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THE RELATIONSHIPS OF THE NORTH AMERICAN  
GENERA *REHNTIA* CAUDELL AND *NEOBARRETTIA* REHN  
(ORTHOPTERA, TETTIGONIIDAE)

BY THEODORE J. COHN

THE genus *Rehntia* has been classified among the Decticinae since its description as a member of that subfamily by Caudell in 1907. Although it shares with the Decticinae two of the diagnostic characters of that subfamily—the presence of dorsoexternal spurs on the fore tibiae and of free plantulae on the hind tarsi—it possesses many other characters divergent from those of true decticines. In particular, it lacks the posterior production of the pronotum and the broad fastigium verticis which are characteristic, though not uniquely diagnostic, of Decticinae, and it is set apart from most North American decticines in having long spines on all thoracic sternites; long, heavily spined forelegs; and eyes that are globose and strongly protuberant.

My first field experience with *Rehntia*, in the summer of 1951, prompted me to undertake a study of that genus and its relatives. I noted its distinctive, nondecticine features at that time, but I did not appreciate their full significance until the following year when, at the Carnegie Museum of Pittsburgh, I was able to study the type of the Brazilian *Macrometopon rantale* Bruner. *Macrometopon*, placed by Bruner in the Listroscelinae near *Carliella* Karny, shows close superficial resemblance to *Rehntia*, and detailed comparison shows that the two genera share many distinctive features. Later examination of material of the genus *Listroscelis* Serville, in the collection of the Academy of Natural Sciences of Philadelphia, and of a male specimen from Brazil of a species of *Cerberodon* Perty, in the collection of the University of Michigan Museum of Zoology, strengthened my conviction that *Rehntia* belongs with these genera in the Listroscelinae.

No precise determination of the relationships of *Rehnia* is possible at this time, partly because of the unavailability of material of some of the listrosceline genera that should be considered, but even more because of the uncertain validity of some of the existing subfamily groupings. Generic relationships within the Decticinae and Listroscelinae are at present poorly understood, and the composition and limits of these and related subfamilies have never been adequately defined. Zeuner (1936a, 1936b, 1939, 1940) has recently revised the classification of the Tettigoniidae, basing his conclusions partly on fossil evidence, partly on venational and other conventional taxonomic characters, and in considerable part on the variations in structure of the prothoracic tracheal apparatus. In his arrangement (1939: 117) he recognizes a number of major stocks; in one of these, the Tettigonioid Group, he places the Decticinae along with the Tettigoniinae, Saginae, Mecopodinae, Phyllophorinae, and (tentatively) Meconeminae; in another, the Conocephaloid Group, he includes the Listroscelinae together with the Salomoninae (including Agraeciinae), Copiphorinae, and Conocephalinae (= Xiphidiinae). He states (1939: 118) that although the Conocephaloid Group is obviously closely akin to the Tettigonioid Group, it is impossible to say whether the former were derived from primitive tettigonioids or whether both groups came independently from a common ancestor; the structure of the prothoracic tracheae shows that "the Conocephaloids cannot be derived from modern Tettigoniinae, [Decticinae], Saginae, or similar forms." Zeuner would thus separate the decticines rather widely from the listroscelines. Nevertheless he points out (1939: 118) that the prothoracic tracheal apparatus of the listrosceline *Hexacentrus* is closely similar to that of the decticine *Decticus*.

Both Uvarov (1924: 492) and Zeuner (1936b: 106) regard the Tettigoniinae and Decticinae as very closely allied, and as probably no more than tribes of a single subfamily, although both authors retain them for convenience as separate subfamilies, especially since the relations of other allied groups such as the Saginae are also in need of revision.

