenagogonus s. str. complex by the following features:

(1) The antennae are short and without sexual differences in the proportional lengths of the first and second segments.
(2) The front leg is sexually dimorphic.
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(3) The pronotum is not or feebly prolonged in the wingless forms.

(4) The mandibular and maxillary plates are almost completely fused.

(5) The lateral longitudinal suture between the mesonotum and mesopleuron is recognizable.

That this subgenus has probably arisen from Tenagogonus s. str. or a similar form is indicated by the fact that the lengths of the middle and hind leg segments resemble those of typical Tenagogonus s. str. species. The secondary reduction of the pronotum in wingless forms occurs also in Tenagogonus (Tenagogonus) madagascariensis independently of this subgenus, suggesting a similar evolutionary potentiality in this respect in the two subgenera.

It was found that in the Limnometra-Tenagogonus s. str. complex the males are larger than the females in the larger and more primitive species, and with reduction in body size and specialization of structures this relation has apparently been reversed so that in a great majority of species of Tenagogonus s. str. the female is larger than the male. In Tenagometra, the male is much smaller than the female as in Tenagogonus s. str.

While the division into Tenagogonus s. str. and Limnometra is quite artificial and purely for the taxonomic convenience, Tenagometra is a distinct natural group.

Genus Tenagometrella Poisson
(Figures 1, 416-420)


Type species: Tenagogonus grandiusculus Poisson, by present designation.

Species examined: T. grandiusculus (Poisson), T. longicornis (Poisson).

Color pattern: Similar to that of Tenagogonus, but different in having a pale yellow median longitudinal stripe instead of black stripe on pronotum, and in the presence of two white oblong spots on mesopleural region.

Structures in wingless forms: Antennae and legs very long in male. Head including eyes a little wider than long. Eye with inner margin strongly emarginated. Antenna in male: very long; first segment longest, almost as long as total length of body; shorter than
second and third segments together; second segment a little shorter than first; third segment a little shorter than second, ciliate on margins; fourth segment shortest, almost one third as long as third segment.* Antenna in female: a little longer than length of body; first segment longest, third segment longer than fourth segment but shorter than second. Antenniferous tubercles slightly dilated in front of eyes. Clypeus with basal margin distinct. Mandibular and maxillary plates distinguishable from each other. Rostrum slender and long, reaching middle of mesosternum; first segment about half as long as head; third segment over five times as long as last segment.

Promotum prolonged to near posterior margin of mesonotum, relatively slender, broadly rounded on apical margin. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesosternum over three and a half times as long as metasternum; paired longitudinal sutures absent; median longitudinal sulcus distinct in anterior half of mesosternum. Metathoracic spiracle located at some distance from pronotum. Metanotum with lateral longitudinal elevation conspicuous, reaching dorsal end of metacetabular suture; median longitudinal sulcus distinct. Metasternum much longer than second ventral abdominal segment; omphalium highly reduced, located at apical third of metasternum; omphalial groove absent. Front leg slender; a little longer than body in male; femur and tibia slender, the latter slightly swollen apically, with a bare shallow depression near apex on inner margin; first and second tarsal segments subequal in length to each other, claws arising from apical fourth of second segment. Middle leg in male with femur longer than total length of body, about as long as tibia; tibia much over four times as long as first tarsal segment; first tarsal segment four times as long as second, claws slender, arising from near apex; middle leg in female much shorter than in male, but proportional lengths of leg segments are much like those in male. Hind leg with femur longer than middle femur in both sexes, a little over twice as long as tibia in male, less than twice as long as tibia in female; tibia about six times as long as first tarsal segment in female, about eight times as long as first tarsal segment in male; first tarsal segment a little over twice as long as second in both sexes.

Abdomen shorter than thorax, gradually narrowed posteriorly. First tergite with usual flattened W-shaped anterior margin; second to sixth segments subequal in length both dorsally and ventrally.

* This may possibly be due to a partial loss of the fourth segment from the specimen examined.
in both sexes, with a slender connexival spine in both sexes. Third to fifth abdominal spiracles placed at middle of each abdominal segment; ventral longitudinal margin of connexivum indistinct, represented by faint depressions; ventral median longitudinal carina absent.

**Male:** Seventh segment simply broadly concave on both dorsal and ventral apical margins. Eighth segment ventrally slightly exposed, broadly concave on ventral apical margin. Ninth segment with suranal plate simple; pygophore simply rounded on apical margin; parameres absent. Endosoma with definitive dorsal plate narrow, reaching apical margin, forked into two thick branches apically (the part of apical plate); ventral plate membranous, bilobed apically; lateral plates slender.

**Female:** Seventh segment longer than sixth ventrally, ventral apical margin feebly bisinuate. Eighth segment slightly exposed ventrally (genitalia were not examined).

**Winged forms:** Pronotum with humeri located far behind middle. Hemelytra with Sc connected with R + M at the point of separation into R and M.

**Distribution:** Africa (Belgian Congo, Liberia, Cameroons).

The genus *Tenagometrella* is distinguishable from the *Limnometra-Tenagogonus* complex by the following characteristics:

1. The conspicuous sexual difference in lengths of the antennae and legs.
2. A higher degree of reduction and different location of the *omphalium*.
3. The yellow instead of black median longitudinal pronotal stripe.

The presence of sexual differences in the proportional lengths of the first and second antennal segments, the proportional lengths of leg and rostral segments, and the degree of specialization of the abdomen are much like those in the more specialized species of *Limnometra* or the more primitive species of *Tenagogonus s. str.* As already noted, there is no significant sexual difference in the proportional lengths of most antennal and leg segments although their absolute lengths are quite different. This fact suggests that the sexual difference lies primarily in the initial growth index b for those segments in allometry equation term. This genus has probably arisen from the *Limnometra-Tenagogonus* complex with acquisition of the above mentioned peculiar features.

Although Poisson (1957) included three species within the sub-
genus *Tenagometrella*, obviously *T. zambezinus* belongs to *Tenagogonus* (Hungerford and Matsuda, 1958). The specimens identified by Poisson as *T.grandiusculus* and *T. longicornis* at the University of Kansas very likely represent the female and male of the same species; they are provisionally treated as the same species in this study.

**Tribe Cylindrostethini Matsuda**

*Color pattern:* Black in ground color in majority of species, with longitudinal silvery stripe laterally on the thorax in most species.

*Structures in wingless forms:* Head between eyes widened posteriorly. Clypeal region well produced anteriorly, with basal margin lost, apical margin straight, connected with labrum by membranous region, thus apical margin appears to be separated from above labrum. Antenna much shorter than body, first segment about as long as or a little shorter than three following segments together; second segment longer than or subequal to third segment, third segment with a distinct basal peduncle; fourth segment curved beyond middle. Antenniferous tubercles divergent anteriorly. Eye with inner margin indented except in *Platygerris*. Mandibular and maxillary plates either indistinct from each other or completely fused. Rostrum short and thick, never extends beyond prosternum, third segment one and half to two and a half times as long as last segment.

Pronotum not prolonged, rather strongly widened posteriorly. Mesosternum without median longitudinal sulcus, anterior margin more or less produced at middle; paired longitudinal sutures recognizable anteriorly in some species of *Cylindrostethus* and *Potamobates*. Interegmental suture between mesonotum and metanotum faint, forming a small subtriangular space anterior to metacetabular suture. Metanotum with median longitudinal sulcus distinct; lateral longitudinal suture nearly reaching metacetabular suture; metacetabular suture joined with dorsal posterior margin of mesonotum. Metasternum with distinct omphalium and omphalial groove leading onto metacetabular region except for *Platygerris*, in which the groove is absent. Front leg with femur thick basally; tibia arched in apical third, inner apical angle with inconspicuous process; tarsus with first segment greatly reduced. Middle leg with femur considerably longer than tibia; tarsus usually flattened and curved, first segment two and a half to seven times as long as second segment. Hind leg always shorter than middle leg; femur one and one fifth to three times as long as tibia; tarsus with first segment about as long as
to nearly three times as long as second segment. *Claws of middle and hind legs present only in Cylindrostethus from the Eastern Hemisphere.*

Abdomen varies greatly in length. Anterior margin of first tergite flattened W-shaped. Well-developed connexival spines present only in *Cylindrostethus*; ventral margin (suture) of connexivum obscure or absent.

**Male:** Seventh segment with ventral apical margin emarginated at middle on concave apical margin; ventral surface either modified or unmodified. Eighth segment not greatly prolonged, or greatly prolonged and its ventral apical margin asymmetrical in some species. Ninth segment with suranal plate more or less greatly, asymmetrically modified on lateral margins; pygophore rotated in

<table>
<thead>
<tr>
<th>Table 9.—Table of significant generic characters in Cylindrostethini.</th>
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<tbody>
<tr>
<td><img src="image" alt="Table 9 Image" /></td>
</tr>
</tbody>
</table>

*In *Potamobates thomasi* Hungerford the spiracles are placed closer to the anterior margin than to the posterior margin.*

For the explanations of symbols see introduction and table 5.
some species, simply rounded on apical margin; parameres inconspicuous or greatly reduced. Endosoma elongate, with excessive apical prolongation in *Platygerris*; dorsal plate extending along dorsal margin of endosoma, bifurcate apically, ventral plate long, number of lateral plates inconstant, often absent.

**Female:** Seventh segment with ventral apical margin bisinuate, or excessively developed. First valvula well sclerotized, divided into basal thicker and apical narrow regions by median membranous area; inner lobe membranous or thinly sclerotized, long and narrow apically. Second valvula with lateral margin strongly sclerotized, apical half narrow, also strongly sclerotized, convergent apically beyond apical margin of intervalvular membrane, where it is also heavily sclerotized and broadly rounded or nearly straight. Vulva inconspicuous, membranous and narrow.

**Winged forms:** Pronotum long, humeri located at apical one third of pronotum. Hemelytra with Sc connected either with R + M at the point of separation into R and M, or with R + M basal to the point of separation of R and M.

**Distribution:** Central and South America, Oriental and Ethiopian regions.

**Relationships of genera**

As noted from the table of significant characters and from the discussion on evolution of the abdomen, antennae, and the rostrum, many characters exhibit linear evolutionary trends. Although the species of *Cylindrostethus* from the Western Hemisphere have taken a slightly different course of evolution in certain minor ways from the members of the same genus from the Eastern Hemisphere, *Potamobates* is apparently nothing but a more specialized group of *Cylindrostethus* from the Western Hemisphere. *P. thomasi* is apparently the border line species between the two genera, as is indicated by the location of the abdominal spiracles and the relatively long body, etc. As already seen, the leg and antennal segments in this species also quite deviate from the allomorphic lines for these segment of *Potamobates*. The genus *Platygerris* is more distinct with a greater and discontinuous reduction of the hind tibia in relation to the total length of the body, which is realized from quite different growth mechanisms for the leg segments as we have already seen. A strong dorsoventral flattening accompanied by broadening of the body emphasizes the distinctness of this genus.
from the other two. The relationships of the genera can be diagrammed as follows (diagram 4):

![Diagram 4](attachment:diagram.jpg)

**Diagram 4.**—Diagram showing the relationships of genera of the *Cylindrostethini*.

Evolutionary tendencies and characteristics peculiar to *Cylindrostethini*

1. Because of the relatively short rostrum, which never extends beyond the prosternum, the median longitudinal groove for the reception of the rostrum has never arisen on the metasternum, and the anterior margin of the mesosternum has even become produced anteriorly at the middle in *Cylindrostethus*.

2. The omphalium and the lateral groove of the omphalium leading onto the metacetabula persist in *Cylindrostethus* and *Potamobates*, although the groove is lost in the most specialized genus, *Platygerris*.

3. The ventral apical margin of the seventh segment of the female is excessively developed in the more specialized genera.

4. An asymmetrical modification of the suranal plate of the male has occurred in varying degrees in most species of all genera.

5. The ventral apical margin of the eighth segment of the male has become asymmetricaly modified in the more specialized genera.

6. The claws have become lost in all species occurring in the Western Hemisphere.

In addition to the above mentioned peculiar evolutionary tendencies, the following structural characteristics common to all genera serve to distinguish this tribe from the other three tribes:

1. The pronotum in wingless forms is never prolonged.

2. The first tarsal segment of the front leg is greatly reduced,
due to a smaller growth ratio for the first segment than for the second segment.

(3) The fourth antennal segment is short and curved beyond the middle.

(4) The apical margin of the clypeus is loosely connected with the base of the labrum by a membranous region.

(5) The hemelytra arise from near apical third of the pronotum; thus the humeri are located considerably more caudad than in the other tribes.

(6) The intersegmental suture between the mesonotum and metanotum in wingless forms is obscure but traceable laterally, forming a subtriangular space anterior to the metacetabular suture, which is well impressed and fused with the dorsal posterior margin of the mesonotum.

Modifications of the abdomen in Cylindrostethini

(Figs. 433-446, 447-451, 470-480, 483, 495-500)

Since the species of *Cylindrostethus* from the Western Hemisphere are different from those of the same genus from the Eastern Hemisphere in certain respects, the evolution of the abdomen is discussed separately for each group. In the three genera of Cylindrostethini occurring in the Western Hemisphere the modification of the genital segments is rather beautifully traceable.

(A) Modifications of the abdomen of Cylindrostethini from the Western Hemisphere.

**The male seventh segment:** In *Cylindrostethus* the seventh segment is at least as long as, or usually longer than the preceding segment ventrally on the median longitudinal axis. In *Potamobates* the length of the seventh segment in relation to the sixth is smallest in *thomasi* and the relative length becomes 2.5 to 3 times as long as the preceding segment in six out of nine species; the relative length of the seventh to the sixth is as 2.5 to 3.5:1 in three species of *Platygerris*. The connexival spine is well developed in *Cylindrostethus* although it is rather inconspicuous in some species; in *Potamobates* and *Platygerris* it has been greatly reduced or lost. The ventral apical margin is simple and concave. An emargination at the middle of the ventral apical margin is small in some species of *Cylindrostethus*; in *Potamobates* the median emargination is least conspicuous in *thomasi*; it becomes progressively more conspicuous in other species of the genus with more specialized ab-
dominal structures (figs. 475-480); the median emargination is conspicuous in all species of Platygerris.

The male eighth abdominal segment: In Cylindrostethus the ventral apical margin is simple and concave or feebly produced medially, and the segment is not prolonged. The segment in Potamobates has become prolonged, its ventral basal region is depressed and the ventral apical margin is modified; first a small rather inconspicuous process occurs on the left side of the ventral apical margin (unidentata, horváthi, figs. 476, 478), then with further prolongation of the eighth segment the process arises near the middle and the right posterior angle became greatly modified (williamsi, variabilis, figs. 479, 480). Simultaneously with the modification on the apical margin, the basal depression on the ventral surface became more well marked. In asymmetricus (fig. 483) and depressus of platygerris the segment is not greatly prolonged and has a conspicuous process on the right side of the ventral apical margin, as in some species of Potamobates; in caeruleus of the same genus (Platygerris) the eighth segment is enormously prolonged (fig. 496), although the ventral apical margin is relatively simple.

The male ninth segment: The suranal plate in Cylindrostethus is symmetrical; the process on each lateral margin of the suranal plate is more and more directed cephalad in the more specialized species of the genus (figs. 436-440). In Potamobates the ninth tergite has become rotated for about 45 degrees and the processes are asymmetrical and more conspicuous on the left side, although they are inconspicuous in thomasi and unidentatus (figs. 475-480); with further development of the process on the left side of the ninth tergite, its apex comes to contact the asymetrically modified apical margin of the eighth segment in some species of Potamobates (figs. 479, 480). The ninth segment is not rotated in Cylindrostethus, the rotation becomes apparent in Potamobates unidentatus and the degree of rotation becomes greater in other species of Potamobates except for thomasi, in which the segment is only feebly rotated; in Platygerris the ninth segment is rotated in all species.

The female seventh segment: The ventral apical margin of the seventh segment in the female of Cylindrostethus is simple, feebly produced at the middle; the connexival spine is also retained in all species. In Potamobates the connexival spine is retained, but the ventral apical margin is highly modified and the eighth segment is
completely hidden by the excessive development of the ventral apical margin except for horváthi and thomasi. In Platygerris the connexival spine becomes even less conspicuous, asymmetrical or lost on the left side, and the excessive development of the ventral apical margin covers the ventral surface of the eighth segment.

(B) Modifications of the abdomen in Cylindrostethus from the Eastern Hemisphere.

The male seventh segment (figs. 435, 441-446): The ventral apical margin of the seventh segment is simple and concave, without a median emargination, in all species. The degree of specialization is thus best seen in relative length of the seventh to the sixth segment. In productus and costalis the seventh segment is considerably shorter than the sixth on the median longitudinal axis, followed by persephone (7th:6th::7:9), naiades (8.5:10), vittipes (7.5:7.5), and sumatranus (9:7.5); the connexival spine is very long in costalis and productus, still conspicuous in naiades, but in all other species it has become increasingly inconspicuous. In sumatranus and persephone the seventh segment is considerably longer than the sixth segment dorsally.

The male eighth segment: The ventral apical margin of the eighth segment is greatly produced posteriorly; the dorsal apical margin is rounded, feebly notched in naiades and persephone.

The male ninth segment: The suranal plate has basal lateral process which are asymmetrical, the process on the left side is always larger. There is no conspicuous difference in degree of modification among the species, but in costalis, productus and vittipes the modification is more conspicuous than in other three species.

The female seventh segment (figs. 447, 451): The degree of specialization, as indicated by the relative lengths of the seventh and sixth segments, is in the following order from more primitive to more specialized: productus, costalis, vittipes, naiades, persephone, and sumatranus. In productus the seventh segment is much shorter than the sixth, in the next three species the seventh segment is a little longer than the sixth, and in the last two species the seventh segment is much longer than the sixth. The connexival spine is long in productus, naiades and persephone, inconspicuous in vittipes and sumatranus. In sumatranus the connexivum is folded back on the dorsum.
Modifications of the other structures in Cylindrostethini.

The rostrum: In the species of Cylindrostethus from the both Hemispheres the third segment is over twice as long as the last segment in the relatively large species with more primitive abdomens, a little less than twice as long as the last segment in the smaller species with more specialized abdomens except for sumatranus; in Potamobates the third segment is about twice as long as in the great majority of species; in Platygerris the third segment is less than one and a half times as long as the last segment in all species. There is thus, throughout the tribe, a clear tendency toward the reduction of the length of the third segment in relation to the fourth, correlated with specialization of the abdomen and with reduction in size of the body.

The antennae: In Cylindrostethus the second segment is definitely longer than the third in all species. In Potamobates the second segment is about as long as the third in all species except for thomasi, in which the second segment is distinctly longer than the third as in Cylindrostethus. In Platygerris the second segment is definitely shorter than the third in all species. The length of the second segment in relation to the third thus appear to have become smaller in the course of evolution.

Genus Cylindrostethus Fieber
(Figs. 17-18, 115-116, 127, 134, 154, 421-459)

Cylindrostethus Kirkaldy, Entomologist, 30:258 (1897).
Cylindrostethus Bergroth, Ent. Month. Mag., 18:258 (1902).

Type species: Cylindrostethus fieberi Mayr, first included species.
Species examined: C. bassleri Drake, C. bilobatus Kuitert, C. costalis Schmidt, C. erythropus (Herrich-Schaeffer), C. hungerfordi Drake and Harris, C. linearis (Erichson), C. naiades Kirkaldy, C.
nietneri Schmidt, C. palmaris Drake and Harris, C. persephone Kirkaldy, C. productus Spinola, C. regulus (B.-White), C. sumatranus Lundblad, C. vittipes Stål.

Color pattern: Ground color somewhat variable, a reddish brown, pale brown and nearly black. Pronotum with a yellow patch or median yellow longitudinal stripe. Mesopleuron with either longitudinal band of silvery pubescence or without it. Mesonotum with more or less distinct paired longitudinal stripes in some species.

Structures in wingless forms: Body elongate and cylindrical. Head between eyes strongly narrowed between anterior half of eyes, then widened posteriorly. Eye large, exserted, emarginated on inner margin. Antenna robust and relatively short; first segment longer than two following segments together; second segment longer than third; fourth segment much longer than third, cylindrical, curved beyond middle. Antenniferous tubercles divergent anteriorly. Clypeus with basal margin completely lost. Mandibular and maxillary plates obscurely defined from each other. Rostrum reaching posterior margin of head; third segment one and a half to two and a half times as long as last segment.

Pronotum hexagonal in shape, shorter than head, posterior margin nearly straight, posterolateral margin oblique. Mesonotum long, posterior margin broadly rounded and feebly notched at middle, with a faint median longitudinal sulcus. Mesosternum twice to three and a half times as long as metasternum, simply convex, simple and concave on posterior margin; paired longitudinal sutures distinct anteriorly in some species, anterior margin roundly elevated and more or less strongly produced forward at middle in some species. Metanotum with median longitudinal sulcus distinct, lateral elevation reaching almost well marked metacetabular suture. Metasternum a little longer than second ventral abdominal segment; omphalium reduced but the groove leading onto metacetabula always well marked near posterior margin; lateral opening of the groove covered with hairs in most species. Front leg with femur thick, a little longer than tibia except for vittipes in which they are subequal in length; tibia in apical third slightly thickened apically, apical margin with a notch, with inconspicuous process at inner apical angle; tarsus with second segment two to four times as long as first segment, claws arising from near apex. Middle leg longer than hind leg; femur about as long as to much shorter than length of body, one and a quarter to twice as long as tibia; tibia a little less
than twice to about three times as long as first tarsal segment; tarsus flattened, first tarsal segment three to seven times as long as second segment; second segment with a pair of long hairs on dorsal margin near apex. Hind leg with femur about one and one fifth to a little over twice as long as tibia; tibia five to over ten times as long as tarsus; first tarsal segment as long as to twice as long as second tarsal segment. Inconspicuous claws from near apex of middle and hind tarsi occur in species from Eastern Hemisphere.

Abdomen long, nearly parallel sided. First tergite with W-shaped anterior margin, much shorter than second tergite, second to sixth tergites subequal in length to each other. Connexivum more or less reflexed. Abdominal spiracles placed closer to anterior margin than to posterior margin of each segment. Ventral longitudinal suture of connexivum represented by rather obscure longitudinal impression on each segment; median longitudinal carina distinct.

Male: Seventh segment with more or less conspicuous connexival spine, ventral apical margin concave or with a small median emargination on concave posterior margin. Eighth segment with dorsal apical margin nearly straight or gently rounded except for naiades and sumatranus, in which it is notched at middle; ventral apical margin simple and concave, slightly produced at middle. Ninth segment not rotated; suranal plate narrowed apically; processes at base asymmetrical, with acute apex directed either cephalad or caudad; pygophore simply rounded on apical margin; parameres rather weakly developed but distinct. Endosoma with definitive dorsol plate extending along the entire dorsal margin of endosoma only (productus), extends from apical margin to basal margin, bifurcate at base and connected with membranous ventral plate which is coiled within endosoma (linearis, erythropus, palmaris, naiades); lateral plates short, located as basal angles of endosoma. (Description of the male genitalia is based on productus, linearis, erythropyus, palmaris, naiades).

Female: Seventh segment with connexival spine as in male, ventrally about as long as or longer than sixth segment, ventral apical margin more or less bisinuate, more or less produced posteriorly at middle. Eighth segment well exposed both dorsally and ventrally; first valvula with inner lobe membranous, acutely pointed, haired on inner margin in erythropus; outer lobe well sclerotized except for median small membranous area, haired throughout inner margin and apical half of outer margin in
erythropus, apex simply narrowed, ramus attached on outer margin of process from ninth tergite. Second valvula well sclerotized, rounded apically; intervalvular membrane with apical margin well sclerotized and broadly rounded, continuous with outer margin of second valvulae; ramus arising from the middle of inner margin of each valvula, rather short. (Description of the female genitalia is based on productus and erythropus).

Winged forms: Pronotum widest at apical one third. Hemelytra with vein Sc connected with R + M at the point of branching into R and M.

Distribution: South America (Brazil, British Guiana, Bolivia, Peru), West Indies (Trinidad), and the Oriental region (Burma, Cambodia, Celebes, Ceylon, Philippines, Sumatra), and the Ethiopian region (Liberia).

The species of Cylindrostethus from the Western Hemisphere are different from the members of the same genus from the Eastern Hemisphere in the following points:

(1) The species of Cylindrostethus from the Eastern Hemisphere have the basal processes of the suranal plate acute and always directed caudad, while they are directed cephalad in the species from the Western Hemisphere.

(2) The middle and hind femora in Cylindrostethus from the Eastern Hemisphere are as long as the body except for productus and costalis, while they are distinctly shorter than the length of body in all species from the Western Hemisphere.

(3) The hind leg is much longer than the body in the species from the Eastern Hemisphere, while it is about as long as length of body in the species from the Western Hemisphere.

(4) A conspicuous modification of the anterior margin of the mesosternum is much more pronounced in some species of Cylindrostethus from the Western Hemisphere than in the species from the Eastern Hemisphere.

(5) The claws are absent in the middle and hind legs in the species from the Western Hemisphere.

The differences in lengths of leg and antennal segments between the two groups of Cylindrostethus is mainly due to the differences in initial growth indices for these segments, as have already been observed.
Genus *Potamobates* Champion

(Figs. 19, 117, 135, 155, 460-480, 490-493)


Type species: *Potamobates unidentatus* Champion, by subsequent designation (Drake and Harris 1934, in the above bibliography).


Color Pattern: Body above predominantly black, mottled with pale yellow markings or stripes. Head black along inner margins of eyes and clypeal region in most species. Pronotum with a median longitudinal yellow stripe or patch, which is confined to anterior lobe in winged forms. Front leg pale yellow, with black stripe at least on inner margin. Mesonotum with or without a median longitudinal yellow stripe and a pair of yellow markings on either side of middle, lateral limit of black area clothed with silvery pubescence. Abdomen above largely dark fuscous to black, each tergite with median yellow spot in some species. Body beneath pale yellow.

Structures in wingless forms: Head wider across eyes than long, strongly narrowed at middle between eyes. Eye exerted posteriorly, large, inner margin emargined posteriorly, covering anterolateral angle of pronotum. Antenna short; first segment definitely longer than two following segments together; second segment subequal to third one except for *thomasi*, apex truncate; fourth segment fusiform, slightly bent at middle or apically. Antenniferous tubercles bent forward, short. Mandibular and maxillary plates completely fused. Rostrum short, scarcely extending beyond prosternum, third segment about twice as long as fourth segment.

Pronotum with posterior margin nearly straight or feebly sinuate, strongly widened anteriorly. Mesonotum with posterior margin roundly produced. Mesosternum three and one third to a little over four times as long as metasternum; paired longitudinal sutures faint but traceable. Metanotum with median longitudinal sulcus distinct at least anteriorly. Metasternum with omphalium vestigial, lateral groove extends onto metacetabulum where it opens, the open-
ing either covered by a tuft of hairs or without them. Front leg with femur thick basally, then gradually thinned apically; tibia incurved and slightly thickened apically, apical margin notched, inner apical angle produced, with apical longitudinal depression on both outer and inner surfaces; tarsus slightly curved; first segment highly reduced; second segment three to three and a half times as long as first segment; claws arise from near apex. Middle leg longer than hind leg; femur about as long as or a little shorter than body, a little less than one and a half times as long as tibia; tibia three times to a little less than twice as long as first tarsal segment; first tarsal segment four times to a little over three times as long as second tarsal segment; apical half of tibia and tarsus flattened and curved, shallowly sulcate on inner margin; second tarsal segment without claws, with a pair of long hairs arising from upper margin near apex. Hind leg with femur about as long as middle femur, twice as long as to a little less than one and a half times as long as tibia; tibia several times as long as tarsus; tibia and tarsus simply narrowed apically; first tarsal segment one and one third to nearly two and one half times as long as second tarsal segment; second tarsal segment with a pair of long hairs arising from upper margin near apex; claws absent.

Abdomen relatively short, subparallel sided or a little narrowed posteriorly. First tergite with W-shaped anterior margin, about as long as or longer than second tergite, second to fifth tergites subequal in length, short, sixth tergite a little longer than fifth tergite. Ventrites with intersegmental suture obscure in some species. Abdominal spiracles placed a little closer to posterior margin than to anterior margin in all species except for thomasi, in which spiracles placed much closer to anterior margin than to posterior margin of each segment. Ventral connexival suture obscure.

**Male:** Seventh segment much longer than sixth segment, both dorsally and ventrally except for thomasi; connexival spine absent or present as short obtuse projection; ventral apical margin always with double emarginations. Eighth segment cylindrically produced posteriorly, almost as long as all preceding segments together in some species, posterior margin more or less greatly modified except for thomasi, ventral surface depressed basally in some species, ventral apical margin always with denticular projection, right posterior angle produced in bizzare shape. Ninth segment rotated to right in all species except for thomasi, in which it is only slightly rotated; suranal plate asymmetrically modified on sides (conspicuous process...
on left side); parameres vestigial. Endosoma long; dorsal plate thick but not bifurcate apically, bifurcate at upper basal angle where it is articulated with sclerotized basal plate; ventral plate sclerotized at least basally; lateral plates simple, sclerotized at middle of dorsal region of endosoma above dorsal plate. (Description of the genitalia is based on horváthi, umidentatus, thomasi).

Female: Seventh segment with ventral basal margin acutely produced cephalad at middle, with more or less well developed connexival spine, ventral surface excessively developed, assuming various shapes on apical margin, covering completely eighth segment above in most species (in thomasi apical margin with a pair of long processes and eighth segment well exposed ventrally); first valvula with inner lobe membranous, folded beneath outer lobe basally, apical half simply narrowed apically; outer lobe robust, basal half of which distinct by oblique narrow membranous region from distal part where is simply narrowed and narowly rounded apically; ramus arising from distal end of basal sclerotized part of outer lobe, connected with process of ninth segment on its outer margin. Second valvula with lateral area in its basal half well sclerotized and continuous with apical margin of intervalvular membrane, where is well sclerotized and freely produced posteriorly in the middle, apical half of second valvula narrow, directed mesad, apex rounded; ramus long. (Description of the female genitalia is based on thomasi and peruvianus.)

Winged forms: Pronotum widest at apical one third, then broadly rounded apically. Hemelytra with Sc united with R + M before the point of branching into R and M respectively.

Distribution: Central and South America (British Honduras, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela).

The genus Potamobates is more primitive than related genus Platygerris in:

(1) Retention of the lateral groove of the omphalium leading onto the metacetabula.
(2) The less flattened body.

The genus Potamobates is more specialized than Cylindrostethus in:

(1) The fusion of the mandibular and maxillary plates.
(2) The less uniform pregenital segments.
(3) Higher degree of modification of the genital segments in both sexes.
The location of the abdominal spiracles, i.e., they are at or a little behind the middles of the segments in a great majority of species.

The loss or great reduction of the connexival spine.

The rotation of the male genital segments.

Genus *Platygerris* Buchanan-White

(Figs. 20, 118, 136, 156, 481-489, 494-504)

*Platygerris* Buchanan-White, Ent. Month. Mag., 20:36(1883)


(Key to species).

Type species: *Platygerris depressus* Buchanan-White, monobasic.

Color pattern: Predominantly black. Head with an orange yellow spot on vertical region. Pronotum with a yellowish median longitudinal stripe, which is confined to anterior lobe in winged forms. Mesothorax with lateral longitudinal stripe composed of silvery pubescence. The color pattern similar to *Potamobates*, but with more dark areas in this genus.

Structures in wingless forms: Body short and strongly flattened. Head between eyes strongly widened posteriorly. Eye indented posteriorly. Antenna short and thick; first segment about as long as three following segments together; second segment linear, thickened anteriorly, apex truncate; third segment always shortest; fourth segment always curved near apex. Antenniferous tubercles thick, divergent anteriorly. Clypeus with basal margin completely lost, anterior margin straight. Mandibular and maxillary plates completely fused. Rostrum short and thick; third segment one and a half times as long as last segment.

Pronotum about as long as head in middle, much wider than head across eyes, posterolateral margin broadly rounded; *propleura widely separated from each other leaving broad prosternum between*. Mesonotum long, wider than pronotum. Mesosternum seven to nine times as long as metasternum; paired longitudinal sutures absent. Metanotum short, median longitudinal sulcus absent; lateral longitudinal elevation weakly developed, not reaching metacetabular suture. Metasternum short; omphalium vestigial but distinct, lateral groove of omphalium absent. Front leg with femur strongly thickened at base, somewhat dorsoventrally depressed in male of *caeruleus*, with a small tubercle at middle on inner margin of *depressus*; tibia always incurved apically, with
rather inconspicuous process at inner apical angle, rather strongly longitudinally impressed on inner margin at apex; first tarsal segment short, second segment at least twice as long as first, claws arising from near apex. Middle leg a little longer than hind leg; femur much longer than body, about two and a half times as long as tibia; tibia flattened at least in apical half, strongly thickened apically, about one and a half times as long as first tarsal segment; tarsus strongly flattened, first segment about three times as long as second; claws absent. Hind leg with femur a little longer than middle femur, a little over three times as long as tibia; tibia at least twice as long as tarsus which is flat, first tarsal segment about twice to nearly three times as long as second segment. Claws absent.

Abdomen slightly narrowed apically in both sexes. First and second tergites have their anterior margins produced anteriorly; third to seventh tergites progressively longer posteriorly; second to sixth ventrites a little longer in female than in male; connexival spine lost. Abdominal spiracles, as well as ventral suture of connexivum, were not studied (the lateral regions of the abdomen are flanked by the metacataylural region and basal leg segments).

**Male:** Seventh segment ventrally strongly depressed, ventral apical margin concave and excave at middle. Eighth segment has spinous process to the left of middle of apical margin in *asymmetricus* and *depressus*; very long and cylindrical, and without process on apical margin in *caeruleus*. Ninth segment always rotated to the right; suranal plate has process like projection on left side and the process meets apically with the apex of process of eighth segment; pygophore rounded apically; parameres vestigial in *P. asymmetricus*. Endosoma with proximal membranous area not well developed (*asymmetricus*) or developed (*caeruleus*); definitive dorsal plate extending along dorsal margin of endosoma, articulated with ventral plate at basal dorsal margin of endosoma; ventral plate sclerotized, long and paired, reaching apex of endosoma; lateral plates located in apical region of endosoma; dorsal margin of endosoma sclerotized at middle above dorsal plate.

**Female:** Seventh segment long ventrally, ventral basal margin acutely produced, trilobed apically and folded on ventral side of eighth segment, with a rather conspicuous spinous process on right side beneath connexivum and with coarse bristles on each side of dorsal posterior margin in *asymmetricus* and *caeruleus*; with small process on both sides near lateral lobes of ventrites, of which the
one on right side a little more conspicuous in *depressus*. First valvula with inner lobe thinly sclerotized, with narrow apex directed mesad; outer lobe robust and well sclerotized, divided into basal and apical halves by intervening membranous area, of which apical area acutely pointed; ramus arises from distal end of basal sclerotized area, connected with process of ninth tergite on its outer margin, apical end of the latter acutely produced on inner edge. Second valvula also divided into basal and distal strongly sclerotized areas by a narrow intervening membranous area, apical half narrow and curved, apex rounded; intervalvular membrane with apical margin straight, strongly sclerotized, the sclerotization extends lateroanteriorly and continuous with basal half of second valvula; ramus arising along inner margin of basal sclerotized area, extending cephalad and again caudad along the ramus of eighth segment, reaching about middle of the process of ninth tergite. Vulva membranous and narrow. (Description of the female genitalia is based on *P. asymmetricus*.)

**Structures in winged forms**: Pronotum widest at the apical one third. Vein Sc connected with R + M before the point of branching into R and M respectively.

**Distribution**: Central America (Costa Rica, Mexico)

This genus is the most specialized in the Cylindrostethini and can readily be distinguished from the other two genera by the absence of the omphalial groove and the flattened body. The extraordinarily long middle and hind femora appear to be produced by extraordinarily high growth ratios for these segments.

** Tribe Charmatometrini Matsuda**

**Color pattern**: Predominantly reddish brown in most species, with a black longitudinal stripe on pronotum in some species.

**Structures in wingless forms**: Head between eyes widened posteriorly. Clypeus with basal margin always lost, directly connected with labrum anteriorly. Antennae shorter than length of body, first segment about as long as or shorter than two following segments together except for *Charmatometra*, in which it is distinctly longer than two following segments together, second segment always shortest, third segment with a distinct basal peduncle, always longer either than second or fourth. Antenniferous tubercles rather small, rounded on outer margins. Mandibular and maxillary plates at least partially distinct from each other. Rostrum extend-
ing beyond prosternum; third segment three to four times as long as fourth segment.

Pronotum always fully prolonged, posterior margin rounded. Mesosternum with median longitudinal sulcus absent; paired longitudinal suture lost in most species. Intersegmental suture between mesonotum and metanotum often obscure laterally. Metanotum with median longitudinal sulcus distinct; lateral longitudinal elevation absent; metacetabular suture poorly developed, not extending dorsally. Metasternum with omphalium and omphalial groove leading onto metacetabula always present. Front leg with femur simple; tibia sometimes with a conspicuous inner apical process (Charmatometra); tarsus with first segment half as long as to about as long as second segment; claws arising preapically. Middle leg longer than hind leg; femur shorter than tibia in all species except for Charmatometra and Eobates. Tarsus with first segment three to a little over five times as long as second segment. Hind leg with femur a little less than twice as long as tibia; tarsus with first segment a little longer than to over two and a half times as long as second segment.

Abdomen moderately long. First tergite always with nearly straight anterior margin enclosing first abdominal spiracle in anterolateral corner of first tergite. Seventh segment without connexival spines; ventral margin of connexivum obscure.

Male: Seventh segment with ventral apical margin subquadrangularly incised, without median emargination, at least a little longer than sixth segment ventrally. Eighth segment more or less prolonged in most species, concave on ventral apical margin, without conspicuous modification on ventral surface. Ninth segment with suranal plate simple; pygophore with apical margin rounded; parameres simply arched and well developed, present in all species. Endosoma with dorsal plate extending along dorsal margin of endosoma, either fused or not fused with basal plate which supports more or less membranous ventral lobe; lateral plates sometimes large.

Female: Seventh segment with ventral apical margin more or less concave in most species, produced medially in some more specialized species of Brachymetra. Eighth segment with first valvula with narrow and short membranous inner lobe folded beneath outer lobe; apex of outer lobe simply rounded. Second valvula apically directed mesad, rounded at apex, extending beyond round apical margin of intervalvular membrane. Vulva with broader

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basal region and apical narrow projection. Vestigial third valvula is recognizable.

Winged forms: Pronotum with humeri located at a little behind middle. Hemelytra with well formed embolium. Sc connected with R + M at the point of separation into R and M.

Distribution: Central and South America.

Table 10.—Table of significant generic characters in Charmatometrini.

<table>
<thead>
<tr>
<th>Character</th>
<th>Charmatometra</th>
<th>Eobates</th>
<th>Brachymetra</th>
<th>Charmatometra</th>
<th>Eobates</th>
<th>Brachymetra</th>
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<td>(-)</td>
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<td>3.1–3.2</td>
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<td>(-)</td>
<td>(-)</td>
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<td>(+)</td>
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For the explanations of symbols see introduction and table 5.

Relationships of genera

The three genera are closely related. Charmatometra is more primitive than the other two in at least three characters, as noted from the table of significant characters. Brachymetra has apparently originated from a Charmatometra-like ancestor with the loss of the characters 17 and 27 in the table, and the shift in location of the abdominal spiracles which has been accompanied by the reduction of the pregenital abdominal segments. The genus Brachymetra can reasonably be regarded as a specialized group of Charmatometra. The genus Eobates, however, is a more distinct genus having a peculiar color pattern and different relative length of the hind tarsal segments from the other two genera. As have already been observed the different proportional lengths of the hind tarsal segments (and possibly also the middle tarsal segments) in Eobates
has resulted from significantly different growth patterns for these segments from the equivalents of the other two genera. The relationships of the genera thus can be diagrammatically shown as follows (diagram 5):

![Diagram 5](image)

**Diagram 5.**—Diagram showing the relationships of genera of the Charmatometrini.

Characters peculiar to Charmatometrini

1. The pronotum in wingless forms is prolonged and secondary reduction has never occurred.
2. The metasternum has the omphalium as well as the omphalial groove in all species of all genera.
3. The connexival spine is absent and presumably has never arisen.
4. In the middle leg the growth ratio for the femur is apparently greater than that for the tibia. Inheriting this growth potential the tibia has become relatively longer (longer than the femur in absolute lengths) with reduction in body size in phylogeny.

In addition to the above-mentioned peculiarities the straight anterior margin of the first abdominal tergite, etc., distinguish this tribe from the other tribes of Gerrinae.

