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# The Cynipoid Genus *Paramblynotus*: Revision, Phylogeny, and Historical Biogeography (Hymenoptera, Liopteridae)

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THE CYNIPOID GENUS *PARAMBLYNOTUS*:  
REVISION, PHYLOGENY, AND  
HISTORICAL BIOGEOGRAPHY  
(HYMENOPTERA: LIOPTERIDAE)

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## ABSTRACT

The genus *Paramblynotus* is the most species-rich genus of the so-called macrocynipoids, the large cynipoid parasitoids of wood-boring and cone-boring insect larvae. The species range in size from some of the largest to the smallest macrocynipoids, comparable in size to microcynipoids. *Paramblynotus* members occur on all continents except Europe and Australia, with most species being tropical or subtropical. The biology is poorly known but a few observations indicate that the species are parasitoids of beetle larvae. In this monographic revision of the genus, we present a species-level cladistic analysis based on qualitative and quantitative features of the external morphology.

For analysis of quantitative features, we present for the first time a novel coding method, the method of Finite Mixture Coding (FMC) based on *k*-means clustering, or FMCK. The new method is similar to the FMC method proposed by previous authors in that they both generate codes (character states) for phylogenetic analysis as the direct output of a statistical procedure, thus avoiding the subdivision of quantitative data into discrete states on the basis of arbitrary criteria as with other coding methods. Through incorporating finite mixture analysis and likelihood estimation as used in FMC and *k*-mean cluster analysis for a priori statistical modeling of component distributions, FMCK is advantageous over FMC in that it can be implemented using readily available statistic programs with *k*-mean cluster analysis, such as STATISTICA, MINITAB or SYSTAT, available on both PC and Macintosh platforms. We were able to identify 8 quantitative characters among 23 as useful for cladistic analysis by using the new coding method. In total, our character matrix has 132 coded characters.

The phylogenetic analysis indicates that species of the previously recognized genus *Decellea* form a monophyletic group deeply nested within *Paramblynotus*. *Decellea* is therefore synonymized with *Paramblynotus*, which is separated into seven monophyletic species groups: the *virginianus*, *scaber*, *yangambicolus*, *nigricornis*, *apeosus*, *ruficollis*, and *punctulatus* groups.

Based on the phylogeny, we reconstruct the historical biogeography of the liopterid subfamily Mayrellinae, consisting of the genera *Paramblynotus* and *Kiefferiella*, using dispersal-vicariance analysis in combination with palaeoenvironmental data. The results suggest that the subfamily originated in the Northern Hemisphere and then expanded its distribution early by way of the Bering area. The divergence between *Paramblynotus* and *Kiefferiella* was apparently associated with the formation of the Rocky Mountains about 50 million years ago. An early *Paramblynotus* lineage dispersed to Africa from the eastern Palearctic by way of Arabia, and it subsequently diversified along with montane forests in Africa. The relatively high diversity of *Paramblynotus* in Southeast Asia is considered to be partly caused by the frequent sea level changes since late Oligocene (29 Ma), which drastically changed the land configuration of this area.

We end this paper with a taxonomic revision of the genus *Paramblynotus*, with a total of 92 species treated, including 72 described as new and 20 previously known, of which 18 are redescribed. Keys to the species groups as defined in this paper and to all known species of each species group are provided. For all species, the available information on their biology and distribution are summarized.

## INTRODUCTION

The genus *Paramblynotus* Cameron, 1908 is one of three currently recognized genera in the liopterid subfamily Mayrellinae. It is by far the most speciose genus of the family, including 20 described and many undescribed species (Ronquist, 1995a). Members of the genus are distributed in all major biogeographical regions except the western Palearc-

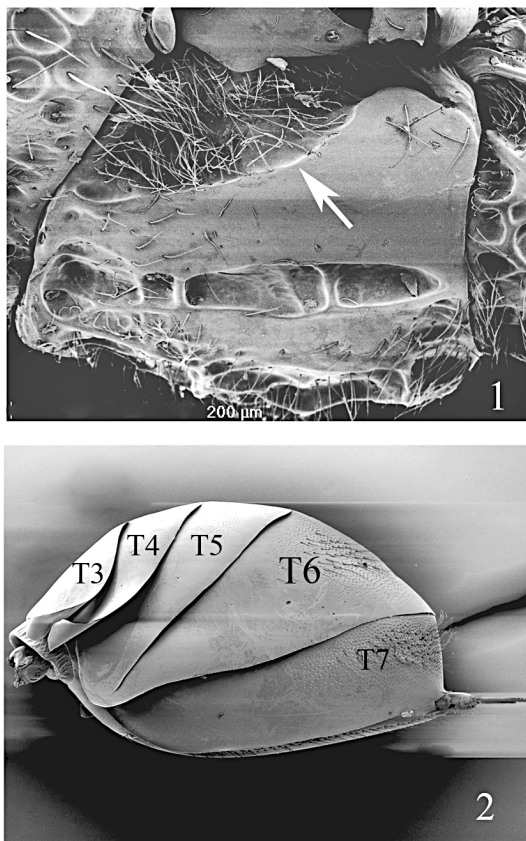
tic and Australia, with the greatest diversity being found in the eastern Palearctic and Oriental regions (Ronquist, 1995a). According to Ronquist (1995a), the closest relative of *Paramblynotus* is the small genus *Decellea* Benoit, 1956, consisting of two species, one of which is undescribed. The distribution of *Decellea* is limited to Africa. The third genus of Mayrellinae is *Kiefferiella* Ashmead, 1903, which is endemic to southwestern North