The composition and relationships of the Meconeminae are also poorly understood. Karny (1924: 105) redefined this subfamily and transferred to it some genera previously assigned to the Listroscelinae. Zeuner (1936b: 107) described the prothoracic tracheal apparatus (which is very different from the types found in decticines and typical listroscelines), and tentatively grouped the meconemines with the

dectices in the Tettigonioid Group. In a later paper (1940: 83-84), however, he shows that there is a gradation of the characters used for defining the Meconeminae by Karny to those typical of certain listroscelines, and states: "It is difficult to regard the line of separation between the Meconeminae and Listroscelinae as clear-cut and natural." Zeuner considers the following genera to be Meconeminae: *Meconema* Serville, *Cyrtaaspis* F. Walker, *Acilacris* Bolivar, *Nicephora* Bolivar, *Cecidophaga* Karny, *Thaumaspsis* Bolivar, *Xiphidiola* Bolivar, *Canariola* Walker (*Orophila* Krauss), *Xiphidiopsis* Redtenbacher, *Amytta* Karsch, *Meconemopsis* Karny, *Phlugis* Stal, *Phlugiola* Karny, and *Phlugiolopsis* Zeuner. *Phisis* Stal, which resembles *Phlugis* in many respects, is left in the Listroscelinae. Zeuner concludes that the Meconeminae and Listroscelinae may ultimately have to be united. "The great differences between the extreme members of the group, such as *Meconema* and *Listroscelis*, are due to their respective herbivorous and carnivorous habits, and the early authors have classified the carnivorous forms as Listroscelinae."

In spite of the unsatisfactory state of knowledge of the higher categories indicated above, comparison of *Rehnia* and *Neobarrettia* with material of the five listrosceline, two meconemine, and twenty-nine decticine genera available to me, supplemented by descriptions of other genera given by Caudell (1908), by Karny (1912), and by other authors, provides ample evidence to justify the reassignment of the two genera in question to the Listroscelinae.

I am indebted to Dr. George Wallace of the Carnegie Museum of Pittsburgh, to Mr. J. A. G. Rehn of the Academy of Natural Sciences of Philadelphia, and to Dr. T. H. Hubbell of the University of Michigan Museum of Zoology for the opportunity to study material of the following genera and species contained in the collections of the institutions named. I wish also to thank Dr. Hubbell for his suggestions and help in the preparation of this paper.

#### MATERIAL EXAMINED

##### Genera under investigation

*Rehnia spinosa* Caudell  
*Rehnia cerberus* Rehn and Hebard  
*Rehnia victoriae* Caudell  
*Rehnia* n. sp.  
*Neobarrettia imperfecta* (Rehn)

*Hexacentrus mundus* (Walker)  
*Hexacentrus dorsatus* Redtenbacher  
*Cerberodon viridis* Perty  
*Listroscelis armata* Serville  
*Macrometopon rantale* Bruner

##### Meconeminae

*Phlugis simplex* Hebard  
*Phlugis poecila* Hebard  
*Phlugiola* species

##### Listroscelinae

*Phisis* species

## Saginae

*Saga vittata* (Fischer v. W.)  
*Clonia* species

## Decticinae (including Tettigoniinae)

*Aglaothorax ovatus* (Scudder)  
*Aglaothorax armiger* Rehn and  
 Hebard  
*Neduba carinata steindachneri*  
 (Hermann)  
*Gampsocleis* (?) *ussuriensis* (Adelung)  
*Gampsocleis obscurus* (Walker)  
*Paradrymadusa ornatipennis* Ramme  
*Capnobotes fuliginosus* (Thomas)  
*Capnobotes occidentalis* (Thomas)  
*Anoplodusa arizonensis* (Rehn)  
*Plagiostira albonotata* Scudder  
*Plagiostira gillettei* Caudell  
*Zacycloptera atripennis* Caudell  
*Apote n. notabilis* Scudder  
*Atlanticus testaceus* (Scudder)  
*Atlanticus monticola davisii*  
 Rehn and Hebard  
*Atlanticus gibbosus* Scudder