Modifications of the abdomen in Charmatometrini

The male seventh segment: The degree of specialization of the segment is indicated by the length of the seventh segment relative to the sixth. In *B. kleopatra*, *B. shawi*, and one unidentified species of *Brachymetra* from Brazil the length of the seventh in relation to the sixth ranges 7.5:6.5 or 4.5:5.5 to 5:8 ventrally, and 7:7 to 5:6.5 dorsally. In smaller species it ranges from 5.5:3.5 in *anduzei* to 9:4.5 in *albinerva incisa* ventrally, or 7:4 in *lata* to 11.5:5 in *anduzei*
dorsally. In *Charmatometra* and *Eobates* the ventral apical margin is simple and concave as in more primitive species of *Brachymetra*, and the relative lengths of the seventh and sixth segments are 15:11 and 10.5:7.5 ventrally respectively.

**The male eighth segment:** In *Brachymetra* the ventral apical margin is concave and the segment is shorter than the seventh in *kleopatra* and *shawi*, while it is about as long as the seventh in *lata*, *albinervia incisa*, and in an unidentified species from Brazil. The highest degree of prolongation of the eighth segment is found in *unca* and *anduzei*, in which the segment is longer than the seventh and the ventral apical margin is roundly produced posteriorly. In *Charmatometra* and *Eobates* the eighth segment is, as in more primitive species of *Brachymetra*, shorter than the seventh ventrally.

**The female seventh segment:** In such larger species of *Brachymetra*, as *kleopatra* and *shawi*, the seventh segment is less than one and five sevenths as long as the sixth segment ventrally and the ventral apical margin is concave; dorsally the seventh segment is as long as the sixth in *shawi*; in smaller and more specialized species the proportional lengths of the seventh and sixth segments range from 10:6.3 in *lata* to 15:6 in *unca* ventrally, 5.7:5 in one unidentified species from Brazil to 11:5.5 in *anduzei* dorsally. The ventral apical margin is more or less produced posteriorly at the middle to cover the eighth segment above, ending in an acute median tip in *unca*. In *Charmatometra*, the seventh ventrite is one and four elevenths times as long as the sixth ventrite, *i.e.*, the seventh ventrite is relatively a little shorter than in the more primitive and larger species of *Brachymetra*. In *Eobates* the seventh is one and two third times as long as sixth segment; dorsally the seventh segment is just a little longer than the sixth (8:7) and the ventral apical margin is concave.

**The female eighth segment:** The eighth segment with the valvifers together are concave on the apical margin in the larger species of *Brachymetra*, such as *shawi*, *kleopatra*, and a species from Brazil; in *anduzei* they are together produced posteriorly and elevated, and the surface is clothed with long hairs (fig. 538). In *Charmatometra* the apical margin of the valvifers is produced. In *Eobates* it is produced.
Genus *Charmatometra* Kirkaldy

(Shig. 21, 113-114, 127, 133, 152, 505-516)


*Charmatometra* Hungerford, Ent. News, 64(7):172-175(redescription).

*Brachymetra* Kirkaldy, Entomologist, 31(420):101-102(1898). (described *B. bakeri*).

Type species: *Brachymetra bakeri* Kirkaldy, by original designation.

Species examined: *Charmatometra bakeri* (Kirkaldy).

Color pattern: Predominantly reddish brown, silvery pubescent on propleuron, mesopleuron and lateral part of abdominal tergites.

Structures in wingless forms: Head between eyes strongly narrowed medially. Eye superposed on pronotum posteriorly. Antenna with first segment thickened anteriorly and truncate at apex, a little shorter than three following segments together; second segment simply thickened anteriorly; third segment a little over one and a half times as long as second; fourth segment elongate fusiform, a little shorter than third. Antenniferous tubercles small, rounded on lateral margins. Clypeus strongly bent forward, basal margin completely lost. Mandibular plate distinct from maxillary plate partially. Maxillary plate large, its anterior margin broadly rounded. Rostrum relatively short, third segment a little over three times as long as last one.

Pronotum with anterior lobe widened anteriorly; posterior lobe narrowed apically, apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum distinct laterally. Mesosternum about five times as long as metasternum; paired longitudinal sutures distinct, divergent posteriorly; median longitudinal sulcus absent. Metanotum short, median longitudinal sulcus distinct. Metasternum a little less than twice as long as second ventrite; omphalium small, but with distinct lateral groove leading onto metacetabulum and its lateral opening covered by a tuft of straight hairs. Front leg with femur slightly narrowed apically, with a small laevigate tubercle near apex on inner margin; tibia strongly widened apically, longitudinally depressed on inner apical area, apex outwardly divided into two parts by deep longitudinal cleft, of which inner part rather conspicuously produced; tarsus long, first and second segments subequal in length; second one with small claws arising subapically. Middle leg with femur longer than length of body, distinctly longer than tibia; tibia somewhat curved and flat-
Study of the Gerridae of the World

Winged forms: Pronotum wide, humeri located at a little behind middle, broadly rounded on apical margin. Intersegmental suture between mesonotum and metanotum distinct between metathoracic spiracle and wing base. Hemelytra were not available for study.

Distribution: South America (Colombia, Ecuador, Venezuela.)
Genus *Brachymetra* Mayr

*(Figs. 23, 113-114, 133, 152, 527-547)*


Type species: *Halobates albinervis* Amyot and Serville, by original designation.


*Color pattern*: Predominantly reddish brown. Head without black marking. Pronotum occasionally with a median longitudinal black stripe and black lateral margin (*anduzei*)

*Structures in wingless forms*: Head narrowed between eyes. Eye exserted posteriorly, inner margin feebly concave, posterior half of inner margin covering anterolateral angle of pronotum. Antenna with first segment always longest; second segment always shorter than third segment; third segment more slender than second segment; fourth segment shorter than third segment. Antenniferous tubercles small. Clypeus with basal margin lost. Mandibular and maxillary plates distinct from each other and of about same sizes. Rostrum rather short, third segment about three to four times as long as last segment.

Pronotum with apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum often obliterated. Mesosternum four and two thirds to six times as long as metasternum; paired longitudinal sutures absent; median ventral longitudinal sulcus absent or indistinct. Metanotum with short and indistinct median longitudinal sulcus. Metasternum distinctly longer than second ventrite; omphalium reduced, lateral groove leading onto metacetabula distinct and the lateral opening covered with a tuft of hairs. Front leg rather long; femur simply narrowed apically; tibia slightly swollen apically, bipartite by an oblique longitudinal cleft in apical region, inner apical process inconspicuous; first tarsal segment a little shorter or about half as long as second segment; claws arising from apical third of second segment and with arolium. Middle leg with femur always shorter than tibia, also always shorter than hind femur; tibia three and a half to seven times as long as first tarsal segment; first tarsal segment four and five sevenths to three and one fifth times as long as second seg-
Hind leg with femur a little less than twice as long as tibia; tibia seven and a half to four times as long as first tarsal segment; first tarsal segment over two and a half times to one and a half times as long as second segment.

Abdomen ovate, gradually narrowed apically. First tergite much longer than second tergite and with a more or less prominent tubercle at middle of posterior margin in females of some species; second tergite with anterior margin slightly produced; third to sixth tergites more or less uniform in shape and length; second to sixth ventrites more or less uniform in shape and length. Abdominal spiracles placed at middle of each segment; ventral margin (longitudinal suture) of connexivum absent.

Male. Seventh and eighth segments well exposed both dorsally and ventrally, posterior margin subquadrangularly concave in both segments. Ninth segment with suranal plate simply narrowed apically; pygophore rounded on apical margin; parameres well developed, simply arched. Endosoma with definitive dorsal plate bifurcate at base (basal plate) and on apical margin of endosoma; ventral plate membranous apically, relatively short; lateral plates simple, large in some species. (Description of the male genitalia is based on kleopatra, lata and shawi.)

Female: Seventh segment longer than sixth segment both dorsally and ventrally. Eighth segment well exposed both dorsally and ventrally in most species. First valvula without well differentiated inner lobe, apex acute, ramus arising from near apex; crescent shaped sclerite loosely connected with apex of the process from ninth tergite and with apical region of ramus of second valvula. Second valvula with apical margin rounded, extending beyond apical margin of intervalvular membrane where it is thinly sclerotized and rounded; ramus arising from beyond middle of second valvula. Vulva with broader basal area and provided with a median narrow production. (Description of the female genitalia is based on lata.)

Winged forms: Pronotum elongate subpentagonal in shape, widest at middle in most species. Intersegmental suture between mesonotum and metanotum is often confluent with elevated lateral margin of metanotum which reaches base of wing.

Distribution: South America (Bolivia, Brazil, British Guiana, Ecuador, Panama, Paraguay, Peru, Venezuela) and Trinidad.

This genus differs from Charmatometra in the following characteristics:
(1) The intersegmental suture between the mesonotum and metanotum is usually unrecognizable laterally in wingless forms.
(2) The middle tibia is longer than the middle femur.
(3) The body size is smaller.

Genus Eobates Drake and Harris
(Figs. 22, 113-114, 133, 152, 517-526)


Type species: Eobates morrisoni Drake and Harris, by original designation.

Species examined: E. vittatus (Shaw).

Color pattern: Pale yellow in ground color. Head with a median and paired black lateral longitudinal stripes. Pronotum with paired black longitudinal stripes and lateral margin black. Connexivum along lateral margin black. Tergites black except for posterior margins paler. Mesothorax with lateral black longitudinal stripe; metanotum black.

Structures in wingless forms: Head between eyes narrowed. Eye with inner margin feebly sinuate. Antenna with first segment longer than two following segments together; second segment slightly thickened apically; third segment a little longer than second one; fourth segment shorter than third. Antenniferous tubercles small. Clypeus with basal margin lost. Mandibular and maxillary plates distinct from each other, the latter larger than the former and broadly rounded on anterior margin. Rostrum relatively long, distinctly extending beyond posterior margin of prosternum; third segment about four times as long as last segment.

Pronotum slightly widened at apical third, posterior margin broadly rounded. Intersegmental suture between mesonotum and metanotum barely recognizable laterally. Mesosternum about four and a half times as long as metasternum; without either median longitudinal sulcus or paired longitudinal sutures. Metanotum with median longitudinal sulcus distinct. Metasternum distinctly longer than second ventrite; omphalium highly reduced but lateral groove well marked at apical third of metasternum, lateral opening of the groove clothed with a tuft of straight hairs. Front leg with femur narrowed apically; tibia with apex slightly swollen,
with an oblique sulcus near apex, inner apical angle slightly pro-
duced; first tarsal segment about two thirds as long as second
segment, second segment with claws arising from apical one fourth
of the segment. Middle leg with femur a little longer than tibia
or than body; tibia about four times as long as first tarsal segment;
first tarsal segment about three times as long as second, both
segments strongly curved, second segment with apical claws. Hind
leg with femur over one and a half times as long as tibia; tibia
about four and a half times as long as tarsus, or over eight times
as long as first tarsal segment; first tarsal segment a little longer
than second segment.

Abdomen ovate. First tergite long, posterior margin concave;
second to sixth tergites subequal in length at middle. Abdominal
spiracles placed at middle of each segment; ventral median longi-
tudinal elevation absent.

Male: Seventh tergite much longer than sixth tergite; seventh
ventrite broadly subrectangularly concave on apical margin. Eighth
segment well exposed both dorsally and ventrally, broadly concave
on ventral apical margin. Ninth segment with suranal plate
rounded on apical margin, largely hidden beneath eighth tergite;
pygophore rounded on apical margin; parameres visible on either
side of pygophore. (The genitalia were not examined.)

Female: Seventh tergite a little longer than sixth tergite; sev-
enth ventrite much longer than sixth ventrite, concave on apical
margin. Eighth segment exposed both dorsally and ventrally.
(The genitalia were not examined.)

Winged forms: Pronotum with humeri located at a little behind
middle, posterolateral margin feebly concave. Intersegmental
suture between mesonotum and metanotum running along dis-
tinctly ridged lateral margin of metanotum as far as wing base.

Distribution: Central and South America (Haiti, Peru).

The genus *Eobates* is distinct from the other genera of Char-
matometrini by the following characteristics:

1. The quite distinct color pattern.

2. The first tarsal segment of the hind leg is only slightly
longer than the second segment.

Tribe *Eotrechini* Matsuda

Color pattern: Reddish brown to black in ground color in most
species. Pronotum and mesonotum usually provided with a yellow
longitudinal stripe or stripes.
Structures in wingless forms: Head between eyes not conspicuously widened posteriorly. Clypeal region strongly bent ventrad in *Amemboa*, basal margin distinct except for *Amemboa*. Antennae slender, first segment as long as or longer than second, usually considerably longer than second, third and second subequal in length in most species, fourth segment longer than third in most species. Antenniferous tubercles reduced in *Amemboa*. Mandibular and maxillary plates distinct from each other except for *Amemboa*. Rostrum extending beyond prosternum, third segment at least twice as long as third.

Pronotum not prolonged. Mesosternum with median longitudinal sulus distinct or obscure; paired longitudinal sutures lost in more specialized genera. Intersegmental suture between mesonotum and metanotum laterally obliterated in *Amemboa*. Metanotum with median longitudinal sulus distinct; metacetabular suture dorsally not reaching intersegmental suture between mesonotum and metanotum; lateral longitudinal suture not reaching intersegmental suture. Metasternum varies greatly in degree of reduction in length; omphalium present but always without lateral omphalial groove leading onto metacetabula. Front leg with femur and tibia greatly modified in males of *Amemboa* and *Chimarrhometra*. Middle leg with femur about one to one and a half times as long as tibia; first tarsal segment about twice to half as long as second segment; claws arise apically, or from near apex, or from near middle of second segment. Hind leg longer than middle leg, or about as long as middle leg, or shorter than middle leg; tibia strongly reduced in more specialized genera (less than half as long as femur); first tarsal segment twice to half as long as second segment; claws arise from various positions on second segment as in middle leg.

Abdomen with anterior margin of first tergite always represented by flattened W-shaped suture. Connexival spine of seventh segment always absent; ventral margin of connexivum obscure or lost.

Male: Seventh segment without median emargination on ventral apical margin, greatly prolonged in more specialized genera. Eighth segment greatly prolonged in more specialized genera. Ninth segment with suranal plate greatly modified in *Amemboa*; pygophore modified on apical margin in *Amemboa* and *Chimarrhometra*; parameres present except for *Amemboa*. Endosoma with round and relatively large apical plate loosely connected with dorsal plate; ventral plate, when present, totally membranous.
Female: Seventh segment prolonged both dorsally and ventrally in more specialized genera. Eighth segment with first valvula long, well differentiated into inner and outer lobes; the former reaching about the middle of the latter. Second valvula extending beyond apical margin of intervalvular membrane. Vulva largely membranous, narrow in Onychotrechus, rather broad in Amemboa.

Winged forms: Pronotum relatively short and humeri located near middle in Amemboa, elongate and humeri located behind middle of pronotum in Eotrechus and Onychotrechus. Sc₂ is joined to R beyond the point of branching of basal R + M in more specialized genus Amemboa.

Distribution: The oriental region. The discontinuous extension of the Malayan fauna into Peninsular India and Ceylon, and a marked difference between the fauna of Ceylon and Southern India on the one hand and that of Northern India on the other are well known. Pradhan (1952) has already discussed the distribution of the genus Amemboa in relation to this problem. Onychotrechus and Eotrechus exhibit the same distributional pattern as Amemboa, which occurs in Southern India, Burma, China, Thailand, Annam, Sumatra, Java, Mindanao, Luzon and Formosa. Chimarrhometra and Rheumatotrechus, however, are known from the Himalayas.

Relationship of genera

Eotrechus is obviously the most primitive genus as seen from table 11, and the ancestral species of this tribe was probably much like Eotrechus, as is evident from the overwhelmingly large numbers of primitive characters in this genus. From this Eotrechus-like ancestor the other four genera have become distinct with acquisition of new characters through reduction and modification of the pre-existing ones. Onychotrechus has apparently become a distinct group with acquisition of peculiar shape and position of the claws, etc., although this genus has still retained a relatively large number of primitive characters. In Amemboa the specialization of structures has reached its maximum, for only one primitive character is retained out of twenty-five tabulated. Chimarrhometra is also highly specialized although it retains more primitive characters than Amemboa. Rheumatotrechus, which I failed to examine, may possibly be a close relative of Chimarrhometra. All the genera of this tribe are not in a linear phylogenetic relationship, and no one genus can be directly derived from any other. They are possibly
remnants of a once diverse group. The phylogenetic relationships of genera can be roughly expressed by diagram 6.

Evolutionary tendencies more or less peculiar to the Eotrechini

(1) The pronotum is not prolonged in wingless forms. Presumably the prolongation has never arisen.

(2) The ventral apical margin of the seventh abdominal segment

Table 11.—Table of significant generic characters in Eotrechini.

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<tr>
<th></th>
<th>Eotrechus</th>
<th>Onychotrehus</th>
<th>Chimarrhometra</th>
<th>Ameoba</th>
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<td>134</td>
<td>(+)</td>
<td>1</td>
<td>(−)</td>
</tr>
<tr>
<td>74</td>
<td>(+)</td>
<td>(+)</td>
<td>(−)</td>
<td>(−)</td>
<td>Total</td>
<td>(+) 24</td>
<td>(±) 4</td>
<td>(−) 8</td>
</tr>
</tbody>
</table>

* According to Esaki (1928).
For explanations of plates see introduction and table 5.
Diagram 6.—Diagram showing the relationships of genera of the Eotrechini.

of the male has never become doubly emarginated in the more specialized forms.

(3) The apical margin of the pygophore has become highly modified in the more specialized genera (Chimarrhometra, Rheumatotrechus, Amemboa).

(4) The hind coxa has become longer than wide in the specialized genera, Onychotrechus, Amemboa. This tendency is also noted in certain groups of Halobatinae and Ptilomerinae.

(5) The vein \( Sc_2 \) has become joined with \( R + M \) before the point of separation into \( R \) and \( M \) in the more specialized genus, Amemboa, due to more distal separation of the \( R + M \) vein into \( R \) and \( M \) veins. This tendency is observed also in Gerrini and Cylindrostethini.

In addition to the above-mentioned tendencies, the absence of the connexival spine, of the omphilial groove even in the most primitive genus Eotrechus, the large round apical plate of the endosoma, and the absence or poor development of the ventral plate in the apical segment of the endosoma separate this tribe from the other three tribes of the Gerrinae.

Modifications of the abdomen in Eotrechini

The most primitive pregenital segments are noted in Eotrechus, in which the segments are subequal in length to one another and the abdominal spiracles are placed closer to the anterior margin than to the posterior margin of each segment; in the other three genera the first to sixth segments have become increasingly shorter roughly in the order of Onychotrechus, Chimarrhometra and Amemboa; the abdominal spiracles have become located at the middle of each segment, and the total lengths of the abdomens in these
genera are considerably shorter than in Eotrechus; in the males of Amemboa and Onychotrechus the ventral surface is longitudinally depressed at the middle.

**The male seventh segment**: In Eotrechus (fig. 548) the ventral apical margin is simply concave and a little shorter than the sixth ventrite on the median longitudinal axis. In Onychotrechus the seventh segment is about one and a half times as long as the sixth ventrally. In Chimarrhometra (figs. 572, 574) the seventh segment is about two and one fifth times as long as the sixth ventrally. In Amemboa (figs. 598, 603) the seventh segment is two and a half to four and a half times as long as sixth. In no species does there occur a small median emargination on the apical margin ventrally.

**The male eighth segment**: The eighth segment in Eotrechus is shorter than the seventh ventrally; in Onychotrechus the eighth segment is a little longer than the seventh ventrally; in Amemboa and Chimarrhometra, however, the eighth segment is greatly prolonged and cylindrical, telescoping the ninth segment at least basally.

**The male ninth segment**: The ninth segment in Eotrechus is provided with the styloide (figs. 551, 552). This structure has apparently been lost in all other genera of the Gerridae. The pygophore in Eotrechus and Onychotrechus is simply rounded on the apical margin. In Amemboa the apical margin has become more or less greatly modified. It is simply rounded only in one species from Thailand (unidentified, fig. 594), in which the pregenital and eighth segments are more primitive than in other species of the genus; in all other species the apical margin of the pygophore is always with a medially produced process and the ventral surface is elevated on the median longitudinal axis. The highest degree of modification is noted in another unidentified species from Thailand (fig. 593), in which the median process on the apical margin is most conspicuous and with a greatly modified rounded lobe on either side of the median process. In Chimarrhometra the modification of the apical margin of the pygophore is even more conspicuous than in Amemboa (figs. 572, 574, 576). The suranal plate is simple in Eotrechus, Onychotrechus and Chimarrhometra; in Amemboa the basal lateral margin has become greatly modified and conspicuous in horváthi, lyra, etc. (fig. 607), although it has remained much less modified in an unidentified species from Thailand (fig. 594). The paramere have been lost in Amemboa only; in Chimarrhometra it is greatly developed and modified (fig. 576). A possible
functional substitution of the modified basal lateral region of the suranal plate for the parameres in *Amemboa* has already been discussed.

**Female:** Since the female specimens of *Eotrechus* and *Chimarrhometra* are not available for study, the comparison of the abdomens in this tribe cannot be complete. It can, however, be said that the seventh segment in *Onychotrechus* is less prolonged than in *Amemboa*. No conspicuous modification, besides the prolongation of the segment, has occurred in these two genera.

Modification of other structures in Eotrechini

As in most other genera of the Gerridae, the length of the third rostral segment relative to the fourth is greatest in the most primitive and the largest (in size) genus *Eotrechus* (4.1:1); in *Onychotrechus* the relative lengths range from 2.86:1 to 3.50:1, and the ratios are definitely greater than in *Amemboa* (2.1:1 to 2.54:1); in *Chimarrhometra* the relative lengths are 3.7:1. In the male of *Chimarrhometra* the front femur is greatly thickened, and in males of *Amemboa* the degrees in modification of the front leg vary from relatively slightly modified condition in an unidentified species from Thailand (fig. 578) to the most highly specialized condition in the femur and tibia of another unidentified species from Thailand (fig. 577). The degree of reduction of the metasternum is least in *Eotrechus* (mesosternum:metasternum :: 1.5:1), and is progressively more pronounced roughly in the order of *Chimarrhometra*, *Onychotrechus* and *Amemboa*.

Genus *Eotrechus* Kirkaldy

(Figs. 25, 127, 153, 548-558)

*Eotrechus* Kirkaldy, Entomologist, 35:137(1902).


Type species: *Eotrechus kal'idasa* Kirkaldy, by original designation.

Species examined: *E. kalidasa* Kirkaldy.

**Color pattern:** Head with a yellow crescent shaped spot. Pronotum with a pair of lateral and median yellow stripes only on anterior lobe. Mesonotum without silvery pubescence.

**Structures in winged forms:** Head including eyes a little wider than long, uppersurface widened between eyes. Antenna slender and long, all segments about equal in length. Antenniferous
tubercles slightly rounded on lateral margin, apex not reaching base of clypeus. Clypeus with basal margin well defined. Mandibular and maxillary plates distinct from each other, mandibular plate extending above maxillary plate anteriorly; maxillary plate with anterior margin broadly rounded. Rostrum long and slender, third segment a little less than four times as long as last segment.

Pronotum in winged form obscurely divided into anterior and posterior lobes, humeri located at apical third of pronotum, broadly rounded on apical margin, strongly elevated posteriorly in posterior lobe. Prosternum relatively long. Hemelytra with vein Sc united to R + M at the point of divergence into R and M respectively. Mesosternum about one and a half times as long as metasternum; paired longitudinal suture extends posteriorly as far as base of metasternal apophyses, median longitudinal sulcus well marked. Primary intersegmental suture between mesonotum and metanotum obliterated laterally. Metacetabular suture not well developed dorsally but well marked on either side of wing. Metasternum relatively long, concave on posterior margin; omphalium highly reduced but distinct, lateral groove of omphalium absent. Front leg with femur slender, slightly thinned apically; tibia much more slender than femur, apical region slightly thickened, without either process or constriction near apex; first and second tarsal segments subequal in length, claws arising apically, with conspicuous arolium. Middle leg with femur slender, about as long as tibia; first and second tarsal segments subequal in length (Esaki, 1928). Hind leg a little longer than middle leg; femur a little shorter than tibia; first and second tarsal segments about equal in length (Esaki, 1928).

Abdomen in male: Relatively long and highly generalized. Second ventrite about half as long as metasternum. Second to seventh segments ventrally subequal in length. Abdominal spiracle placed distinctly closer to anterior margin than to posterior margin of each segment from second to seventh segment. Ventral longitudinal suture (ventral margin) of connexivum obliterated in first two segments. Ventrites without median longitudinal impression.

Male: Seventh connexival segment without spine, ventral apical margin of seventh segment simply concave. Eighth ventrite shorter than seventh ventrite, concave on apical margin, eighth tergite broadly rounded on apical margin. Ninth segment with suranal plate narrow and simple; pygophore with conspicuous styloide on each side; parameres slender, apically rounded. Endosoma with definitive dorsal plate bifurcate at base, thickened on lower
margin near base, apically reaching near apical margin of endosoma, not fused with large apical plate; lateral plates simple and long; without basal plate; ventral plate (?) membranous and short. (Description of the genitalia is based on *kalidasa*).

**Female:** Specimen was not available for study.

**Distribution:** Burma.

The genus *Eotrechius*, which is represented by only one species, *E. kalidasa*, has the following peculiar primitive characteristics:

1. The prosternum is relatively long.
2. All the antennal segments are subequal in length.
3. The mesosternum is only one and a half times as long as the metasternum.
4. The sternal and pleural regions of the mesothorax are distinctly defined by paired longitudinal sutures, which reach posteriorly to the bases of the mesosternal apophyses.
5. The second to seventh ventrites are subequal in length.
6. The hind leg is longer than the middle leg.
7. The tibia is a little longer than the femur in the hind leg.
8. The claws arise apically in all legs.
9. The pygophore is provided with the styloide.
10. The apical plate of the endosoma is separated from the dorsal plate.

The genus, however, is specialized in high degree of reduction of the omphalium and the loss of the lateral groove leading from the omphalium onto the metacetabular regions. This genus is apparently a relict.

**Genus Onychotrechus** Kirkaldy

(Figs. 26, 127, 153, 559-571, 599, 602)

*Onychotrechus* Kirkaldy, Entomologist, 36:44-45(1903).


*Gerris* Kirkaldy, Entomologist, 34:117(1901) (described *Gerris* (Linnometra) *sakuntala*, which was assigned to *Onychotrechus* by Distant, 1904).

Type species: *Onychotrechus rhexenor* Kirkaldy, by original designation.

Species examined: *O. sakuntala* (Kirkaldy), *O. rhexenor* Kirkaldy.

**Color pattern:** Yellowish brown in ground color. Head above with a pair of black longitudinal stripes. Pronotum and propleuron each with two dark fuscous stripes, which are continuous onto mesonotum and mesopleuron. Mesopleuron with a longitudinal
stripe of silvery pubescence between the dark stripes. Abdomen above predominantly dark fuscous.

Structures in wingless forms: Head between eyes much longer than wide, uppersurface convex, widened posteriorly. Eye with inner margin emarginate in posterior half. Antenna slender, first segment longer than second; second and third segments subequal in length; fourth segment a little longer than third. Antenniferous tubercles inconspicuous. Clypeus with basal margin distinct. Mandibular and maxillary plates clearly separated from each other, mandibular plate subtriangular, covering apically basal half of upper margin of maxillary plate. Rostrum with third segment over three times as long as last segment.

Pronotum about as wide as head including eyes, posterior margin broadly convex. Intersegmental suture between mesonotum and metanotum distinct both dorsally and laterally. Mesonotum with posterior margin feebly concave; median longitudinal sulcus recognizable posteriorly, but difficult to recognize due to presence of golden hairs. Mesosternum almost six times as long as metasternum, median longitudinal sulcus distinct only in anterior half. Paired longitudinal sutures distinct anteriorly, posterior margin of metasternum concave. Metacetabular suture poorly developed, not reaching lateral longitudinal suture of metanotum dorsally. Metanotum with median longitudinal sulcus indistinct, overgrown by golden hairs; lateral longitudinal elevation continuous with abdominal connexivum posteriorly, obliterated before posterolateral angle of mesonotum. Metasternum about twice as long as second abdominal ventrite; omphalium present at posterior one third of metasternum. Front leg slender; femur with a black protuberance at apical one fourth of inner margin in female of *rhexenor*; tibia slightly swollen at apex; second tarsal segment about twice as long as first segment, claws arising from apical one third of second segment, with a fine apically curled arolium. Middle leg about as long as hind leg; femur simply narrowed apically, about one and a half times as long as tibia; tibia about five to six times as long as tarsus; tarsus with first segment about half as long as second, claws well developed and with a simple long arolium, arising from apical one third of second segment. Hind leg slender, as slender as middle leg; femur over one and a half times as long as tibia; tibia about five times as long as tarsus; first tarsal segment about half as long as second segment, claws arising from apical one third of second
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segment, well developed and with a simple arolium. *Mesocoxa and metacoxa relatively long.*

Abdomen rather strongly narrowed posteriorly. Connexivum rather strongly reflexed. Abdominal segments not uniform in length and shape. First tergite much longer than second tergite; tergites increasingly longer in posterior segments, so are ventrites; fourth to seventh ventrites with median longitudinal depression in male. Abdominal spiracles placed at middle of each segment.

**Male:** Seventh ventrite with apical margin concave. Eighth segment well developed, oblique on dorsal margin, concave on apical margin. Ninth segment with suranal plate simple; pygophore well exposed ventrally; parameres short and robust. Endosoma with dorsal plate fused with paired round apical plates on apical margin of endosoma; lateral plates slender, ventral lobe totally membranous, without sclerotized basal support. (Description of the genitalia is based on *sakuntala.*)

**Female:** Seventh segment well developed both dorsally and ventrally, over three times as long as sixth segment ventrally in *sakuntala.* Eighth segment ventrally partly exposed; first valvula with inner lobe simply narrowed apically, short, about half as long as outer lobe, apex with a mass of long hairs; outer lobe simply narrowed apically, acute at tip; ramus on outer margin of outer lobe arising from about apical one fourth of the lobe, indistinguishably fused with process of ninth tergite. Second valvula with apex narrowly rounded, extending beyond apical margin of intervalvular membrane which is rounded; intervalvular membrane with narrow sclerotized region on each side and they are convergent apically. Vulva membranous, narrow, connected with inner lobes of first valvulae, narrowly rounded at apex, with a narrow median longitudinal stripe. (Description of the genitalia is based on *sakuntala.*)

**Winged forms:** Pronotum elongate, widest behind middle, apical margin broadly rounded. Intersegmental suture between mesonotum and metanotum laterally recognized as an elevated ridge leading anteriorly to wing base. Hemelytra with vein Sc₂ connected with R + M at the point of branching into R and M.

**Distribution:** Oriental region (Burma, Ceylon, Southern India).

The genus *Onychotrechus* is related to *Amemboa,* but can be distinguished from it by the following more primitive characteristics:

(1) The intersegmental suture between the mesonotum and metanotum is traceable laterally.
The middle and hind legs are subequal in length.

The parameres are present.

The suranal plate lacks modification.

The apical margin of the pygophore is simple.

The vein Sc₉ is united with R + M vein at the point of divergence into R and M, due to the more basal separation of R and M.

This genus is also peculiar in that the claws arise far more basally than in other genera on the extraordinarily long second tarsal segments of the middle and hind legs. The claws themselves are better developed than in the other genera of Eotrechini.

Genus Chimarrhometra Bianchi
(Figs. 27, 153, 572-583)


Type species: Halobates orientalis Distant, by original designation.

Species examined: C. orientalis (Distant).

Color pattern: Ferruginous in ground color. Head with basal yellow crescent shaped marking obscure. Pronotum with a median and a pair of yellow stripes.

Structures in wingless forms: Head including eyes a little wider than long, rather strongly bent ventrad anterior to eyes. Eye emarginated on inner margin. Antenna slender; first segment longest, last three segments subequal in length to one another. Antenniferous tubercles about as long as eyes. Clypeus with basal margin distinct. Mandibular and maxillary plates distinct from each other. Rostrum rather thick, extending far beyond posterior margin of prosternum; third segment about four times as long as last segment.

Pronotum with posterior margin nearly horizontal, produced laterally. Intersegmental suture between mesonotum and metanotum distinct laterally. Posterior margin of mesonotum straight. Mesonotum with a pair of well sculptured oblique grayish impressions arising from anterior margin. Mesosternum about three and a half times as long as metasternum; median longitudinal sulcus obliterated; paired longitudinal sutures absent. Metacetabular suture not extending onto dorsum. Metanotum with median longitudinal sulcus obliterated posteriorly; metanotal lateral elevation extending as far as metacetabular suture. Metasternum with omphalium located at apical one fifth of metasternum, a tuft of long
hairs arising from it; omphalia groove absent. Front leg with femur strongly thickened at base, then narrowed apically; tibia curved, slightly narrowed at middle, apex with bare depression on inner margin; tarsus with first segment much shorter than second, claws arising from near apex, with fine arolium. Middle leg a little longer than hind leg; femur about one and a half times as long as tibia; tibia a little over three times as long as first tarsal segment; tarsus with first segment a little over twice as long as second tarsal segment, claws arising from very near apex. Hind leg armed with numerous black small spines as in middle leg; femur a little shorter than middle femur, a little less than twice as long as tibia; tibia over four times as long as first tarsal segment; tarsus with first segment a little over twice as long as second tarsal segment, claws arising from very near apex.

Abdomen highly reduced ventrally in male; first tergite longer than second tergite. Abdominal spiracles placed at middle of each segment; ventral longitudinal suture of connexivum absent; ventral median longitudinal impression absent.

**Male:** Seventh segment a little shorter than five preceding segments dorsally, or a little shorter than three preceding segments ventrally, without connexival spine, feebly sinuate on dorsal apical margin, deeply concave on ventral apical margin. Eighth segment greatly developed dorsally and with round apical margin, ventral apical margin deeply concave. Ninth segment with suranal plate mostly hidden beneath eighth tergite, slender and long, rounded on apical margin, without conspicuous modification; pygophore forked into a pair of well developed processes on apical margin; parameres greatly developed and directed ventrad apically. Endosoma with definitive dorsal plate extending along dorsal margin, loosely connected with large apical plate; lateral plates located along ventral margin near base; ventral lobe (ventral plate) small and membranous, supported by small and slender basal plate which is clearly separated from dorsal plate; apical plate directed ventrally and with broadly rounded apical margin. (Description of the genitalia is based on *orientalis.*)

**Female:** Female specimen was not available for study.

This genus is peculiar among the genera of Eotrechini in the following characteristics:

(1) The mesonotum is provided with a pair of oblique impressions arising from the anterior margin.

(2) A tuft of long hairs arises from the omphalium.
(3) The front femur of the male is greatly thickened.
(4) The development of the parameres and the modification of the apical margin of the pygophore are more conspicuous than in any other genus of the tribe Eotrechini.

Genus *Amemboa* Esaki

(Figs. 24, 153, 584-598, 600-601, 603-608)


Type species: *Amemboa fumi* Esaki, by original designation.

Color pattern: Reddish brown, mottled with dark to fuscous markings. Head always with median longitudinal black stripes which are confluent posteriorly, and also with a pair of black longitudinal stripes along eyes. Pronotal region with two pairs of black stripes, median pair of them are confluent anteriorly; propleural region also with two black stripes. Mesonotum with median and lateral pairs of dark fuscous stripes, each one of lateral and median pairs are connected by a transverse band. Mesopleural region with two longitudinal black stripes, silvery pubescent between them and on mesoacetabula and metacetabula. Abdomen above almost totally black to dark fuscous. General color pattern is similar to that of *Onychotrechus*.

Structures in wingless forms: Head rather strongly bent ventrad, longer than wide between eyes, uppersurface convex. Eye with inner margin slightly sinuate at middle. Antenna slender, a little shorter than body. First segment longer than second; second one usually a little shorter than third; fourth segment longest. Antenniferous tubercles inconspicuous, directed downward apically, their lateral margins slightly rounded. Clypeus with basal margin indistinct. Mandibular and maxillary plates almost completely fused, with a faint suture separating them, apical region of both sclerites always black. Rostrum relatively short, third segment a little over twice as long as last segment.

Pronotum about as long as head, wider than head including eyes, rounded on lateral and posterior margins. Intersegmental suture between mesonotum and metanotum obliterated laterally. Mesonotum with median longitudinal sulcus recognizable in posterior
third or half. Mesosternum several to almost ten times as long as metasternum, feebly or not impressed on median longitudinal axis; paired longitudinal sutures absent. Metacetabular suture not reaching lateral elevation of metanotum. Metanotum with median longitudinal sulcus faintly recognizable; lateral longitudinal elevations convergent anteriorly. Metasternum with posterior margin less concave than anterior margin; omphalium distinct, located behind middle of metasternum; omphalial groove absent, remnant of lateral opening of the groove recognizable as a black spot on metacetabula. Front leg shows sexual dimorphism; femur thicker in male than in female and usually with two thick bundles of short black bristles, one near middle and another at apical one fourth of inner margin in male; tibia at basal third of inner margin always outcurved and with a bump at basal one third of inner margin in male; tarsus with first segment about half as long as second or a little shorter than second segment, claws arising from before middle of second segment, with apically curved arolium. Middle leg longer than hind leg; femur about one and a half times as long as tibia; tibia a little over twice as long as first tarsal segments; tarsus with first segment about twice as long as second segment; claws arising preapically and small. Hind leg with femur about two and a half times as long as tibia; tibia over twice as long as first tarsal segment; tarsus with first segment less than twice as long as second segment; claws arising from apical one fourth of second tarsal segment, arolium as in middle leg.

Abdomen elongate subtriangular in shape. Abdominal segments more reduced ventrally than dorsally, flanked laterally by well developed meso- and metacetabula, so that abdominal spiracles are hidden from view. Second connexital segment often fused with third dorsally. First abdominal tergite longer than second tergite, second to sixth tergites quadrangular in shape, of which sixth one is a little longer than the preceding one; ventrites often depressed on median longitudinal axis in male.

Male: Seventh segment ventrally well developed, a little longer than second to sixth together dorsally, ventral surface much shorter than dorsal surface, but longer than sixth ventrite. Eighth segment well developed both dorsally and ventrally, forming a cylinder-like cavity to ensheath ninth segment, dorsally about as long as seventh, ventrally a little longer than entire preceding abdominal segments together. Ninth segment with suranal plate
differentiated into three regions in most species, i.e., apical hairy region bearing tenth segment apically; middle region differentiates into long spinous process laterally; and lower subquadrangular plate bearing internally a process which holds upper apical region of endosoma: Pygophore modified into various shapes in various species on the apical margin; parameres lost. Endosoma with dorsal plate loosely connected with paired large round apical plates on apical margin; ventral lobe small and totally membranous, directly supported by the base of dorsal plate; lateral plates slender. (Description of the genitalia is based on horváthi and two unidentified species.)

Female: Seventh segment well developed both dorsally and ventrally, forming a deep cavity ensheathing genital segments, dorsally distinctly longer than sixth tergite; ventrally about as long as entire preceding abdominal segments together. Eighth segment exposed only dorsally, completely covered by seventh segment ventrally; first valvula with inner lobe simply narrowed apically, reaching middle of outer lobe; outer lobe well sclerotized on inner half, with short hairs on inner margin throughout, ramus indistinguishably fused to process of ninth tergite. Ninth segment with second valvulae sclerotized along lateral and apical margins, apical lobe small, rounded and reflexed, slightly extending beyond apical margin of intervalvular membrane which is concave. Vulva largely membranous, apical margin nearly straight except at middle, where it is sclerotized and slightly produced. (Description of the genitalia is based on lyra.)

Winged forms: Pronotum strongly constricted at anterior third, forming distinct anterior and posterior lobes, posterolateral margin broadly rounded. Intersegmental suture distinct as an elevated carina connecting metathoracic spiracle and wing base. Hemelytra with veins scattered with golden hairs. Vein Sc₂ joined with R + M before the point of branching into R and M.

Distribution: Oriental region (Annam, Burma, Formosa, India, Java, Luzon, Mindanao, Sumatra.)

The genus Amemhoa is peculiar in the Eotrechini in the following characteristics:
(1) The suranal plate is highly modified.
(2) The parameres are lost.
(3) The vein Sc₂ is united to R + M before the point of branching into R and M.
Genus *Rheumatotrechus* Kirkaldy


Type species: *Rheumatotrechus himalayanus* Kirkaldy, mono-basic.

Specimens of the type species were not available for study. The following description is copied from Kirkaldy (1908):

"This genus has somewhat the appearance of *Ptilomera* of the Gerridae, but the legs are much shorter, especially the fore tarsi.

"Head as in *Ptilomera*, but the eyes are less oblique, and much less emarginate, the vertex being elongate, and subparallel as far as the articulation of the antennæ; first segment of the antennæ little longer than second; labrum much as in *Ptilomera*. In the aperuous form the pronotum is well rounded at the sides, extending laterally much farther than eyes. The nota and tergites are much as in *Ptilomera*, but the whole insect is much shorter and broader in proportion, the abdominal sclerites much less elongate, the mesonotum also more rounded laterally. The fore femora are a little incrassate, and are scarcely longer than the tibiae, fore tarsi very short. Middle and hind legs much shorter than in *Ptilomera*.