*Pediodes haldemaniae* (Girard)  
*Anabrus simplex* Haldeman  
*Anabrus longipes* Caudell  
*Peranabrus scabricollis* (Thomas)  
*Pholidoptera aptera* (Fabricius)  
*Montana carpetana* (Bolivar)  
*Platycleis intermedia* (Serville)  
*Metriopectera brachyptera* (Linnaeus)  
*Sphagniana sphagnorum* (Walker)  
*Eremopedes scudderii* Cockerell  
*Eremopedes covilleae* Hebard  
*Atelopus schwarzi* Caudell  
*Idiostatus aequalis* (Scudder)  
*Acrodesctes philopagus*  
 Rehn and Hebard  
*Idionotus tehachapi* Hebard  
*Decticita brevicauda* (Caudell)  
*Glinopleura minuta* Caudell  
*Steiroxys pallidipalpus* (Thomas)  
*Steiroxys trilineatus* (Thomas)  
*Gtenodecticus pygmaeus* auct. ?  
 (det. Uvarov)  
*Tettigonia viridissima* Linnaeus  
*Hubbellia marginifera* (Walker)

COMPARISON OF *Rehnia* WITH LISTROSCELINAE (S.L.)  
 AND DECTICINAE (S.L.)

*Fastigium verticis*

The most evident and perhaps the most significant feature demonstrating the relationship of *Rehnia* to the Listroscelinae is the form of the fastigium verticis. Among the listroscelines proper only *Lipotactes* has a broad fastigium, this structure being narrow and relatively small in all other genera; in the meconemines *Phlugis* and *Phlugiola* it is almost entirely suppressed. The South American genera *Macrometopon* and *Cerberodon* and the genera *Listroscelis* and *Hexacentrus* and their allies have a compressed, almost lamellate fastigium which is separated by a distinct groove from the apex of the weakly developed frontal fastigium. In the two first-named genera it projects from the head at a level well below the summit of the occiput, and in most (but not all) of the species of *Listroscelis* and *Hexacentrus*, as well as in *Macrometopon* and *Cerberodon*, the dorsal surface of the fastigium joins the curvature of the vertex at a slight angle as seen in profile.

In the Decticinae the fastigium verticis is in general a broad, prominent structure, its dorsal surface continuing the slope and curvature of the vertex and its sides gradually converging between

the eyes. Its apex is usually in broad contact with the apex of the fairly well-developed frontal fastigium. In some decticine genera the fastigium is more strongly narrowed (*Capnobotes*, *Plagiostira*) or considerably reduced (*Apote*, *Zacycloptera*), and in at least one species (*Aglaothorax armiger*) its apex does not touch the frontal fastigium. In none of these genera, however, does the fastigium approach the degree of compression or the reduction in size characteristic of the Listroscelinae.

The fastigium verticis of *Rehnia* conforms in all respects to the listrosceline pattern, and differs only in small details from those of *Cerberodon* and *Macrometopon*. Its lamellate form in *Rehnia* suffices in itself to distinguish that genus at a glance from all North American Decticinae.

#### *Other features of the head*

The eyes of Listroscelinae (and Meconeminae) are characteristically conspicuous, strongly protruding, globose, and located far forward on the head. In contrast, the eyes of Decticinae protrude but little, and are placed laterally on the head, well behind the apex of the usually broad fastigium verticis. In a few decticine genera, such as *Capnobotes*, the eyes are more protuberant and the fastigium is somewhat reduced or narrowed, but never to such a degree as in Listroscelinae. The eyes of *Rehnia* are prominent, globose, and anteriorly located; they are typically listrosceline in aspect. Many groups of actively predatory insects that find their prey by sight have prominent, anteriorly located eyes, and in the Tettigoniidae such eyes occur not only in the Listroscelinae (and Meconeminae) and in *Rehnia*, but also in the strongly predatory Saginae (*Saga* and *Clonia*).

An elongated head is also characteristic of many predatory insects. In the Listroscelinae, Meconeminae, and Saginae the frons, labrum, and mandibles are distinctly elongated in most genera, in contrast to the shorter, wider face of the Decticinae. *Rehnia* possesses the elongate face characteristic of the listroscelines.

#### *Food habits and raptorial adaptations of the forelegs*

The modifications of the eyes and face suggest that the Listroscelinae (and Meconeminae) are more strongly predatory than the Decticinae, and the structure of the forelegs in the two groups is in

general consistent with this conclusion. The forelegs of all Listroscelinae (and most Meconeminae) are highly modified. They are longer than the middle legs, their ventral spurs are long to very long as compared with those of most other Tettigoniidae,<sup>1</sup> and their ventral femoral spines are usually well developed. It is generally assumed that listroscelines are largely or exclusively carnivorous, and this has been given as a characteristic separating them from related subfamilies (see quotation from Zeuner (1940: 83-84), above, and the additional discussion in that paper). There is surprisingly little published information on the feeding habits of the listrosceline-meconemine group, but so far as it goes it confirms the assumption that the members of this assemblage are active predators. Henry (1934) reports that *Decolya* captures insect prey "by leaping upon it and dexterously grasping it with the strongly spurred fore- and mid-legs," and that *Phisis kelletti* Henry captures small flies by "a clap-net action of the fore- and mid-legs." Eichler (1938) states that *Phlugiola dahlemica* catches small flies by sudden jumps, and holds the prey tightly between the spines of the forelegs while eating it. In *Meconema* and *Phlugiolopsis* the spurs of the anterior tibiae are not exceptionally long; according to Zeuner (1940) the former is herbivorous and the latter is a predator on slow-moving insects such as plant lice and caterpillars which it seizes directly with its mandibles. I am informed by T. H. Hubbell that crop contents of species of *Hexacentrus* that he has examined consisted entirely of insect remains, including fragments of ants, small winged Hymenoptera, beetles, and flies.

The Decticinae do not possess highly modified forelegs, although many (*Tettigonia*, for example) have them armed with strong ventral spines. I have never seen any decticine use its legs for capturing live prey in a manner comparable to that of *Decolya* and *Phisis*. Dr. Stanley K. Gangwere, who has made an extensive study of food habits in Orthoptera (MS.), concludes from his observations on *Atlanticus testaceus* and from published information on other decticines that

<sup>1</sup> The ventrocephalic spurs are usually longer than the ventrocaudal, and those near mid-length of the tibia are longer than those at the base and apex. The ratio of length of longest spur to dorsoventral tibial depth at mid-length of tibia in specimens of a few representative species was determined by measurement to be as follows: Decticinae: *Atlanticus testaceus*, ♂ 1.3; *Pediodes haldemanni*, ♂ 1.3; *Ctenodecticus pygmaeus*, ♂ 1.3; *Tettigonia viridissima*, China, ♂ 2.3, ♀ 2.1, Sweden, ♀ 1.6; *Hubbellia marginifera*, ♂♂ 1.9, 1.8. Listroscelinae: *Hexacentrus dorsatus*, ♂ 3.7, ♀ 4.5; *H. mundus*, ♂ 4.4; *Macrometopon*, last instar juv. ♂ 3.0; *Phisis* sp., ♀ 7.3. Meconeminae: *Phlugiola* sp., ♀ 5.2; *Phlugis* sp., ♀ 5.8; *Rehnia victoriae*, ♂ 2.0, ♀ 2.2; *Rehnia* sp., ♂ 1.7.

the members of this group are probably omnivorous from necessity, though carnivorous by preference. He classes them as carnivorous scavengers rather than as active predators.

*Rehnia* has strongly modified forelegs very similar to those of Listroscelinae, although the ventral tibial spurs are much shorter than those of *Hexacentrus*, *Cerberodon*, and *Macrometopon*, and are matched in degree of development by those of some members of the decticine genus *Tettigonia*. My caged individuals were maintained on a diet of live insects alone, and were quite successful in capturing active prey. They did not use their forelegs in the manner described for *Phisis* and *Decolya*, but simply pounced and sat upon their victims—a method suited to such large, powerful, heavy-bodied creatures.

#### *Sternal and coxal armature*

*Rehnia* and such typical Listroscelinae as *Listroscelis*, *Hexacentrus*, *Macrometopon*, and *Cerberodon* are provided with long, almost cylindrical spines on the prosternum and on the meso- and metabasisternites. In the listroscelines *Phisis* and *Decolya* the prosternum bears slender spines but the processes of the mesosternum are reduced to prominent, round, semipedunculate tubercles and those of the metasternum to conical tubercles. In the meconemine genera *Meconema*, *Phlugiolopsis*, *Phlugiola*, *Phlugis*, and *Xiphidiopsis* the prosternum and metasternum are unarmed, and the mesosternum bears rounded knobs. Zeuner (1940: 84) points out that in the mesosternal armature a complete transition can be traced from the small rounded knobs of *Meconema* to the long pointed spines of *Hexacentrus*.