"(1) *Himalayanus*, sp. nov. Pale castaneous or fulvous; head with an elongate oval mark on vertex (the interior castaneous) and some lateral marks, dark fuscous. Apex of first segment and apical fourth of second dark fuscous. Eyes dark. Last segment of labium black. Pronotum dark castaneous; a central line and lateral sinuous one on each side, yellow, the central one narrowly and rather obscurely margined with black, this spreading out a little apically. The mesonotum has a small, subtriangular, fuscous mark on each side subanteriorly. Legs yellowish-fulvous; apex of tibiae and tarsi blackish. Tergite dark castaneous, verging on piceous on abdomen proper and inward half of pleurites; one or two smaller brown spots medially. Beneath yellowish fulvous, a lateral, sinuous, dark castaneous line on the mesosternum on each side, edged with silver; also some obscure marks. The first segment of the antennæ one fifth longer than the second. Fore femora scarcely longer than the tibiae, which are nearly four times as long as tarsi; last tarsal segment more than twice as long as penultimate. Middle femora slender, as long as body from base of clypeus to base of pygophor; scarcely longer than tibiae and tarsi together; tibiae about twice and a half as long as tarsi, first tarsal segment twice as long as second. Hind femora one-third longer than the middle pair; scarcely longer than the tibiae and tarsi; tibiae slightly more than
twice as long as tarsi; first tarsal segment not twice as long as second. The hind part of the metanotum is triangular, the sides shortly truncate, and the base a little emarginate.

"Male: The pygophor is very remarkable, and I hope to figure it in my forthcoming 'Notes on the Gerridae'; the hooks, etc., are yellowish-fulvous, the apices blackish. Length—8 mm."

The genus is probably close to Chimarrhometra as Kirkaldy indicated by saying "This genus has considerable resemblance to Chimarrhometra orientalis (Distant)." The proportional lengths of the first and second tarsal segments, those of hind tibia and the hind tarsus, of the first hind tarsal segment and second tarsal segments, the remarkably modified pygophore, and the type locality lead one to strongly suspect that this genus might be a relative of Chimarrhometra. Hind femora being one third longer than middle pair, etc., however, definitely distinguish this genus from Chimarrhometra. Distant (1910) failed to locate the type specimens of this species in the Belgian Museum. I also was unable to borrow the type specimens from the same Museum where they are supposed to be preserved. The location of the types of Rheumatotrechus himalay anus thus remains as enigma. Although its systematic position is uncertain this genus is provisionally treated as belonging to the Eotrechini.

**Subfamily Ptilomerinae Bianchi**


**Structures in wingless forms:** Body cylindrical or oval, large in size. Head with anterior margin with three projections, median clypeal region and lateral antenniferous tubercles in all genera except for Rheumatogonus, in which anterior margin is rounded. Clypeus with basal margin obliterated. Eye small and globular, its inner margin emarginated. Dorsal surface of head between eyes widened posteriorly, posterior margin feebly produced posteriorly. Antenniferous tubercles well developed and divergent except for Rheumatogonus. Antenna long; first segment longer than three following segments together in majority of genera; second segment longer than third or vice versa; fourth segment with apical half always curved and with a longitudinal slit. Mandibular and maxillary plates distinct from each other in all genera. Rostrum short, not extending beyond prosternum; third segment twice to three times as long as last segment.

Pronotum not prolonged, a little wider than long in most genera,
lateral margins divergent anteriorly, posterior margin nearly straight or feebly concave. Intersegmental suture between mesonotum and metanotum always distinct dorsilaterally in all genera. Mesonotum without median longitudinal suture, with lateral longitudinal suture demarcating mesonotum from mesopleural region distinct in *Potamometra*. Mesosternum convex; paired longitudinal sutures defining mesosternum from mesopleural region distinct in some species of some genera; secondary well demarcated median flattened area extending from anterior margin of mesosternum to apical abdominal segments occurs in females of *Hetrobates*. Metanotum with or without median longitudinal suture; metanotal lateral longitudinal suture absent; metacetabular suture dorsally reaching anterior end of first connexival segment, dividing thus metacetabulum into anterior and posterior areas. Metathoracic spiracle conspicuous, located longitudinally. Metasternum more reduced than in Gerrinae. Omphalium reduced but present in all genera, located on median longitudinal axis of metasternum closer to posterior margin than to anterior margin; omphalial groove absent. Front leg longer than body except in *Rheumatogonus*. Femur robust, slightly narrowed apically, a little longer than tibia; tibia always with conspicuous process at inner apical angle; first tarsal segment as long as or longer than second tarsal segment; claws arising from near apex and with arolium. Middle leg longer than hind leg in all genera except for *Ptilomera* and *Potamometra*; femur much longer than length of body; with a conspicuous fringe of long hairs in males of *Ptilomera*, considerably longer and thicker than tibia; tibia with a conspicuous row of hairs in all genera; first tarsal segment several times as long as second tarsal segment; second tarsal segment with or without claws. *Hind leg with coxa more or less prolonged in some genera*, with a more or less conspicuous spinous process on apical margin in some genera; femur much longer than tibia, often three or four times as long as tibia; tibia with a row of rather short hairs on inner margin of most genera; tarsus very short, first tarsal segment shorter than second, or both segments fused, with or without claws.

*Abdomen in male*: First tergite with anterior margin distinct and nearly straight; second to sixth tergite subequal in length to each other in most species. Connexivum nearly horizontal or slightly reflexed, ventral longitudinal margin of connexivum distinctly recognizable as oblique suture in *Ptilomera*, obliterated or overgrown by silvery pubescence in other genera. Abdominal spiracles placed closer to anterior margin than to posterior margin.
of each segment in *Ptilomera*, or at middle between the margins in other genera. Seventh segment prolonged, ventral apical margin concave. Eighth segment more or less prolonged, ventral surface with a basal transversely depressed area and an obscurely elevated area in apical half in some genera, ventral apical margin concave or produced at middle. Ninth segment with suranal plate widened at middle, more or less strongly flattened, conspicuously widened apically in *Ptilomera*; pygophore more or less greatly prolonged in most genera; parameres present in all genera, simple in most genera, highly modified in *Ptilomera s. str.* Endosoma with dorsal plate never reaching apex of endosoma except for *Ptilomera* and *Potamometra*; basal plate always fused with dorsal plate; ventral plate slender and long, not bilobed and largely sclerotized.

**Abdomen in female:** Basal abdominal tergites more or less greatly narrowed and anterior margin of first tergite obliterated due to strong reflection of connexivum in some genera. Abdomen, except for first tergite, telescoped into thoracic cavity dorsally in *Potamometra* and *Potamometroides*; first and sixth tergites modified in some species. Abdominal spiracles and ventral longitudinal margin of connexivum as in males. Seventh segment with ventral apical margin always lobately produced, covering eighth segment above, posterolateral area also excessively developed and modified in various shapes in most genera. Eighth segment with first valvula without well differentiated inner lobe, densely clothed with long obliquely adpressed hairs on inner half of each valvula. Second valvula well sclerotized along outer margin, with well differentiated slender, well sclerotized apical processes; intervalvular membrane also with a pair of smaller processes on apical margin, always with a pair of dark spots above the processes, the spots are often confluent apically forming a single large spot; point of connection of ramus of first valvula to the process of ninth tergite distinct. Vulva largely membranous, or thinly sclerotized. First ventrite absent in both sexes.

**Winged forms:** Hemelytra with Sc and C distinct basally in *Ptilomera*; R + M and Cu also distinct basally in *Ptilomera, Rheumatogonus, Rhyacobates*, but fused basally in *Potamometra*. A connected with Cu at apical third of hemelytra. Pronotum with humeri located at apical third, anterior lobe well defined from posterior lobe by a transverse suture, posterior margin behind humeri broadly rounded.

**Distribution:** Oriental region, and one genus, *Potamometroides*, is known from Madagascar.
Table 12.—Table of significant generic characters in Ptilomerinae.

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<tr>
<th>Propilomera</th>
<th>Ptilomera s. str.</th>
<th>Potanometra</th>
<th>Potamometridae</th>
<th>Potamometropis</th>
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## Table 12.—Table of significant generic characters in Ptilomerinae.—Concluded

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*Pygophore is subquadrangular in shape.

For the explanations of symbols see introduction and table 5.

### Relationships of genera

There appear to be three major groups of genera and two genera whose phylogenetic positions are ambiguous in this subfamily.

The first group, the *Propilomera-Ptilomera s. str.* complex, of which the latter is nothing but a more specialized group of the former, is a widely distributed group of the Ptilomerinae in the Oriental region. The peculiarities of this group are the longer hind leg than the middle leg, fused tarsal segments in the middle and hind legs although the claws are retained, the highly specialized apical abdominal segments in both sexes of the latter group, etc.

The second group is the *Rheumatogonus-Potamometropsis* group. The two genera are quite distinct, but their basically close relationship is indicated by the relatively short first antennal segment, the more nearly horizontal metacetabular suture, much less specialized apical abdominal segments in both sexes than in the other genera, etc. As noted from table 12, *Potamometropsis* and *Rheumatogonus* have more characters in common than with other genera.

The third group includes *Rhycobates, Heterobates*, and possibly *Pleciobates*. This group is characterized by the relatively longer first antennal segment, the basally strongly reflexed connivium, and the highly modified apical abdominal segments in the female, etc. This group is generally highly specialized as will be noted from the relatively few numbers of primitive characters, and their closely related more primitive genera are not known.
Potamometra is very similar to the Proptilomera-Ptilomera complex in the structures of the middle and hind legs, i.e., the hind leg is longer than the middle leg, the tarsal segments being fused though the claws are retained. These characters are peculiar to these two genera in the Ptilomerinae. Potamometra, however, is rather drastically different from the Proptilomera-Ptilomera s. str. complex in certain other characters, such as the withdrawn abdomen of the female, the modified first abdominal tergite of the female, retention of the suture demarcating the mesonotum from the mesopleural region, the more specialized wing venation than in any other genera, etc. These characters preclude any possibility that this genus is closely related to Proptilomera or Ptilomera s. str. Potamometroides is the only African genus (Madagascar) thus far described. The genus simulate Potamometra in that the female abdomen is withdrawn into the thoracic cavity. In fact, however, this genus shares more characteristics in common with Rhyacobates or Heterobates than with Potamometra. The withdrawal of the abdomen of the female into the thoracic cavity is apparently a case of parallelism.

The above discussion is summarized roughly in the following diagram.

![Diagram 7](image-url)

Diagram 7.—Diagram showing the relationships of genera of the Ptilomerinae.
Evolutionary tendencies and characters peculiar to Ptilomerinae

The insects belonging to this subfamily always live in swift and turbulent currents. Esaki (1923) already pointed out that the extremely long first antennal segment, the long and robust femora in all legs, the presence of a fringe of hairs in the middle tibia in all genera and in the middle femur in the male of Ptilomera are adapted characters to this peculiar habitat. Pradhan (1952), referring to Heterobates rihandi (Pradhan), thinks that the triangular well demarked area on the meso- and metasterna, and abdomen in the female of the species probably helps these insects to adhere to the stones and partly submerged rocky boulders lying at the edge of water or in the bed of fast running hill streams.

In spite of these apparently adapted characters, the subfamily has certain characters which are more primitive than their counterparts in the Gerrinae, i.e. (1) the mandibular and maxillary plates are clearly separated from each other in all genera; (2) the primary intersegmental suture between the meso- and metanota being always distinct laterally, while it is often obliterated laterally in the Gerrinae; (3) the veins R + M and Cu being basally distinct from each other in four genera out of five investigated, while they are always fused basally in the Gerrinae.

In addition to the above-mentioned characters, the following are characteristics peculiar to this subfamily and of diagnostic importance:

(1) The metacetabular suture reaches dorsally the anterior end of the first definitive connexival segment, thus the metacetabular region is divided obliquely into the anterior and posterior halves. (In some genera of Halobatinate the metacetabular suture reaches the anterior end of the first abdominal tergite, but the metacetabular region is not divided into two laterally defined portions, since the intersegmental suture between the mesonotum and metanotum is laterally obliterated).

(2) The first connexival segment never extends into the metanotal region. (In Charmatometrini of the Gerrinae and some genera of Halobatinae the first connexival segment also does not extend into the metanotal region).

(3) The female seventh abdominal segment with the ventral apical margin is always lobately produced, and the same segment is excessively developed lateroposteriorly and variously modified. (Modification of the seventh abdominal segment of the female fre-
quently occurs in other groups of the Gerridae, but very rarely the posterolateral region of the segment is as greatly modified as in Ptilomerinae).

Genus *Ptilomera* Amyot and Serville
(Figs. 33, 36, 119-120, 137, 157, 166, 609-641)

*Ptilomera* Amyot and Serville, Hist. nat. insectes, Hémiptères, p. 413 (1843).  

Type species: *Gerris laticauda* Hardwicke, by original designation.


**Color pattern:** General color yellowish brown to ferrugineous red, or rarely nearly black. Clypeus, apices of antenniferous tubercles black. Mesopleural region with a black longitudinal stripe or stripes clothed with short silvery pubescence. Abdominal tergites along lateral margins black and silvery pubescence. Body beneath except head almost totally silvery pubescent.

**Structures in wingless forms:** Male and female of about equal size. Head with anterior region not bent ventrad, widened posteriorly between eyes, posterior margin of head nearly straight. Eye small, broadly rounded on outer margin, sinuate on inner margin. Antenniferous tubercles divergent anteriorly. Antenna slender, shorter than length of body. First segment longer than three following segments together; third segment longer than second and than fourth; fourth segment curved in apical third. Rostrum not extending beyond prosternum, third segment about three times as long as last segment.

Pronotum subquadrangular in shape, about as wide as or a little wider than head including eyes, wider than long at middle, lateral margins broadly rounded, posterior margin nearly straight or feebly concave. Mesonotum about twice to two and a half times as long as pronotum, without either longitudinal sulcus or lateral longitudinal suture separating mesonotum from mesopleuron. Mesosternum with paired longitudinal sutures present in some species,
less than ten times as long as metasternum in most species. Metasternum with distinct median longitudinal sulcus extending throughout entire length of metasternum; metacetabular suture strongly oblique, ventrolateral margin of metacetabulum feebly concave. Metasternum with reduced omphalium located closer to posterior margin than to anterior margin. Front leg with femur simple, a little longer than tibia; tibia with a conspicuous process at inner apical angle; apical inner surface of femur and basal inner surface of tibia with some tubercles; tarsus a little shorter than tibia; first segment about twice to a little less than three times as long as second segment; second segment thickened near apex, claws arising from near apex and with distinct arolium, without significant sexual difference in length of tarsus relative to tibia. Middle leg relatively longer in male than in female; femur in male robust, with a fringe of long hairs except in basal one fourth, femur in female bare and slender, a little less than twice as long as tibia in both sexes; tibia more or less strongly curved, with shorter fringe of hairs on inner margin in both sexes; first tarsal segment about ten times as long as second segment; second segment with small claws arising from near apex. Hind leg longer than middle leg, relatively longer in male than in female; coxa with a small spine on apical margin except for Proptilomera, shorter than wide; femur a little less than twice as long as tibia; both femur and tibia without fringe of hairs; first and second tarsal segments completely fused, very short, claws arising from near apex.

Abdomen long, nearly parallel-sided as far as sixth segment. Anterior margin of first tergite clearly retained, triangularly defined. Anterolateral angle of the tergite elevated and with spiracle; second tergite much longer than first, second to sixth tergites subequal in length to each other, with dense mass of adpressed silvery hairs on sides. Connexivum nearly flattened or slightly reflexed. Second to sixth ventrites subequal in length. Spiracles of second to sixth segments placed closer to anterior margin than to posterior margin of each segment.

Male: Seventh segment longer than sixth segment both dorsally and ventrally, dorsal apical margin nearly straight or slightly concave, broadly concave ventrally. Eighth segment more or less greatly prolonged; ventral surface with basal transverse depression in all species and apical median longitudinal elevation in some species, ventral apical margin more or less produced posteriorly at middle. Ninth segment with suranal plate provided with more
or less conspicuous process on lateral margin in most species; pygophore more or less greatly prolonged in most species, with round apical margin in most species, upper margin with a conspicuous process near middle; parameres long, curved laterally at apex, densely clothed with shaggy hairs in most species. Endosoma with dorsal plate reaching apically to apex of dorsal margin in laticaudata(?) and curved back along apical margin and rounded at apex in Proptilomera; basal plate indistinguishably fused with dorsal plate and gives support apically to slender, long and membranous ventral lobe; lateral plates absent in Proptilomera, but with two pairs of small lateral plates and basal dorsal region sclerotized in laticaudata(?). [Description of genitalia is based on himalayensis and laticaudata(?).]

Female: Seventh segment conspicuously lobately produced laterally, the lobe splits further into upper and lower lobes in Ptilomera s. str. Shape and degree of development of the lobes vary greatly in various species, often among individuals within the same species; ventral apical margin always lobately produced in all species, covering ventral eighth segment. First valvula along inner margin with apical cleft dividing the valvula into two lobes apically, lateral sclerotized area short, densely clothed with oblique long hairs on the area between outer margin and inner membranous region. Second valvula with lateral margin broadly sclerotized, apex directed mesad, narrowly rounded and well sclerotized; intervalvular membrane with a pair of apical processes armed with straight hairs, with a pair of oblique dark spots at bases of apical processes. [Description of the genitalia is based on laticaudata(?).]

Winged forms: Pronotum with anterior lobe well defined by transverse groove; humeri located at apical third of pronotum, posterior margin broadly rounded. Hemelytra with R + M and Cu veins basally distinct from each other, the two veins basally connected by a cross vein beyond middle of hemelytra. Vein A connected with Cu at about apical third of the wing. Hind leg with vein A distinct and connected with Cu at apical third of wing.

Distribution: The Oriental region (Annam, Burma, Celebes, Ceylon, China, Formosa, India, Java, Nepal, Philippines, Sumatra).

Subgenus Ptilomera Amyot and Serville s. str.

For type designation and citations refer to generic bibliography. Body larger. Middle coxa with a spinous process on apical margin. Male eighth abdominal segment often with median
longitudinal elevation on ventral surface; pygophore often prolonged; parameres bent apically and with a mass of shaggy hairs in many species. Female seventh abdominal segment modified posterolaterally; lobate ventral projection large.

Subgenus Proptilomera Hungerford and Matsuda


Type species: Ptilomera himalayensis Hungerford and Matsuda.

Body relatively short. Middle coxa without spinous process on apical margin. Male eighth abdominal segment without either basal depression or longitudinal elevation on ventral surface; pygophore simply rounded on apical margin; parameres simple, without a mass of shaggy hairs apically. Female seventh abdominal segment without modification posterolaterally; lobate ventral projection small.

Modification of the abdomen and some structural characteristics

As will be noted from the above description, all the characters in Proptilomera are more primitive than their counterparts in Ptilomera s. str. From the primitive conditions in Proptilomera, the genital segments have become modified variously in various species as described below.

The male eighth segment: The segment has become more and more prolonged; its ventral surface has become longitudinally elevated medially in the apical half or almost entire length of the pygophore (figs. 624-628), and the ventral apical margin has become produced posteriorly at middle. The median production of the ventral apical margin also occurs in some species of Rhyacobates.

The male ninth segment: The suranal plate has become more and more widened apically in most species (figs. 620-623), has become widened preapically in some species. The pygophore also has become greatly prolonged and narrowed (figs. 624-629), the highest degree of prolongation is noted in werneri (fig. 629) from the Philippines, in which the apex is even acutely pointed; the ventral surface is greatly longitudinally elevated in pamphagus, and the lateral margin of the pygophore is also provided with a more or less conspicuous process basally in all species of Ptilomera s. str. The parameres have become clothed with a dense mass of shaggy hairs in most species, or the apex has become strongly
bent in *canace* (fig. 626), or thickened and bifurcate as seen in *werneri* (fig. 629), although the parameres are quite simple and without hairs in *Proptilomera*.

The female seventh segment: The simplest modification of the upper lateral region of the segment is the production of the spinous process arising from the basal region of the seventh connexival segment only, as seen in one species from Himalaya (fig. 632); the apical lateral region has become further developed and finally the third projection (ventrolateral) has become formed in some species (figs. 634, 635). The degree of development of these lobate projections are even individually highly variable, as pointed out by Lundblad (1933).

The genus shares some peculiar characteristics in common with *Potamometra* as follows:

1. The hind leg is longer than the middle leg.
2. The hind tarsal segments are fused.
3. The length of the front tarsus relative to the front tibia is without sexual difference.

Genus *Potamometra* Bianchi
(Figs. 28, 119-120, 642-655)


Type species: *Potamometra berezowskii* Bianchi, by original designation.

Species examined: *P. Berezowskii* Bianchi, *P. tibetensis* Esaki.

Color pattern: Predominantly black in ground color. A median yellow longitudinal stripe from middle of head down to metanotum, short yellow hairs rather densely scattered on black ground color giving a grayish tinge, silvery adpressed hairs distributed on pleural regions of all three thoracic segments, thus giving an appearance of a broad white band on each side of the body. Legs yellow with black stripes, apical regions on femora of all legs pale yellow.

Structures in wingless forms: Large and broad, with extremely long legs. Head somewhat obliquely directed anteriorly, strongly widened posteriorly between eyes, posterior margin nearly straight. Antenniferous tubercules divergent apically. Eye globular and small, inner margin strongly concave. Antenna shorter than length of body; first segment longer than three following segments together,
relative length of second to first greater in female than in male; fourth segment shortest. Rostrum rather slender, third segment over twice as long as last segment.

Pronotum with lateral margin broadly rounded or convergent anteriorly, wider than head including eyes, posterior margin feebly sinuate on either side of middle or nearly straight. Mesonotum laterally well defined from mesopleural region by a longitudinal suture from behind posterolateral angle of pronotum to intersegmental suture between mesonotum and metanotum. Mesosternum less than ten times as long as metasternum, about three times as long as second abdominal ventrite in male. Metanotum without distinct median longitudinal sulcus; metacetabular suture strongly oblique dorsally. Metasternum relatively longer in male than in female; omphalium placed midway between anterior and posterior margins of metasternum. Front legs longer than body. Femur about one and one sixth times as long as tibia, thick, with numerous small black tubercles on inner margin; tibia with process on inner apical angle conspicuous; tarsus about as long as tibia in both sexes, first segment over three times as long as second; second segment thickened apically, claws arising from near apex, with fine arolium. Middle leg with femur almost twice as long as total length of body, over one and a half times as long as tibia, without hairs on inner margin; tibia with a fringe of long hairs on inner margin except in basal and apical regions, a little less than twice as long as first tarsal segment; first tarsal segment over ten times as long as second segment; second tarsal segment with small claws. Hind legs longer than middle leg; coxa about as long as wide, with a process at inner apical angle projecting posteriorly, the process much more developed in female than in male; femur longer than middle femur, a little less than one and a half times as long as tibia; first and second tarsal segments fused, with small claws arising from near apex.

Abdomen in male: First abdominal tergite very short, its anterior margin distinct; second to sixth tergites inclined posteriorly, seventh tergite sometimes folded beneath the preceding segment. Connexival segments nearly vertically reflexed, second to sixth ventrites strongly reduced, seventh segment ventrally greatly developed and much longer than all preceding segments together. Eighth segment greatly prolonged, cylindrical, lifted upward apically (thus in fig. 643 dorsal apical margin looks concave). Ninth segment with suranal plate roundly produced at middle of lateral margin, apex rounded; pygophore well exposed, subquadrangular in shape and a
little shorter than preceding segment, apical margin slightly produced, with a dark process arising on lateral margin anterior to the base of parameres; parameres long, protruded beyond apex of pygophore. Endosoma with dorsal plate slender, reaching apex of endosoma, basally indistinguishably fused with basal plate, this in turn bears dark slender thread like ventral plate; lateral plates simple and long. (Description of the genitalia is based on *berezowskii*).

**Abdomen in female:** First tergite with anterior margin concave at middle, produced posteriorly as a long process at middle; tergites from second segment on folded to be telescoped into thoracic cavity; ventrally only four basal segments are exposed, the rest telescoped into thoracic cavity. First valvula broad, inner region membranous, a dense mass of straight adpressed hairs located lateral to inner membranous region, long and narrow sclerotized area lateral to the haired area reaching apex of valvula; ramus robust. Second valvula with lateral sclerotized area tapering apically, apex directed posteromesially, rather thick, sclerotized except at extreme apex, broadly rounded; paired processes on apical margin of intervalvular membrane sparsely bearing straight hairs, with a pair of oblique slender sclerotized pieces basal to the processes. (Description of the genitalia is based on *berezowskii*.)

**Winged forms:** Pronotum with humeri located at apical one third, posterior margin broadly rounded. Forewing with R + M and Cu fused basally as in typical gerrinae, but Sc, not connecting Sc and R + M. Hind wing with A reaching to Cu beyond the middle of wing.

**Distribution:** China.

The genus *Potamometra* is peculiar in the following points, which set this genus off from all other genera of the subfamily:

1. The mesonotum is provided with the lateral longitudinal sutures defining the mesopleura laterally.

2. The first abdominal tergite of the female has a conspicuous median projection; the same in the male is very short.

3. The pygophore is subquadrangular in shape.

**Genus Rhyacobates** Esaki

(Figs. 29, 119-120, 656-680)


Type species: *Rhyacobates takahashii* Esaki, by original designation.


Color pattern: Predominantly black dorsally. Head with a median black spot and marginal yellowish brown area. Pronotum black, with a median yellowish brown spot, marginal area of pronotum in winged forms yellowish brown. Mesonotum black, with silvery pubescence, median longitudinal yellowish brown stripe not reaching anterior margin. Legs yellowish brown. Abdomen with connexivum pale yellowish brown or black and silvery pubescent. Meso- and metacetabular regions yellowish brown, silvery pubescent.

Structures in wingless forms: Female much larger than male. Head with anterior margin not bent ventrad, widened posteriorly between eyes. Antenniferous tubercles divergent anteriorly, obtuse at tips. Antenna with first segment longer than three following segments together; second segment subequal to or shorter than third; fourth segment curved in apical half, shortest. Rostrum short, not extending beyond prosternum; third segment over twice as long as last segment.

Pronotum transverse, subquadrangular in shape, lateral margins divergent anteriorly, posterior margin feebly sinuate or nearly straight. Mesonotum about three times as long as pronotum in males, over three times as long as pronotum in females, without lateral longitudinal suture separating mesonotum from mesopleural regions. Mesosternum about ten times as long as metasternum; paired longitudinal sutures sometimes present. Metanotum with median longitudinal sulcus distinct throughout entire length of metanotum; metacetabular suture strongly oblique dorsally. Metasternum with reduced omphalium located at a little behind middle. Front leg longer than body. Femur robust, slightly tapering apically, longer than tibia with inner apical process more or less conspicuous in both sexes; first tarsal segment about one third as long as tibia in male, or a little over half as long as tibia in female, one and three fifths to almost twice as long as second tarsal segment in male, over twice as long as second in female; claws arising from near apex, robust, with hair like arolium arising from base of claws. Middle leg with femur about twice or a little less than twice as long as tibia in both sexes, without dense fringe of long
hairs on inner margin; tibia with a row of short hairs on entire inner margin; first tarsal segment several times as long as second tarsal segment, strongly curved; second tarsal segment without claws. Hind leg shorter than middle leg; coxa longer than wide, without spine on apical margin; femur a little longer than middle femur, about two and a half to three and a half times as long as tibia; tibia with a row of shorter hairs on inner margin; first tarsal segment a little shorter than second tarsal segment; second segment without claws. Abdomen with anterior margin of first tergite slightly produced anteriorly, with a more elevated sub-triangularly defined area laterally, each enclosing first abdominal spiracle within; first to sixth tergites in male transverse, seventh tergite subquadrangular, about twice as long as sixth in male. Connexivum in female strongly reflexed, lateral margins often meet each other above tergites in females, ventrites progressively longer posteriorly. Abdominal spiracles on third to sixth segments placed a little closer to anterior margin than to posterior margin.

**Male:** Seventh segment about one and a half times as long as sixth ventrally. Eighth segment with ventral apical margin slightly produced posteriorly, densely clothed with long hairs; ventral surface transversely depressed basally, longitudinally elevated in middle of apical half. Ninth segment with suranal plate widened in apical half, basal lateral angle with a foot shaped process; pygophore well exposed, rounded on apical margin; parameres simply curved and slender. Endosoma with dorsal plate not reaching middle of endosoma, bifurcate apically, indistinguishably fused with basal plate, which in turn gives support to long and slender ventral lobe, without either well defined lateral plates or apical plate; ventral margin of endosoma more or less sclerotized. (Description of the genitalia is based on lundbladi and takahashii).

**Female:** Seventh segment ventrally about twice or over twice as long as sixth, posterior margin bisinuate, with an inconspicuous median projection; connexivum with posterolateral region of seventh segment modified as shown in figures 671, 673, 676. Eighth segment with first valvula membranous, with or without a small spinous process on inner margin near apex, ventral surface densely clothed with long and straight hairs which are obliquely adpressed, apex narrowly rounded, outer margin sclerotized. Second valvula with lateral margin broadly sclerotized, apex narrowly rounded; intervalvular membrane with a pair of small haired sclerotized processes
on apical margin, with dark spots above the processes on intervalvular membrane.

Winged forms: Pronotum with humeri located much behind middle, broadly rounded behind humeri. Tergites in *lundbladi* much like in wingless forms of the same species. Wing venation (Esaki, 1925) as in *Ptilomera* and *Rheumatogonus*. R + M and Cu veins are basally separated and they are connected by a cross vein.

**Distribution:** The Oriental region (Formosa, Southern China).

**Genus Heterobates Bianchi**

(Figs. 31, 119-120, 681-701)


Type species: *Heterobates dohrandti* Bianchi, by original designation.


**Color pattern:** Black in ground color, clothed with short silvery pubescence dorsally. Head with a median black spot and marginal ochraceous area. Pronotum with or without median longitudinal ochraceous stripe. Mesonotum with a median longitudinal ochraceous stripe. Proacetabular region, coxae and trochanters of all legs ochraceous. Abdomen beneath and mesosternum along median longitudinal axis ochraceous.

**Structures in wingless forms:** Head not bent ventrad, widened posteriorly between eyes. Antenniferous tubercles divergent anteriorly. Antenna about as long as body in male, considerably shorter than body in female. First segment longer than three following segments together; second segment longer than third; fourth segment shortest, curved in apical half. Rostrum thick and densely clothed with gray hairs; third segment over twice as long as last segment.

Pronotum a little wider than head including eyes, posterior margin feebly concave but feebly produced medially, lateral margins slightly divergent anteriorly. Mesonotum about three times as long as pronotum in male, about four times as long as pronotum in female. Mesosternum about ten times as long as metasternum, without longitudinal suture separating mesonotum from meso-
pleural region; with distinctly demarcated median flattened area extending the entire surface of mesosternum and further onto apical abdominal segments in female. Metanotum has distinct median longitudinal sulcus. Metacetabular suture dorsally strongly oblique. Metasternum with highly reduced omphalium located closer to posterior margin than to anterior margin of metasternum. Front leg with femur sparsely clothed with long hairs on inner margin, about one and one fifth times as long as tibia; tibia with a conspicuous process at inner apical angle; tarsus a little over half as long as tibia in male, or about two thirds as long as tibia in female; first tarsal segment about one and a half to about twice as long as second segment; second segment with claws arising from apical one fourth and with membranous arolium which is apically curled. Middle leg with femur longer than body, relative length of femur to body greater in male than in female, a little over twice as long as tibia; tibia with fringe of rather conspicuous hairs in both sexes; tarsus strongly curved and flattened; first segment several times as long as second, fringed with hairs in basal one fourth; second segment without claws. Hind leg shorter than middle leg. Coxa longer than wide, without spine on apical margin; femur over four times as long as tibia; tibia strongly curved apically, with inconspicuous fringe of hairs on entire inner margin; first tarsal segment shorter than second segment; second segment without claws.

**Abdomen in male:** Anterior margin of first tergite recognizable, produced anteromesially, first abdominal spiracle clearly recognizable, anterior margin of second tergite produced anteriorly; third to fifth subequal in length; sixth a little longer than fifth; ventrally second to sixth subequal in length; seventh a little longer than sixth, its posterior margin broadly concave. Eighth segment with dorsal apical margin rounded, slightly produced posteromesially on ventral apical margin. Ninth segment with suranal plate widened preapically and flattened laterally; pygophore well exposed, narrowly rounded on apical margin; parameres well exposed, slender and long, narrowly rounded on apical margin. Endosoma with dorsal plate hook-shaped, bent obliquely cephalad apically, extending beyond middle of endosoma, indistinguishably fused with basal plate, which in turn is fused with narrower ventral plate; ventral plate membranous apically; lateral plates oblique, located basally; apical plates connected posteriorly to each other by a narrow transverse bridge, the bridge in turn connected with apex of dorsal plate. (Description of the genitalia is based on *dohrandti*).
Abdomen in female: Basal tergites obliterated due to reflection of connexivum. Connexivum slanting towards middle basally, exposed area of tergites triangular, each tergite becoming progressively larger posteriorly, posterolateral angle of sixth connexival segment subrectangularly produced inward; spiracles of second to sixth ventrites placed at middle of each segment. Seventh segment broadly rounded on dorsal apical margin, lobately produced laterally, with rather acute or broadly rounded apex, ventral lobate apical margin straight, totally or not totally covering eighth segment above. Eighth segment with dorsal apical margin broadly rounded. First valvula with inner half largely membranous and densely clothed with straight, long and adpressed hairs which are directed caudad, apex sclerotized and narrowly rounded, outer margin well sclerotized; ramus robust, arising from beyond apex of lateral well sclerotized area. Second valvulae with outer margin broadly rounded, membranous near apex, apices directed mesad and rounded; intervalvular membrane with two small membranous processes bearing hairs on apical margin, black spot at bases of processes obliterated. (Description of the genitalia is based on dohrandti.)

Distribution: Nepal, Northern India, Turkestan.

This genus is closely related to Rhyacobates, but differs by the following characteristics:

(1) The ventral side of the body with distinctly demarcated area extending from the mesosternum to the apical abdominal segments in the female.

(2) The hind femur is over four times as long as tibia; it is less than three and a half times as long as tibia in Rhyacobates.

(3) The middle femur is over twice as long as the middle tibia; it is less than twice as long as tibia in Rhyacobates.

(4) The second antennal segment is always longer than the third; the second is as long as or shorter than third in Rhyacobates.

(5) The anterolateral angle of the mesonotum is somewhat produced.

Genus Potamometroides Hungerford
(Figs. 35, 119-120, 702-712)


Type species: Potamometroides madagascariensis Hungerford, by original designation.

Species examined: P. madagascariensis Hungerford.

Color pattern: Body above predominantly black. Head with a black spot continuous with black marginal area along eyes. Clyp-
eus and basal region of head yellowish brown. Pronotum black, with median yellowish brown stripe. Mesonotum totally black, with lateral longitudinal stripes composed of silvery pubescence reaching posteriorly to metathoracic spiracle. Abdomen entirely black above, pro-, meso- and metapleural regions yellowish brown. Meso- and metasternal regions black. Legs yellowish brown to nearly black.

**Structures in wingless forms:** Head not bent anteriorly, strongly widened posteriorly between eyes, posterior margin nearly straight or feebly concave. Antenniferous tubercles divergent anteriorly. Antenna a little longer than length of body in male; first segment longer than three following segments together; second segment as long as third; fourth segment curved and shortest. Rostrum not extending beyond prosternum; third segment twice as long as last segment.

Pronotum widened anteriorly, wider than head including eyes, posterior margin produced posteriorly at middle in female, nearly straight in male. Mesonotum about three times as long as pronotum in both sexes, without lateral longitudinal suture separating mesonotum from mesopleuron, posterior margin concave dorsally. Mesosternum over ten times as long as metasternum. Metanotum without median longitudinal sulcus. Metacetabular suture dorsally strongly oblique. A long process arising from dorsal apical angle of mesoacetabulum superposed on metacoxa in female. Metasternum with reduced omphalium, posterior margin less concave in female than in male. Front leg with femur one and one fifth to one and one sixth times as long as tibia; sparsely clothed with long straight hairs on inner margin; tibia with inner apical process conspicuous, twice as long as first tarsal segment in female, three times as long as first tarsal segment in male; first tarsal segment a little less than twice as long as second segment; second tarsal segment with claws arising from near apex, claws with slender membranous arolium. Middle leg with coxa rather short; femur a little less than twice as long as tibia, without fringe of hairs; tibia with fringe of long hairs on inner margin, narrowed apically; first tarsal segment strongly curved, about five times as long as second; second segment without distinguishable claws. Hind leg shorter than middle leg; coxa about three times as long as wide, slightly narrowed apically; femur relatively longer in male than in female, about four times as long as tibia in male, about three times as long
as tibia in female; first tarsal segment a little shorter than second segment; second segment without claws.

**Abdomen in male:** Shorter than mesonotum and metanotum together. First tergite with anterior margin distinct, obliquely ridged laterally; second tergite with anterior margin broadly produced, long; third to fifth tergites subequal in length; sixth tergite longer than fifth; seventh tergite much longer than sixth, broadly rounded on apical margin; second to sixth ventrites greatly reduced; seventh segment ventrally over twice as long as sixth at middle and broadly concave on apical margin. Eighth segment greatly prolonged and cylindrical, convex on dorsal apical margin and nearly straight on ventral apical margin. Ninth segment with lateral projection not conspicuous; pygophore well exposed, rather strongly narrowed apically, apical margin rounded; parameres well developed. Endosoma with dorsal plate indistinguishably fused with basal plate, thinly sclerotized, boot-shaped process on ventral margin of dorsal plate, reaching middle of endosoma; ventral plate fused with basal plate at basal ventral angle of endosoma, broad and strongly sclerotized, membranous and lobate apically, ventral margin of endosoma lobately produced apically, without well defined lateral plate. (Description of the genitalia is based on madagascariensis.)

**Female:** Abdomen, leaving first tergite dorsally and second ventrite ventrally, completely telescoped into thoracic cavity. First tergite as in male; seventh ventrite simply elongate and with feebly concave apical margin. First valvula densely clothed with straight adpressed hairs directed caudad on inner half, apex narrowly rounded, sclerotized in apical region, upper lateral margin sclerotized; ramus attached to the process of ninth tergite at apex. Second valvula with lateral margins well pigmented, apical well sclerotized process located mesal to apical end of sclerotized lateral margin; ramus fine, arising from near apex of lateral margin of second valvula, basally reaching apex of process of ninth tergite; intervalvular membrane with a pair of small processes, sparsely clothed with hairs on apical region of intervalvular membrane, crescent shaped spot above base of apical processes of intervalvular membrane. (Description of the genitalia is based on madagascariensis.)

**Distribution:** The Ethiopian region (Madagascar).

The genus *Potamometroides* and *Potamometra* are the only genera in which the abdomen of the female is telescoped into the thoracic cavity. This, however, does not suggest any close rela-
tionship between the two genera. As already noted elsewhere, *Potamometra* shares a few peculiar characteristics in common with *Ptilomera*, and it has three peculiar characters which set this genus off from all the other genera. The withdrawal of the abdomen in the female of these two genera is apparently a case of parallelism. It is interesting also to point out that a well-developed conspicuous process occurs on the posterior margin of the first tergite and at the inner apical angle of the hind coxa in the female of *Potamometra*, while a similar process occurs at the inner apical angle of the metacetabulum in the female of *Potamometroides*.

Genus *Potamometropsis* Lundblad

*(Figs. 30, 119-120, 713-731)*


Type species: *Potamometropsis obnubila* Lundblad, by original designation.


Color pattern: Uppersurface predominantly black and silvery pubescent. Head with a large black spot on centre, yellowish brown marginally. Pronotum with median yellowish spot or stripe. Meso- notum with or without yellowish brown spots, with lateral silvery stripe from anterior margin to metathoracic spiracle. Abdomen above black except for connexivum of *P. hoogstraali* which is yellowish brown. Body beneath largely yellowish brown, silvery pubescent throughout the entire surface.

Structures in wingless forms: Head not bent anteriorly, slightly widened posteriorly between eyes, much narrower than anterior region, posterior margin of head concave. Antenniferous tubercles divergent anteriorly. Antenna a little shorter than length of body. First segment about as long as three following segments together; second segment shorter than third segment; relative length of second to third is a little greater in male than in female; third segment truncate at apex; fourth segment shorter than third, curved at middle. Rostrum not extending beyond prosternum; third segment a little over twice to about three times as long as last segment.