In the Decticinae many genera lack sternal processes, but when such are present they are located as in Listroscelinae. Those of the mesosternum usually form only triangular lobes, but in some genera they are spinous processes which are, however, more or less lamellate except near the tip. The processes of the metasternum are less often developed, and when present are rarely more than angulate lobes.

A similar situation exists with respect to the ventral coxal armature. In its fullest development this consists of a large, heavy, more or less acute tooth formed from the distal border of the ventral side of the coxa, and a smaller, more acute tooth on the surface of the coxa near the proximoventral border. These teeth are strongly developed in *Rehnia*, *Cerberodon*, *Macrometopon*, and *Hexacentrus*; they are weakly developed or absent in *Phisis* and the meconemine

genera. In the Decticinae they are only occasionally (and then weakly) developed. In many genera of that subfamily the distoventral margin of the coxa is angulate, but it never forms a large acute tooth, and the proximal tooth is absent in all the decticinae that I have examined. Considering the manner in which *Rehnia* captures its prey, by pouncing and sitting upon it, the sternal and coxal spines may be useful in holding a struggling insect.

#### *Pronotal characters*

Most Listroscelinae (and Meconeminae) as well as *Rehnia* have a pronotum which is approximately semicylindric in cross section, either throughout or anteriorly. In *Hexacentrus* and in a few other genera the caudal part is dorsally flattened and has short, weakly indicated shoulders. In *Rehnia*, in *Hexacentrus*, and in *Listroscelis* and *Cerberodon* and their allies, the pronotum is distinctly narrower than the enlarged head for most of its length, with the anterior part flared slightly for the reception of the head. In *Macrometopon*, *Cerberodon*, *Listroscelis*, *Monocerophora*, and *Rehnia* the caudal border is elevated slightly into a distinctive but short flange. The pleuron and episternum are firmly joined to the very edge of the lateral lobes in these genera, and this, together with the narrowness of the greater part of the pronotum, gives the latter the appearance of being closely appressed to the body.

In the Decticinae the pronotum, though quite varied in form, usually presents a very different appearance. It is often flattened above and provided with lateral carinae or rounded shoulders. It is usually as wide as or wider than the head, or if constricted it is so only near or cephalad of its mid-length, widening rapidly cephalad and caudad of the narrowest part. Only rarely does it have an elevated posterior flange, which is at most only weakly developed, and the anterior and ventral margins of the lateral lobes form a free, unappressed border in most of the genera examined. As a result, the pronotum of decticinae appears relatively bulky, and gives the impression of not being closely attached to the underlying structures. In most of the genera it is produced caudad into a large "shield" covering most or all of the stridulatory field of the tegmina, and accounting for the name "shield-backed katydids" commonly applied to the group. The shield is not, however, a universal feature in the Decticinae, and a comparable prolongation of the pronotum is present



in several genera of Listroscelinae. There is no shield in *Rehnia* nor in those South American listrosceline genera to which *Rehnia* appears to be most closely related, *Macrometopon*, *Cerberodon*, and *Carliella*. In this respect *Rehnia* resembles most Listroscelinae, and in its other pronotal characteristics it shows no strong resemblance to those Decticinae in which a shield is not developed.

#### *Other morphological features*

Since Zeuner (1936a,b) has founded his classification of the tettigoniid subfamilies in considerable part on the structure of the prothoracic tracheal apparatus, and on this basis has assigned the decticines to his Tettigonioid Group and the listroscelines to his Conocephaloid Group, it would seem that the condition of these structures in *Rehnia* should afford clear evidence of the relationships of this genus. However, Zeuner himself has called attention (1939: 118) to the close similarity of the listrosceline *Hexacentrus* and the decticine *Decticus* in respect to this apparatus. I am informed by T. H. Hubbell, who has examined the prothoracic tracheal structures in *Rehnia* and in a number of the other genera in question, that *Rehnia* agrees with *Hexacentrus* and *Macrometopon* in having a very large, rounded oblong femoral stigma with bare margins, trumpet-shaped vesiculae femoralis connected by a short slender communicating trachea, and a common stem from which the truncal tracheae branch at some distance from the truncal stigma. Unfortunately for present purposes, all these features also occur in the decticines. In most of the latter, however, the margins of the femoral stigma are furnished with hairs or bristles, sometimes slender and few in number, sometimes (as in *Atlanticus*) broad-bladed, forked, and so long and thickly set as to almost occlude the stigmal opening. Among the genera of true listroscelines examined, only *Phisis* was found to have scattered slender hairs along the stigmal margins. In *Phlugis*, *Phlugiola*, and other meconemine genera the prothoracic tracheal apparatus is so reduced, aberrant, and unlike that found in *Hexacentrus* and *Rehnia* as to bring into question the presumed close relationship of the meconemines to the listroscelines.

The internal armature of the proventriculus in Orthoptera affords many indications of relationship, and has been too little used by taxonomists. I am again indebted to T. H. Hubbell for the following information on its features in *Rehnia* and other genera. Wilde (1877)

described and figured the proventricular armature of *Tettigonia* and *Meconema*, and Norris (MS.) and Judd (1948) have made comparative studies of many genera and species. The six columns of tooth-like structures are well developed in most tettigonioids and conocephaloids, and in these groups the structure of the toothlike appendages is generally similar. Hubbell states that the armature of *Rehnia* and *Hexacentrus* resembles that of such decticine genera as *Atlanticus* and *Pediodes*, but differs from the condition in these and most other decticine genera in the lesser number and slightly different form of the central teeth. In the decticine genera there are usually from 14 to 18 teeth in each longitudinal row, whereas in *Rehnia* and *Hexacentrus* there are only 8 or 9. In most decticine genera, furthermore, the central teeth have a prolonged, inwardly and backwardly directed apical point best seen in side view, while in *Rehnia* and *Hexacentrus* the somewhat jagged rim of the tooth is not thus prolonged, and shows, in all but the most caudal teeth, a tendency (most pronounced in *Hexacentrus*) to be slightly reflexed forward on the crest of the tooth. In the meconemine genera the armature is much reduced, the reduction reaching an extreme in *Phlugis*, in which there are only 6 or 7 small, weakly sclerotized, bluntly rounded median and lateral teeth in each column. Here again the pronounced differences of meconemines from true listroscelines suggest a somewhat distant rather than a close relationship between the two assemblages.

*Rehnia* resembles certain listrosceline genera in particular features of the terminal structures of the male abdomen. The cerci of *Hexacentrus*, *Cerberodon*, *Macrometopon*, and *Listroscelis* and its allies are simple, thick at the base, and thence narrowed abruptly to the curved distal part, which is prolonged to an acuminate apex. The cerci of *Rehnia* are similar, but differ in the less abrupt curvature of the shaft, the less acuminate apex, and in having on the dorsointernal surface of the basal half a ridge that is enlarged apically to form a weak tooth. In the Decticinae the form of the cerci is quite varied, and generally more complex than in the Listroscelinae; often the cerci are provided with an internal tooth more discrete than that of *Rehnia*. The cerci of the latter more closely resemble those of the listrosceline genera named above than they do those of any of the decticine genera. The same is true of the structure of the supra-anal plate of the male. In *Macrometopon*, *Cerberodon*, and *Hexacentrus* this plate is simple, not at all produced, and slightly emarginate distad; in *Rehnia* it is also simple but more sharply and deeply emarginate

distad, and with the lateral parts slightly produced into lobes; in the Decticinae the plate is usually much more specialized and often produced into long apical lobes.

One of the most distinctive characteristics of *Rehnia* (and *Neobarrettia*) is the lack of titillators. Their complete absence was determined by dissection of alcoholic material of *Rehnia cerberus* and *R. victoriae*, and by examination of the relaxed abdomen of a specimen of *R. spinosa*. This unusual condition is shared with the listrosceline genus *Macrometopon*, examination of the relaxed type of *M. rantale* having failed to disclose any sclerotized structures within the genital chamber. All other genera of both the Listroscelinae and the Decticinae that I have examined, or for which there are adequate published descriptions, possess well-developed titillators.