Pronotum wider than head including eyes, lateral margin broadly rounded, posterior margin either concave or convex. Mesonotum about two and a half times as long as pronotum, relatively a little longer in female, posterior margin of mesonotum feebly concave at
middle; lateral longitudinal suture separating mesonotum from mesopleuron absent. Metanotum with median longitudinal sulcus obsolete; metacetabular suture dorsally gently oblique, nearly horizontal. Metasternum with vestigial omphalium located close to posterior margin. Front leg with femur one and one fourth to one and one third times as long as tibia, a little thicker in male than in female; tibia with inner apical process more conspicuous in female than in male; first tarsal segment less than twice as long as second, second segment with claws arising from near apex, claws with arolium. Middle leg with coxa short; femur straight, much longer than length of body, a little less than twice as long as tibia, without fringe of hairs on inner margin; tibia strongly curved and with fringe of long hairs throughout entire inner margin in both sexes; first tarsal segment between three and four times as long as second segment; second segment with distinct claws arising from near apex. Hind leg shorter than middle leg; coxa a little longer than wide; femur between two and three and a half times as long as tibia; tibia fringed with hairs throughout the entire inner margin; first tarsal segment much shorter than second segment; second segment with distinct claws.

Abdomen with anterior margin of first tergite distinct, first tergite with median elevation arising from anterior margin in female of werneri; sixth tergite with median apical production in female of hoogstraali. Connexivum either flattened horizontally or subvertically erected, apical angle of sixth connexival segment strongly produced in female of hoogstraali; second ventral segment much shorter than metasternum; second to sixth ventrites subequal in length. Abdominal spiracles of second to sixth segments located at about middle of each segment.

Male: Seventh segment dorsally over twice as long as sixth tergite, ventral apical margin broadly concave, also over twice as long as sixth ventrite. Eighth segment strongly produced except for hoogstraali, its dorsal apical margin broadly rounded. Ninth segment with suranal plate simply widened preapically; pygophore well exposed and long; parameres conspicuous and long. Endosoma with dorsal plate hook-shaped, apex directed obliquely cephalad, thinly pigmented and completely fused with thick and dark basal plate, which in turn gives support to ventral lobe; ventral lobe largely membranous; lateral plates obliquely placed. (Description of the genitalia is based on hoogstraali).
Female: Seventh segment ventrally excessively developed, and ventral apical region greatly varies in shape in various species. Eighth segment ventrally completely covered by apical region of seventh ventricle except for obnubila, in which seventh segment is least prolonged and eighth segment apically exposed ventrally. First valvula broad, inner half densely clothed with long straight hairs directed caudad, with sclerotized area lateral to inner haired area, apex narrowly rounded; ramus reaching apical third of valvula. Second valvula with lateral margin broadly sclerotized, apical lobe directed posteromesially, broadly rounded apically; intervalvular membrane with a pair of small apical processes bearing straight hairs, with strongly pigmented U-shaped spot above apical margin; ramus slender, arising from near apex of second valvula, not much extending caudad along lateral margin of the valvula. (Description of the genitalia is based on hoogstraali.)

Distribution: The Oriental region (Sumatra, Philippines).

The genus Potamometropsis shares two important characters in common with Rheumatogonus, i.e., the nearly horizontal metacetabular suture and the absence of the modification of the posterolateral region of the seventh abdominal segment of the female. They are probably more closely related to each other than to others, but Potamometropsis differs from Rheumatogonus in the anterior margin of the head which is not rounded and in the first antennal segment which is relatively longer.

Genus Rheumatogonus Kirkaldy
(Figs. 32, 119-120, 127, 732-747)


Type species: Ptilomera luzonicus Kirkaldy, monobasic.
Species examined: R. burmanus (Distant), R. intermedius Hungerford.

Color pattern: Predominantly yellowish brown, tergites fuscous to nearly black, or sometimes yellowish brown. Metanotum with median black longitudinal stripe in intermedius.

Structures in wingless forms: Relatively small in size and cylindrical in shape. Head with anterior region of head strongly bent ventrad and anterior margin broadly rounded, widened posteriorly between eyes, posterior margin of head nearly straight. Eye large
and long, exserted. Antenniferous tubercles with cavities open ventrad. Antenna considerably shorter than length of body; first segment considerably shorter than three following segments together; second segment equal to or longer than third; fourth segment shorter than third, slightly curved in apical third. Rostrum not extending beyond prosternum; third segment with paired long hairs near apex on dorsal surface, a little over twice to three times as long as last segment.

Pronotum with lateral margins divergent anteriorly or rounded, about as wide as head including eyes, posterior margin slightly sinuate on either side of middle. Mesonotum with dorsal posterior margin feebly concave, its relative length to pronotum a little over twice as long as pronotum in male, over two and a half times as long as pronotum in female. Mesosternum with posterior margin slightly concave, about ten times as long as metasternum. Metanotum with median longitudinal sulcus not recognizable in intermedius, normally distinct in burmanus, lateral longitudinal suture separating mesonotum from mesopleuron absent; metacetabular suture dorsally nearly horizontal. Metasternum with omphalium inconspicuous, located at apical third of metasternum. Front leg a little shorter than body; femur one and one third to one and a half times as long as tibia, sparsely clothed with dark hairs on inner margin; tibia gradually thickened apically, inner apical process not conspicuous; relative length of tarsus to tibia considerably greater in female than in male, ranging from one and seven tenths to two and one third times as long as tibia; first tarsal segment as long as or shorter than second in male, or a little longer than second in female, claws arising from apical third of second segment. Middle leg with coxa short; femur less than twice as long as tibia, without fringe of hairs; tibia curved, about three times as long as first tarsal segment; first tarsal segment four to five times as long as second, both segments highly curved, second one with distinct claws. Hind leg shorter than middle leg; coxa a little longer than wide; femur about three times as long as tibia; tibia about ten times as long as tarsus, strongly curved apically; first tarsal segment a little shorter than second segment, which is without claws.

Abdomen with anterior margin of first tergite distinct, feebly convex, with anterolateral subtriangularly defined area enclosing spiracle, short; second tergite about as long as wide, much longer than either first or third tergite; third to sixth tergites subequal in length, narrowed apically. Connexivum more or less reflexed,
neither greatly modified nor folded on dorsum. Abdominal spiracles of second to sixth ventrites placed at middle of each segment.

**Male:** Seventh segment about twice as long as sixth segment both dorsally and ventrally, broadly rounded on dorsal apical margin and concave on ventral apical margin. Eighth segment more or less greatly prolonged, telescoping basal ninth segment within. Ninth segment with lateral production of suranal plate not conspicuous; pygophore well exposed, broadly rounded on apical margin; parameres well developed, simply curved upward and tapered apically. Endosoma membranous, dorsal plate thinly sclerotized and short, basally fused with strongly sclerotized oblique and robust basal plate, which bears apically slender, short and membranous ventral plate; without well-defined lateral plates. (Description of the genitalia is based on *intermedius*.)

**Female:** Seventh segment greatly prolonged, ventrally with median lobate process covering eighth segment, laterally simply acutely pointed, dorsally nearly straight on apical margin. Eighth segment with first valvula rather narrow, long adpressed hairs relatively scarce, apex obtusely rounded; ramus rather slender, attached to outer apical angle of process from ninth tergite. Second valvula with lateral margin broadly sclerotized; ramus fine, apical process arising mesal to apical region of the valvula, narrow and long, directed more or less mesad, apical paired processes of intervalvular membrane without conspicuous mass of hairs, with an inversed V-shaped spot above base of apical processes of intervalvular membrane. (Description of the genitalia is based on *intermedius*.)

**Winged forms:** Pronotum widest at apical one third, broadly rounded on apical margin. Hemelytra with $R + M$ and $Cu$ are connected by a cross vein at basal one fourth; $Cu$ and $A$ are united at a little beyond middle of hemelytron.

The genus *Rheumatogonus* is specialized in that the anterior margin of the head is strongly bent ventrad, but it is more primitive than any other genera in that the first antennal segment and the femora of all legs are relatively much shorter than in other genera, in other words, they have not been as greatly prolonged as in other genera in adaptation to their peculiar habitat (swift and turbulent currents). Another primitive feature is that the seventh abdominal segment of the female is not modified on the posterolateral area.
Genus *Pleciobates* Esaki


Type species: *Pleciobates tuberculatus* Esaki, by original designation.

The specimens of this genus have not been available for study. The following is the original description by Esaki:

"*Apterous form; female*: Body oblong, fusiform. Head much longer than broad between eyes, anteocular portion not longer than the rest of head. Eyes much rounded laterally, slightly emarginate interiorly. Antennae very long and slender, not longer than body, first segment longer than the rest of antennae, second and fourth segments subequal in length, third one-third the length of first, a little longer than the second. Rostrum not passing the anterior coxae, third segment much the longest, a little swollen at middle. Pronotum transverse, anterior and posterior margins nearly straight. Mesonotum very large, three times as long as pronotum, lateral margins not quite parallel. Metanotum much shorter than mesonotum, a little longer than pronotum, lateral portions more or less confluent with mesothorax, separated into two portions antero-posteriorly, posterior portion much shorter than the anterior portion. Anterior legs slender, femur stoutest, slightly tapering towards the apex, tibia more slender and shorter than femur with an acute process at the inner side of apex, tarsus much longer than half the length of tibia, first segment one and a half times as long as second. Intermediate and posterior legs very long and slender; intermediate femur much longer than body; tibia more slender than femur, a little longer than half of the latter; tarsus about one half of tibia, much thinner than tibia, tapering towards the apex, first segment about six times as long as second; posterior femur slightly shorter and much thinner than intermediate femur, tibia about a half of femur tapering towards the apex, tarsus very short, not longer than one tenth of tibia, first segment about twice the length of the second. Intermediate and posterior acetabula lateral to the abdomen. Abdomen broad and short, about as long as mesonotum. Dorsal segments very broad, first four segments subequal in length, fifth longer than the two preceding segments together, sixth shorter than the fifth. Ventral segments ring-shaped, first five segments equal in breadth, the sixth much narrower, more or less tube-like. Female genital segments very small, slightly protruding the end of abdominal segment. Connexivum broad, almost perpendicularly erected, ending into a very long, stout spine-like process,
which is much projecting beyond the end of abdominal segment. “Male and the macropterous form unknown.

“Type: Pleciobates tuberculatus sp. nov.

This genus undoubtedly belongs to the subfamily Ptilomerinae. It differs from the other genera of the subfamily in the shorter head, very remarkable structure of the connexivum, and in some other less important characters. The female of Ptilomera Amyot et Serville have an apparently similar structure of the connexivum to that in this genus, but in the former the apical prolongation is rather filament-like, whereas in the latter the same is stout and spine-like. As a matter of fact this genus is more closely allied to Rhycobates Esaki, than to Ptilomera Amyot et Serville.

“Pleciobates tuberculatus sp. nov.

“Apterous female: Body black with brown markings, and grayish pubescence. Head dark brown, a large middle spot on the anterior part of vertex, basal margin of head, antenniferous tubercles, extreme apex of frons black, with minute brown pubescence. Eyes black, shining. Antennae totally black. Rostrum very pilose, dark brown with the apical half of the third and the entire fourth segment black. Dorsal surface of thorax pitchy black, more or less shining, a conspicuous longitudinal brown marking in the middle of pronotum; lateral sides, suture between meso- and metanotum and a small area on each side of the median longitudinal line of mesonotum with silvery, grayish pubescence. Prosternum pale brown with the same coloured pubescence, with a very small black spot at the end of the acetabular suture. Mesosternum black, except the posterior area and acetabulum which are pale brown, with very dense grayish pubescence. Metasternum (apparently the first ventral abdominal segment) pale brown, thickly pubescent. Anterior coxa, trochanter and femur brown, extreme base and apex of femur, three conspicuous stripes on the femur, tibia and tarsus black. Intermediate and posterior legs black with the coxae, trochanters and the base of the intermediate femur brown. Dorsal surface of abdomen pitchy black, coarsely covered with grayish pubescence, apex of the last genital segment brown. Connexivum pitchy black with the apical prolonged portion pale brown. Ventral surface of abdomen pale brown, sixth segment much darker; thickly covered with silvery grayish pubescence.

“Body fusiform, about three times as long as broad. Antennae a little shorter than body, first segment longer than the rest of the antennae, ratio of the antennal segments: 18:5:6:5, the last segment
slightly flattened near apex. Pronotum transverse, anterior and posterior margins straight; mesonotum very large, moderately convex, a little widened posteriorly; metanotum about one half of the mesonotum in length, lateral portions much protruded anteriorly, divided into two portions by a distinct transverse ridge, the anterior portion about five times as long as the posterior one, with a conspicuous tubercle-like process in the middle of the ridge (well observable in profile). The characters of the legs are given in the generic description. Abdomen broad and short, about as long as mesonotum, narrowed posteriorly; first four segments nearly equal in length, fifth slightly shorter than the preceding three segments taken together, sixth a little shorter than the fifth. Connexivum broad, almost perpendicularly erect, forming a very conspicuous, long, stout spine-like process at the end, which is almost as long as the last two dorsal abdominal segments taken together, directed inwardly and crossed with each other at the apex. First four ventral abdominal segments very short, increasing the length from first to fourth; fifth much longer than fourth, nearly as long as third and fourth taken together; sixth very long, nearly as long as three preceding segments taken together, much rounded and narrowed posteriorly. Genital segments very small, mostly inserted in the sixth segment.

"Length of body 7 mm., breadth of body 2.3 mm., length of intermediate femur 9.5 mm., length of intermediate tibia 5.5 mm., length of posterior femur 8.5 mm., length of posterior tibia 3.5 mm.

"Male and macropterous forms are unknown.

"Habitat: Malay Peninsula."

The above original description and the figures given by Esaki require reinterpretations in certain respects. Esaki evidently believed that the metanotum is divided into two portions, i.e., anterior and posterior portions as in his previous works on the Gerridae, but the posterior portion is actually the first abdominal tergite. Thus the italicized part in the above description should be read "anterior margin of first tergite distinct, metanotum much longer than first tergite." In his figure a, the metacetabular suture runs obliquely forward, instead of rearward, to reach the intersegmental suture between the mesonotum and metanotum. The direction of the suture is very probably wrong, the suture in all other genera of the subfamily runs obliquely caudad dorsally to reach the anterolateral angle of the first abdominal tergite. He says that the first tarsal segment of the hind leg is twice the length of the second segment.
If this is true this genus is quite unique in this character, since the first tarsal segment of the hind leg is always about as long as or even shorter than the second segment in all other genera of the Ptilomerinae.

**Subfamily Halobatinae Bianchi**


**Structures in wingless forms: Body small, a little longer than wide.** Head with anterior margin broadly rounded except for marine genera. Clypeus with basal margin obliterated except for marine genera. Eye with inner margin feebly rounded, covering posteriorly at least anterior half of pronotum. Antenniferous tubercles not or weakly developed except for marine genera. Antenna slender, shorter than length of body; first segment longest, shorter or longer than second and third segments together; **relative length of second to third segment greater in males than in females except for marine genera**; third segment modified in males of *Esakia*; fourth segment slender and simple in most genera, or short and more or less strongly curved in some genera. Mandibular and maxillary plates distinct from each other. Rostrum relatively short; third segment less than three times as long as last segment in great majority of species.

Pronotum not prolonged, much shorter than head in some genera. Intersegmental suture between mesonotum and metanotum dorsally represented by posterior margin of mesothoracic scutocutellum, laterally obliterated except for *Asclepios*. Longitudinal suture separating mesopleuron from mesonotum absent in all genera. Mesosternum without paired longitudinal suture. Metanotum with median longitudinal sulcus indistinct or absent, metanotal lateral longitudinal suture rather weakly developed except for *Esakia*. Metacetabular suture dorsally approaching anterolateral angle of first tergite in some genera. Metathoracic spiracle small and longitudinally placed. Metasternum much reduced, represented by a short transverse subtriangular plate either reaching or not reaching metacetabula laterally or by omphalium alone; omphalium borne on apical margin of metasternum; omphalial groove absent. Front leg with femur and tibia have modification on inner margin in some genera; tarsus with first segment highly reduced except for *Halobates*; second segment much longer than first except for *Halobates*;
plates always produced roundly longer than times several which sclerotized along inner dorsal of plate dorsal claws always margin. Second ventral apical plate slender Eurymetropsis, in apical with anterior simple; pygophore of segment ventrally, segments of species of which inner margin more or less prolonged in marine genera; tibia about half as long as or less than half as long as femur; first tarsal segment about as long as second segment in majority of species, first and second tarsal segments fused in Halobates.

Abdomen with ventrite more or less greatly reduced; first tergite with anterior margin distinct in most species, nearly straight; second and third tergites with their anterior margins, when distinct, roundly produced anteriorly. First ventrite absent. Connexivum with anterior segments often fused, not reflexed on dorsum, without connival spine.

Male: Seventh segment longer than a preceding segment or segments ventrally, simply concave or nearly horizontal on ventral apical margin. Eighth segment more or less greatly prolonged, modified dorsally in Halobates. Ninth segment with suranal plate simple; pygophore with apical margin simply rounded except for Eurymetropsis, in which it is strongly bifurcate; rotated in some species of Halobates; parameres present except for marine genera, in which it is highly reduced or lost. Endosoma with definitive dorsal plate always curved back along apical margin of endosoma (fused part of apical plate); basal plate arising from behind base of dorsal plate or indistinguishably fused with dorsal plate; lateral plates always present, usually in basal half of endosoma; ventral plate slender and long, membranous apically.

Female: Seventh segment greatly prolonged, simply concave in ventral apical margin except for Metrocoris, in which ventral apical margin more or less greatly developed and modified in shape. First valvula either membranous or thinly sclerotized along outer margin; inner lobe small and fused with vulva except for Esakia, in which inner lobe is folded beneath outer lobe; outer lobe differentiated or split into hairy inner region and outer region in marine genera; ramus connected with process of ninth tergite on its outer margin. Second valvulae convergent apically; intervalvular membrane always with paired lateral membranous lobes which converge apically, a fine transverse dark stripe above apical margin of intervalvular membrane. Vulva simply rounded, membranous or thinly sclerotized along apical margin in most species.
Table 13.—Table of significant generic characters in Halobatinae.

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TABLE 13.—Table of significant generic characters in Halobatinae.—\textit{Concluded}

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For the explanations of symbols see introduction and table 5.

\textit{Winged forms:} Hemelytra with embolium always well formed along front margin of hemelytra. \( R + M + Cu \) branched into anterior \( R + M \) and posterior \( Cu \). \( R + M \) either connected or not connected with embolium by oblique vein; \( Cu \) joined with A apically. Line of weakness absent.

Relationships of genera

The marine Halobatini, which includes two genera, *Asclepios* and *Halobates*, are quite distinct from the fresh water genera by some characters adaptive to the marine habitat and by peculiar modifications in the male apical abdominal segments, while retaining some characters more primitive than any fresh water genus. *Halobates* is nothing but a specialized group of *Asclepios*.

Among the fresh water genera, *Metrocoris* and *Eurymetra* have the highest number of primitive characters and they are closely related. While *Metrocoris* is confined to the Oriental region, *Eurymetra* occurs in Africa. In Africa there occur two other *Eurymetra*-like genera, *Eurymetropsis* and *Eurymetropsiella*. They have become distinct from *Eurymetra* by further specialization in certain structures as noted from table 13. The other rather remotely related genera, *Ventidius* and *Esakia*, occur solely in the Oriental region. They are different from the rest in the shorter pronotum, larger eyes, and the rather strongly flattened metacetabula, etc. *Ventidius* (*Ventidioides*) is nothing but a specialized group of *Ventidius* *s. str.*, but *Esakia* has become quite distinct from *Ventidius* with acquisition of some specialized characters, such as the strongly modified third antennal segment in the male, etc. *Eurymetropsielloides*, though occurring in Africa, shares some more or less important characters in common with the *Ventidius-Esakia* complex, such as the shorter pronotum and large eyes, but the narrow and simple metacetabulum is like that of *Metrocoris*.

The relationships of genera may be expressed as in diagram 8.

![Diagram 8](image-url)

*Diagram 8—Diagram showing the relationships of genera of the Halobatinae.*
Tribe Halobatini Bianchi

Color pattern: Predominately black dorsally, clothed with short velvety hairs. Head yellow to orange along eyes.

Structures in wingless forms: Head with anterior margin feebly produced medially and on each side of the middle; basal margin of clypeus distinct. Antenniferous tubercles produced forward. Interssegmental suture between mesonotum and metanotum absent dorsally in most species. Metasternum greatly reduced but reaching laterally metacetabular regions. Front leg has tibia without conspicuous inner apical process; first tarsal segment about as long as or a little shorter than second in most species. Middle leg with tibia provided with a row of hairs in all species; first tarsal segment with a row of hairs in most species. Hind leg with tarsal segments fused in Halobates; coxa longer than wide. Abdomen has the anterior margin of first tergite obliterated in most species. Male eighth segment with dorsal apical angle produced in most species; ventrolateral angle of male eighth segment with conspicuous process in all species. Ninth segment with suranal plate provided with more or less conspicuous projection at middle in most species; parameres highly reduced or absent.

Distribution: Temperate and tropical zones of the Pacific, the Indian, and the Atlantic oceans, and the Red sea.

Evolutionary tendencies peculiar to Halobatini

Both Asclepios and Halobates, while maintaining the same basic structural pattern as the fresh water genera of the same subfamily, exhibit some quite peculiar evolutionary trends as follows:

(1) The body surface is clothed with short velvety hairs.
(2) The wings are always absent.
(3) The body size has apparently become larger in the course of evolution.
(4) The first tarsal segment of the front leg has presumably become longer in the course of evolution.
(5) A row of long hairs on the middle tibia occur in both Asclepios and Halobates, the row of long hairs occurs also on the middle first tarsal segment in addition to the middle tibia in the specialized genus, Halobates.
(6) The hind coxa has apparently become prolonged.*
(7) The hind tarsal segments have become fused in the more specialized genus, Halobates.*

* Occurs also in other subfamilies.
(8) Modifications of the posterior ventrolateral and dorsolateral angles of the eighth segment in the male (process) have become more conspicuous in the more specialized genus, Halobates.

(9) The parameres have become vestigial or lost, while well retained in the fresh water genera.

(10) The suranal plate has become conspicuously widened at the middle in the more specialized genus, Halobates.*

While some of the above-mentioned evolutionary tendencies are adaptive ones to the marine habitat, others appear to have nothing to do with the peculiar habitat (e.g., modifications of the abdomen). In spite of the high degrees of specialization of the above mentioned structures, the tribe Halobatini has remained more primitive than the fresh water genera in the following structures:

(1) The basal margin of the clypeus is distinctly retained.

(2) The antenniferous tubercles are also retained and the anterior margin of the head in dorsal view is, therefore, not simply rounded as in the fresh water genera.

(3) The intersegmental suture between the mesonotum and metanotum is clearly retained laterally and is continuous to the metathoracic spiracle in Asclepios and some species of Halobates.

(4) The metasternum, though much reduced, reaches the metacetabular region laterally.

Modifications of the abdomen in Halobatini
(Figs. 751, 756, 770-776)

The male seventh segment: In Asclepios the seventh segment is prolonged but the ventral apical margin is concave, and the segment is transverse ventrally (fig. 751). In Halobates the segment is more prolonged and the ventral apical margin is nearly straight or even slightly produced medially. In H. proavus, sericeus, japonicus, sobrinus, and hayanus the seventh ventrite is twice as wide as long; in H. mariannarum (fig. 774) the seventh segment is less than twice as wide as long; in H. splendens, flaviventris and micans (fig. 770) the seventh ventrite is only slightly wider than long; in H. hawaiensis (fig. 773) it is almost as long as wide.

The male eighth segment: In Asclepios (figs. 748, 751) the eighth segment is well exposed both dorsally and ventrally; the dorsal apical margin is simply rounded or feebly concave and the ventral processes are relatively short and simply rounded apically. In Halobates the eighth segment is more or less hidden beneath the more prolonged seventh segment. The dorsal lateral angle is pro-

* Occurs also in other subfamilies.
ved with an obtuse process of varying degrees of development. The ventral paired lateral processes are simple but longer in *H. hayanus*, *sericeus*, *japonicus*, *sobrinus*, *flavicentris* and *proavus* than in *Asclepios*; they are thickened and truncate at apices in *hawaiiensis* (fig. 772); they are strongly asymmetrical in *mariannarum* (fig. 774) *splendens* and *micans*.

**The male ninth segment:** The suranal plate in *Asclepios* is simple although widened at middle. In *Halobates* the median widening is least conspicuous in *mariannarum*; more conspicuous and nearly rectangularly produced laterally at the middle in *germanus*, *japonicus*, *sericeus*, *splendens*, and *hayanus*; subrectangularly produced laterally and with a fine process at the middle of each side in *hawaiiensis* and *micans*; with a conspicuous process at the middle in *flavicentris* and *sobrinus*. The pygophore is not rotated in *Asclepios*, but it is rotated in *H. splendens* and *H. mariannarum* (fig. 774).

**The female seventh segment:** In *Asclepios* the seventh ventrite is broadly concave and relatively short. In some species of *Halobates* (*proavus*, *sericeus*) the seventh ventrite is relatively short and the ventral apical margin is somewhat concave, but in all others the seventh ventrite is more prolonged and the apical margin is nearly straight or even slightly produced at the middle; in *hawaiiensis* (fig. 771) the basal margin of the seventh ventrite is broadly concave and the apical margin is feebly bisinuate.

**Modifications of the other structures in Halobatini**

**The body size:** As already noted, *Asclepios* is more primitive in many characters than in *Halobates* but the size of the body (45-57)* is definitely smaller than *Halobates**. In *Halobates*, as noted from the preceding discussion of the evolution of the abdomen, there is a rather striking tendency for the body size to be generally smaller in the species with more primitive abdomens, such as *proavus* (56), *sericeus* (54), *germanus* (58), *hayanus* (69), *sobrinus* (67), *japonicus* (69) than in the species with generally more specialized abdomens such as *mariannarum* (75), *hawaiiensis* (87), *splendens* (81). It appears that the prolongation of the seventh segment in both sexes is at least a great contributing factor toward the enlargement of the body in the larger species. The body size has apparently become larger in the evolution of these marine genera, contrary to the tendency toward reduction of the body size which prevails in the great majority of the groups of the Gerridae.

* The numerical values represent values for the male body length.
** According to Dr. R. L. Usinger (in conversation) *Asclepios annandalei* Distant is quite large in size.
Genus Asclepios Distant
(Figs. 40, 138, 159, 748-759, 765-766)


Type species: Asclepios annandalei Distant, monobasic.

Species examined: A. apicalis Esaki, A. coreanus Esaki, A. coreanus miyamotoi Esaki.

Color pattern: Predominately grayish black above. Head orange yellow with a black spot on centre. Pronotum with posterior margin and on median longitudinal axis, meso- and metapleural regions orange yellow. Legs, antennae, and body beneath orange yellow to yellow.

Structures in wingless forms: Head between eyes wider at base than long at middle. Eye small, exserted, posteriorly covering anterolateral angle of pronotum. Antenniferous tubercles somewhat developed. Antenna has first segment longest, about as long as or a little longer than two following segments together, sparsely armed with small black bristles; second segment simply slightly thickened apically, apex truncate, a little longer than third segment; third segment simply slightly thickened anteriorly, apex truncate, also sparsely armed with short bristles; fourth segment about as long as or a little longer than third, fusiform. Rostrum short and robust, third segment a little less than twice as long as last segment.

Intersegmental suture between mesonotum and metanotum more or less distinct, traceable laterally as far as metathoracic spiracle, anteriorly produced obtuse angulately at middle. Mesonotum without distinct median longitudinal sulus, simply convex; metacetabular suture almost reaching anterolateral angle of first tergite. Metasternum very short, about as long as second ventrite but extends laterally as far as inner margin of posteriorly produced metacorubula; omphalium vestigial, represented by a small tubercle on middle of posterior margin. Front leg has femur strongly thickened at base, then straightly narrowed apically in male and with many short and fine black spines on inner margin; tibia thickened on inner margin, inner apical process conspicuous; tarsus with first segment very short; second segment several times as long as first, claws arising from inner margin at basal third, with fine arolium. Middle leg with femur a little longer than tibia; tibia ciliated on almost entire inner margin, a little over twice as long as first tarsal segment; first tarsal segment slightly curved and thickened at base, a little over twice as long as second segment;
second segment with highly reduced claws. Hind leg shorter than middle leg, femur twice or a little less than twice as long as tibia; tibia eight to nine times as long as first tarsal segment or three to a little less than three times as long as first and second segments together; first tarsal segment much shorter than second segment; second segment with paired claws arising from basal region of inner margin, with fine arolium, fine hairs arising from apex and dorsal margin.

Abdomen strongly declivent. Anterior margin of first tergite distinctly retained, those of first and second produced anteriorly at middle. Ventrites greatly reduced in length.

**Male:** Seventh segment ventrally a little shorter than whole preceding abdominal segments together. Eighth segment cylindrically prolonged, ventrally with a pair of processes protruding posteriorly on each side. Ninth segment with suranal plate narrowed apically, dilated at middle, longitudinally elevated on dorsal surface along median longitudinal axis; pygophore with apical margin rounded; parameres vestigial. Endosoma with definitive dorsal plate extending along apical margin of endosoma, robust and bifurcate apically, basally extending along basal margin of endosoma; ventral plate slender, rising from upper part of basal margin of endosoma, reaching apical margin of endosoma; paired lateral plates long; a slender U-shaped sclerite extends over dorsal plate from both sides. (Description of the genitalia is based on *coreanus*.)

**Female:** Seventh segment a little longer than second to sixth segments together ventrally, apical margin broadly concave. Eighth segment well developed ventrally. First valvula with inner lobe short and fused with membranous vulva; outer lobe with oblique rows of hairs on almost entire surface of inner half, apical region of the lobe membranous, acute at tip; ramus arising from near apex of outer lobe; apex of process of ninth tergite with crescent shaped plate. Second valvula with two apical lobes, outer one more conspicuous, inner lobe hook-shaped, directed caudally at apex. (Description of the genitalia is based on *coreanus* *miyamotoi*.)

**Distribution:** Off or along the coasts of India, Formosa, Japan, Korea.

The genus *Asclepios* is more primitive than *Halobates* in the following characters:

1. The intersegmental suture between the mesonotum and the metanotum is always distinct and traceable laterally as far as the metathoracic spiracle.
(2) The first and second tarsal segments of the hind leg are distinct from one another.

(3) The row of long hairs on the middle leg is confined to the tibia.

(4) The anterior margins of the basal abdominal tergites are distinct.

(5) The suranal plate is less strongly widened posteriorly.

(6) The male genitalia have the parameres retained and the eighth abdominal segment of the male much less modified.

Genus Halobates Eschscholtz

(Figs. 41, 138, 159, 760-766, 767-776)

Halobates Eschscholtz, Entomographien, p. 102(1822).


Halobates Van Duzee, Cat. Hem., p. 431(1917).


Halobates Esaki, Botany and Zoology, 1:771-784(1933).


Type species: Halobates micans Eschscholtz, by subsequent designation (Laporte, 1833 in the above reference).


Color pattern: Black in ground color, gray pubescent throughout almost entire body in varying densities in various species. Head always with a pair of orange yellow spots, which are often confluent. Body beneath concolorous with body above.

Structures in wingless forms: Head wider at base than long in middle. Eye small, covering anterolateral angle of pronotum. Antenniferous tubercles somewhat developed. Antenna with first segment considerably longer than second and third segments together in most species, thickened and truncate at apex; second segment about as long as or more often longer than third segment, apex truncate; fourth segment fusiform, always longer than third
segment. Rostrum short and robust, third segment less than twice as long as last segment.

Intersegmental suture between mesonotum and metanotum normally lost though present in nymphs, occasionally recognizable as a faint suture in adults. Metanotum without distinct median longitudinal sulcus; metacatetabular suture dorsally approximated to anterolateral angle of first abdominal tergite. Metasternum very short, but reaching laterally to inner basal angle of posteriorly produced metacatetabular; omphalium vestigial, represented by a small tubercle at middle of posterior margin of metasternum. Front leg with femur sparsely armed with long fine hairs on inner margin, with some stiff, black bristles on inner margin at base, thicker and flattened at base in males of some species; tibia thickened apically on inner margin, process at inner apical angle conspicuous; tarsus relatively long, first segment shorter than second segment in most species, but at least one third as long as the latter, second segment with claws arising from inner margin before middle, claws with fine arolium. Middle femur one and one third to a little over twice as long as tibia; tibia ciliated on inner margin, usually less than twice as long as first tarsal segment; second segment with apex clothed with short hairs, straight long hairs arising from dorsal margin near apex, highly reduced fine claws arising from near apex. Hind leg shorter than middle leg; femur about twice as long as tibia except for splendens and micans, in which femur a little longer than tibia; tibia about three to a little less than four times as long as tarsus; tarsus with first and second segments completely fused, claws arising from beyond middle, with fine arolium, apex with a short hair, and a long hair arising from upper margin near apex.

Abdomen strongly declivent. Anterior margins of basal abdominal tergites at least medially obliterated normally, those of first and second produced anteriorly when traceable. Ventrites strongly reduced in lengths.

Male: Seventh segment strongly developed ventrally, longer than all preceding segments together in some species, as long as or a little shorter than sixth segment dorsally. Eighth segment with dorsal apical margin rounded produced, with a pair of lateral processes of various shapes in some species, ventrally with a pair of slender lateral processes, their apices vary in shape in various species, asymmetrical in some species. Ninth segment with suranal plate provided with a more or less conspicuous projection at middle of each side in most species; pygophore more or less rotated in some
species; parameres absent. Endosoma with definitive dorsal plate strongly thickened, turned back and bifurcate at apex, represented by two slender plates medially, reaching basal margin of endosoma; ventral plate indistinguishably fused with dorsal plate, broad and thin, apically membranous, circled dorsoccephalad; long, U-shaped slender plate not stretching over dorsal plate; lateral plates rather short and robust, placed in basal half of endosoma. (Description of the genitalia is based on H. sohrinus).

Female: Seventh segment well developed ventrally, longer than all preceding ventrites together in some species, transverse and trapezoidal in shape in most species, simply concave or bisinuate on ventral apical margin. Eighth segment exposed both dorsally and ventrally. First valvula split into inner hairy region and outer shorter region, both simply narrowed apically, their apices subacute, inner lobe fused with vulva; process of ninth tergite, to which ramus of first valvula is attached, is lacking crescent shaped plate at apex. Second valvulae convergent apically, acute at tips; intervalvular membrane on apical margin bilobed and each lobe acutely pointed. (Description of the genitalia is based on H. sohrinus.)

Distribution: Temperate and tropical zones of the Pacific, Indian, and Atlantic oceans and the Red sea. Eskai (1933) listed two species of Halobates (H. micans and H. inermis) as occurring in the Atlantic ocean.

Tribe Metrocorini Matsuda

Color pattern: Uppersurface of body mottled with yellow and black stripes, bands, or spots.

Structures in wingless forms: Head with anterior margin broadly rounded. Clypeus with basal margin obscure or lost. Antenniferous tubercles scarcely developed.

Intersegmental suture between mesonotum and metanotum distinct dorsally in most species, lost laterally in all species. Metasternum laterally not reaching metacetabular regions. Front leg has inner apical process of tibia conspicuous; first tarsal segment always short, much shorter than second segment in most species. Middle tibia without conspicuous row of hairs in most genera. Hind tarsal segments always distinct from one another; coxa about as long as wide.

Abdomen with anterior margin of first tergite distinct in most species. Male eighth segment prolonged in some species, with-
out conspicuous modification. Male ninth segment with suranal plate simple; parameres always present.

**Distribution:** Temperate and tropical zones of the Eastern Hemisphere.

**Genus Metrocoris** Mayr

(Figs. 45, 108, 121, 139, 158, 167, 777-796)

Metrocoris Meinert, Ent. Medd., 1:140(1888).
Metrocoris Kirkaldy, Entomologist, 37:61(1904).

Type species: **Metrocoris brevis** Mayr, monobasic.


**Color pattern:** Pale yellow in ground color. Head usually with a median large black marking. Pronotum in wingless forms with a single median and a pair of lateral longitudinal black stripes which are confluent anteriorly. Mesonotum with a single median and two pairs of lateral black stripes, the outer pair often confluent with transverse black stripe on intersegmental suture; black along anterior margin of mesonotum. Metanotum with median longitudinal and a pair of lateral oblique black stripes which meet laterally with the stripes from the intersegmental suture and the stripe coming from metathoracic spiracle; black transverse stripe along metacetabular suture and metacetabula has a black longitudinal stripe. Abdomen largely black on upper surface, pale yellow to yellow on undersurface. Pronotum in winged form always with median longitudinal black stripes reaching near apex, with a pair of lateral black stripes in posterior lobe, black along anterior margin of pronotum. Hemelytra nearly black, with darker veins.
Structures in wingless forms: Male larger than female in some species. Head including eyes usually over twice as wide as long in the middle. Eye exerted, covering most part of anterolateral angle of pronotum. Antenna relatively longer in male than in female; first segment much longer in male than in female, longest in both sexes, often longer than second and third segments together, third segment with inconspicuous basal peduncle, both second and third segments gradually thickened anteriorly and subtruncate at apices, relative length of second to third greater in male than in female; fourth segment shortest. Rostrum slightly extending beyond posterior margin of prosternum; third segment about three times as long as last segment.

Pronotum shorter than head at middle, lateral margin rounded, posterior margin concave. Intersegmental suture between mesonotum and metanotum more or less concave dorsally, obliterated laterally. Metanotum without median longitudinal sulcus; metacetabular suture distinct, reaching dorsally anterolateral angle of first tergite; metacetabulum narrow, posterior margin simply oblique, posterolateral angle not flattened; metanotal lateral longitudinal suture weakly developed, not reaching intersegmental suture. Metasternum highly reduced, represented by small transverse subtriangular plate bearing omphalium at middle of posterior margin. Front leg with femur lacks tubercle, occasionally thickened and with conspicuous processes on inner margin in male (strangulator); tibia strongly thickened apically, with conspicuous inner apical angle which is defined by oblique depression on inner and outer surfaces, lacks a row of denticles on inner margin; tarsus with first segment very short, second segment long, claws arising from middle or beyond middle of the segment, and with membranous arolium. Middle leg with femur thickest, about one and one fifth to one and a half times as long as tibia; tibia gradually tapering apically, twice to a little over twice as long as first tarsal segment; first tarsal segment four and two thirds to six and a half times as long as second segment, second tarsal segment with claws arising preapically and with fine arolium. Hind leg with femur one and one fourth to a little over one and a half times as long as tibia; tibia about ten times as long as first tarsal segment; first tarsal segment about as long as second or shorter than second in some species, claws arising preapically.

Abdomen with anterior margin of first tergite bisinuate or sometimes obliterated; second tergite strongly angularly produced
on anterior margin, to a lesser extent so is third tergite; fourth to seventh tergites subequal in length to each other. Connexivum reflexed. Ventrites much more strongly reduced than tergites. Abdominal spiracles, when recognized, placed closer to posterior margin than to anterior margin except for those of sixth ventrite which are at middle, those of seventh closer to anterior margin than to posterior margin.

**Male:** Seventh segment ventrally much longer than sixth segment, broadly concave on ventral apical margin. Eighth segment broadly rounded on apical margin dorsally, broadly concave on apical margin ventrally. Ninth segment with suranal plate usually hidden beneath well developed eighth tergite, simple, ventral basal angle with a foot shaped process on each side; pygophore broadly rounded on apical margin or rarely broadly dilated in apical half; parameres well developed and conspicuous. Endosoma with definitive dorsal plate turned cephalad on apical margin of endosoma, represented by two slender sclerites along dorsal margin; indistinguishably fused with ventral plate; ventral plate tapering apically and membranous, curved upward anterior to apical margin of endosoma; lateral plates two paired, upper one not well sclerotized. (Description of the genitalia is based on ståli(?).)

**Female:** Seventh segment ventrally strongly developed and modified in various shapes apically in various species (figs. 787, 788, 790), completely enclosing eighth segment above. First valvula with inner lobe short, more strongly sclerotized and fused to membranous vulva; outer lobe long and membranous, with acute tip; ramus extending on outer margin as far as apical third of the outer lobe and basally on outer margin of process of ninth tergite. Second valvula apically bilobed, outer one more robust, basally free from inner lobe, which is directly continuous with concave apical margin of intervalvular membrane; ramus fine. Vulva membranous, with short median projection. (Description of the genitalia is based on ståli(?).)

**Winged forms:** Pronotum subpentagonal in shape, with subhorizontal anterior margin and acute tip. Hemelytra with well developed embolium. \( R + M + Cu \) branches into two veins at basal third of the wing \((R + M \text{ and } Cu)\); two apical cells are formed beyond middle of wing. Vein A joins apically with apical end of lower one of the closed cells, also connected with rear margin of wing at middle by a short cross vein.
Study of the Gerridae of the World

Distribution: The palearctic and Oriental regions (Annam, Arabia, Burma, Ceylon, China, Formosa, India, Japan, Korea, Malaya, Nepal, Persia).

Genus *Eurymetra* Esaki
(Figs. 47, 797-807)


Type species: *Metrocoris natalensis* Distant, by original designation.

Species examined: *E. natalensis* (Distant), *E. nitidulus* (Esaki), *E. angolensis* Hoberlandt, and one unidentified species.

Color pattern: Essentially as in *Metrocoris*, more lustrous in most species.

Structures in wingless forms: Head including eyes over twice as wide as long. Eye strongly exserted, covering most part of antero-lateral margin of pronotum, anterior half of inner margin slightly rounded. Antenna relatively longer in male than in female; first segment relatively longer in male than in female, slightly curved and longest, usually about twice as long as second, truncate at apex; second segment nearly as long as or shorter than third; third segment with small simple peduncle; fourth segment fusiform, always shortest. Rostrum has third segment a little less than four times as long as last segment.

Pronotum short, lateral margins rounded and divergent posteriorly, posterior margin sinuate. Intersegmental suture between mesonotum and metanotum slightly concave at middle dorsally, directed obliquely forward laterally, lost in front of metathoracic spiracle. Metanotum without median longitudinal sulcus; lateral longitudinal suture weakly developed. Metacetabulum relatively wide, dorsal apical margin simply concave. Metasternum represented by a small transverse, subtriangular plate; omphalium distinct. Front leg with trochanter lacks tubercle; femur simple, slender, slightly curved and narrowed apically, with long hairs on inner margin at basal half, without tubercles on inner margin; tibia thickened apically, with rather conspicuous process at inner apical angle, which is defined by an oblique depression both on outer and inner surfaces, lacks denticles on inner margin; tarsus with first segment short; second segment three to five times as long as first segment, claws arising from near middle of lower margin of
second segment and with membranous arolium. Middle leg with femur gradually tapering apically, one and a half to two and a third times as long as tibia; tibia two and two thirds to three and one third times as long as first tarsal segment; first tarsal segment a little over four to six and a half times as long as second segment, claws arising preapically and with arolium. Hind leg with femur over twice to about one and a half times as long as tibia; tibia eight to ten times as long as first tarsal segment; first tarsal segment a little longer than second segment, claws arising preapically.

Abdomen wider than in Metrocoris. First tergite with bisinuate anterior margin; second tergite with anterior margin strongly produced anteriorly, to a lesser degree so is anterior margin of third tergite; fourth to sixth tergites subequal in length. Connexivum more or less strongly reflexed. Abdominal spiracles of sixth and seventh segments located at middle between anterior and posterior margins.

**Male:** Seventh segment ventrally twice as long as sixth segment or about as long as second to sixth segments together (*nitidulus*), concave on ventral apical margin. Eighth segment well developed dorsally, covering suranal plate. Ninth segment with suranal plate subcylindrical, with a conspicuous pair of foot-shaped processes at outer basal angles; pygophore rounded on apical margin; parameres well developed. Endsoma with dorsal plate robust and turned cephalad apically, loosely connected with basal plate at dorsal basal angle of endsoma, slender looped sclerite stretches along and above dorsal plate; ventral plate indistinguishably fused to dorsal plate, slender and sclerotized except for apex which is membranous; lateral plates composed of two pairs, upper one of them stretch over the entire length of endsoma. (Description of the genitalia is based on *natalensis*.)

**Female:** Seventh segment well developed but not covering eighth segment ventrally. Eighth segment with first valvula sclerotized on outer margin, the rest membranous and with acute tip, inner lobe fused with vulva. Second valvula sclerotized along outer margin, apices convergent; intervalvular membrane with a pair of membranous processes converging apically. Vulva rounded on apical margin and with a median longitudinal ridge. (Description of the genitalia is based on *natalensis*.)

**Winged forms:** Not available for study.

**Distribution:** The Ethiopian region (Angola, Cameroons, Ethiopia, Ivory coast, Madagascar, Natal, Nigeria, South Africa).
The genus is closely related to *Metrocoris*, but can be distinguished by the union of the following characteristics:

1. The body, especially the abdomen, is strongly widened at least in some species.
2. The male genital segment is not prolonged as in *Metrocoris*.
3. The uppersurface of the body lustrous.
4. The seventh segment ventrally does not extend beyond the eighth segment in the female.

**Genus Eurymetropsiella** Poisson

(Figs. 48, 808-816, 818)


Type species of the genus: *Eurymetropsiella schoutedeni* Poisson, by original designation.

Species examined: *E. schoutedeni* Poisson.

**Color pattern:** Predominantly black. Dark yellow spots on anterior and basal regions of head. Pronotum dark yellow on margin. Mesothorax and metathorax with several pairs of yellow spots as shown in figure 48. Legs nearly black. Body beneath largely pale yellow.

**Structures in wingless forms:** Body nearly globular and flattened. Mesonotum and metanotum greatly widened. Head including eyes over twice as wide as long. Eye covering anterolateral margin of pronotum, posterior end nearly reaching posterolateral angle of pronotum. Antenna thicker in male; first segment much longer than second, but shorter than second and third together; third segment shorter than second but longer than fourth, basal peduncle simple. Rostrum short and thick, extending beyond prosternum, third segment about twice as long as fourth segment.

Pronotum shorter than head, posterolateral angle rounded, posterior margin nearly straight. Mesothorax with humeral area slightly produced on either side of pronotum, widened posteriorly on either side of metacetabular region. Intersegmental suture between mesonotum and metanotum nearly straight and distinct only dorsally. Metanotum without median longitudinal sulcus; metanotal lateral suture absent; metacetabular suture absent. Metacetabula narrow, posterolateral angle not produced. Metasternum represented by small omphalium only, transverse subtriangular metasternal plate lost. Front leg sexually dimorphic, a mass of shaggy hairs on trochanter and femur occur only in male. Femur distinctly longer than tibia and slender; tibia with inner apical process
separated by a longitudinal groove, acute at tip, bearing long curled hairs; tarsus a little shorter than tibia, first segment a little over half as long as second, claws arising from apical one third of second segment. Middle leg with femur thicker at base, about one and a half times as long as tibia; tibia curved, with two rows of hairs on inner margin throughout, a little less than twice as long as tarsus. Hind leg with coxa a little longer than wide; trochanter densely haired, femur about two and a half times as long as tibia; first tarsal segment a little shorter than second, second segment in lateral view much finer in apical half, claws not recognized in the specimen examined.

Abdomen in female: Dorsally strongly declivent. Anterior margin of first tergite distinct, broadly roundly produced at middle; anterior margins of second and third tergites also produced anteriorly; from sixth tergite on completely folded beneath fifth. First three connexival segments completely fused. Second to fifth ventrites greatly reduced, sixth ventrite as long as four preceding segments together.

Male: Parameres well developed. Pygophore narrowly rounded on apical margin (based on Poisson's figures and description, 1950).

Winged forms: Unknown.

Distribution: The Ethiopian region (Belgian Congo, French Congo, Togo).

The genus *Eurymetropsiella* is more specialized than *Eurymetra* in the following points:

1. The antennae are sexually dimorphic.
2. The second to fifth ventrites are more reduced.
3. The metasternum is represented by the omphalium alone.
4. The first three connexival segments are completely fused.
5. The seventh abdominal segment of the female is ventrally greatly prolonged and apically infolded within the abdominal cavity.

The genus can be separated from *Eurymetropsis* Poisson by the following characteristics:

1. The pygophore is simply rounded on the apical margin, while it is deeply notched on the apical margin in *Eurymetropsis*.
2. The body is much wider.
3. The intersegmental suture between the mesonotum and metanotum nearly straight dorsally.
4. The metasternum is represented by the omphalium alone.
5. The relatively long first tarsal segment of the front leg.
Genus *Eurymetropsielloides* Poisson
(Fig. 49, 845-853)


Type species: *Eurymetropsielloides milloti* Poisson, monobasic.

Since this genus was described for only a single species represented by a single male specimen which was not available for study, it has not been possible to redescribe it. The followings are the original description by Poisson and the additional remarks based on the drawings given by Poisson with his original description. The figures are copied from his work.

*Original description:* "*Eurymetropsielloides Milloti* n. g., n. sp.

"Cet Halobatinae est à rapprocher des genres *Eurymetropsis* Poiss. (Type *E. Carayoni* Poiss. du Cameroun), et *Eurymetropsiella* Poiss. (Type *E. Schoutedeni*, espèce africaine de l’Ituri à laquelle s’ajoute *E. congoensis* Poisson (1955), du Congo.

"Pigmentation générale noir sépia; une bande jaunâtre au bord postérieur du vertex; deux tâches triangulaires de même teinte contre le bord postérieur du pronotum. Une bande jaune-flave de part et d’autre sur les côtés du thorax simulant un oiseau les ailes étendues vu postérieurement. Deux bandes jaunâtres, étroites, mésonotalies, postérieures, précédées de deux petites taches presque rondes et plus centrales sur le disque du mésonotum. Une tâche médiane ovaire transversalement sur le septième tergite, accompagnée d’autres tâches sur les hanches distribuées comme l’indique la figure (fig. 49 in this work). Une fine et courte pilosité cuivrée tapisse les tergites abdominaux II à V.

"Antennes noires; le 1 article jaunâtre à la base, le 4 article légèrement contourné en S:

55-35-(3)-31-(1.5)-21

Pattes antérieures noires, sauf la base du fémur jaunâtre; fémur armé de trois longues soies raides, implantées ventralement vers la base de L’article. Tibia non denté, seulement revêtu sur son bord ventral d’une courte et dense pilosité et prolongé par un éperon pré-tarsien, terminé par une courte brosse:

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"Pattes intermédiaires: les plus longues; 1er article tarsien quelque peu renflé à son extrémité antérieure et finement poilu en dessous:

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<td>98</td>
<td>62</td>
<td>22.5 + 4</td>
</tr>
</tbody>
</table>
Pattes postérieures

F. T. t.
101 41 8 + 9

8e segment abdominal cylindrique, mais quelque peu renflé vers l'avant (fig. 7, A). Capsule génitale peu acuminée et non bifurquée. Paramères symétriques, incurvés et spatulés.

"Longueur: 3.5 mm; largeur au niveau du mésothorax: 2.2 mm.

"Distrib.—1 mâle aptère, Sandrangato, Moramanga (Madagascar) (J. Millot, 1954).

"Obs.—Le genre Eurymetropsielloides n. g. diffère d'Eurymetropsis par la capsule génitale du mâle non bifurquée à l'extrémité, les tibias antérieures non armés de denticules, l'aspect général plus massif; il diffère d'Eurymetropsiella par ses pattes antérieures proportionellement plus courtes, aux articles plus épais, les tibias non finement dentés, seulement pourvus de courts poils densés; les fémurs non armés d'un denticule pileux; la capsules génitale moins conique; les paramères non aciculés; le vertex proportionellement plus large; les yeux débordant assez largement les côtes du pronotum.

"La tête est un peu plus large entre les yeux qu'elle n'est longue vue dorsalement; avec les yeux, elle est trois fois au moins plus large que longue. Corps : 1.5 fois a 1.6 fois plus long que large."

Remarks: The genus Eurymetropsielloides appears to be more closely related to Ventidius than to Eurymetropsis or Eurymetropsiella with which Poisson has compared it. The similarities to Ventidius are indicated in the following characters:

(1) The broad head between eyes. In the related genera of Poisson, the head between eyes is relatively narrow as in Eurymetra or Metrocoris, but in Ventidius and Esakia the head between eyes is broad as in Eurymetropsielloides.

(2) The eyes are elongate. In Eurymetra and related genera described by Poisson from Africa, the eyes are much shorter and more rounded on the anterior margin, not as much exerted as shown in figure 4 for Eurymetropsielloides milloti, while in Ventidius and Esakia the eyes are more elongate and completely cover the lateral margins of the pronotum, much as in Eurymetropsielloides.

(3) The pronotum is short as in Ventidius or Esakia, not as long as in the other genera occurring in Africa.

(4) The proportional lengths of antennal segments and leg segments are much as in a typical species of Ventidius.
This genus, however, differs from *Ventidius* by the metacetabula which are not flattened posterolaterally and by the different color pattern. Poisson apparently missed one abdominal segment (tergite) in his figure.

All abdominal tergites are clearly distinct from each other in his figure but the number of tergites is one less than it should be. The intersegmental suture between the mesonotum and metanotum is indicated only laterally in his figure.

**Genus Eurymetropsis** Poisson

(Figs. 46, 872-880)


Type species: *Eurymetropsis carayoni* Poisson, by original designation.

Species examined: *E. carayoni* Poisson.

**Color pattern:** Predominantly black. Head black except along dorsal basal margin of head and behind clypeus yellow. Antenna black. Pronotum along basal and lateral margins yellow. Mesonotum with a yellow longitudinal stripe extending back above mesocoxa; a pair of small yellow spots above intersegmental suture between mesonotum and metanotum, another pair of small yellow spots inside mesopleural yellow longitudinal stripe. Metanotum with two paired yellow spots in front of first tergite and metacetabular suture, and one spot of the same color on metacetabula. Legs black except bases yellow. Body beneath pale yellow.

**Structures in wingless forms:** Relatively elongate in body shape. Head including eyes much over twice as wide as eyes. Eye covering anterior half of lateral margin of pronotum. Antenna a little shorter than body; first segment longest, shorter than second and third segments together, dilated at basal third; second segment longer than third; third segment with a ear-shaped basal peduncle; fourth segment shortest and curved. Rostrum with third segment about two and a half times as long as last segment.

Pronotum relatively long, posterior margin slightly produced anteriorly at middle, lateral margin rounded, a little narrower than head including eyes. Mesonotum slightly widened posteriorly. Intersegmental suture between mesonotum and metanotum produced anteriorly at middle, obliterated laterally. Metanotum with a faint median longitudinal sulcus anteriorly, lacks metanotal lateral longitudinal elevation; metacetabular suture not reaching anterolateral angle of first tergite; metacetabulum relatively nar-
row, dorsal posterior margin simple and oblique, posterolateral angle not rounded. Male front leg with coxa lacks tubercle; femur provided with a small dark tubercle on inner margin at middle, sparsely clothed with long hairs on inner margin of trochanter and femur; tibia with a rather conspicuous process at inner apical angle, inner margin with a series of small black tubercles along inner margin; tarsus with first segment greatly reduced, second segment slender and long, claws arising from a little beyond middle of inner margin of second segment and with arolium. Middle leg with femur a little less than twice as long as tibia; tibia about twice as long as tarsus; tarsus with first segment five times as long as second segment. Hind leg with femur a little over twice as long as tibia; tibia about eight times as long as first tarsal segment; tarsus with first segment a little shorter than second segment.

Abdomen with anterior margin of first tergite obliterated, much longer than second tergite; basal abdominal tergites densely clothed with adpressed hairs and segmentations obscured; fifth to seventh tergites highly reduced in length. Ventrites also greatly reduced; seventh ventrite a little longer than the preceding.

Male: Eighth segment with a paired needle shaped processes (?), greatly prolonged. Ninth segment with pygophore strongly bifurcate apically. Parameres symmetrical and conspicuous. (Description is based on Poisson’s figures on carayoni (1948.)

Winged forms: Unknown.

Distribution: The Ethiopian region (Cameroons).

Poisson says “8 segment abdominal du mâle présentent postérieurement des prolongement aciculés (fig 2, C),” but his figure 3A and B, (figs. 878, 879 in this work) which actually show the dorsal and ventral sides of the eighth segment, show no such modified structure. Figure 2, C (fig. 880) which Poisson thought to represent the eighth segment appears to be actually the suranal plate, and the spinous structures are probably the basal lateral foot-shaped processes of the suranal plate which frequently occur in the Gerridae. Unfortunately, the eighth and ninth segments are detached from the specimens which Dr. Poisson kindly lent for study, and are therefore not available for study to make this interpretation certain.

The genus Eurymetropsis can be differentiated from Eurymetropsiella by the following characteristics:

(1) The pygophore is strongly bifurcate on the apical margin.
(2) The anterior margin of the first abdominal tergite is obliterated.

(3) The intersegmental suture between the mesonotum and the metanotum is produced anteriorly at the middle.

(4) The body is more slender.

Genus *Ventidius* Distant

(Figs. 42-43, 122, 140, 160, 819-844)


Type species: *Ventidius aquarius* Distant, monobasic.


Color pattern: Head including eyes over twice as wide as long in middle. Eye elongate, exserted, covering lateral margin of pronotum and anterolateral angles of mesonotum. Antenna slender and long, longer in male than in female. First segment always longest, sparsely armed with black bristles, with a tuft of hairs at distal end in *malayensis*; apex truncate; second segment has its relative length to third greater in male than in female; third segment shorter than second segment in larger species, or a little longer than second in smaller species, with a small basal peduncle; fourth segment longer than third (*malayensis*) subequal to or a little shorter than third. Rostrum short, third segment twice to a little over three times as long as last segment.

Pronotum short and transverse, both anterior and posterior margins concave, lateral margins rounded. Intersegmental suture indistinct though traceable dorsally in most species, the suture laterally obliterated in front of metathoracic spiracle in all species. *Mesosternum with a small black tubercle on median longitudinal axis in kuiterti*, Metanotum without median longitudinal sulcus; lateral longitudinal suture not reaching intersegmental suture; metacetabular suture reaching dorsally anterolateral angle of first abdominal tergite; metacetabulum relatively broad, posterolateral angle more or less flattened and somewhat produced. Metasternum
represented by a small transverse subtriangular plate bearing omphalium on it. Front leg relatively long and slender; trochanter lacks tubercle; femur with a small tubercle on inner margin of male in *kuiterti*, slender and simple in other species, sparsely clothed with some long hairs on inner margin at base; tibia with a narrow inner apical process defined by an oblique depression on both outer and inner surfaces; tarsus with first segment greatly reduced; second segment much longer than first, claws arising from near base or middle of second segment and with distinct arolium. Middle leg with femur straightly narrowed apically, one and two thirds to twice as long as tibia; armed with spinous bristles sparsely; tibia straightly narrowed apically, about one and a half to almost twice as long as first tarsal segment; first tarsal segment about four and a half to almost eight times as long as second tarsal segment, claws arising from a little beyond middle of second segment. Hind leg also progressively tapering apically; femur straightly narrowed apically, sparsely clothed with spinous bristles, about two to two and a half times as long as tibia; tibia five to six times as long as first tarsal segment; first tarsal segment nearly as long as to twice as long as second tarsal segment; second segment with slender claws arising from near middle.

Abdomen with first tergite, when recognizable, nearly straight on anterior margin; second and third tergites with anterior margins produced anteriorly, but obliterated medially in majority of species; connexivum slightly reflexed, anterior margin of third connexival segment lost in some species. Anterior ventrites strongly reduced in length. Abdominal spiracles were not studied (abdomen is flanked by metacetabula and hind legs).

**Male:** Seventh segment ventrally a little shorter or longer than all preceding ventrites together. Eighth segment with dorsal posterior margin broadly rounded. Ninth segment with suranal plate simple, with foot-shaped process at base of lateral margin; pygophore small, apical margin simply rounded; parameres well retained, asymmetrical in *kuiterti*. Endosoma with definitive dorsal plate turned back along apical margin of endosoma, robust and bifurcate at apex (the part of apical plate), basally branched into two slender parallel plates, and fused with basal plate which in turn fused with ventral plate; ventral plate membranous apically; lateral plates simple and elongate. (Description of the genitalia is based on *chinai, malayensis, kuiterti.*
Female: Seventh segment ventrally a little shorter or longer than all preceding segments together, concave on posterior margin. Eighth segment well exposed ventrally; first valvula with outer lobe acutely pointed at apex, inner lobe fused with vulva; ramus reaching apical third of valvula on its outer margin, basally connected with process of ninth tergite on its outer margin, which is provided with a crescent shaped plate at its apex. Second valvula sclerotized along outer margin, apical lobe membranous and directed mesad apically, with another poorly developed membranous apical lobe above; intervalvular membrane with its apical margin broadly concave, with a fine dark line above apical margin. Vulva large, broadly rounded on apical margin. (Description of the genitalia is based on V. kuiterti).

Winged forms: Pronotum with humeri located much in front of middle of pronotum, nearly straightly narrowed apically from humeri. Hemelytra as in Metrocoris but lower cell longer and vein A joined at its extremity. R + M + Cu vein indistinct.

Distribution: The Oriental region (Burma, Ceylon, India, Java, Malaya, Philippines).

Subgenus Ventidius Distant s. str.

For type designation and citations see generic bibliography.


Subgenus Ventidioides Hungerford and Matsuda


Type species: Ventidius kuiterti Hungerford and Matsuda, by original designation.

Body smaller. Second antennal segment shorter than third. Front femur with a tuberculous bump on inner margin in male. Mesosternum with a small tubercle (pore?) led by longitudinal canal internally on median longitudinal axis. Metacetabulum with posterolateral angle with two obtuse projections. Parameres asymmetrical.

The subgeneric distinction lies primarily in the presence or absence of the porous tubercle on the mesosternum. All other characters that characterize Ventidioides are evidently more specialized
conditions of their counterpart in *Ventidius s. str*. The difference in proportional lengths between the second and third antennal segments probably has been derived from much the same growth mechanism for the segments.

Modification of the abdomen of the male

In the larger species, *malayensis, usingeri*, the seventh segment is distinctly or a little shorter than the five preceding segments together ventrally; in smaller species (*e.g.*, *wernerii, kuiterti, henryi*) the seventh segment is relatively long. The eighth segment is largely withdrawn beneath the seventh in *malayensis*; in all other species the eighth segment is more or less greatly prolonged. The parameres are distinct in all species, but they are somewhat reduced in size in the otherwise most primitive species, *malayensis*. The parameres are asymmetrical in the specialized species, *kuiterti*.

Modification of the other structures

*The antennae*: The second antennal segment is definitely longer than the third segment in both sexes in the larger species, *malayensis* and *usingeri*; in the smaller species the second segment is about as long as or even shorter than the third segment. It is apparent that the length of the second segment in relation to the third has become smaller with reduction in size of the body, and this is due presumably to a greater growth ratio for the second segment than for the third segment common to all species of this genus.

*The rostrum*: The third rostral segment is about three times as long as the fourth in the larger species, *malayensis* and *usingeri*, but in the smaller species the third segment is definitely less than three times as long as the fourth. As in other genera the length of the third segment in relation to the fourth has evidently become smaller with reduction of the body size in evolution.

Genus *Esakia* Lundblad

(Figs. 44, 854-871)


Type species: *Esakia ventidioides* Lundblad, monobasic.


*Color pattern*: Predominantly black, with a large pale yellow spot on mesonotum and metanotum and with a whitish spot on mesoacetabulum and metacetabulum in *usingeri*. 
Study of the Gerridae of the World

Structures in wingless forms: Small and flattened. General shape wider anteriorly than in related genera, such as Ventidius. Head including eyes over twice as wide as long in middle. Eye strongly exserted, extending slightly beyond lateral limit of pronotum, covering a part of mesonotum. Antenna a little longer in male than in female, placed on ventral surface of body; first segment longest, longer than two following segments together, swollen at middle, slightly constricted near apex in some species, apex truncate, sparsely clothed with fine bristles; second segment club shaped, simply and gradually thickened anteriorly, apex truncate, a little shorter than third; third segment in male strongly flattened, with ear shaped basal peduncle, lateral margin fringed with stiff black hairs; fourth segment fusiform, with inconspicuous basal peduncle and stiff hairs on basal lateral margins. Rostrum short, nearly reaching posterior margin of prosternum, short and robust; third segment twice or less than twice as long as last segment.

Pronotum short, much shorter than head, posterior margin nearly straight, or feebly concave, lateral margin rounded. Intersegmental suture feebly produced anteriorly, obliterated laterally. Metanotum without median longitudinal sulcus, lateral elevation of metanotum reaching intersegmental suture between mesonotum and metanotum; metacetabular suture evanescent apically, not reaching lateral longitudinal elevation of metanotum. Metasternum highly reduced, represented by a small, transverse, subtriangular plate bearing omphalium. Front leg with tronchanter lacks tubercle; femur considerably longer than tibia, simple; tibia gradually thickened apically, with narrow inner apical process defined by oblique depression on both surfaces; tarsus with first segment very short, second segment with claws arising from near middle, with distinct arolium, several times as long as first segment. Middle leg with femur one and a half to one and two thirds times as long as tibia; tibia about two and a half to about three times as long as first tarsal segment, with a fringe of hairs on inner margin basally; first tarsal segment a little over four times to a little over six times as long as second tarsal segment, claws arising preapically. Hind leg with femur over three times as long as tibia; tibia about six times as long as first tarsal segment; first tarsal segment about two thirds as long as second tarsal segment in most species; second segment with claw arising from a little beyond middle of the segment.

Abdomen has anterior margin of first tergite usually recognizable; anterior margins of second and third tergites roundly produced;
third to sixth tergites subequal in length. Connexivum reflexed. Ventrites much more reduced than tergites.

**Male:** Seventh segment ventrally about as long as two preceding segments together in *usingeri* or longer in *kuiterti*, concave on ventral apical margin. Eighth segment broadly rounded on apical margin dorsally, broadly concave on ventral apical margin. Ninth segment with suranal plate long and slender; pygophore feebly concave on ventral apical margin; parameres conspicuous and lobate. Endosoma with definitive dorsal plate membranous apically, curved back on apical margin, basally distinct from ventral plate at upper basal angle of endosoma; ventral plate wide and paired, flat apically, curved back along dorsal margin of endosoma; lateral plates located in upper basal half of endosoma; thin U-shaped sclerite goes across apical portion of dorsal plate. (Description of the genitalia is based on *kuiterti*)

**Female:** Seventh segment well developed, as long as or a little shorter than all preceding segments together, posterior margin concave. Eighth segment well exposed ventrally, dorsal apical margin produced posteriorly. First valvula thickened apically and acutely pointed at inner apical angle, membranous except on outer margin which is sclerotized, inner lobe infolded beneath outer lobe, shorter and tapering apically. Second valvula with two pairs of apical lobes directed mesad, outer lobe more heavily sclerotized, and superposed on inner lobe which is membranous; short apical margin of intervalvular membrane between inner lobes straight, intervalvular membrane also with an arched, thinly sclerotized slender bar above apical margin; process of ninth-tergite obliquely connected basally with lateral area of ninth tergite.

**Winged forms:** Pronotum subpentagonal in shape, widest in front of middle in *usingeri*. Forewing coriaceous along upper basal margin. \(R + M + Cu\) send a fine oblique branch from middle of the wing to be united with vein A, without forming apical cells.

**Distribution:** The Oriental region (Burma, Java, Philippines). This genus is related to *Ventidius* Distant but can be recognized from it by the following characteristics which indicate greater degrees of specialization in *Esakia*:

1. The forewing venation is more reduced.
2. The third antennal segment is peculiarly modified in the male.
(3) The presence of the lateral longitudinal elevation of the metanotum reaching the definitive intersegmental suture between the mesonotum and metanotum.

(4) The shape of the body is more widened anteriorly.

**Subfamily Rhagadotarsinae Lundblad**


**Structures in wingless forms:** Head between eyes subquad-rangular in shape, dorsal surface usually with a more or less distinct median longitudinal depression; anterior margin with three distinct projections, i.e., median clypeal region and lateral antenniferous tubercles. Clypeus elevated and short, well defined basally. Eye small, inner margin not concave, covering anterolateral angle of pronotum. Antenniferous tubercles well developed. Antenna slender and relatively short, greatly modified in males of many species of *Rheumatobates*. Mandibular and maxillary plates well defined from each other, the latter well developed and produced, forming bucculae, and enclosing base of rostrum. Rostrum slender and relatively short, third segment less than twice as long as last segment.

Pronotum not prolonged, posterior margin concave. Definitive intersegmental suture between mesonotum and metanotum represents posterior margin of mesothoracic postnotum dorsally and laterally metacetabular suture in winged forms, well impressed and broadly roundly produced posteriorly at middle. Mesonotum laterally defined by longitudinal suture. Mesoacetabular region dilated posteriorly. Mesoacetabular region more or less displaced lateroventrally by first connexival segment. Metathoracic spiracle placed obliquely anterior to definitive intersegmental suture between mesonotum and metanotum, small. Metanotum short, with or without median longitudinal sulcus, laterally defined by first connexival segment. Metacetabular region more or less displaced lateroventrally by first connexival segment which extends anteriorly into metanotal region. Metasternum relatively long; omphalium as well as omphal-ial groove absent. Front leg with femur slender, about twice as long as tibia; tibia greatly thickened apically, with or without apical projection. First tarsal segment always greatly reduced; second segment with or without longitudinal cleft apically, claws arising from base of cleft in *Rheumatobates*. Middle leg longer
than hind leg. Coxa prolonged in males of some species of Rheumatobates; femur and tibia modified in males of many species of Rheumatobates; tarsal segments distinct from each other. Hind leg more or less greatly modified in coxa, trochanter, femur, and tibia in males of many species of Rheumatobates. First and second tarsal segments distinct from each other.

Abdomen with first segment greatly intruded into metathoracic region. First connexival segment almost reaching or reaching intersegmental suture between mesonotum and metanotum, its posterior margin distinct; first ventrite clearly present behind metasternum; first tergite with anterior margin distinct only laterally. Second to sixth segments subequal in length to each other both dorsally and ventrally.

Winged forms: Hemelytra with $R + M + Cu$ forked into two branches, anterior branches ($R + M$) either connected or not connected with Sc by oblique cross vein behind middle of hemelytra; posterior branch (Cu) either connected or not connected with A at the middle of hemelytra; the anterior branch apically either fused with Sc to form a cell along anterior margin of hemelytra or not forming a cell. Thinly pigmented line of weakness present. Pronotum with humeri located behind middle, posterior margin broadly rounded.

**Male:** Seventh segment longer than sixth, its ventral apical margin simply concave, prolonged and longitudinally depressed in Rhagadotarsus. Eighth segment simple, prolonged in Rhagadotarsus. Ninth segment with suranal plate simple; pygophore with apical margin broadly rounded; parameres absent. Endosoma with apical, dorsal, basal, and ventral plates completely fused together, forming a ring.

**Female:** Seventh segment with ventral apical margin simply concave. Eighth segment more or less greatly prolonged. Female genitalia forming complete ovipositor. Second valvulae completely fused apically to enclose first valvulae; both first and second valvulae are basally connected with black subtriangular region of process of ninth tergite.

**Distribution:** The Oriental, Ethiopian, Nearctic, and Neotropical regions.

The Rhagadotarsinae is a peculiar group in which some highly primitive characters are combined with some highly specialized characters. As already noted, this subfamily is related to Trepo-
batinae but the subfamily is more primitive than Trepobatinae in the following characteristics:

1. The mandibular and maxillary plates are well defined from each other, the latter is especially well developed and forms the bucculæ to accommodate the rostrum between. This is peculiar to this subfamily.

2. The clypeus with the basal margin is well defined; the basal margin is obliterated in most genera of the Trepobatinae.

3. The antenniferous tubercles are much more well developed than in Trepobatinae.

4. The mesonotum is provided with the lateral longitudinal suture which defines the mesonotum from the mesopleural region. The suture occurs only in Potamometra of Ptilomerinae and few genera of Gerrinae in which the pronotum is not prolonged in wingless forms.

5. The first connexival segment with the posterior margin is distinct; it is completely obliterated and the segment is almost indistinguishably fused with the metacetabular region in Trepobatinae.

6. The first ventral abdominal segment is well retained. This is peculiar to this subfamily in the Gerridae.

7. Associated with the longer body, the metasternum as well as the abdominal segments are longer than in the Trepobatinae.

8. The female genitalia is the well formed ovipositor. This is peculiar to this subfamily.

9. The forewing venation is more primitive than that in the Trepobatinae.

The Rhagadotarsinae, however, is more specialized than the Trepobatinae in the following characteristics:

1. The antennal and leg segments are highly modified in males of many species of Rheumatobates.

2. The omphalium has been completely lost, while it is retained in two genera of the Trepobatinae.

3. The parameres have been completely lost, while they are retained in a majority of genera of the Trepobatinae.

4. The endosoma with the apical, dorsal, basal, and ventral plates are completely fused to form a loop; while they are not completely fused in the Trepobatinae.
Evolutionary tendencies in Rhagadotarsinae

At the subgeneric or generic level the more primitive characters are associated with the genus Rhagadotarsus or the subgenera of Rhagadotarsus, which are larger in size. The maxillary plate and the antenniferous tubercles are most well developed in Caprivia which is the largest in size; they are less developed in Rhagadotarsus s. str. than in Caprivia; least developed in Rheumatobates which is the smallest in size. The metasternum and abdominal segments are the longest in Caprivia and shortest in Rheumatobates. The modification of the antennal and leg segments has arisen only in Rheumatobates which is smallest in body size. It may thus safely be concluded that the structures have become more specialized with reduction of body size at the subgeneric and generic level in evolution of the Rhagadotarsinae.

At the species level, however, this relation is reversed in Rheumatobates. As will be noted from the following table the species with more specialized antennal and leg segments in males are generally greater in body length than the species without or with a slight modification of the antenna and legs. This tendency is much more pronounced in the male than in the female. It should be also noted that the two species belonging to the subgenus Hynesia of Rheumatobates do not conform to this tendency.

Genus Rhagadotarsus Breddin
(Figs. 37, 38, 123, 141, 161, 168, 881-903)


Type species: Rhagadotarsus kraepelini Breddin, monobasic.

Color pattern: Black in ground color. Head along eyes and posterior margin reddish. Pronotum yellow to orange yellow at middle. Both mesonotum and abdominal tergites largely whitish black. Coxae, trochanters, and basal regions of femora paler. Body beneath concolorous with body above.

Structures in wingless forms: Head with an obscure median longitudinal sulcus or sometimes without it, posterior margin concave. Antenniferous tubercles especially well developed in subgenus Caprivia, in which they reach almost to tip of clypeus. Antenna slen-
Table 14.—Lengths of body in species of *Rheumatobates*.

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
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<tbody>
<tr>
<td>Without modification in males:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. petilus</em></td>
<td>1.89–2.3 mm.</td>
<td>2.55–2.77 mm.</td>
</tr>
<tr>
<td><em>R. drakei</em></td>
<td>1.728 mm.</td>
<td></td>
</tr>
<tr>
<td><em>R. bonariensis</em></td>
<td>1.89–2.1 mm.</td>
<td>2.25–2.52 mm.</td>
</tr>
<tr>
<td><em>R. minutus</em></td>
<td>1.6 mm.</td>
<td>1.785–2.2 mm.</td>
</tr>
<tr>
<td><em>R. minutus flavidus</em></td>
<td>1.6–1.89 mm.</td>
<td>2.68–2.95 mm.</td>
</tr>
<tr>
<td><em>R. vegatus</em></td>
<td>2.0–2.24 mm.</td>
<td></td>
</tr>
<tr>
<td>The front leg only modified in males:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. clanis</em></td>
<td>2.1–2.38 mm.</td>
<td>2.37–3.17 mm.</td>
</tr>
<tr>
<td><em>R. mangrovensis</em></td>
<td>2.8 mm.</td>
<td>3.3 mm.</td>
</tr>
<tr>
<td><em>R. trinitatis</em></td>
<td>3.1 mm.</td>
<td>3.7 mm.</td>
</tr>
<tr>
<td>The hind and middle legs modified and third antennal segment unmodified in males:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. klaget</em></td>
<td>2.27–2.52 mm.</td>
<td>2.8–3.0 mm.</td>
</tr>
<tr>
<td><em>R. crassifemur crassifemur</em></td>
<td>2.0–2.22 mm.</td>
<td>2.5–2.86 mm.</td>
</tr>
<tr>
<td><em>R. crassifemur schroederi</em></td>
<td>2.02–2.4 mm.</td>
<td>2.52–3.15 mm.</td>
</tr>
<tr>
<td><em>R. crassifemur esakii</em></td>
<td>2.05–2.39 mm.</td>
<td>2.5–2.94 mm.</td>
</tr>
<tr>
<td>The hind and middle legs modified and the third antennal segment modified in males:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. carvalhoi</em></td>
<td>2.9–3.0 mm. (for male and female?)</td>
<td></td>
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<tr>
<td><em>R. creaseri</em></td>
<td>2.55 mm.</td>
<td>2.9 mm.</td>
</tr>
<tr>
<td><em>R. citatus</em></td>
<td>2.52 mm.</td>
<td>2.52–2.69 mm.</td>
</tr>
<tr>
<td><em>R. praeposterus</em></td>
<td>2.02–2.2 mm.</td>
<td>2.56–2.9 mm.</td>
</tr>
<tr>
<td><em>R. hungerfordi</em></td>
<td>2.6–2.94 mm.</td>
<td>2.73–3.25 mm.</td>
</tr>
<tr>
<td><em>R. trulliger</em></td>
<td>2.5–2.8 mm.</td>
<td>2.73–3.15 mm.</td>
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<td><em>R. tentipes</em></td>
<td>2.44–2.86 mm.</td>
<td>2.94–3.28 mm.</td>
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<td><em>R. spinosus</em></td>
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<td><em>R. mexicanus</em></td>
<td>2.18–2.52 mm.</td>
<td>2.7–2.86 mm.</td>
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<td><em>R. rileyi</em></td>
<td>2.2–2.5 mm.</td>
<td>2.64–3.15 mm.</td>
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<td><em>R. rileyi paloisi</em></td>
<td>2.7–2.94 mm.</td>
<td>2.64–3.36 mm.</td>
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<td><em>R. bergrothi</em></td>
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<td><em>R. meintert</em></td>
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<td>3.06 mm.</td>
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The length of body is after Hungerford (1954).

...der; first segment much longer than second; second segment always shorter than third; third segment slender; fourth segment slender, about as long as third or longer. Eye small, covering only anterolateral angle of pronotum posteriorly. Mandibular and maxillary plates well defined from each other, the former small, the latter well developed and produced anteriorly on each side of rostrum, thus forming bucculae. Rostrum rather short, basally telescoped be-
between bucculae; third segment less than twice as long as last segment.

Pronotum very short, basal margin concave, lateral margin rounded, narrower than head including eyes. Intersegmental suture between mesonotum and metanotum produced posteriorly at middle. Mesonotum laterally defined by longitudinal suture which extends entire length of mesonotum, median longitudinal sulcus more or less distinct throughout entire length of mesonotum. Meso-acetabular region strongly dilated laterally. Mesosternum broadly concave on apical margin. Metanotum short, with or without a more or less distinct median longitudinal sulcus. Metasternum slightly depressed near anterior margin, posterior margin concave, less than half as long as mesosternum. Front leg with coxa short; femur slender and without sexual difference in shape, slightly thickened apically; tibia strongly narrowed basally, less than half as long as femur, apical margin concave, flattened, shallowly depressed on inner surface in apical half; tarsus with first segment greatly reduced, second segment rather thick, rounded especially on anterior margin; apical half splits into two parts by cleft, anterior part thicker than posterior part; claws arising from base of the cleft, with distinct membranous arolium. Middle leg with coxa short; femur slender and straight, subequal in thickness throughout, over one and one fifth times as long as tibia; tibia more slender than femur, about two and one fifth (Rhagadotarsus s. str.) to a little less than three times (s. g. Caprivia) as long as first tarsal segment. First tarsal segment one and a half to two and a half times as second segment; second segment with apical hairs and claws arising from near apex. Hind leg with coxa relatively long; femur a little over twice as long as (Rhagadotarsus s. str.) or about two and a half times as long as tibia (s. g. Caprivia); tibia about five times as long as first tarsal segment; first tarsal segment as long as or a little shorter than second segment; second segment with claws arising from a little beyond middle of second tarsal segment.

Abdomen long, nearly straightly narrowed posteriorly. First abdominal tergite with anterior margin distinct only laterally; second to fifth tergites subequal in length. Connexivum rather strongly reflexed. First connexival segment with posterior margin distinct, anteriorly nearly reaching intersegmental suture between mesonotum and metanotum. Ventrites subequal in length throughout second to sixth segments, with a shallow laevigate depression on
each segment in male; first ventrite broadly rounded on anterior margin and a little longer than second ventrite. Abdominal spiracles placed closer to posterior margin than to anterior margin or at middle between anterior and posterior margins.

Male: Seventh segment longer than sixth segment both dorsally and ventrally, straight on apical margin dorsally, or concave ventrally, with a rather deep depression ventrally. Eighth segment cylindrical, over twice as long as seventh segment, strongly longitudinally depressed ventrally. Ninth segment with suranal plate simple, elevated longitudinally; pygophore with apical margin simply rounded; parameres absent. Endosoma with apical, dorsal, basal, and ventral plates completely fused, forming a loop and extends beyond apex of endosoma; lateral plates small and inconspicuous. (Description of the genitalia is based on R. (R.) kraepelini.)

Female: Seventh segment much longer than sixth segment, concave on ventral apical margin. Eighth segment cylindrical. Valvifers narrowed apically, extending beyond apical margin of eighth tergite. First valvula well sclerotized, simply narrowed apically and with acute tip, basally connected with a subtriangular part at apex of ninth tergal process, which is membranous and long. Second valvulae completely fused apically, forming a complete sheath and with acute tip; ramus very fine but distinct as far as near apex of valvula, connected basally with tip of black plate at apex of ninth tergal process. Ninth tergite slender, slightly thickened at middle, with round apical margin. (Description of the genitalia is based on R. (R.) kraepelini and R. (C.) hutchinsoni.)