#### *Similarities of Rehnia to Listroscelinae and to Decticinae*

From the evidence presented above it is apparent that *Rehnia* resembles certain of the listrosceline genera in precisely those characteristics by which the Listroscelinae differ from the Decticinae, or in features which *Rehnia* shares only with those genera. Where differences from conditions found in listrosceline genera exist, as in the shape of the stridulating field of the male tegmina and in details of form of the pronotum, the supra-anal plate, and the cerci, *Rehnia* shows little specific resemblance to the Decticinae. This genus does, however, share with the Decticinae two diagnostic characters which require further consideration.

The first is the presence in *Rehnia* of dorsal spurs on the outer side of the fore tibia which appear homologous with those of Decticinae. None of the genera presently accepted as Listroscelinae have such spurs, which are always present in the Decticinae except in the genera of the group Atrypteroes (Uvarov, 1924: 503). If *Rehnia* is actually a listrosceline, as the weight of evidence indicates, then it must either have independently developed dorsal spurs on the fore tibia, which seems unlikely, or have retained an armature present in the ancestral listroscelines but lost in other modern genera of the subfamily.

The second point of resemblance of *Rehnia* to the Decticinae, the presence of free plantulae on the basitarsus, constitutes less of a problem. These structures are probably nothing more than the halves of

a modified pulvillus, formed by retraction of the posterior membranous border between the sclerotized ventral plates of the pulvillus and the basitarsus. The plantulae are variously developed in the Decticinae, from a condition in which they are scarcely more than an enlarged and sclerotized pulvillus (in *Anoplodusa* and *Tettigonia*, for example) to very long paired plates which in some instances (*Gtenodecticus*, for example) equal the combined length of the two proximal tarsal segments.

Uvarov (1924: 493), in discussing the artificiality of separating the Tettigoniinae from the Decticinae on the basis of absence or presence of the plantulae, remarks that "it must be assumed that the presence of the plantulae in the Decticinae is an obvious adaptation to life on the ground, where the plantulae serve to secure a firmer footing before jumping, while the majority of Tettigoniinae are climbers on trees and bushes and seldom descend to the ground. Thus, it seems that the plantulae are a purely adaptational character acquired as a result of a change in habits, and, as such, can hardly be of great taxonomic value." Regardless of the evolutionary implications of this statement, it is scarcely borne out by observation. None of the North American genera of Decticinae with which I am familiar can be considered exclusively terrestrial except the boreal *Acrodictes*. Most decticine, especially the stridulating males, spend much or even almost all of their time in shrubs and other vegetation. Furthermore, in those genera whose members are usually on the ground, such as *Anabrus* and *Atlanticus*, the plantulae are not much more developed than they are in strongly thamnophilous and arboreal species, such as those of *Capnobotes* and *Eremopedes*. *Acrodictes philopagus*, which lives on the talus slopes of Mount Whitney in California and is as nearly terrestrial as any decticine can be said to be, has very poorly developed plantulae. Therefore, there seems to be no clear evidence concerning the functional significance of these structures, at least so far as the North American decticine are concerned.

The occurrence of plantulae is not restricted to the Decticinae; similar structures occur in the Saginae (*Saga*), and the enlarged sclerotized basal pulvillus of the listrosceline genera *Macrometopon* and *Cerberodon* might be regarded as a step toward the development of plantulae. Only minor changes would be needed to convert it into the type of plantulae found in *Rehnia*, in which the basal pulvillus has been enlarged and the two halves of its ventral surface sclerotized,

but in which the tips of the lobes do not project beyond the normal extent of the pulvillus, with which the lobes maintain a direct membranous connection.