Winged forms: Hemelytra with R + M + Cu forked into two branches, anterior branch connected with Sc by an oblique vein at the point behind middle of hemelytra, and apically fused with Sc; posterior branch connected with A at the middle of hemelytra; a rather obscure straight line of weakness recognizable at middle of apical half of hemelytra. Vein A connected with rear margin of hemelytra by a short oblique vein. Hind wing as in fore wing, but upper (anterior) branch of R + M + Cu not fused with Sc apically, and A not connected with posterior margin of wing by a short cross vein.

Distribution: The Oriental region (Burma, China, Formosa, India, Java, Philippines, Malaya) for Rhagadotarsus s. str., and the Ethiopian region (South Africa, French Congo, Belgian Congo, Sudan) for Caprivia.
Rhagadotarsus s. str. and the subgenus Caprivia can be distinguished by comparing the following description for each subgenus.

Subgenus Rhagadotarsus Breddin s. str.

For type designation and citations see generic bibliography.

Body relatively short. Bucculae and antenniferous tubercles relatively weakly developed. Middle tibia a little over twice as long as first tarsal segment. Hind femur a little over twice as long as first tarsal segment.

Subgenus Caprivia China


Type species: Rhagadotarsus hutchinsoni China, by original designation.

Body almost cylindrical. Bucculae and antenniferous tubercles well developed. Middle tibia a little less than three times as long as first tarsal segment. Hind femur about two and a half times as long as tibia.

Genus Rheumatobates Bergroth

(Figs. 39, 123, 141, 161, 168, 904-961)

Rheumatobates Bergroth, Insect Life, 4:321(1892).

Type species: Rheumatobates rileyi Bergroth.


Structures in wingless forms: Head with an obscure median longitudinal impression usually recognizable in anterior half of uppersurface. Antenniferous tubercles more well developed in males than in females of some species in which antennae greatly modified. Antenna in female short and slender in all species; first segment shorter than second and third segments together, second segment shortest, third one usually with two long hairs arising from apex and near middle of inner margin; fourth segment fusiform. Antennae in males highly variable in shape and proportional lengths of segments, greatly modified in many species. Mandibular and maxillary plates clearly separted from each other, the latter well developed and rounded on upper apical margin. Rostrum slender, relatively short; third segment usually about twice as long as fourth segment.

Pronotum longer in males than in females in some species, strongly produced posteriorly on each side, posterior margin concave. Intersegmental suture between mesonotum and metanotum broadly convex dorsally. Mesonotum laterally defined from mesopleural regions by a longitudinal suture; median longitudinal sulcus distinct; mesoacetabular region dilated. Mesosternum broadly concave on apical margin. Metanotum short, median longitudinal sulcus often absent, laterally defined by first abdominal connexival segment which intrudes anteriorly into metanotal region; metacetabular region somewhat displaced lateroventrally by first connexival segment. Metasternum about half as long as mesosternum, posterior margin less concave than anterior margin. Front leg in female with simple and slender femur and short and thick tibia. Front leg in male with femur sparsely clothed with long hairs on inner margin, strongly thickened and with some black long hairs in some species; tibia about half as long as femur, rather strongly thickened apically, inner apical angle lobately produced; tarsus a little shorter than tibia; first segment greatly reduced and basally hidden under hairy apical margin of tibia; second segment rounded on anterior margin, apex acute and without cleft, long claws arising from near middle of inner margin. Middle leg
with femur and tibia have a row of long hairs on inner margin in males of some species, and the former thickened apically or curved and peculiarly thickened in males of some species; femur longer than tibia in most species; tarsus with first segment a little less than twice to a little over three times as long as second segment in females; second segment with small claws arising from beyond middle. *Hind leg greatly modified from coxa to tibia in males of some species.* Femur over one and a half times as long as tibia in most species; tarsus with first segment a little less than twice to a little over three times as long as second segment in females of all species, or much longer than second in males of some species in which the preceding segments are greatly modified; second tarsal segment with well developed long claws.

Abdomen obovate. Anterior margin of first tergite roundly produced anteriorly, usually obliterated medially. First segment greatly encroaching into metathoracic region pleurosternally; first connexival segment with posterior margin distinct and at about the same level as first abdominal spiracle, anteriorly reaching definitive intersegmental suture between mesonotum and metanotum, ventrally first ventrite clearly retained and longer than second abdominal ventrite. Second to sixth segments subequal in length both dorsally and ventrally, anterior margin of second tergite slightly produced anteriorly.

**Male:** Seventh segment longer than sixth, simple on ventral apical margin. Eighth segment rather strongly drawn out and more or less cylindrical. Ninth segment with pygophore rounded on apical margin; parameres absent. Endosoma with apical, dorsal, basal and ventral plates completely fused, forming a loop, not extending beyond apex of endosoma apically, with small lateral plates. *(Description of the genitalia is based on *R. (R.) crassifemur.)*

**Female:** Seventh abdominal segment with ventral apical margin concave. Eighth segment strongly prolonged. First valvula long, acutely pointed, inner lobe darker basally, with a fine apical process almost reaching near apex of outer lobe; ramus connected with a dark subtriangular plate basally. Second valvulae fused apically, forming a narrow sheath to enclose first valvulae within, connected basally with black subtriangular region of the process from ninth tergite on its inner margin. *(Description of the genitalia is based on *R. (R.) crassifemur.)*

**Winged forms:** Hemelytra with $R + M + Cu$ connected with Sc by an oblique vein at basal third, anterior branch not connected
with Sc apically; posterior branch apically not connected with A. Vein A extending only in basal third. T-shaped white line of weakness spreading in apical two thirds of hemelytra. *Hind wing venation as in forewing venation, much more reduced than in Rhagadotarsus.*

**Distribution:** The Western Hemisphere (Large part of the United States, Argentina, Brazil, British Guiana, British Honduras, Cuba, Mexico, Paraguay, Panama, Peru, Puerto Rico).

The genus *Rheumatobates* is distinguishable from *Rhagadotarsus* by the following characters:

1. The wing venation is more reduced, i.e., the apical cell is not formed and the line of weakness is T-shaped, while in *Rhagadotarsus* the hemelytra with its venation is more developed and forms an apical cell along the anterior margin of the wing, and the whitish line of weakness is simply horizontal.

2. The second tarsal segment of the front leg is without cleft, whilst it is split into two parts by a narrow longitudinal cleft in *Rhagadotarsus*.

3. *Rheumatobates* is obviously much more specialized than *Rhagadotarsus* as seen in the higher degrees of specialization in the antennae and legs in males of many species.

The genus *Rheumatobates* is divided into two subgenera, i.e., *Rheumatobates* s. str. and *Hynesia* China. The differences between the two subgenera are only in the males.

**Subgenus Rheumatobates** Bergroth s. str.

For type designations and citations see generic bibliography.

Male antennal segments greatly modified in most species. Fourth antennal segment at least not much longer than third. Male front leg with femur modified but not much thickened and without a row of conspicuous spines on entire inner margin.

**Subgenus Hynesia** China


Type species: *Hynesia trinitatis* China, by original designation.

Male antennae long, not greatly modified; fourth antennal segment very long in *trinitatis*. Male front femur much longer and thicker than in *Rheumatobates* s. str., with a row of conspicuous spines on entire inner margin.

Two species, *R. (H.) trinitatis* (China) and *R. (H.) mangrovensis* (China) from Trinidad belong to this subgenus.
Subfamily Trepobatinae Matsuda

Structures in wingless forms: Relatively homogeneous, highly specialized group including thirteen genera of small body size. Shape of body elliptical or sometimes globular.

Head with anterior margin more or less broadly rounded in dorsal view. Clypeus with basal margin either obliterated or retained. Eye not entirely covering lateral margin of pronotum, more or less rounded on inner margin. Antenniferous tubercles scarcely or poorly developed. Antennal cavities open anterior to eyes. Antenna slender; first segment longest in most genera, strongly incrassate in males of Metrobatopsis; relative lengths between second and third segments vary considerably in various genera, second and third modified distally in Metrobates; fourth segment as long as or longer than third in most genera. Mandibular and maxillary plates distinct from each other in some genera. Rostrum relatively short, third segment not over three times as long as last.

Pronotum never prolonged, shorter and narrower than head in many genera. Intersegmental suture between mesonotum and metanotum represented dorsally by posterior margin of metathoracic postnotum in winged forms, and laterally by metacetabular suture in winged forms. Mesonotum with or without median longitudinal sulcus; lateral longitudinal suture defining mesonotum from mesopleuron absent. Mesosternum with paired longitudinal suture defining mesosternum from mesopleuron absent in all genera. Metathoracic spiracle inconspicuous, placed subparallel with intersegmental suture between mesonotum and metanotum laterally. Metanotum with median longitudinal sulcus absent in most genera. Metacetabular region dilated posteriorly, elevated as far as the intersegmental suture anteriorly. Metasternum a little longer than second abdominal ventrite in most genera; omphalium absent in most genera. Front leg with femur modified in some species of some genera; tibia without conspicuous process at inner apical angle, modified in males of some species; tarsus with first segment greatly reduced; second segment often several times as long as first, claws arising from near middle of second segment. Middle leg longer than hind leg; femur thick and short; tibia always longer than femur, about twice as long as femur in some genera; tarsus with first segment always longer than second except for Metrobates, in which second segment longer than first. Hind leg with femur always longer than middle femur and than hind tibia; tarsus with first and
second segments fused in some genera, second segment much longer than first and with conspicuous claws in *Metrobates*.

Abdomen has anterior margins of first and second tergites obliterated in some genera, broadly rounded when recognizable, both segments much longer than third tergite. First ventrite absent; ventrites more reduced than tergites, but less than in Halobatini. Connexivum extends into well elevated metacetabular region and indistinguishably fused with the latter in some genera, nearly horizontal or slightly reflexed in most genera. Abdominal spiracles, when recognized, located at middle or a little closer to posterior margin than to anterior margin of segments.

**Male:** Seventh segment with ventral apical margin simply concave or nearly horizontal. Eighth segment dorsally more well developed, more or less greatly prolonged in some genera. Ninth segment with suranal plate armed with a spinous process directed cephalad apically on each lateral margin in some genera. Pygophore simple in great majority of genera; parameres retained in most genera and simple. Endosoma with dorsal plate apically either fused with or distinct from apical plate; basal and ventral plates absent in most genera, they are weakly developed when present; lateral plates sometimes not well defined.

**Female:** Seventh segment ventrally longer than sixth; ventral apical margins simply concave or nearly horizontal in great majority of species; apical tergites modified in some species of *Metrobotopsis*. Eighth segment well exposed in some genera. First valvula with inner lobe always folded beneath outer lobe, always well pigmented, typically with two apical processes of different length, or they are lost in some genera; ramus of first valvula pigmented, located typically along outer margin of process of ninth tergite. Second valvula long, rounded apically, extending beyond apical margin of intervalvular membrane. Vulva relatively well developed, often extending beyond middle of first valvula; ramus fine and long.

**Winged forms:** Hemelytra long, basal half to one third coriaceous, forming embolium along anterior margin of hemelytron. R + M + Cu forked into two oblique branches near extremity of basal coriaceous area, upper one united with lower apical angle of basal coriaceous area, then together sending a straight vein into apical membranous region, lower branch united with A near extremity of basal coriaceous region, then send a lower straight vein into
Table 15—Table of significant generic characters in Triplaxifiles.

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*Table 15—Table of significant generic characters in Tropobatinae—Continued.*
| Genus          | No. | Symbol 1 | Symbol 2 | Symbol 3 | Symbol 4 | Symbol 5 | Symbol 6 | Symbol 7 | Symbol 8 | Symbol 9 | Symbol 10 | Symbol 11 | Symbol 12 | Symbol 13 | Symbol 14 | Symbol 15 | Symbol 16 | Symbol 17 | Symbol 18 | Symbol 19 | Symbol 20 |
|----------------|-----|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| Pleurobatus    | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Rhipidomermata| (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Hyporhynchus  | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Cymophanes    | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Naphydus      | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Schisteus     | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Rhipidomermataconicola | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| Oelandera     | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Haplodactylus | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Thelodontura  | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Trigoniodontida | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Trigonoidea   | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |
| Notoptera     | (+) | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      | (+)      |

* For the female only.

For the explanations of symbols see introduction and table 5.
apical membranous region (this vein is obliterated in Metrobatopsis). Line of weakness always present between the two apical straight veins in membranous region.

Distribution: Temperate and tropical zones of the Eastern and Western Hemispheres.

Relationships of genera

As noted from the table of characters, the number of primitive characters varies relatively little among genera in comparison with other subfamilies, indicating a relatively high degree of homogeneity of the subfamily. Derivation of certain genera from certain other existing genera is hard to conceive in this subfamily. Another important fact is that no one genus occurs in both the Eastern and the Western Hemispheres. The distribution of Metrobates, Telmatometra, Trepobatoides, Trepobates, Halobatopsis and Ovatametra is confined to the Western Hemisphere; Hynesionella, Metrobatopsis, Rheumatometra, Rheumatometroides, Stenobates, Cryptobates, and Naboandelus occur solely in the Eastern Hemisphere.

Among the genera from the Western Hemisphere, Metrobates is unique in the highly flattened body, the modified antennae, the long middle tibia and hind femur, etc., and it is not closely related to any one genus from the Western Hemisphere. Telmatometra is more closely related to Halobatopsis than to Trepobates, as is indicated mainly by a similar proportional lengths of leg segments. Ovatametra has possibly been derived from Telmatometra or Halobatopsis like ancestor with reduction in the body size, etc. Trepobatoides is structurally similar both to Telmatometra and Trepobates; it is, however, quite distinct from both of them by its different proportional lengths of the antennal and leg segments.

Among the genera from the Eastern Hemisphere, Stenobates and Rheumatometroides are evidently closely related, as indicated by the retention of the omphalium, the metacetabula being dorsally convergent, etc. These characters are peculiar to these genera. Rheumatometroides has been known from the Solomon Islands and Stenobates from Singapore. Metrobatopsis and Rheumatometra are known from New Guinea, the Solomon Islands, and Northern Australia. They are not closely related. Rheumatometra is similar to Metrobates from the Western Hemisphere in certain characters, such as the shape of the body, retention of the median longitudinal sulcus on the mesonotum, the wide head, a similar female genitalia, etc., although both genera are quite distinct from each other by
certain specialized characters peculiar to each one of them. Cryptobates is relatively more generalized and similar to Telmatometra from the Western Hemisphere, especially in the proportional lengths of antennal and leg segments. It is, however, distinct from Telmatometra by the complete loss of the anterior margins of the first and second abdominal tergites, etc. Naboandelus may be somewhat closely related to Hynesionella, although its phylogenetic position is obscure to me because of the absence of the male specimens available for study. Hynesionella has hitherto been known only from Africa. The genus is unique in having the carinate definitive intersegmental suture between the mesonotum and metanotum; the modification of the male apical segments is also peculiar, although the suranal plate is provided with a spinous process on the lateral margin as in the other three genera of this subfamily.

Although the intergeneric relationships are often obscure, the following diagram 9 indicating the relationships of genera is tentatively presented:

![Diagram 9. Diagram showing the relationships of genera of the Trepobatinae.](attachment:image)
Evolutionary tendencies and some structural peculiarities in Trepobatinae

As noted elsewhere, the subfamily is rather highly homogenous and well defined. There is, however, no good evidence to indicate that certain genera have been derived from other existing genera, and the great majority of genera have attained independently about the same degree of structural specialization. It is thus relatively difficult to discuss the process of evolution of structures at the generic level. The following points, however, appear to deserve noting as evolutionary tendencies and structures more or less peculiar to this subfamily.

(1) The relatively short and thick middle femur, which is always shorter than the middle tibia, has been well fixed in this subfamily. This relatively short femur is apparently realized by the smaller growth ratio and smaller initial growth index for the femur than those for the tibia (P<0.05 in Trepobates knighti).

(2) The growth ratio for the first antennal segment is relatively high. Because of this there is a tendency for this segment to vary greatly in length among the related species without great difference in the body length.

(3) The spinous process on the lateral margin of the suranal plate of the male has arisen in four genera, and the apex of the process is directed cephalad.

(4) The seventh abdominal segment has remained relatively simple, though prolonged. Conspicuous modification of the segment has arisen only in females of certain species of Metrobatopsis.

Genus Trepobates Uhler

(Figs. 60, 110, 124, 142, 162, 169, 962-980)

_Trepobates_ Drake and Harris, Psyche, 39(4):112(1932).
_Kallistometra_ Kirkaldy, Entomologist, 32:28(1899) (type species, _Kallistometra taylori_ Kirkaldy).
Type species: *Halobates pictus* Herrich Schaeffer, by original designation.


Color pattern: Variegated yellow (or rarely orange yellow) and black. Head usually with a median longitudinal black stripe. In some species the dark markings on dorsal surface are greatly reduced or partially obliterated, whereas in others the color is almost entirely black, the yellow being replaced by black. Meso-thorax typically with a median and two pairs of lateral longitudinal black stripes.

Structures in wingless forms: Body oval, moderately pubescent. Head between eyes widened posteriorly, posterior margin nearly straight. Eye exserted, covering anterolateral angle of pronotum. Antennal cavities open cephaloventrad, located on or just above the lines across anterior margins of eyes. Antenna slender, extending back beyond middle of body. First segment longest, a little shorter than second and third segments together; second segment shortest in most species, relative length of second to first greater in female than in male; third segment a little longer than second, third segment in males of some species with long pilosities on lower margin, both second and third segments slightly and simply thickened anteriorly and truncate at apices; fourth segment about as long as or a little longer than third. Mandibular and maxillary plates indistinguishably fused. Rostrum rather slender, reaching mesosternum, third segment about twice as long as last segment in most species.

Pronotum transverse subquadrangular in shape, narrower than head including eyes, posterior margin broadly concave or nearly straight. Mesonotum without distinctly impressed median longitudinal sulcus, a little over twice as long as pronotum in most species. Intersegmental suture between mesonotum and metanotum nearly straight dorsally. Metanotum without distinct median longitudinal sulcus, laterally defined by longitudinal elevation continuous from abdominal connexivum, reaching intersegmental suture between mesonotum and metanotum. Metasternum with omphalium as well as omphalial groove completely lost, longer than second ventrite, less than one tenth as long as mesosternum. Front leg relatively long; femur curved, depressed and concave on inner
margin in male; tibia simple, considerably shorter than femur; tarsus with first segment extremely reduced, second segment often several times as long as first segment, claws arising from beyond middle and with fine arolium. Middle leg with femur much thicker than tibia, ciliated on lower margin in males, a little over half as long as tibia; tibia a little over three times as long as first tarsal segment; tarsus with first segment a little longer than second segment in most species, second segment with small claws. Hind leg with femur much more slender but much longer than middle femur, about twice as long as tibia; tibia over twice as long as first tarsal segment; first tarsal segment less than twice as long as second segment.

Abdomen gradually narrowed posteriorly. Connexivum strongly reflexed, especially so in female. First and second abdominal tergites with anterior margins strongly produced anteriorly, anterior margin of first often obliterated medially. Ventrally haired in some species.

Male: Seventh segment much longer than sixth segment and broadly concave on ventral apical margin. Eighth segment about as long as seventh or longer than seventh ventrally, ventral apical margin concave, with a feeble median notch or simply concave on dorsal apical margin. Ninth segment with suranal plate largely hidden beneath eighth tergite, simply rounded on apical margin; pygophore exposed in apical half, broadly rounded on apical margin; parameres robust and simply curved upward apically. Endosoma with dorsal plate turned backward apically, distinctly split into two arms basally; basal plate separated from base of dorsal plate; ventral plate short and membranous, strengthened by black slender sclerite arising from basal plate; lateral plates long and simple. (Description of the genitalia is based on knighti and trepidus.)

Female: Seventh segment much longer than sixth segment ventrally, broadly concave on apical margin in most species, with long and straight pilosity on apical margin in some species; connexivum strongly reflexed on dorsum, with spinous process apically in knighti. Eighth segment with apical half exposed. First valvula with inner lobe dark, split into two lobes, outer one of them almost reaching apex of outer lobe; outer lobe clothed with straight oblique hairs basally, apex membranous, roundly folded; ramus extending along outer margin of process of ninth tergite, which is provided with dark arched crescent shaped sclerite apically. Second val-
vulae with apices roundly folded and convergent apically; ramus slender, extending basally along ramus of first valvula. Vulva membranous, acutely pointed. (Description of the genitalia is based on knighti.)

Winged forms: Hemelytra with well formed embolium. R + M + Cu vein sends short branches both anteriorly and posteriorly, anterior branch connected with Sc and extends into apical membranous region, posterior branch united with vein A at extremity of basal coriaceous region. T-shaped line of weakness recognized basally along apical margin of coriaceous region, and horizontally at middle between two veins in membranous region and reaches apex of hemelytra. Hind wing with Sc connected by oblique branch from R + M at middle, with two apical veins evanescent apically; Cu vein obscure, apically fused with A beyond middle of hind wing. Pronotum widest at middle or a little behind middle.

Distribution: Canada, greater part of the United States, West Indies, Central and South America (Guatemala, Mexico, Panama, Peru, Venezuela).

Genus Telmatometra Bergroth
(Figs. 59, 80-81, 125, 142, 143, 169, 981-991)

Telmatometra Bergroth, Ohio Nat., 8:374(1908).

Type species: Telmatometra whitei Bergroth, monobasic.


Color pattern: Variegated yellow and black, predominantly yellow in some species. Head with longitudinal black stripes along eyes. Mesonotum with two longitudinal dark stripes on each side, with additional stripe mesad of them in some species.

Structures in wingless forms: Body oval. Male smaller and more slender than female. Pronotum in relation to mesonotum longer in male than in female. Head between eyes strongly widened posteriorly, posterior margin straight. Eye exserted, extending to nearly anterior half of pronotum. Antenniferous tubercles scarcely developed; antennal cavities open on or a little below straight line across anterior margins of eyes. Antenna over half as long as body, greater in absolute and relative length to body in male, but without significant difference in proportional lengths of segments between sexes. First segment strongly curved
in basal half, much longer than second segment, but not over twice as long as the latter; second segment shortest, truncate at apex; third segment always over twice as long as second, slender, simple at apex; fourth segment about as thin as third, a little shorter than third. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum relatively long and slender, reaching mesosternum; third segment three times as long as last segment.

Pronotum shorter and much narrower than head, anterior margin straight, posterior margin variable, lateral margin rounded. Mesonotum with median longitudinal sulcus obscure, recognizable posteriorly; over two and a half times as long as pronotum. Intersegmental suture between mesonotum and metanotum slightly produced anteromesially. Metanotum laterally defined by longitudinal elevation, median longitudinal sulcus normally recognizable throughout the entire length. Metasternum highly reduced, less than one tenth as long as mesosternum but a little longer than second ventrite, without either omphalium or omphalial groove. Front leg slender and relatively long; femur slightly longer than tibia; tibia simply thickened apically, without conspicuous process, inner surface with longitudinal shallow depression apically; tarsus with first segment highly reduced, second segment three to five times as long as first segment, claws arising from beyond middle and with membranous arolium. Middle leg with femur robust, much thicker than tibia, between two thirds and three fourths as long as tibia; tibia over three times as long as first tarsal segment; first tarsal segment longer than second tarsal segment, but not over one and a half times as long as second; second segment with poorly developed claws. Hind leg with femur a little less than twice to a little over twice as long as tibia; tibia over four times as long as first tarsal segment; first tarsal segment about as long as second tarsal segment, second segment with claws.

Abdomen has connexivum strongly reflexed, but not folded on dorsum in female. Anterior margins of first and second tergites convex, which are often obliterated medially, both segments much longer than any one segment that follows posteriorly.

Male: Seventh segment at least twice as long as sixth segment, concave on ventral apical margin. Eighth segment prolonged in some species, simply concave or notched at middle on ventral apical margin, ventral surface with a median longitudinal groove and densely clothed with hairs on either side of the groove (indentata),
or depressed in some species. Ninth segment with suranal plate laterally hidden beneath eighth tergite; pygophore exposed at least apically; parameres simply curved upward, short but robust. Apical segment of endosoma with dorsal plate basally bifurcate, fused anteriorly with large apical plate which extends along ventral apical area of endosoma; lateral plates slender, reaching anteriorly near point of fusion or dorsal plate with apical plate, extending posteriorly beyond base of dorsal plate; without ventral plate. (Description of the genitalia is based on whitei, indentata, and fusca.)

Female: Seventh segment ventrally much longer than sixth segment, deeply concave on ventral apical margin. Eighth segment ventrally well exposed beyond concave ventral apical margin of seventh segment. First valvula with outer lobe simply narrowed apically, inner lobe membranous, folded beneath outer lobe but not reaching apex of outer lobe, a dark thread-like structure arising from near base and extending as far as apex of outer lobe. Second valvulae constricted near apices, extending far beyond apical margin of intervalvular membrane which is concave; process of ninth tergite robust. Vulva slender, reaching apical one fourth of first valvulae. (Description of the genitalia is based on whitei.)

Winged forms: Forewing with well formed hairy embolium, anterior branch from basal R + M + Cu is connected with embolium at its lower apical angle; posterior branch is connected with vein A before middle of hemelytron. In apical membranous region there are two veins, the anterior one from apex of embolium and lower one from the point of union between A and the posterior branch from R + M + Cu. The line of weakness represented by pale straight region spreading entire membranous region at middle, basal line of weakness is represented by fine thinly pigmented line behind basal coriaceous region. Hind wing with Cu evanescent apically. No vein A is recognized. Pronotum subpentagonal in shape, widest at a little behind middle, apex broadly rounded.

Distribution: Central and South America (Bolivia, Brazil, British Honduras, Costa Rica, Colombia, Mexico, Panama, Peru, Puerto Rico).

The genus Telmatometra is distinguishable from Trepobates by the following characteristics:

1. Sexual difference in proportional lengths of the first and second antennal segments is absent.

2. The male has relatively and absolutely longer antennae than the female.
(3) The length of the third rostral segment relative to the second is greater than in *Trepobates*.

(4) The length of the tibia in relation to the femur in the front leg is greater than in *Trepobates*.

(5) The first tarsal segment is about as long as second in the hind leg, while it is distinctly longer than second in *Trepobates*.

(6) The intersegmental suture between mesonotum and metanotum is produced anteromesially.

(7) There is evidence that the growth ratio for the third antennal segment is greater than those for the first and second segments in *Telmatometra*.

**Genus Trepobatoides** Hungerford and Matsuda

(Figs. 52, 125, 142, 169, 992-1002)


Type species: *Trepobatoides boliviensis* Hungerford and Matsuda, by original designation.

Species examined: *T. boliviensis* Hungerford and Matsuda.

**Color pattern:** Predominantly pale yellow. Head with median black longitudinal stripe. Pronotum with a median black longitudinal stripe and a pair of black spots on either side of middle; mesonotum with a median black longitudinal stripe and a pair of lateral longitudinal stripes of the same color extending for entire length of mesonotum; mesopleural region with a black longitudinal stripe which extends back as far as metathoracic spiracle. Metanotum with a pair of large black spots along anterior margin. Each abdominal tergite with both anterior and posterior margins black.

**Structures in wingless forms:** Body elongate ovate, much narrowed anteriorly. Head between eyes longer than wide, widened posteriorly, posterior margin slightly produced posteriorly. Eye oblong, covering anterolateral angle of pronotum. Antennal cavities open just above anterior margins of eyes. Antenna slender, a little shorter than length of body. First segment distinctly longer than two following segments together; second segment shortest, its relative length to first segment greater in male than in female; third segment with apex truncate; fourth segment much longer than third segment. Clypeus with basal margin obliterated. Mandibular and maxillary plates completely fused. Rostrum long, extending far beyond prosternum; third segment about two and a half times as long as last segment.
Pronotum much narrower than head, posterior margin feebly concave, posterolateral angle broadly rounded. Mesonotum without distinct median longitudinal sulcus, its relative length to pronotum greater in male than in female. Intersegmental suture between mesonotum and metanotum feebly concave dorsally. Metanotum laterally defined by longitudinal elevations with a faint median longitudinal sulcus. Metasternum a little less than one tenth as long as mesosternum, without omphalium. Front leg considerably thicker and longer than tibia; tibia slightly thickened apically, without armature on inner apical angle in both sexes; tarsus a little less than half as long as tibia; first segment strongly reduced; second segment three times as long as first, claws arising from middle of inner margin, with hair like arolium, Middle leg with femur thick, about two thirds as long as tibia; tibia a little over three times as long as first tarsal segment; first tarsal segment a little less than twice as long as second tarsal segment; claws very small. Hind leg with femur about twice as long as tibia; tibia slightly thickened at base, then tapering apically, five to six times as long as first tarsal segment; first tarsal segment a little shorter than second segment, claws inconspicuous.

Abdomen oblong, a little narrower in male. Connexivum not strongly reflexed. First tergite with anterior margin roundly produced and distinct; second segment also produced on anterior margin; third to sixth tergites subequal in length in both sexes; second to sixth ventrites subequal in length in both sexes.

**Male:** Seventh segment ventrally over twice as long as sixth segment. Eighth segment strongly prolonged and cylindrical, ventrally about twice as long as seventh in the middle, roundly depressed along posterior margin. Ninth segment with suranal plate widened posteriorly; pygophore well exposed, nearly truncate on apical margin, densely clothed with adpressed hairs on ventral surface; parameres simply curved upward. Endosoma long. Dorsal plate thick and bifurcate basally, apically fused with apical plate via narrow bridge; without well defined lateral plates; broadly sclerotized along ventral margin of endosoma; without either ventral or basal plate.

**Female:** Seventh segment ventrally about three times as long as sixth segment, ventral apical margin broadly concave. Eighth segment ventrally well exposed. First valvula with inner lobe dark, with two apical processes, inner one of them shorter and attached to vulva, outer one almost reaching apex of outer lobe of first
valvula. basally covering outer lobe beneath; with a tuft of straight long hairs on lower lateral margin of the dilated base of outer lobe. Second valvula directed mesad apically and broadly rounded apically; intervalvular membrane directly continuous with apices of valvulae, dark along outer margin; ramus slender and long, without crescent shaped sclerite at apex of process of ninth tergite.

**Distribution:** South America (Bolivia).

The genus *Trepobatooides* is related to *Telmatometra* and its allies but peculiar in the following characteristics:

1. The head above has a black longitudinal stripe. This is true of *Trepobates* but not of *Telmatometra* (except for *rozeboomii*), *Halobatopsis, Cryptobates*, etc.
2. The first antennal segment is much longer than the two following segments together. In no other genera of Trepobatinae is the first segment much longer than two following segments together.
3. The length of the second antennal segment in relation to the first is greater in the male than in the female. In the related genus *Trepobates* the length of the second segment relative to the first is greater in the female than in the male.
4. The female genitalia are peculiar in that: (1) The inner lobe of the first valvula covers the outer lobe beneath basally, and has a tuft of long hairs on the lateral margin of each side of outer lobe, and (2) the second valvulae are apically so approximated as to obliterate the apical margin of the intervalvular membrane.
5. The relative lengths of the first and second tarsal segments of the middle leg are close to 2:1; while the same proportion never exceeds 1.5:1 in *Trepobates* and *Telmatometra*.

Although the relative lengths of the leg segments are more like those of *Telmatometra*, the relatively short rostrum suggests a relationship to *Trepobates*. The extremely long first antennal segment suggest a closer relationship to *Trepobates* than to *Telmatometra*, in which the first antennal segment is not the longest. The male genital segment is, however, similar to that of *Telmatometra acuta*. This genus thus represents an intermediate between *Trepobates* and *Telmatometra*. Different proportional lengths of antennal and leg segments from those in the related genera are apparently derived from different growth patterns from those in the related genera, considering the fact that the body length of this genus is about the same as in *Trepobates, Telmatometra*, etc.
Genus Halobatopsis Bianchi
(Figs. 50, 143, 163, 1003-1011, 1019-1025)


Type species: Halobates platensis Berg, by original designation.
Species examined: H. platensis (Berg), H. spiniventris Drake and Harris.

Color pattern: Variegated black and pale yellow to pale brown.
Structures in wingless forms: Head between eyes strongly widened posteriorly, posterior margin feebly concave. Eye exserted, extending posteriorly as far as middle of pronotum. Antenniferous tubercles scarcely developed; antennal cavities open on or above line across anterior margins of eyes. Antenna over half as long as body, without sexual difference in relative lengths between segments, and in relative length of antenna to length of body. First segment slightly curved at base, twice or a little less than twice as long as second; second segment shortest; third segment less than one and a half times as long as second segment, apex truncate; fourth segment about as long as or longer than third segment. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum with third segment relatively thick basally and about two and a half times as long as last segment.

Pronotum narrower than head including eyes, lateral margins broadly rounded, posterior margin concave at middle. Relative length of mesonotum to pronotum greater in female than in male. Mesosternum with posterior margin concave. Intersegmental suture between mesonotum and metanotum slightly produced anteriorly at middle. Metanotum laterally defined by longitudinal elevations, without median longitudinal sulcus. Metasternum highly reduced, less than one tenth as long as mesosternum, without omphalium, distinctly longer than second ventrite. Front leg with femur strongly arched in male of spiniventris; tibia distinctly shorter than femur, strongly curved, constricted beyond middle and with a dense row of short black hairs on inner surface; tarsus with first segment greatly reduced, second segment with claws arising from beyond middle of second segment. Middle leg with femur two thirds to three fourths as long as tibia; tibia a little less than three times
as long as first tarsal segment; first tarsal segment less than one and a half times as long as second segment, second segment with poorly developed claws. Hind leg with femur about twice as long as tibia; tibia over four times as long as first tarsal segment; first tarsal segment subequal in length to second; second segment with claws longer than those in middle leg.

Abdomen with connexivum strongly reflexed but not folded on dorsum in female of spiniventris. Anterior margins of first and second tergites produced anteriorly, obliterated at middle, both segments much longer than any one of following segments.

**Male:** Seventh segment over two and a half times as long as sixth segment and concave on ventral apical margin. Eighth segment concave on ventral apical margin or with a median spinous process (spiniventris). Ninth segment with suranal plate simple; pygophore exposed in apical half, broadly rounded on apical margin; parameres robust. Endosoma with dorsal plate bifurcate basally, apically directed cephalad along ventral margin of endosoma (fused apical plate); without well defined lateral plates, sclerotized along ventral margin of endosoma; without either ventral or basal plate. Description of the genitalia is based on spiniventris.)

**Female:** Similar to Telmatometra. Seventh segment deeply concave on ventral apical margin. Eighth segment thus ventrally well exposed behind seventh ventrite. First valvula with inner lobe folded beneath outer lobe, split apically into two lobes and both nearly reaching apex of outer lobe, largely fused with vulva on inner margin. Second valvula far extending beyond apical margin of intervalvular membrane, folded upward and rounded apically, apical margin of intervalvular membrane concave and sclerotized; ramus very long. Vulva long, reaching near apex of first valvula. (Description of the genitalia is based on spiniventris.)

**Winged forms:** Hemelytra with well formed hairy embolium. R + M + Cu sends two branches, anterior one of them united with inner apical angle of embolium, then sending a branch into apical membranous region; the posterior branch united with A before middle of wing, then extending into membranous region. Line of weakness represented by a transverse weakly pigmented area, which stretches throughout the middle of the entire membranous region of wing. Hind wing with vein A obscure, connected with R + M beyond the cross vein connecting Sc and R + M. Pronotum sub-pentagonal, widest behind middle.
Distribution: South America (Argentina, Brazil, Uruguay.)

The genus *Halobatopsis* differs from *Telmatometra* by the following characteristics:

1. There is no conspicuous sexual difference in proportional lengths of antennal segments or in the length of the antenna in relation to the total length of body in *Halobatopsis*.

2. The third antennal segment is distinctly less than twice as long as the second, while it is distinctly over twice as long as the second in *Telmatometra*.

3. The abdomen is predominantly black, while it is predominantly yellow in *Telmatometra*.

The genus *Halobatopsis* is also closely related to *Trepobates*, but can be distinguished from it by:

1. The eyes extending beyond the middle of the pronotum in lateral view, while they do not extend beyond middle in *Trepobates*.

2. The hind tibia is over twice as long as the tarsus, while it is distinctly less than twice as long as the tarsus in *Trepobates*.

3. The abdomen is relatively wider in *Halobatopsis* than in *Trepobates*.

Genus *Ovatametra* Kenaga

(Figs. 55, 125, 143, 163, 1026-1036)


Type species: *Halobatopsis peruvianus* Drake and Harris, by original designation.

Species examined: *O. fusca* Kenaga, *O. obesa* Kenaga, *O. minima* Kenaga, one unidentified species.

Color pattern: Variegated pale yellow to pale brown and black. Head with a pair of lateral and median black longitudinal stripes which are often confluent posteriorly. Pronotum with a pair of lateral black spots and a median black stripe. Mesonotal region typically with a pair of lateral and median longitudinal stripes; mesopleural region with two black longitudinal stripes. Metanotum and abdominal tergites largely black.

Structures in wingless forms: Oval. Female considerably longer and wider than male. Head between eyes widened posteriorly, posterior margin weakly concave. Eye exserted, extending posteriorly, covering a large part of lateral margin of pronotum. Antenniforous tubercles scarcely developed; antennal cavities open above line across anterior margins of eyes. Antenna slender, over half the
length of body, without significant difference in proportional lengths of antennal segments between sexes. First segment distinctly longer than second segment, but shorter than two following segments together; second segment as long as or a little shorter than third segment; third segment with apex truncate; fourth segment longer than third. Clypeus with basal margin obliterated. Mandibular and maxillary plates indistinguishably fused. Rostrum with third segment less than twice as long as last segment.

Pronotum narrower than head including eyes, posterior margin rounded produced posteriorly in female, nearly straight in male of *minima*, lateral margin rounded. Relative length of mesonotum to pronotum greater in female than in male, without median longitudinal sulcus. Intersegmental suture between mesonotum and metanotum concave dorsally. Metanotum laterally defined by longitudinal carina, without median longitudinal sulcus. Metasternum highly reduced, without omphalium, less than one tenth as long as mesosternum. Front leg with femur distinctly longer than tibia; tibia over twice as long as tarsus; tarsus with first segment greatly reduced, claws arising from near middle. Middle leg with femur robust, about two thirds as long as tibia; tibia a little less than three times as long as first tarsal segment; first tarsal segment a little longer than second segment. Hind leg with femur twice or a little less than twice as long as tibia; tibia about two and a half times as long as first tarsal segment; first tarsal segment a little longer than second segment.

Abdomen with connexivum usually strongly reflexed. Anterior margins of first and second tergites rounded produced anteriorly but more or less obliterated at middle; both segments longer than any one following segment.

Male: Seventh segment with ventral apical margin concave and feebly notched at middle in *minima*, or simply concave and less than three times as long as sixth segment ventrally. Eighth segment with ventral surface strongly depressed and hairy in *minima*. Ninth segment telescoped within cavity formed by elongated eighth segment; suranal plate simple; pygophore apically exposed; parapmeres robust and simply curved upward. Endosoma with dorsal plate thickened at base, extending anteriorly along apical margin of endosoma (probably fused with apical plate); lateral plates two paired, one along dorsal plate, the other along ventral margin of endosoma; without well defined basal and ventral plates. (Description of the genitalia is based on *minima* and one unidentified species.)
Female: Seventh segment ventrally less than three times as long as sixth segment, its ventral apical margin broadly concave. First valvula with inner lobe well pigmented, folded beneath outer lobe, with basal thickening and apical thread like process; outer lobe simply narrowed apically, membranous and rounded apically. Second valvula with apex rounded and convergent from each side; apical margin of intervalvular membrane thus obliterated, with V-shaped, dark area on the membrane; ramus fine and long; process of ninth tergite with a crescent shaped sclerite at apex at the point of union with ramus of first valvula. Vulva membranous, slender, free from inner lobe of first valvula. (Description of the genitalia is based on O. fusca and one unidentified species.)

Distribution: South America (Bolivia, Brazil).

The genus Ovatametra is closely related to Halobatopsis, from which it can be separated by the following characteristics:

1. The body is smaller in Ovatametra than in Halobatopsis.
2. The head has a median black longitudinal stripe in Ovatametra.
3. The endosoma is provided with two pairs of lateral plates in Ovatametra, while it is without well differentiated lateral plates in Halobatopsis.
4. The third antennal segment is only slightly longer than or equal to the second in Ovatametra, while it is distinctly longer than the second segment in Halobatopsis.
5. The third rostral segment is less than twice as long as the last segment in Ovatametra, while it is about two and a half times as long as the last segment in Halobatopsis.
6. The middle tibia is not as long as the body in Ovatametra, while it is as long as the body in Halobatopsis.
7. The hind femur is less than twice as long as the front femur in Ovatametra, while it is over twice as long as the front femur in Halobatopsis.
8. The middle tarsus is subequal to or longer than the middle femur in Ovatametra, while the same is shorter than the middle femur in Halobatopsis.