#### THE GENUS *Neobarrettia*

Known as yet only by the single species *Neobarrettia imperfecta* from Guerrero, Mexico, this genus is very closely allied to *Rehnia*, as the close similarity of the two in all the features discussed above indicates. The fastigium is less compressed and not as deep, and the femoral spination is much weaker, but the basic structural similarity to the corresponding parts in *Rehnia* is evident. *Neobarrettia* shares with *Rehnia* a short, acutely conical projection on the middle of the penultimate sternite of the female, a characteristic I have found in no other genus. The structure of the male cerci is of the same basic type as in *Rehnia*; the cerci are thickened at the base, taper to a curved acute apex, and are provided proximad with a weak ridge on the dorsointernal surface. Finally, *Neobarrettia*, like *Rehnia* and *Macrometopon*, lacks titillators, a condition which, so far as I can determine, is restricted to these genera.

In their description of *Rehnia sinaloae*, Rehn and Hebard (1919) mentioned its "pronounced tendency toward *Neobarrettia*," presumably referring to the shape of the hind part of the pronotum and the short tegmina. *Rehnia sinaloae* is the only member of its genus known from the Pacific slope of the continent; the other species are spread over the southern Great Plains (from Kansas southward), the coastal plain of Texas, and the coastal plain and eastern sierras of northern Mexico. Since recent field work has shown that in this eastern region *Rehnia* is not uncommon, it is not improbable that its apparent absence from much of Mexico is a result of inadequate collecting, and that the genus has a much wider range than is now known. There is, therefore, a possibility that *Rehnia* and the southern Mexican *Neobarrettia* may be linked by a series of as yet undiscovered species.

It seems clear that Caudell (1907: 305) was wrong in stating that in spite of their superficial resemblance *Rehnia* and *Neobarrettia* are unrelated. He based this conclusion on the fact that *Neobarrettia* has only two apical ventral spines on the hind tibia and *Rehnia*, like most other tettigonioids, has four. Using this criterion, he placed

*Neobarrettia* in the group Rhacoclees and *Rehnia* in the group Gampsoclees of the Decticinae. The presence of only two apical spurs in *Neobarrettia* must be regarded as no more than a peculiarity of the genus, together with such other characteristics as the absence of wings, the inflated tegmina, and the flaring of the caudal part of the pronotum. In the last-mentioned feature, *Neobarrettia* is more similar to *Cerberodon* than is *Rehnia*.

#### GENERAL CONCLUSIONS

*Rehnia* and *Neobarrettia* resemble the Listrosclinae in several characteristics that may be used to distinguish most listrosclines from decticines, and they are similar to the listroscline genera *Cerberodon* and *Macrometopon* not only in general habitus, but also in a number of important structural features. They share with the Decticinae only two significant characters: the presence of plantulae on the hind basitarsus, and of dorsal spines on the fore tibiae. Plantular development has been shown above to be variable in the decticines, and not restricted to the members of that subfamily. The presence of the dorsal spines on the fore tibia in *Rehnia* and *Neobarrettia* may have resulted from evolutionary convergence toward the decticines, but is more likely to be owing to retention of a feature common to the ancestors of both decticines and listrosclines that was lost in most of the modern genera of the latter group.

I conclude that *Rehnia* and *Neobarrettia* should be transferred from the Decticinae to the Listrosclinae. There they may be tentatively grouped with *Macrometopon*, *Cerberodon*, and possibly also with *Carliella* and *Isocarliella* (Mello-Leitão, 1940). With these genera they represent a trend among the Listrosclinae toward heavy bodies, enlarged heads with compressed fastigia set well below the level of the vertex, short tegmina, and simple cerci. There are, however, species within the genera *Rehnia* and *Neobarrettia* which are small (*Rehnia pulchella* Tinkham, 1944), species with only weakly enlarged heads (*R. victoriae*), species with broader fastigia than is normal for the group (*Neobarrettia imperfecta*), and species with long wings (an undescribed species of *Rehnia* in my collection). Revisionary studies will be required to determine whether *Rehnia* and *Neobarrettia* are in fact closely related to *Macrometopon* and *Cerberodon*, as suggested above, or whether two separate phyletic lines showing

parallel modifications are represented, one leading to the two last-named genera and the other to the larger, short-winged species of *Rehnia* that have maximally compressed fastigia (*Rehnia spinosa* and *R. cerberus*). Plans have been laid for study of the problems involved.

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