The above-mentioned differences in proportional lengths may be attributable to similar allometric growth patterns for the segments, since Ovatametra is definitely shorter in body size than in Halobatopsis. The differences, therefore, need to be reinvestigated in terms of allometric changes.
Genus *Rheumatometroides* Hungerford and Matsuda

(*Figs. 56, 1037-1049*)


Type species: *Rheumatometroides browni* Hungerford and Matsuda, by original designation.

Species examined: *R. browni* Hungerford and Matsuda.

Color pattern: Predominantly black, with testaceous markings. Head with broad black median longitudinal stripe. Pronotum with testaceous spot at middle. Mesonotum with a large W-shaped testaceous marking. Mesopleuron and metapleuron with broad black bands, the former with a band of grayish pile superimposed. Thoracic venter pale testaceous; abdominal tergites predominantly black; venter more or less brown.

Structures in wingless forms: Head between eyes widened posteriorly, slightly dilated just in front of eyes, dorsal posterior margin of head straight. Eye covering anterolateral angle of pronotum, inner margin slightly sinuate. Antennal cavities placed much anterior to eyes. Antenna shorter than length of body; first segment longest, with spinous hairs sparsely scattered; second segment a little longer than third, second and third segments together longer than first; fourth segment a little longer than third. Clypeus with basal margin obliterated, laterally well defined. Mandibular and maxillary plates almost completely fused. Rostrum with first segment relatively long; third segment less than twice as long as last segment.

Pronotum narrower than head including eyes, posterior and lateral margins rounded. Mesonotum over twice as long as pronotum, with distinct median longitudinal sulcus, with medially keeled longitudinal groove extending throughout entire length of mesonotum in female, posterior margin concave and incised at middle. Interssegmental suture between mesonotum and metanotum anteromesially produced. Metasternum about one tenth as long as mesosternum. Metacetabular region convergent anteriorly in female. Metanotum without median longitudinal sulcus. Metasternum rather strongly produced anteriorly on basal margin in male; omphalium present, more distinct in male, located closer to anterior margin than to posterior margin of metasternum. Front leg slender, without sexual difference in shape; tibia simply thickened apically and flattened; first tarsal segment greatly reduced, second segment three and a half times as long as first segment, claws arising from
near middle. Middle leg with femur robust and a little shorter than tibia; tibia a little over three times as long as first tarsal segment; first tarsal segment as long as second. Hind leg with femur about two and a half times as long as tibia; tibia about six times as long as first tarsal segment; first tarsal segment shorter than second tarsal segment, claws inconspicuous in both middle and hind legs.

Abdomen with connexivum strongly reflexed and folded on dorsum in both sexes. Anterior margin of first tergite distinct, roundly produced anteriorly, first tergite much longer than second tergite, anterior margin of succeeding segments well impressed and straight.

**Male:** Seventh ventrite greatly prolonged, over twice as long as sixth. Eighth segment broadly rounded on dorsal apical margin, nearly straight on ventral apical margin. Ninth segment with suranal plate provided with a pair of lateral long processes directed cephalad; pygophore with apical margin simply rounded; parameres reduced but distinctly recognizable. Endosoma with definitive dorsal plate extending to apical margin and turned backward, basally indistinguishably fused with basal plate, which in turn bears apically slender black sclerite apparently giving support to membranous ventral plate, as in *Trepobates*. (Description of the genitalia is based on *browni*.)

**Female:** Seventh ventrite over twice as long as sixth, produced posteriorly at middle. Eighth segment with first valvula simply narrowed apically, apex membranous; inner lobe not distinct from outer lobe, attached largely to vulva, apex of outer lobe membranous, membranous lobe arising from near base and directed laterally; ramus attached to the apex of process of ninth tergite. Second valvula simply narrowed apically, serrulate on outer margin apically; intervalvular membrane produced, reaching near apices of second valvulae; ramus slender, extending back beyond middle of second valvulae and rounded at apex; process of ninth tergite sclerotized, simply narrowed at apex. Vulva with apex rounded, thinly sclerotized, reaching middle of first valvulae. (Description of the genitalia is based on *browni*.)

**Distribution:** The Solomon Islands.

The genus *Rheumatometroides* is quite peculiar in the following characteristics:

(1) The first rostral segment is long.

(2) In the female the mesonotum is provided with a distinct medially keeled longitudinal groove.
(3) The omphalium is present.

(4) The suranal plate in the male is provided with a conspicuous lateral process.

In the female of *Rheumatometra philarete* Kirkaldy the mesonotum also has a median longitudinal groove, but only posteriorly. In *Hynesionella* and *Metrobatopsis* the suranal plate also has conspicuous process on each side, but these have probably developed independently in these genera. The omphalium occurs in this species and *Stenobates*. As mentioned elsewhere this genus is closely related to *Stenobates*.

**Genus Stenobates** Esaki

(Figs. 58, 1050-1057)


Type species: *Stenometra biroi* Esaki, by original designation.
Species examined: *S. biroi* (Esaki).

**Color pattern:** Head with three longitudinal dark stripes on yellow ground color. Pronotum with a pair of yellow round spots along anterior margin, the rest black. Mesonotum with two pairs of pale yellow longitudinal stripes on black ground color. Abdomen above black. Body beneath, rostrum and legs predominantly yellow.

**Structures in wingless forms:** Head longer than wide at base between eyes, posterior margin straight. Eye covering anterolateral angle of pronotum. Antennal cavities located far beyond anterior margins of eyes. Antenna slender, shorter than body. First segment simple, longer than two following segments together; second and third segments simple; second segment longer than third; fourth segment about as long as third. Clypeus widened anteriorly, basal margin obliterated. Mandibular and maxillary plates almost completely fused. Rostrum very thick, first segment relatively long; third segment concave on upper margin, strongly thickened basally on lower margin, less than twice as long as last segment.

Pronotum shorter than head, posterior margin broadly rounded. Mesothorax gently widened posteriorly, median longitudinal sulcus (groove) distinct posteriorly in male. Intersegmental suture between mesonotum and metanotum produced anteromesially. Metanotum without median longitudinal sulcus. Metacetabular regions
well elevated and defined from metanotal region, convergent anteriorly. Metasternum angularly produced anteriorly, much longer than second abdominal ventrite, about one fourth as long as mesosternum in male; highly conspicuous omphalium located at intersegmental suture between mesosternum and metasternum. Front leg with femur slender; tibia strongly widened apically, flattened and thin; tarsus a little shorter than tibia, first segment highly reduced; second segment about six times as long as first, slender claws and membranous arolium arising from near middle. Middle leg slender; femur five sixths as long as tibia, relatively long and slender; tibia about three times as long as first tarsal segment; tarsus with first segment a little longer than second. Hind leg much shorter than middle leg. Femur about three times as long as tibia; tibia over five times as long as first tarsal segment; first tarsal segment a little shorter than second.

Abdomen in male: Connexivum reflexed on dorsum. First tergite with anterior margin distinct and roundly produced anteriorly; second and third tergites with anterior margins distinct; ventrites not highly reduced. Seventh ventrite longer than two preceedings together. Eighth tergite well developed and broadly rounded on apical margin. Ninth segment with suranal plate having conspicuous process on each side; pygophore small, rounded on apical margin.

Female: Female specimen was not available for study.

Distribution: The Oriental region (Singapore).

The genus Stenobates, which is known only from the type species, is apparently closely related to Rheumatometroides as is evidenced by the following characteristics which they share in common:

1. The relative lengths of leg segments are very similar.
2. The intersegmental suture between the mesonotum and metanotum is produced anteriorly at the middle.
3. The dorsal posterior margin of the head is straight.
4. The thick and reflexed rostrum.
5. The elevated metacetabular regions are convergent anteriorly.
6. The omphalium is retained.
7. The suranal plate is provided with a spinous process on each lateral margin.
8. The front tibia is strongly flattened, and simply but strongly widened apically.
The genus *Stenobates*, however, can easily be separated from *Rheumatometroides* by the quite distinct shape of the front tibia in the male and the omphalium being much more conspicuous and located at the anterior limit of the metasternum where it is strongly produced anteriorly.

**Genus Cryptobates** Esaki

(Figs. 51, 1058-1071)


Type species: *Gerris raja* Distant, by original designation.

Species examined: *C. kuiterti* Hungerford and Matsuda, *C. raja* (Distant).

**Color pattern:** Pale yellow in ground color, black along inner margins of eyes; pronotum with either a broad single or paired black median longitudinal stripes, and paired lateral stripes of the same color; mesonotum with three black longitudinal stripes; abdominal tergites variable in color, first tergite with a transverse yellow spot on each side. Hemelytra dark fuscous.

**Structures in wingless forms:** Head between eyes a little longer than wide, widened posteriorly, posterior margin straight. Eye exserted, inner margin slightly rounded, covering anterolateral angle of pronotum. Antennal cavities open just above anterior margins of eyes. Antenna slender and about as long as body in female (not known for male). First antennal segment much longer than second but shorter than third or fourth, incrassate apically; second segment shortest and more slender than first, apex thick and truncate; third segment much more slender than second, over twice as long as second; fourth segment as thin as third, as long as or just a little shorter than third, clothed with hairs which are considerably longer than those on third. Clypeus with basal margin faint but recognizable. Mandibular and maxillary plates recognizable by faint suture separating them. Rostrum very long, reaching near middle of mesosternum; first segment about half as long as head on ventral surface; third segment three times as long as last segment.

Pronotum a little narrower than head including eyes; lateral margins divergent posteriorly, posterior margin broadly rounded and produced posteriorly or feebly bisinuate, mesonotum convex, about two to three times as long as pronotum. Mesosternum convex, posterior margin concave. Intersegmental suture between
mesonotum and metanotum nearly straight dorsally. Metanotum declivent posteriorly, completely fused with first abdominal tergite, without median longitudinal sulcus, laterally defined by strongly elevated area. Metasternum greatly reduced, a little less than one twentieth as long as mesosternum, omphalium absent. Front leg slender and long, a little shorter than total length of body. Femur slender, about the same in thickness throughout, a little longer than tibia; tibia simply thickened apically, inner apical angle without conspicuous process in both sexes; tarsus with first segment greatly reduced, but relatively longer than in other genera of the subfamily; second tarsal segment three and a half times as long as first segment, claws arising from apical third of inner margin of second segment. Middle leg with femur thick, slightly narrowed beyond middle, a little shorter than tibia; tibia about three times as long as first tarsal segment; first tarsal segment less than one and two thirds times as long as second segment; second tarsal segment slightly curved apically, claws very inconspicuous. Hind leg with femur two to two and one half times as long as tibia; tibia about three to four times as long as first tarsal segment; first tarsal segment as long as or a little shorter than second tarsal segment, second segment has claws rather inconspicuous.

Abdomen strongly declivent posteriorly. Connexivum nearly vertically erected. Anterior margins of first and second tergites obliterated, anterior margin of third tergite straight and distinct.

Male: Seventh segment ventrally a little shorter than five preceding ventrites together. Eighth segment greatly prolonged, its ventral apical margin feebly bisinuate. Ninth segment with suranal plate long, widened in apical two thirds; pygophore ventrally well exposed, its apical margin feebly notched at middle; parameres greatly developed. Endosoma with dorsal plate extending as far as apical margin of endosoma, separated from apically bifurcate apical plate in kuiterti, basally extending along basal margin of endosoma; ventral plate membranous or short but sclerotized in kuiterti, basally detached from dorsal (or dorsal plus basal) plate; lateral plates long and oblique; apex of endosoma sclerotized and slightly produced. (Description of the genitalia is based on raja and kuiterti.)

Female: Seventh segment a little shorter than five preceding segments together ventrally, ventral apical margin concave. Eighth segment well exposed ventrally. First valvula with inner lobe well pigmented, forked into two slender processes, one of them
reaching near apex of outer lobe; outer lobe simply narrowed apically, apex acute; ramus reaching basal region of outer margin of the process of ninth tergite. Second valvula well pigmented on outer margin, apex broadly rounded and directed mesad or simply rounded apically, extending far beyond apical margin of intervalvular membrane. Vulva membranous and slender, largely free from inner lobe of first valvula. (Description of the genitalia is based on *ktiiferti*.)

Winged forms: Hemelytra with basal coriaceous region occupies about basal two fifths, with broad embolium; two apical veins in membranous region, anterior one coming from lower (posterior) apical angle of embolium, the posterior one from the point of union of \( R + M + Cu \) and \( A \). Line of weakness white and distinct, along apical margin of basal coriaceous region and horizontally on middle of hemelytron.

Distribution: The Oriental region (Burma, Southern India).

The genus *Cryptobates* appears to be related to *Telmatometra* in having a long rostrum, the first antennal segment not being the longest, the long front legs, etc., but can be distinguished from it by the following characteristics:

1. The middle tibia is only slightly longer than the middle femur.
2. The anterior margins of the first and second abdominal tergites are completely lost.
3. The basal margin of the clypeus and the suture separating the mandibular and maxillary plates are recognizable.
4. The metanotum is without median longitudinal sulcus.

Esaki (1929) believed that this genus is most closely related to *Amemboa*, but *Amemboa* actually belongs to the other subfamily, Gerrinae.

Genus *Naboandelus* Distant

(Figs. 61, 1072-1080)


Type species: *Naboandelus signatus* Distant, monobasic.

Species examined: *N. bergevini* Bergroth, *N. signatus* Distant, and two unidentified species.

Color pattern: Predominantly black. Head with a large black spot surrounded by yellow to yellowish brown area on dorsal
surface. Pronotum with a median yellow spot. Legs predominantly yellow or brown.

Structures in wingless forms: Head between eyes slightly widened posteriorly, posterior margin nearly straight or feebly convex. Eye semicircular in shape, posteriorly covering antero-lateral angle of pronotum. Antennal cavities placed just above anterior margins of eyes. Antenna with first segment slightly curved at base, longest but distinctly shorter than second and third segments together; second segment a little longer than third; third segment shortest; fourth segment fusiform. Clypeus well elevated, basal margin distinct. Mandibular and maxillary plates fused. Rostrum moderately thick; third segment less than twice as long as last segment.

Pronotum shorter and narrower than head, posterior margin broadly rounded or nearly straight, lateral margin rounded. Mesonotum without median longitudinal sulcus. Mesosternum with apical margin concave. Intersegmental suture between mesonotum and metanotum feebly anteromesially produced. Metanotum without median longitudinal sulcus, laterally defined by longitudinal elevation. Metasternum about one seventh as long as mesosternum in bergevini. Front leg with femur slender, about one and one third as long as tibia; tibia simply thickened apically and without conspicuous apical process in female; tarsus with first segment highly reduced; second segment three to four times as long as first segment, claws arising from a little beyond middle, with hair like arolium. Middle leg with femur thick, about two thirds to three quarters as long as tibia; tibia two and a half to three times as long, as first tarsal segment; first tarsal segment less than one and a half times as long as second segment; second segment with claws inconspicuous. Hind leg with femur a little less than two and a half times as long as tibia; tibia about five times as long as first tarsal segment; first tarsal segment much shorter than second; second tarsal segment with claws slender and not conspicuous.

Abdomen in female: Rather strongly declivent posteriorly on dorsal surface. Connexivum reflexed, more strongly so from fourth segment on posteriorly and ventral surface more or less exposed dorsally. First tergite with anterior margin indicated only by lateral pits, completely lost medially in bergevini; second tergite rather strongly roundly produced anteriorly at middle, third to seventh tergites subequal in lengths; second ventral segment less than half as long as metasternum; seventh ventrite twice as long
as sixth ventrite, its posterior margin feebly concave; posterior tergites reflexed upward, thus eighth segment subvertically exposed behind seventh segment. Genitalia similar to those in *Rheumatometra* and *Hynesionella*. First valvula with inner lobe darker, broad at base, reaching apical region of outer lobe; ramus well pigmented, extending basally along outer margin of process of ninth tergite, apex of the process with a crescent shaped sclerite. Second valvula well pigmented except for apical region, which is rounded and slightly extending beyond apical margin of inter-valvular membrane; ramus of second valvula slender. Vulva membranous, acutely pointed at middle and at each side. (Description of the female genitalia is based on *bergevini*.)

**Winged forms:** Hemelytra long and slender, far extending beyond tip of abdomen. Coriaceous region occupies basal one third of wing; venation as in other genera of Trepobatinae, R + M + Cu branches into two oblique veins more proximally than in other genera; line of weakness not quite reaching basal coriaceous region, narrow. Pronotum widest behind middle, broadly rounded on posterior margin.

**Distribution:** Oriental and Ethiopian regions (Angola, Arabia, Belgian Congo, Cameroons, Egypt, India, Madagascar, Somalia).

Although the phylogenetic position of this genus is not clear because of the absence of the male specimens available for study, this genus is probably close to *Hynesionella* from Africa. A close relationship to *Hynesionella* is indicated by:

1. The similiar general color pattern.
2. The rather strongly reflexed connexivum in the posterior abdominal segments in the female.
3. The similar proportional lengths of the leg segments except for those in the distal middle leg segments.
4. The similar proportional lengths of the antennal segments.

**Genus Hynesionella** Poisson

(Figs. 54, 1081-1092)


Type species: *Hynesionella aethiopica* Poisson, by original designation.


**Color pattern:** Predominantly grayish black, with bluish tinge. Head with a large black spot, reddish brown along eyes and
posterior margin of head. Pronotum with a median pale yellow spot.

Structures in wingless forms: Female much larger than male. Oval and robust. Head between eyes slightly widened posteriorly, basal margin feebly concave or nearly straight. Eye with inner margin emarginated in posterior half, covering anterolateral angle of pronotum. Antenniferous tubercles feebly developed; antennal cavities open on line across anterior margins of eyes. Antenna with first segment longest, slightly curved, shorter than two following segments together; second segment longer than third segment; third segment with apex truncate; fourth segment subequal to or a little longer than third. Clypeus short, basal margin recognizable. Mandibular and maxillary plates fused. Rostrum extending beyond prosternum; third segment about twice as long as last segment.

Pronotum with posterior margin produced posteriorly in the middle, lateral margins divergent anteriorly. Mesonotum widely and evenly depressed on median longitudinal axis; mesopleural region above coxa slightly narrowed; mesosternum with posterior margin concave, surface smooth and slightly convex. Intersegmental suture between mesonotum and metanotum well raised and carinate, produced posteriorly at middle in omer-cooperi. Metanotum without median longitudinal sulcus, short at middle, laterally defined by strong elevation reaching intersegmental suture between mesonotum and metanotum; metacetabular region rounded on lateral margin and convergent posteriorly. Metasternum much more reduced in length than in most other genera, a little longer than second ventrite. Front leg with femur thick near base, then narrowed apically, inner surface depressed and densely clothed with gray pubescence in omer-cooperi, incised near base on inner margin in male of aethiopica; tibia with inner apical angle more produced in male than in female. Middle leg with femur thick, about two thirds as long as tibia; tibia a little over twice to about three times as long as first tarsal segment; first tarsal segment a little over twice as long (?) or about as long as second segment; claws arising from near tip of second segment, inconspicuous. Hind leg with tibia half or a little less than half as long as femur, over seven times as long as first tarsal segment; first tarsal segment less than half as long as second segment; claws arising from beyond middle of second segment, slender and relatively long.

Abdomen strongly narrowed posteriorly in anterior half. Con-
nexivum strongly reflexed. First tergite roundly produced on anterior margin, obliterated medially in male of omer-cooperi; second segment produced anteromesially, third to sixth tergites subequal in length. Ventrites more reduced.

**Male:** Seventh segment ventrally about half as long as second to fifth segments together. Eighth segment enormously developed ventrally, a little longer than all preceding segments together ventrally, about as long as third to seventh segments together dorsally, posterior half narrowed and narrowly rounded on apical margin dorsally; ventral surface with yellowish elevation laterally, slightly raised along median longitudinal axis. Ninth segment with lateral process of suranal plate conspicuous; pygophore exposed apically, apical margin broadly rounded; parameres highly vestigial. Endosoma with definitive dorsal plate extending along both apical and basal margins, bifurcate on both apices; lateral plates located beneath the base of dorsal plate, robust; ventral plate short and membranous, supported basally by slender oblique sclerite arising from near basal end of dorsal plate. Endosoma not prolonged apically. Proximal segment of endosoma sclerotized and lobate apically. (Description of the genitalia is based on omer-cooperi.)

**Female:** Seventh segment ventrally about twice as long as sixth segment; ventral apical margin simply concave. Eighth segment ventrally exposed. First valvula with inner lobe slender, folded beneath outer lobe, well sclerotized except for apical membranous region, reaching near apex of outer lobe, another shorter membranous lobe arising more cephalad; outer lobe greatly narrowed apically, sclerotized in outer half, a membranous lobe arising from base of outer lobe; ramus darkly pigmented, extending posteriorly along entire outer margin of process of ninth tergite, which is highly membranous and with sclerotized apical crescent shaped sclerite. Second valvula dark except for apical region, which is membranous, roundly folded and approximated to each other beyond apical margin of intervalvular membrane, which is dark and feebly notched at middle; ramus dark and slender. (Description of the genitalia is based on H. omer-cooperi.)

**Distribution:** Africa (East Cape Province, Ethiopia).

The genus *Hynesionella* is unique in the carinate, posteromesially produced definitive intersegmental suture between the mesonotum and metanotum.
Genus *Metrobates* Uhler

(Figs. 57, 126, 144, 164, 1093-1108)


Type species: *Metrobates hesperius* Uhler, monobasic.


Color pattern: Variegated grayish blue and black dorsally in most species. Grayish region entirely replaced by black in some species. Head always with reddish brown area at base. Pronotum with a median paler spot.

Structures in wingless forms: More or less strongly dorsoventrally flattened. Female much wider than male, without conspicuous sexual difference in length of body. Head between eyes strongly widened posteriorly, posterior margin nearly straight. Eye exserted, covering anterolateral angle of pronotum. Antenniferous tubercles scarcely developed; antennal cavities placed anterior to anterior margins of eyes. Antenna over half the length of body, without difference in proportional lengths of segments between sexes. First segment longer than three following segments together in some species, at least longer than two following segments together, strongly curved at base, thickened at middle, apex truncate, inner margin sparsely clothed with straight hairs in males, simply gradually thickened apically in females; second and third segments slightly curved and thickened apically, with comb shaped mass of short and thick hairs on inner distal angles of both segments more or less pronounced in most species, third segment always shorter than second; fourth segment a little longer than third in all species except *Plaumanni*. Clypeus with basal margin obliterated. Mandibular and maxillary plates, though clothed with hairs, recognizable from each other, and the latter smaller than former. Rostrum rather short, clothed with long hairs; third segment about twice as long as last segment.

Pronotum narrower than head including eyes, posterior margin variable, concave or convex, lateral margins broadly rounded.
Mesonotum with a faint median longitudinal sulcus throughout entire length. Mesosternum with a median longitudinal impression in most species, with a pair of tubereulous processes on postero-lateral angles near base of mesocoxae in male of *porcus*. Inter-segmental suture between mesonotum and metanotum more or less anteromesially produced. Metanotum without distinct median longitudinal sulcus, laterally defined by longitudinal elevations reaching the intersegmental suture. Metasternum over one tenth as long as mesosternum, without omphalium. Front leg with femur much longer than tibia, with a tubercle at middle of inner margin in male of *denticornis*; tibia with inner apical angle somewhat produced in male, longitudinally depressed near apex on inner margin; tarsus with first segment greatly reduced; second segment with claws arising from near middle on inner margin and with arolium. Middle leg with femur half to two thirds as long as tibia, thick and straight; tibia considerably longer than body, about seven times as long as first tarsal segment in most species; first tarsal segment much shorter than second segment, about one third as long as second in most species; second segment with claws arising from near apex of the segment and inconspicuous. Hind leg with femur over two and a half times as long as tibia; tibia two and a half times to three times as long as tarsus, and over ten times as long as first tarsal segment; first tarsal segment much shorter than second; second segment with claws arising from near middle and well developed.

Abdomen with connexivum not strongly reflexed. First and second tergites with their anterior margins distinct, both segments long. Ventrites considerably shorter than tergites.

**Male:** Seventh segment ventrally much longer than sixth segment, but never much over three times as long as sixth, ventral apical margin concave, nearly straight or feebly concave dorsally. Eighth segment cylindrical, strongly developed and with round apical margin dorsally, simply concave ventrally. Ninth segment with suranal plate exposed in apical half and with round apical margin; pygophore rounded on apical margin; parameres vary in shape and degree of development, conspicuous in most species and exposed on either side of pygophore. Endosoma with definitive dorsal plate extending along entire dorsal margin of endosoma, bifurcate on both ends; large apical plate (?) not connected with apex of dorsal plate; without either well defined lateral or ventral plate. (Description of the genitalia is based on *hesperius.*)
Female: Seventh segment about twice as long as sixth segment ventrally in most species, simply concave on ventral apical margin. Eighth segment ventrally well exposed. First valvula with inner lobe well sclerotized, folded beneath outer lobe, with two long apical processes, basally fused with vulva; outer lobe simply narrowed apically. Second valvula with apex directed somewhat mesad, rounded and membranous, considerably extending beyond apical margin of intervalvular membrane, where is well pigmented; ramus slender and long. Vulva largely membranous, medially produced on apical margin. (Description of the genitalia is based on hesperius.)

Winged forms: Hemelytra with basal coriaceous region occupying basal half of hemelytron, with broad embolium. Anterior apical vein arising from apex of embolium, lower (posterior) apical vein arising from point of union of vein A and R + M + Cu. Line of weakness broad. Pronotum in apical half broadly rounded, with a round pale spot near anterior margin at middle.

Distribution: Greater portion of the United States, Central and South America (British Honduras, Cuba, Guatemala, Haiti, Jamaica, Mexico, Peru, Puerto Rico, Venezuela).

The genus Metrobates is quite distinct from all other genera of the subfamily by the following characteristics:
(1) The strongly flattened body.
(2) The second and third antennal segments being conspicuously modified apically.
(3) The relatively long middle tibia.
(4) The conspicuous claws in the hind and middle legs and the long second tarsal segment bearing them.
(5) The presence of the median longitudinal impression on the mesosternum.

Genus Rheumatometra Kirckaldy
(Figs. 62, 63, 1110-1121, 1135-1141)

Rheumatometra Kirckaldy, Entomologist, 35:281(1902).

Type species: Rheumatometra philarete Kirckaldy, monobasic.
Species examined: R. philarete Kirckaldy.

Color pattern: Head behind clypeus and along posterior margin with a yellow transverse band; the rest black on dorsal surface. Antennae black except for base of first segment yellow. Pronotum has a median longitudinal yellow stripe or spot. Mesonotal region with a longitudinal yellow stripe at middle in posterior half, the

**Structures in wingless forms: Female much larger than male.** Head between eyes wide, wider at base than long at middle, posterior margin concave on either side of middle. Eye covering anterolateral angle of pronotum posteriorly. Antenniferous tubercles feebly developed; antennal cavities open on horizontal line across anterior margins of eyes. Antenna much shorter than body. First segment a little longer than second in male or much longer than second in female; second and third segments unmodified apically; second segment slightly longer than third; third segment a little shorter than fourth. Clypeus with basal margin distinct. Mandibular and maxillary plates distinct from each other. Rostrum rather thick; third segment about twice or less than twice as long as last segment.

Pronotum transverse, much shorter than head, about four times as wide as long at middle, posterior margin feebly produced posteriorly. Mesonotum with median longitudinal sulcus distinct and depressed towards intersegmental suture in posterior two thirds in female, without a distinct median longitudinal sulcus in male. Intersegmental suture between mesonotum and metanotum anteromesially produced. Mesothorax strongly widened posteriorly, more so in female. Mesopleural region with an oblique laevigate depression above mesocoxa outside mesoacetabular cleft. Metanotum without median longitudinal sulcus, defined laterally by elevated metacetabular region. Metasternum much longer than second ventrite, without either omphalium or omphalial groove, less than one sixth as long as mesosternum in female. Front leg with femur long and strongly arched in male; tibia also arched in male; both femur and tibia in female simple and the latter is shorter than former and without conspicuous apical thickening; first tarsal segment greatly reduced; claws arising from beyond middle of second tarsal segment. Middle leg with femur thicker in basal half, about two thirds as long as tibia, relatively shorter in male than in female; tibia a little less than twice as long as first tarsal segment, much thinner than femur; first tarsal segment over twice as long as second tarsal segment, relatively longer in female than in male. Hind leg with femur over twice as long as tibia in male, or less than twice
as long as tibia in female; tibia about twice as long as tarsus in male; first and second tarsal segments fused.

Abdomen more strongly narrowed in male than in female. Connexivum not folded on tergum. First abdominal tergite with anterior margin obliterated medially; second tergite with anterior margin roundly produced at middle; third to sixth tergites and second to sixth ventrites subequal in length to each other.

Male: Seventh segment a little less than twice as long as sixth segment both dorsally and ventrally. Eighth segment with posterior margin simply concave ventrally, slightly concave on dorsal apical margin. Ninth segment largely telescoped within cavity formed by eighth segment. Suranal plate simple; pygophore small and simply rounded on apical margin; parameres rather small, arising from deep inside pygophore and exposed only apically. Endosoma with dorsal plate bifurcate basally, thickened apically and extends along apical margin of endosoma (probably fused part of apical plate); lateral plates slender and simple; without either basal or ventral plate. Basal segment of endosoma apically produced and sclerotized.

Female: Seventh segment a little less than twice as long as sixth segment ventrally; ventral apical margin simply concave. Eighth segment ventrally well exposed. Genitalia much like those of Metrobates. First valvula with inner lobe folded beneath outer lobe, well pigmented, branched into two apically, of which inner branch longer and extending to about middle of outer lobe; outer lobe narrowly pigmented along inner margin, apex membranous; ramus slender, attached to outer apical angle of well pigmented process of ninth tergite. Second valvula simply rounded apically, slightly extending beyond apical margin of intervalvular membrane, which is pigmented and notched at middle; ramus slender. Vulva simply rounded on apical margin, membranous basally and free from inner lobes of first valvulae.

Winged forms: Forewing with basal third of upper margin coriaceous, forming embolium. R + M + Cu forks into two apical branches at basal one fourth of wing; anterior branch goes obliquely to be united with inner apical angle of embolium, then sending further a branch into membranous region; posterior branch united with vein A, sending a vein apically. Line of weakness in membranous region evanescent basally. Hind wing much shorter than forewing. Pronotum relatively short, posterior half broadly rounded.
Distribution: Australia.

The genus Rheumatometra resembles Metrobates from the Western Hemisphere by the following similar characteristics:

1. The similar general shape of the body and color pattern.
2. The head is wide and the dorsal posterior margin is produced posteriorly.
3. The clypeus with the basal margin well defined.
4. The similar female genitalia.
5. The presence of a median longitudinal sulcus on the mesonotum.
6. The relatively long metasternum.

The genus, however, can easily be separated from Metrobates by the following characteristics:

1. The quite distinct proportional lengths of antennal segments, and the absence of the distal comb on the second and third segments.
2. The first and second tarsal segments are fused.
3. The hind legs have the claws not conspicuous.
4. The female is much larger than the male.
5. The front leg of the male is greatly arched.
6. The shorter pronotum.
7. Quite distinct proportional lengths of leg segments.
8. The absence of the median longitudinal impression on the mesosternum.

Genus Metrobatopsis Esaki
(Figs. 53, 1122-1134, 1142-1144)


Type species: Metrobatopsis flavonotatus Esaki, by original designation.

Species examined: M. affinis Esaki, M. flavonotatus Esaki, E. solomonensis Hungerford and Matsuda, two unidentified species.

Color pattern: Predominantly black. Pronotum always with a broad pale yellow spot at middle. Mesonotum with a single or a pair of round yellow spots.

Structures in wingless forms: Body oval, male much narrower than female. Head between eyes a little longer than wide, feebly widened at base, dorsal posterior margin nearly straight or feebly produced posteriorly. Eye exserted, covering anterolateral margin
of pronotum. Antennal cavities open anterior to anterior margins of eyes. Antenna with first segment curved at base, more or less strongly incrassate in males of some species, longer than second; second segment always longer than third; third segment subequal to fourth segment; fourth segment fusiform and flattened. Clypeus elevated, basal margin distinct. Mandibular and maxillary plates fused. Rostrum extending beyond prosternum; third segment over twice as long as last segment.

Pronotum much narrower than head including eyes, posterior margin broadly rounded, lateral margins rounded, convergent anteriorly. Mesonotum depressed in posterior half at middle, without median longitudinal sulcus. Mesosternum simple, posterior margin concave. Intersegmental suture between mesonotum and metanotum anteromesially produced. Metanotum without median longitudinal sulcus, laterally defined by subparallel longitudinal elevation. Metasternum about one tenth as long as mesosternum in female, more strongly reduced in male, without either omphalium or omphalial groove. Front leg with femur considerably longer and thicker than tibia, thickest and strongly curved near base; tibia simply incrassate apically; tarsus with first segment greatly reduced, second segment three to four times as long as first segment, claws arising from beyond middle of second segment and with membranous arolium. Middle leg longer than hind leg; femur thick, subequal in thickness throughout, a little over two thirds as long as tibia; tibia slightly incrassate basally and tapering apically, about twice as long as first tarsal segment; first tarsal segment about twice to a little less than three times as long as second segment; second segment curved, slightly thickened at apex, claws small and inconspicuous. Hind leg with femur longer than middle femur, two and one fourth to three times as long as tibia; tibia about three times as long as tarsus; first and second tarsal segments fused.

Abdomen with connexivum strongly reflexed for all segments. Anterior margin of first tergite obliterated medially, that of second segment broadly roundly produced anteriorly, second tergite much longer than third tergite. Ventrites strongly reduced.

Male: Seventh segment greatly prolonged. Eighth segment greatly prolonged except for *M. affinis*, cylindrical. Ninth segment with suranal plate with a slender process on lateral margin near apex (except possibly for *affinis*); pygophore vertically rotated anteriorly except for *affinis*, with a median spinous process on median longitudinal axis except for *affinis*; parameres absent. Endosoma
long, curved upward apically; apical segment of endosoma tightly ensheathed within heavily sclerotized basal segment of endosoma, definitive dorsal plate small, bifurcate apically; paired lateral plates slender, located in basal region of endosoma; without either ventral or basal plate. (Description of the genitalia is based on flavonotatus.)

Female: Sixth tergite pointed apically at middle in some species. Seventh segment well developed ventrally, covering eighth segment (valvifers) in most species. Eighth segment has first valvula well differentiated into outer and inner lobes; inner lobe well pigmented and short, folded beneath outer lobe; outer lobe simply narrowed apically, apex rounded and membranous; ramus extending basally along process of ninth tergite, which is provided with a crescent shaped sclerite apically. Second valvula pigmented on outer margin except for apex where is membranous, slightly constricted near apex, apex rounded and slightly extending beyond apical margin of intervalvular membrane where is rounded. Vulva short, simply rounded on apical margin. (Description of the female genitalia is based on flavonotatus?.)

Winged forms: Hemelytra with basal third subcoriaceous, venation as in Rheumatometra except for obliteration of lower vein in apical membranous region. Pronotum a little wider than long, widest at a little behind middle, posterior margin broadly rounded.


The genus Metrohatopsis is somewhat similar to Rheumatometra, but differs from it by the following characteristics:

(1) The eighth abdominal segment in the male is strongly prolonged in most species. The ninth segment in the same sex with suranal plate has lateral spinous process, the pygophore is vertically rotated and the parameres are lost; while in Rheumatometra the eighth segment is not as greatly prolonged in two species of Metrobatopsis (solomonensis, flavonotatus), the suranal plate is unmodified, the pygophore is not rotated, and the parameres are retained.

(2) The first antennal segment in male is longer and more strongly incrassate than in Rheumatometra.

(3) The front femur of the male is thickened near base but simply narrowed apically; in Rheumatometra it is greatly thickened and strongly arched.

(4) The dorsal surface of the head is only feebly widened in the female; in Rheumatometra it is greatly widened posteriorly.
The mesonotum without a well impressed median longitudinal sulcus; in *Rheumatometra* the median longitudinal sulcus is well impressed in the female.

The inner lobe of the first valvula is short; in *Rheumatometra* it is long and branched into two.

The hemelytra have the lower (posterior) apical vein obliterated in *Metrobatopsis*.

Modification of the abdomen

**Male:** In relatively large species, *affinis*, the eighth segment is not prolonged although its ventral apical margin is provided with a pair of processes (fig. 1142), in the other two species (*solomonensis* and *flavonotatus*) the eighth segment is greatly prolonged and the ventral surface has a broad depressed area. The pygophore in *flavonotatus* and *solomonensis* is rotated vertically, exposing only the apical region of the pygophore; the suranal plate is also provided with a process on the lateral margin near apex in these two forms; in the larger species, *affinis*, the pygophore is not rotated vertically and without the process on the median longitudinal axis, and the suranal plate does not appear to have the lateral process (not dissected).

**Female:** In the female of an undescribed species the ventral apical margin of the seventh segment is simply concave (fig. 1138), and the eighth segment is exposed both dorsally and ventrally. This species is the largest in size. In the smaller species the seventh segment is greatly prolonged ventrally (figs. 1143, 1144), in *flavonotatus* the sixth tergite is acutely pointed on the posterior margin at the middle, and the seventh and eighth tergites are folded beneath the sixth tergite (fig. 1122), so is true with a species from the Solomon Islands (fig. 1144). In another species, however, the seventh and eighth tergites are well exposed without the sixth tergite being modified (1143).

Modification of the other structures

*The antennae:* In the relatively large and structurally primitive species, *affinis*, the first antennal segment of the male is simple; it is somewhat greatly thickened in the apical half in *solomonensis*, *flavonotatus* which are smaller.

The genus *Metrobatopsis* exhibits much more structural diversity than in the other genera of Trepobatinae, as noted from the foregoing account. We have already found also indication that the
growth patterns for the antennal and leg segments are presumably considerably different at the specific level in this genus.

On Hermatobatinae  
(Figs. 64, 1145-1151)

The Hermatobatinae was excluded from the Gerridae in an earlier part of this section (Classification). This group of water-striders are fundamentally different from the other groups of the Gerridae by the following highly unique characteristics:

(1) In the male the mesothorax and metathorax are completely fused both dorsally and ventrally.

(2) In the female the paired lobes arising from the anterior margin of the mesonotum develop posterolaterally as far as the apex of the abdomen, and the abdominal spiracles are placed laterally on the lobes.

(3) The vestigial dorsal scent gland openings are recognized on the basal region of the fourth abdominal tergite (figs. 1146, 1148).

(4) The pregenital abdominal segments are ventrally completely fused in the female and extremely reduced in the male.

(5) The front tarsus is distinctly three segmented.

(6) The eyes are granulated and the pronotum is extremely short.
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<th>Name of species</th>
<th>Length of body</th>
<th>Antennae 1:2:3:4</th>
<th>Rostrum</th>
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Table 16.—Measurements of leg and antennal segments.—Continued

### Gerrinae

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Table 16.—Measurements of leg and antennal segments.—Continued

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<td>83</td>
<td>22:16:5:15:5:17</td>
<td>14:5.5</td>
<td>27.5:25:2.7:5.5</td>
<td>86:58:3:9</td>
<td>92:53:5:3:5:8</td>
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**Halobatinae**

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<th>Halobates sericeus ♂</th>
<th>54</th>
<th>12.5:4.5:4.5:10</th>
<th>4.5:3</th>
<th>21.5:17.5:3:3.5:8</th>
<th>58.27:26:4</th>
<th>43:23:5.8 (1+2 segs.)</th>
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<tr>
<td>Halobates hawaiensis ♂</td>
<td>87</td>
<td>30:10.7:9</td>
<td>6:3.5</td>
<td>33:27:4.5:5.5</td>
<td>95:70:35:11</td>
<td>80:40:11.5 (1+2 segs.)</td>
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<tr>
<td>Name of species</td>
<td>Length of body</td>
<td>Antennae</td>
<td>Rostrum</td>
<td>Front leg</td>
<td>Middle leg</td>
<td>Hind leg</td>
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<td>M. sp. (India) ♂</td>
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<td>30.2:14:15:9</td>
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<td>36:29:2:10</td>
<td>100:37:30:5</td>
<td>100:50:15:5</td>
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<td>83</td>
<td>26:12:5:16:10</td>
<td>11.3</td>
<td>34:42:2.5:12</td>
<td>103:72:26:5:4</td>
<td>110:54:5.5:5</td>
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<td><em>V. kuerti</em> ♂</td>
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<td>20:6:5:7:8:5</td>
<td>5.7:2.5</td>
<td>18.5:15:0.3:1.5</td>
<td>50:27:14:3</td>
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<td>E. weisingeri ♂</td>
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<td>E. kuiteri ♂</td>
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<td>E. ventidioides ♂</td>
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<td>Ptilomera (P. himalayensis)</td>
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<td>Ptilomera (P. pamphaga) ♂</td>
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<tr>
<td>P. (Pt.) lacustris ♂</td>
<td>200</td>
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<td>130:30:40:28</td>
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<td>P. (Pt.) dromas ♂</td>
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<td>P. (Pt.) werneri ♂</td>
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<td>P. (Pt.) aello ♂</td>
<td>257</td>
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<td>P. (Pt.) sp. (India)</td>
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<td>112:29:34:24</td>
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<tr>
<td>Potamometra berezowskii ♂</td>
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<td>P. tibetensis ♀</td>
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<td>77:27</td>
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Table 16.—Measurements of leg and antennal segments.—Continued

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Length of body</th>
<th>Antennae 1:2:3:4</th>
<th>Rostrum</th>
<th>Front leg</th>
<th>Middle leg</th>
<th>Hind leg</th>
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<tr>
<td><em>Rhyacobates chinensis</em> ♂</td>
<td>105</td>
<td>58:15:17:11.5</td>
<td>9.6</td>
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<td><em>H. bilobatus</em> ♂</td>
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<td>7.54</td>
<td>57:46:18:10</td>
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<td>168</td>
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<td><em>P. obnubila</em> ♂</td>
<td>107</td>
<td>62:20</td>
<td>10.5:4.5</td>
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<td>*Rheumatobates petilus ♀</td>
<td>100</td>
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<td>10:4</td>
<td>27:13:10:5</td>
<td>70:59:30:10:5</td>
<td>47.2:73.5:8.5</td>
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<td>Name of species</td>
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<td>Front leg</td>
<td>Middle leg</td>
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<td>*R. praeposterus ♀</td>
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<td>22:11;10 (1+2 segs.)</td>
<td>60:30;33:10</td>
<td>47:29:7:8.5</td>
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<td>Front leg</td>
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<td>*T. knighti ♂</td>
<td>130.5</td>
<td>34:18.5:20:21</td>
<td>19:8.5</td>
<td>52:35:3:14</td>
<td>68:128:5.73 (1+2 segs.)</td>
<td>101:45:5.31 (1+2 segs.)</td>
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<td>*T. taylori ♂</td>
<td>113.5</td>
<td>33:15:18:20</td>
<td>18:11</td>
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<td>62:119</td>
<td>89:45</td>
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<td>Length</td>
<td>Width</td>
<td>Ratio</td>
<td>Male or Female</td>
<td>Length</td>
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<td>H. spinicentrus ♂</td>
<td>71</td>
<td>17.8:5:11.5:11</td>
<td>11:4.7</td>
<td>27.5:21:2.0:8.5</td>
<td>47:70:23:17</td>
<td>58.5:30:7.6</td>
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<td>Ornatometra fusca ♀</td>
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<td>7.5:5.6:8</td>
<td>6.3:3</td>
<td>14:10</td>
<td>20:33.5:12.5:12.5</td>
<td>25.5:15:6:4.5</td>
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<td>O. minima ♂</td>
<td>34</td>
<td>7.5:4.3:4.7:6.5</td>
<td>5.5:3</td>
<td>12:10:1(?)3</td>
<td>18:28:10:8</td>
<td>21:10.5:4:3.5</td>
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<td>Hynesionella omercooperi ♂</td>
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<td>8.5:6:4.8:5.1</td>
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<td>Naboandels signatus ♀</td>
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<td>8:5:5.5</td>
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<td>N. bergezini ♀</td>
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<td>38:15.5:2.5:5.5</td>
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<td>N. sp. (Formosa) ♀</td>
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<td>4:2.8</td>
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Table 16.—Measurements of leg and antennal segments.—Concluded

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Length of body</th>
<th>Antennae 1:2:3:4</th>
<th>Rostrum</th>
<th>Front leg</th>
<th>Middle leg</th>
<th>Hind leg</th>
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<tbody>
<tr>
<td><em>Metrobatopsis flavonotatus</em> ♂</td>
<td>73</td>
<td>23:15.5:9:10.5</td>
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<td>27.5:20:2.8</td>
<td>61:83:15:20</td>
<td>80:29:11</td>
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<td></td>
<td></td>
<td>(1+2 segs.)</td>
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<td>(1+2 segs.)</td>
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</table>

The lengths of body in parentheses for the species of *Limnogonus* are the individuals from which the measurements of antennal segments were made.
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Snodgrass, R.

Sprague, I.

Taylor, L.

Thompson, D’Arcy.

Usinger, R., and Matsuda, R.

Westoll, T.

Wigglesworth, V. B.

Woodland, J.
Figures 65-69

65. Lateral view of the head, *Gerris remigis* Say.
68. Sagittal section of the head, *Gerris remigis* Say.
69. The epipharynx, *Gerris remigis* Say.
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70, 71. Sagittal sections of the head, *Cerris remigis* Say.
Figures 72-77

72 Ptilomera sp. (winged form)

73 Ptilomera sp. (wingless form)

74 Gerris remigis (winged form)

75 Gerris remigis (wingless form)

76 Metrocoris stolii (?) (winged form)

77 Metrocoris stolii (?) (wingless form)

72, 73. Dorsal view of the thorax, _Ptilomera_ sp. from South India.
74, 75. Dorsal view of the thorax, _Gerris remigis_ Say.
76, 77. Dorsal view of the thorax, _Metrocoris stolii_ (Dohrn). (?)
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82. The hind wing, *Gerris remigis*, Say.
83. The forewing, *Gerris remigis* Say.
84. The forewing base, *Gerris remigis* Say.
85. The hind wing base, *Gerris remigis* Say.
86. Ventral view of the thorax, *Eotrechus kalidasa* Kirkaldy.
87. Ventral view of the thorax, *Gigantometra gigas* (China).

89. Dorsal view of the thorax, showing internal structures, *Gerris remigis* Say.

90. Dorsal view of the thorax, showing internal structures, *Metrocoris stali* (Dohrn) (?).
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91. Middle coxa, Gerris remigis Say.
92. Hind coxa, Gerris remigis Say.
93. Dorsal view of the metathorax, showing internal structures, Gerris remigis Say.
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95. Dorsal view of the body, *Gerris remigis* Say.
Figures 94-97

94 Gerris remigis

95 Gerris remigis

96 Rhagadotarsus krapelini

97 Rhagadotarsus krapelini
Figures 98-101

100. Lateral view of the male ninth and tenth abdominal segments, *Gerris remigis* Say.
Figures 98-101

8th segment (ventral)
8th segment (dorsal)
Pygophore
Suranal plate (9th tergum)

Suranal plate (9th tergum)

Apical sclerotized part of endosoma
Tenth segment
Paramere

Pygophore

Apical plate + Dorsal plate + Basal plate

Ventral plate
Lateral plate
Basal segment of endosoma
Apical segment of endosoma
102.-104. Diagrammatic drawings of sclerotized plates in endosoma of Gerridae.
106. Female genitalia, *Gerris remigis* Say.
107. Diagram showing evolution of thoracic and basal abdominal sutures in Gerridae. Broken lines indicate the sutures that have been lost.
Figure 108

108. Postembryonic growth of antennal segments in *Metrocoris histrio* B.-White, broken lines are for female. Each connected point is mean value at different stages.
Figure 108

Antennal segments

Length of body
Figure 109

109. Postembryonic growth of hind leg segments in *Gerris remigis* Say. Broken lines are for female. Each connected point is mean value at different stages.
110. Postembryonic development of the hind leg segments in *Trepobates Knighti* Drake. Broken lines are for females. Each connected point is mean value at different stages.
111. Antennal segments in Gerris. Each connected point is mean value at different stages.
Figure 112

112. Antennal segments in *Tachygerris*.

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113. Second and third antennal segments in Charmatometrini.
114. First and fourth antennal segments in Charmatometrini.
Figure 115

115. Antennal segments in Cylindrostethus from the Eastern Hemisphere. S. is Cylindrostethus sumatranus Lundblad.
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116. Antennal segments in *Cylindrostethus* from the Western Hemisphere.
117. First and fourth antennal segments in *Potamobates*. 
Figure 118

Antennal segments in *Platygeris*.
Figure 119

Antennal segments in *ptilomerinae.*
Figure 120

120. Second and third antennal segments in *ptilomerinae.*
Figure 121

121. Antennal segments in Metrocoris. Each connected point is mean value at different stages.
Figure 122

Antennal segments vs. length of body in *Ventidius*.

122. Antennal segments in *Ventidius*.
123. Antennal segments in Rhagadotarsinae. Each connected point is mean value at different stages (2 individuals at each stage).
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124. Antennal segments in *Trepobates*. Each connected point is mean value at different stages.
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125. Antennal segments in *Telmatometra* and related genera.
126. Antennal segments in *Metrobates.*
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Hypothetically primitive growth line for the antennal segment in Gerridae.
Figure 128

128. Diagram showing the evolution of growth gradient for antennal segments.
129. Hind leg segments in *Gerris*. Each connected point is mean value at different stages.
130. Hind leg segments in the *Limnometra-Tenagognus s. str.* complex. Round points are *Limnometra*, triangles represent *Tenagognus s. str.*
131. Hind leg segments in *Limnogonus*. Round points are *Limnogonus s. str.* triangle points represent *Limnogonellus*. 
Figure 132

Hind leg segments in *Tachyngerris*.
Figure 133

133. Hind leg segments in Charmatometrini. E E' are for a species from Ecuador; p p' are for a species from Panama.
134. Hind leg segments in *Cylindrostethus*. Triangles for species from the Eastern Hemisphere; round spots for the species from the Western Hemisphere.
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135. Hind leg segments in *Potamobates*.
136. Hind leg segments in *Platygerris*.
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137. Hind leg segments in *Ptilomera*. 
138. Hind leg segments in *Halobatini*. 
139. Hind leg segments in *Metrocoris*. Each connected point represents mean value at different stages.
140. Hind leg segments in Ventidius. Growth line is for V. henryi.
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141. Hind leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.
142. Hind leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.
143. Hind leg segments in *Telmatometra* and related genera.
144. Hind leg segments in *Metrobates*. 
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145. Hind leg segments in *Hynesionella* and *Rheumatometra*.
146. Hind leg segments in *Cryptobates* and *Rheumatometroides*. 
147. Evolution of hind leg segments (femur and tibia) in Gerridae, a is allomorphic line.
148. Middle leg segments in Gerris. Each connected point represents mean value at different stages.
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149. Middle leg segments in the Limnometra-Tenagogenus s. str. complex.
150. Middle leg segments in *Tachygerris*.
151. Middle leg segments in *Limnogonus s. str.-Limnogonellus* complex. Round points for *Limnogonus s. str.*, triangle points for *Limnogonellus*. White points for tibiae.
152. Middle leg segments in *Charmatometrini*.
153. Middle leg segments in *Eotrechini.*
154. Middle leg segments in *Cylindrostethus*. Round points for species from Eastern Hemisphere; triangle points for species from Western Hemisphere. *Cylindrostethus sumatranus* Lundblad is not plotted.
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155. Middle leg segments of *Potamobates*.
156. Middle leg segments of *platygerris*. 
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157. Middle leg segments in Ptilomera.
158. Middle leg segments in *Metrocoris*. Each connected point represents mean value at different stages.
159. Middle leg segments in Halobatini.

160. Middle leg segments in Ventidius.
161. Middle leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.
Figure 162

Middle leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.
163. Middle leg segments in *Telmatometra* and related genera.
164. Middle leg segments in *Metrobates*.
165. Front leg segments in *Gerris*. Round points for *Aquarius*; triangle points for *Gerris s. str.* Each connected point represents mean value at different stages.
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166. Front leg segments in ptilomera.
167. Front leg segments in *Metrocoris*. Each connected point represents mean value at different stages.
168. Front leg segments in Rhagadotarsinae. Each connected point represents mean value at different stages.
169. Front leg segments in *Trepobates* and related genera. Each connected point represents mean value at different stages.
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170. Diagram showing relation of ontogeny to phylogeny.
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171. Dorsal view of body, Gigantometra gigas (China), winged male.
172. Lateral view of head, Gigantometra gigas (China).
173. Ventral view of metathorax, Gigantometra gigas (China).
174. Ventral view of male apical abdominal segments, Gigantometra gigas (China).
175. Lateral view of the male ninth and tenth abdominal segments, Gigantometra gigas (China).
176. Front tarsus, Gigantometra gigas (China).
177. Middle tarsus, Gigantometra gigas (China).
178. Hind tarsus, Gigantometra gigas (China).
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179. Dorsal view of whole body, wingless male of *Gerris (Aquarius) cinereus* (Puton).

180. Ventral view of whole body, wingless male of *Gerris (Aquarius) cinereus* (Puton).


183. Front leg, *Gerris (Aquarius) paludum* (Fabricius).

184. Middle tarsus, *Gerris (Aquarius) najas* (De Geer).


186. Female genitalia, *Gerris (Aquarius) elongatus* (Uhler).

187. Dorsal view of whole body, wingless female of *Gerris (Gerris) incognitus* Drake and Harris.

188. Lateral view of head, *Gerris (Gerris) thoracicus* Schummel.

189. Antenna, *Gerris (Gerris) thoracicus* Schummel.

190. Front leg, *Gerris (Gerris) thoracicus* Schummel.

191. Middle tarsus, *Gerris (Gerris) costae* (Herrich-Schaeffer).

192. Hind tarsus, *Gerris (Gerris) costae* (Herrich-Schaeffer).
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193. Ventral view of male apical abdominal segments, Gerris (Aquarius) elongatus (Uhler).

194. Same, Gerris (Gerris) gilbifer Schummel.

195. Same, Gerris (Aquarius) remigis Say.

196. Same, Gerris (Aquarius) paludum (Fabricius).

197. Same, Gerris (Gerris) thoracicus Schummel.

198. Same, Gerris (Gerris) odontogaster (Zetterstedt).

199. Same, Gerris (Gerris) agrenticollis Parshley.

200. Same, Gerris (Gerris) firmus Drake and Harris.

201. Same, Gerris (Gerris) gillettei Lethiery et Severin.

202. Same, Gerris (Gerris) pingreensis Drake and Harris.

203. Lateral view of abdomen, Gerris (Gerris) firmus Drake and Harris.

204. Ventral view of female apical abdominal segments, Gerris (Aquarius) elongatus (Uhler).

205. Same, Gerris (Gerris) marginatus Say.

206. Same, Gerris (Aquarius) antigone Kirkaldy.

207. Same, Gerris (Gerris) odontogaster (Zetterstedt).

208. Same, Gerris (Aquarius) remigis Say.
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209. Female genitalia, Gerris (Gerris) gillettei Drake and Harris.
210. Female genitalia, Gerris (Gerris) marginatus Say.
211. Male genital segment, Gerris (Aquarius) paludum (Fabricius).
212. Male genital segment, Gerris (Aquarius) elongatus (Uhler).
213. Apical segment of endosoma, Gerris (Aquarius) remigis Say.
214. Same, Gerris (Aquarius) chilensis (Berg).
215. Same, Gerris (Aquarius) amplus Drake and Harris.
216. Same, Gerris (Aquarius) paludum (Fabricius).
217. Same, Gerris (Aquarius) ventralis (Fieber).
218. Same, Gerris (Aquarius) antigone Kirkaldy.
219. Same, Gerris (Aquarius) conformis (Uhler).
220. Same, Gerris (Aquarius) cinereus (Paton).
221. Same, Gerris (Gerris) thoracicus Schummel.
222. Same, Gerris (Gerris) marginatus Say.
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226. Dorsal view of the thorax in winged form, *Gerris (Limnoporus) dissorits* Drake and Harris.
230. Hind wing, *Gerris (Limnoporus) dissorits* Drake and Harris.
231. Female genitalia, *Gerris (Limnoporus) notabilis* Drake and Hottes.
232. Apical segment of endosoma, *Gerris (Limnoporus) dissorits* Drake and Harris.
233. Same, *Gerris (Limnoporus) canaliculatus* Say.
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234. Ventral view of wingless male, Gerriselloides brachynotus (Horváth).
235. Dorsal view of wingless male, Gerriselloides brachynotus (Horváth).
236. Lateral view of head, Gerriselloides brachynotus (Horváth).
237. Ventral view of male apical abdominal segments, Gerriselloides brachynotus (Horváth).
238. Lateral view of female apical abdominal segments, Gerriselloides brachynotus (Horváth).
239. Male front leg, Gerriselloides brachynotus (Horváth).
240. Male antenna, Gerriselloides brachynotus (Horváth).
241. Middle leg, Gerriselloides brachynotus (Horváth).
242. Hind leg, Gerriselloides brachynotus (Horváth).
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243. Dorsal view of winged male, Gerrisella settembrinoi (Poisson).
244. Dorsal view of wingless male, Gerrisella settembrinoi (Poisson).
245. Lateral view of female head, Gerrisella settembrinoi (Poisson).
246. Ventral view of female abdomen, Gerrisella settembrinoi (Poisson).
247. Lateral view of male apical abdominal segments, Gerrisella settembrinoi (Poisson).
248. Female antenna, Gerrisella settembrinoi (Poisson).
249. Male front leg, Gerrisella settembrinoi (Poisson).
250. Male middle tarsus, Gerrisella settembrinoi (Poisson).
251. Male hind tibia and tarsus, Gerrisella settembrinoi (Poisson).
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255. Ventral view of male abdomen, *Tenagogerris euphrosyne* (Kirkaldy).
257. Lateral view of male genital segment, *Tenagogerris euphrosyne* (Kirkaldy).
259. Female genitalia, *Tenagogerris euphrosyne* (Kirkaldy).
262. Male hind tarsus, *Tenagogerris euphrosyne* (Kirkaldy).
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263. Dorsal view of wingless male, Eurygerris mexicanus (Champion).
264. Dorsal view of wingless male, Eurygerris fuscinervis (Berg).
265. Dorsal view of wingless female, Eurygerris flavolineatus (Champion).
266. Forewing, Eurygerris cariniventris, (Champion).
267. Lateral view of head, Eurygerris fuscinervis (Berg).
268. Pronotum in winged form, Eurygerris fuscinervis (Berg).
269. Front leg, Eurygerris fuscinervis (Berg).
270. Lateral view of male genital segment, Eurygerris fuscinervis (Berg).
271. Apical segment of endosoma, Eurygerris mexicanus (Champion).
272. Apical segment of endosoma, Eurygerris fuscinervis (Berg).
273. Antenna, Eurygerris fuscinervis (Berg).
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276. Ventral view of male apical abdominal segments, *Eurygerris carmelus* (Drake and Harris).
278. Apical segment of endosoma, *Eurygerris carmelus*, (Drake and Harris).
280. Lateral view of female apical abdominal segments, *Eurygerris carmelus* (Drake and Harris).
281. Female genitalia, *Eurygerris mexicanus* (Champion).
283. Same, *Eurygerris mexicanus* (Champion).
284. Same, *Eurygerris cariniventris* (Champion).
285. Same, *Eurygerris carmelus* (Drake and Harris).
286. Same, *Eurygerris kahli* (Drake and Harris).
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289. Ventral view of male abdomen, *Limnogonus (Limnogonus) hypoleucus* (Gerstaecker).
292. Lateral view of head, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
293. Lateral view of head, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
297. Antenna, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
298. Front leg, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
299. Front leg, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
300. Middle tarsus, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
301. Middle tarsus, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
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304. Same, *Limnogonus (Limnogonellus) aduncus* Drake and Harris.
305. Same, *Limnogonus (Limnogonellus) aduncus* Drake and Harris.
306. Same, *Limnogonus (Limnogonellus) hyalinus* (Fabricius).
308. Same, *Limnogonus (Limnogonellus) Lundbladi* Usinger.
309. Dorsal view of male apical abdominal segments, *Limnogonus (Limnogonus) visendus* Drake and Harris.
313. Same, *Limnogonus (Limnogonellus) ignotus* Drake and Harris.
314. Ventral view of female apical abdominal segments, *Limnogonus (Limnogonellus) hyalinus* (Fabricius).
318. Same, *Gerris (Limnoporus) canaliculatus* Say.
320. Same, *Gerris (Limnoporus) canaliculatus* Say.
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321. Lateral view of male genital segment, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
322. Lateral view of male genital segment, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
323. Female genitalia, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
324. Female genitalia, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
325. Apical segment of endosoma, *Limnogonus (Limnogonus) aduncus* Drake and Harris.
326. Same, *Limnogonus (Limnogonus) cereiventris leptocerus* (Reuter).
327. Same, *Limnogonus (Limnogonus) hyalinus* (Fabricius).
328. Same, *Limnogonus (Limnogonus) australis* (Skuse).
329. Same, *Limnogonus (Limnogonus) fossarum* (Fabricius).
330. Same, *Limnogonus (Limnogonus) hypoleucus* (Gerstaecker).
331. Same, *Limnogonus (Limnogonus) nitidus* (Mayr).
333. Same, *Limnogonus (Limnogonellus) visendus* Drake and Harris.
334. Same, *Limnogonus (Limnogonellus) hesione* (Kirkaldy).
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336. Ventral view of male abdomen, *Trachygerris celocis* (Drake and Harris).
337. Dorsal view of structures beneath wings, *Tachygerris celocis* (Drake and Harris).
342. Lateral view of male genital segment, *Tachygerris celocis* (Drake and Harris).
343. Female front leg, *Tachygerris adamsoni* (Drake).
344. Middle tarsus, *Tachygerris spinulatus* (Kuitert).
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347. Same, *Tachygerris celocis* (Drake and Harris).

348. Same, *Tachygerris spinulatus* (Kuitert).

349. Same, *Tachygerris adamsoni* (Drake).


352. Female genitalia, *Tachygerris opacus* (Champion).

353. Ventral view of apical abdominal segments, *Tachygerris celocis* (Drake and Harris).


355. Same, *Tachygerris celocis* (Drake and Harris).

356. Same, *Tachygerris quadrilineatus* (Champion).

357. Male front leg, *Tachygerris celocis* (Drake and Harris).

358. Male front tarsus, *Tachygerris celocis* (Drake and Harris).
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360. Lateral view of head, *Tenagogonus (Limnometra) ciliatus* (Mayr).
361. Lateral view of male genital segment, *Tenagogonus (Limnometra) ciliatus* (Mayr).
362. Female genitalia, *Tenagogonus (Limnometra) ciliatus* (Mayr).
364. Hind wing, *Tenagogonus (Limnometra) cursitans* (Fabricius).
367. Middle tarsus, *Tenagogonus (Limnometra) annulicornis* (Breddin).
368. Hind tarsus, *Tenagogonus (Limnometra) annulicornis* (Breddin).
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378. Lateral view of male genital segment, *Tenagogonus (Tenagogonus) albovittatus* Stål.


381. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

382. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.

383. Same, *Tenagogonus (Limnometra) femoratus* (Mayr).

384. Female genitalia, *Tenagogonus (Limnometra) femoratus* (Mayr).


386. Same, *Tenagogonus (Tenagogonus) madagascariensis* Hoberlandt.

387. Same, *Tenagogonus (Tenagogonus) albovittatus* Stål.
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388. Lateral view of male apical abdominal segment, Tenagogonius (Limnometra) insularis (Hungerford and Matsuda).
389. Same, Tenagogonius (Limnometra) anadyomene (Kirkaldy).
390. Same, Tenagogonius (Tenagogonius) kuiterti Hungerford and Matsuda.
391. Same, Tenagogonius (Tenagogonius) zambezinus (Poisson).
392. Same, Tenagogonius (Tenagogonius) divergens Hungerford and Matsuda.
393. Same, Tenagogonius (Tenagogonius) madagascariensis Hoberlandt.
394. Same, Tenagogonius (Tenagogonius) albocittatus Stål.
395. Same, Tenagogonius (Tenagogonius) kampaspe Kirkaldy.
396. Ventral view of male apical abdominal segments, Tenagogonius (Limnometra) fluviorum (Fabricius).
397. Same, Tenagogonius (Limnometra) octopunctatus (Hungerford).
398. Same, Tenagogonius (Limnometra) lipovskii (Hungerford and Matsuda).
399. Same, Tenagogonius (Tenagogonius) kuiterti Hungerford and Matsuda.
400. Same, Tenagogonius (Tenagogonius) albocittatus Stål.
401. Same, Tenagogonius (Tenagogonius) madagascariensis Hoberlandt.
402. Same, Tenagogonius (Tenagogonius) robustus Hungerford and Matsuda.
403. Ventral view of female apical abdominal segments, Tenagogonius (Limnometra) ciliatus (Mayr).
404. Same, Tenagogonius (Limnometra) octopunctatus (Hungerford).
405. Same, Tenagogonius (Tenagogonius) pravipes bergrothi Hungerford and Matsuda.
406. Same, Tenagogonius (Tenagogonius) fijiensis Hungerford and Matsuda.
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408. Dorsal view of wingless male, *Tenagogonus* (*Tenagometra*) sp.
409. Lateral view of head, *Tenagogonus* (*Tenagometra*) sp.
410. Ventral view of male apical abdominal segments, *Tenagogonius* (*Tenagometra*) sp.
412. Lateral view of male genital segment, *Tenagogonus* (*Tenagometra*) sp.
413. Apical segment of endosoma, *Tenagogonus* (*Tenagometra*) sp.
414. Ventral view of female apical abdominal segments, *Tenagogonus* (*Tenagometra*) sp.
415. Female front leg *Tenagogonus* (*Tenagometra*) sp.
419. Lateral view of male genital segment, *Tenagometrella grandiusculus* (Poisson).
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421. Dorsal view of wingless male, Cylindrostethus erythropus (Herrich-Schaeffer).

422. Ventral view of metathorax and basal abdomen, Cylindrostethus erythropus (Herrich-Schaeffer).

423. Dorsal view of structures beneath wings, Cylindrostethus productus Spinola.

424. Lateral view of thorax, Cylindrostethus productus Spinola.

425. Dorsal view of female metathorax and basal abdomen, Cylindrostethus bilobatus Kuitert.

426. Ventral view of male mesothorax, Cylindrostethus bilobatus Kuitert.

427. Antenna, Cylindrostethus erythropus (Herrich-Schaeffer).

428. Forewing, Cylindrostethus erythropus (Herrich-Schaeffer).

429. Hind wing, Cylindrostethus erythropus (Herrich-Schaeffer).

430. Front leg, Cylindrostethus erythropus (Herrich-Schaeffer).

431. Middle tarsus, Cylindrostethus productus Spinola.

432. Hind tarsus, Cylindrostethus productus Spinola.
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434. Same, *Cylindrostethus hungertfordi* Drake and Harris.
435. Same, *Cylindrostethus costalis* Schmidt.
436. Same, *Cylindrostethus palmaris* Drake and Harris.
437. Same, *Cylindrostethus bilobatus* Kuitert.
438. Same, *Cylindrostethus erythrophus* (Herrich-Schaeffer).
439. Same, *Cylindrostethus bassleri* Drake.
440. Same, *Cylindrostethus linearis* (Erichson).
441. Same, *Cylindrostethus productus* Spinola.
442. Same, *Cylindrostethus naiades* Kirkaldy.
443. Same, *Cylindrostethus sumatranus* Lundblad.
444. Same, *Cylindrostethus vittipes* Stål.
446. Same, *Cylindrostethus nietneri* Schmidt.
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447. Lateral view of female apical abdominal segments, *Cylindrostethus productus* Spinola.
448. Lateral view of female apical abdominal segments, *Cylindrostethus palmaris* Drake and Harris.
452. Lateral view of head, *Cylindrostethus erythropus* (Herrich-Schaeffer).
453. Female genitalia, *Cylindrostethus productus* Spinola.
454. Female genitalia, *Cylindrostethus erythropus* (Herrich-Schaeffer).
455. Lateral view of male genital segment, *Cylindrostethus erythropus* (Herrich-Schaeffer).
456. Apical segment of endosoma, *Cylindrostethus productus* Spinola.
457. Same, *Cylindrostethus erythropus* (Herrich-Schaeffer).
458. Same, *Cylindrostethus palmaris* Drake and Harris.
459. Same, *Cylindrostethus naiades* Kirkaldy.
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468. Middle tarsus, *Potamobates peruvianus* Hungerford.
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472. Same, *Potamobates unidentatus* Champion.
473. Same, *Potamobates variabilis* Hungerford.
479. Same, *Potamobates variabilis* Hungerford.
480. Same, *Potamobates williamsi* Hungerford.
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Figures 481-493

481. Dorsal view of wingless male *Platy Gerris depressus* B.-White.
489. Middle tibia and tarsus, *Platy Gerris asymmetricus* Hungerford.
492. Same, *Potamobates horváthi* Esaki.
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496. Ventral view of male apical abdominal segments, *Platygerris caeruleus* Champion.
504. Last hind tarsal segment, *Platygerris asymmetricus* Hungerford.
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505. Dorsal view of wingless female, *Charmatometra bakeri* (Kirkaldy).
506. Lateral view of head, *Charmatometra bakeri* (Kirkaldy).
507. Ventral view of abdomen, *Charmatometra bakeri* (Kirkaldy).
508. Antenna, *Charmatometra bakeri* (Kirkaldy).
509. Male front leg, *Charmatometra bakeri* (Kirkaldy).
510. Apical part of male front femur, *Charmatometra bakeri* (Kirkaldy).
511. Last middle tarsal segment, *Charmatometra bakeri* (Kirkaldy).
512. Hind tarsus, *Charmatometra bakeri* (Kirkaldy).
513. Ventral view of male apical abdominal segments, *Charmatometra bakeri* (Kirkaldy).
514. Lateral view of male genital segment *Charmatometra bakeri* (Kirkaldy).
515. Apical segment of endosoma, *Charmatometra bakeri* (Kirkaldy).
516. Female genitalia, *Charmatometra bakeri* (Kirkaldy).
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518. Dorsal view of wingless male, \textit{Eobates vittatus} (Shaw).
519. Ventral view of male abdomen, \textit{Eobates vittatus} (Shaw).
520. Lateral view of thorax, \textit{Eobates vittatus} (Shaw).
521. Lateral view of head, \textit{Eobates vittatus} (Shaw).
523. Male front leg, \textit{Eobates vittatus} (Shaw).
524. Hind tarsus, \textit{Eobates vittatus} (Shaw).
525. Ventral view of apical female abdomen, \textit{Eobates vittatus} (Shaw).
526. Ventral view of male apical abdominal segments, \textit{Eobates vittatus} (Shaw).
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530. Forewing, *Brachymetra lata* Shaw.
532. Ventral view of metathorax and basal abdomen, *Brachymetra lata* Shaw.
536. Female genitalia, *Brachymetra lata* Shaw.
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Figures 537-547

538. Same, *Brachymetra anduzei* Drake and Harris.
539. Same, *Brachymetra lata* Shaw.
540. Same, *Brachymetra unca* Shaw.
542. Same, *Brachymetra anduzei* Drake and Harris.
543. Same, *Brachymetra lata* Shaw.
545. Same, *Brachymetra lata* Shaw.
546. Same, *Brachymetra sp.* from Brazil.
547. Lateral view of male genital segment, *Brachymetra kleopatra* Kirkaldy.
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555. First and second antennal segments, *Eotrechus kalidasa* Kirkaldy.
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561. Lateral view of head, *Onychotrechus sakuntala* (Kirkaldy).
563. Forewing, *Onychotrechus sakuntala* (Kirkaldy).
564. Hind wing, *Onychotrechus sakuntala* (Kirkaldy).
566. Male front leg, *Onychotrechus sakuntala* (Kirkaldy).
567. Middle tarsus, *Onychotrechus sakuntala* (Kirkaldy).
568. Hind tarsus, *Onychotrechus sakuntala* (Kirkaldy).
569. Lateral view of male genital segment, *Onychotrechus sakuntala* (Kirkaldy).
570. Apical segment of endosoma, *Onychotrechus sakuntala* (Kirkaldy).
571. Female genitalia, *Onychotrechus sakuntala* (Kirkaldy).
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572. Dorsal view of wingless male, *Chimarrhometra orientalis* (Distant).
573. Lateral view of head, *Chimarrhometra orientalis* (Distant).
574. Ventral view of male metathorax and abdomen, *Chimarrhometra orientalis* (Distant).
575. Male antenna, *Chimarrhometra orientalis* (Distant).
576. Lateral view of male genital segment, *Chimarrhometra orientalis* (Distant).
577. Male front leg, *Amemboa* sp. from Thailand.
578. Same, *Amemboa* sp. from Thailand.
580. Same, *Chimarrhometra orientalis* (Distant).
581. Middle tarsus, *Chimarrhometra orientalis* (Distant).
582. Hind tarsus, *Chimarrhometra orientalis* (Distant).
583. Apical segment of endosoma, *Chimarrhometra orientalis* (Distant).
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584. Forewing, *Amemboa* sp. from Thailand.
585. Hind wing, *Amemboa* sp. from Thailand.
587. Middle tarsus, *Amemboa horváthi* Esaki.
589. Ventral view of male apical abdominal segments, *Amemboa* sp. from Thailand.
593. Ventral view of male apical abdominal segments, *Amemboa* sp. from Thailand.
594. Lateral view of male genital segment, *Amemboa* sp. from Thailand.
595. Apical half of endosoma, *Amemboa* sp. from Thailand.
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599. Lateral view of thorax in winged form, *Onychotrechus sakuntalai* (Kirkaldy).
600. Same, *Amemboa* sp. from Thailand.
602. Ventral view of metathorax and abdomen, *Onychotrechus sakultala* (Kirkaldy).
606. Female front leg, *Amemboa horváthi* Esaki.
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611. Lateral view of head, *Ptilomera* (*Ptilomera*) *laticaudata* (Hardwicke) (?).

612. Forewing, *Ptilomera* (*Ptilomera*) sp. from Southern India.

613. Hind wing, *Ptilomera* (*Ptilomera*) sp. from Southern India.


616. Female front leg, *Ptilomera* (*Ptilomera*) sp.

617. Hind tibia and tarsus, *Ptilomera* (*Ptilomera*) sp. from Southern India.

618. Hind tarsus, *Ptilomera* (*Ptilomera*) sp. from Southern India. Showing tarsal segmentation after treatment with KOH.

619. Middle femur, *Ptilomera* (*Ptilomera*) *laticaudata* (Hardwicke) (?).
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621. Same, *Ptilomera (Ptilomera) hylactor* Breddin.

622. Same, *Ptilomera (Ptilomera) dromas* Breddin.


625. Same, *Ptilomera (Ptilomera) pamphaga* Breddin.


627. Same, *Ptilomera (Ptilomera) harpalus* Schmidt.

628. Same, *Ptilomera (Ptilomera) aello* Breddin.

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Figures 630-641

630. Ventral view of metathorax and basal abdomen, *Ptilomera dromas* Breddin.


632. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

633. Dorsal view of female apical abdominal segments, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).


635. Same, *Ptilomera (Ptilomera) pamphaga* Breddin.


637. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).


639. Same, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).

640. Same, *Ptilomera (Ptilomera) sp.*

641. Female genitalia, *Ptilomera (Ptilomera) laticaudata* (Hardwicke) (?).
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651. Lateral view of male genital segment, *Potamometra berezowskii* Bianchi.
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663. Female front leg, *Rhyacobates takahashii* Esaki.
666. Middle tarsus, *Rhyacobates takahashii* Esaki.
667. Middle tarsus, *Rhyacobates lundbladi* (Hungerford).
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696. Apical segment of endosoma, Heterobates dohrandti Bianchi.
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790. Ventral view of female abdomen, Metrocoris stáli (Dohrn). (?)
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912. Middle last tarsal segment, Rheumatobates rileyi Bergroth.
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914. Male antenna, Rheumatobates clanis Drake and Harris.
915. Same, Rheumatobates mangrovensis (China).
916. Same, Rheumatobates trinitatis (China).
917. Same, Rheumatobates bonariensis (Berg).
918. Same, Rheumatobates drakei Hungerford.
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925. Same, *Rheumatobates rileyi* Bergroth.
927. Same, *Rheumatobates trulliger* Bergroth.
929. Female antenna, *Rheumatobates mangrovensis* (China).
931. Same, *Rheumatobates clanis* Drake and Harris.
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936. Same, *Rheumatobates vegatus* Drake and Harris.
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942. Female front leg, *Rheumatobates petilus* Drake and Hottes.
943. Same, *Rheumatobates creascri* Hungerford.
946. Same, *Rheumatobates klagei* Schroeder.
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958. Same, *Rheumatobates klagei* Schroeder.
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First valvula

Second valvula

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996. Apical segment of endosoma, Trepobatoides boliviensis Hungerford and Matsuda.
997. Lateral view of male genital segment, Trepobatoides boliviensis Hungerford and Matsuda.
998. Female genitalia, Trepobatoides boliviensis Hungerford and Matsuda.
999. Male antenna, Trepobatoides boliviensis Hungerford and Matsuda.
1000. Female front leg, Trepobatoides boliviensis Hungerford and Matsuda.
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1015. Female antenna, *Telmatometra whitei* Bergroth.
1016. Middle tarsus, *Telmatometra whitei* Bergroth.
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1019. Lateral view of head, *Halobatopsis spiniventris* Drake and Harris.
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1023. Lateral view of male genital segment, *Halobatopsis spiniventris* Drake and Harris.
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1028. Ventral view of head, *Ovatametra minima* Kenaga.
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1030. Ventral view of male apical abdominal segments, *Ovatametra obesa* Kenaga.
1031. Lateral view of male apical abdominal segments, *Ovatametra sp*.
1033. Same, *Ovatametra sp*.
1034. Female antenna, *Ovatametra obesa* Kenaga.
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1042. Female front leg, *Rheumatometroides browni* Hungerford and Matsuda.

1043. Middle tarsus, *Rheumatometroides browni* Hungerford and Matsuda.


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1058. Dorsal view of wingless female, Cryptobates raja (Distant).
1059. Ventral view of head, Cryptobates raja (Distant).
1060. Lateral view of head, Cryptobates raja (Distant).
1061. Pronotum in winged form, Cryptobates raja (Distant).
1062. Forewing, Cryptobates raja (Distant).
1063. Ventral view of female abdomen, Cryptobates raja (Distant).
1064. Antenna, Cryptobates raja (Distant).
1065. Front leg, Cryptobates raja (Distant).
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First valvulae folded cephalad.
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1074. Lateral view of head, Naboandelus bergevini Bergroth.
1075. Ventral view of head, Naboandelus signatus Distant.
1076. Ventral view of female abdomen, Naboandelus signatus Distant.
1077. Female front leg, Naboandelus bergevini Bergroth.
1078. Middle tarsus, Naboandelus bergevini Bergroth.
1079. Hind tibia and tarsus, Naboandelus bergevini Bergroth.
1080. Female genitalia, Naboandelus sp. from Burma. First valvulae folded cephalad.
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1093. Dorsal view of wingless female, "Metrobates denticornis" (Champion).
1094. Ventral view of head, "Metrobates denticornis" (Champion).
1096. Ventral view of male abdomen, "Metrobates denticornis" (Champion).
1098. Forewing, "Metrobates denticornis" (Champion).
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1103. Lateral view of male apical abdominal segments, Metrobates hes-
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1104. Apical segment of endosoma, Metrobates hesperius Uhler.
1105. Antenna, Metrobates denticornis (Champion).
1106. Middle tarsus, Metrobates plaumanni Hungerford.
1107. Hind tarsus, Metrobates denticornis (Champion).
1108. Female genitalia, Metrobates hesperius Uhler. First valvulae folded cephalad.
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First valvula

Second valvula
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1110. Dorsal view of wingless male, Rheumatometra philarete Kirkaldy.
1111. Ventral view of male abdomen, Rheumatometra philarete Kirkaldy.
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1117. Lateral view of male apical abdominal segments, Rheumatometra philarete Kirkaldy.
1118. Apical segment of endosoma, Rheumatometra philarete Kirkaldy.
1119. Middle tarsus, Rheumatometra philarete Kirkaldy.
1120. Hind tarsus, Rheumatometra philarete Kirkaldy.
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1122. Dorsal view of wingless female, Metrobatopsis flavonotus Esaki.
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1125. Forewing, Metrobatopsis flavonotus Esaki.
1126. Ventral view of male abdomen, Metrobatopsis flavonotus Esaki.
1127. Lateral view of male apical abdominal segments, Metrobatopsis solomonensis Hungerford and Matsuda.
1128. Lateral view of apical segment of endosoma, Metrobatopsis flavonotus Esaki.
1129. Dorsal view of apical segment of endosoma, Metrobatopsis flavonotus Esaki.
1130. Pronotum in winged form, Metrobatopsis flavonotus Esaki.
1131. Male antenna, Metrobatopsis solomonensis Hungerford and Matsuda.
1132. Female antenna, Metrobatopsis flavonotus Esaki.
1133. Male front leg, Metrobatopsis solomonensis Hungerford and Matsuda.
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1140. Female front leg, *Rheumatometra philarete* Kirkaldy.
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1147. Lateral view of male, *Hermatobates weddi* China.