America and consists of one fossil species and four extant species, two of which are described (Ronquist, 1995a).

The current knowledge of the biology of the Mayrellinae is based on a few rearing and collecting records. These suggest that the *Paramblynotus* species are parasitoids of wood-boring Coleoptera of the families Cerambycidae (Diaz, 1973; Yang and Gu, 1994; Ronquist, 1995a) and Curculionidae, and possibly also Hymenoptera of the family Siricidae (Yang and Gu, 1994). *Decellea* has been reared from Coleoptera as well as from Lepidoptera (Ronquist, 1995a), and species of *Kiefferiella* are parasitoids of Buprestidae (Coleoptera) (Weld, 1956). In all cases, mayrellines have been associated with broad-leaved trees and bushes (Weld, 1956; Ronquist, 1995a), never conifers; the plant records include members of the families Asteraceae, Chenopodiaceae, Euphorbiaceae, Fabaceae, Fagaceae, Lauraceae, Myrtaceae, Oleaceae, Pteroxylaceae, and Ulmaceae (Ronquist, 1995a and references therein; this study; Schick, personal commun.). The circumscription of the genus *Paramblynotus* has changed considerably since its establishment by Cameron (1908). Several genera have been synonymized with *Paramblynotus*, including *Paraegilips* Kieffer, 1910 (Hedicke and Kerrich, 1940; Weld, 1952; Ronquist, 1995a), *Allocynips* Kieffer, 1914 (Weld, 1930), *Holocynips* Kieffer, 1916 (= *Diholocynips* Rohwer and Fagan, 1917) (Ronquist, 1995a), *Mayrella* Hedicke, 1922 (Weld, 1952), *Paribalia* Weld, 1922 (Ronquist, 1995a), *Stylobrachys* Belizin, 1951 (Kovalev, 1994), *Baviana* Barbotin, 1954 (Weld, 1962), and *Decellea* Benoit, 1956 (Weld, 1962; but see Ronquist, 1995a). The concept of the genus adopted in this study is based on Ronquist (1995a) except for a few changes motivated by the results of the phylogenetic analysis.

The genus *Paramblynotus* is considered a monophyletic group supported by two derived features (Ronquist, 1995a): (1) ventral margin of mesopleural triangle well defined and evenly curved (fig. 1), and (2) abdominal tergum 6 of females distinctly expanded dorsally to form the largest metasomal tergum (fig. 2). The first character is shared by all *Paramblynotus* species except



Figs. 1, 2. Apomorphies for *Paramblynotus*. 1, Ventral margin of mesopleural triangle is smoothly curved and well defined (*P. virginianus*); 2, metasomal tergum 6 dorsally distinctly expanded, representing the largest metasomal tergum in females (*P. dyak*).

those in the small African *yangambicolus* species group, which is characterized by a less well-defined mesopleural triangle. Based on this character and other evidence, Ronquist (1995a) treated the *yangambicolus* group as a genus (*Decellea*) distinct from *Paramblynotus*, reverting the previous synonymization of the two genera by Weld (1962). Here we show that the *yangambicolus* group is deeply nested within *Paramblynotus*, and therefore the lack of a distinct ventral mesopleural margin in these species must be interpreted as a secondary reversal. In all other Iliopterids, as well as in ibaliids and *Austrocynips*, the ventral margin of the mesopleural triangle is irregular and usually not well defined; in the rare cases where the mesopleural triangle is more

distinctly defined, its ventral margin is not evenly curved (Ronquist, 1995b). Thus, despite the secondary loss in the *yangambiculus* group, the ventrally defined mesopleural triangle remains a viable synapomorphy for *Paramblynotus* species.

The second *Paramblynotus* synapomorphy, the dorsally enlarged sixth abdominal tergum, is a unique feature for *Paramblynotus* among all cynipoids. In the Oberthuerellinae, the sixth abdominal tergum is also the largest metasomal tergum, but in this subfamily the tergum is expanded ventrally as well as dorsally, giving it a completely different shape that has apparently been independently derived. Within *Paramblynotus*, there are two obvious subsequent modifications of the sixth tergum. In *P. mixtus* of the *yangambiculus* group, tergum 6 has become subequal to the three proceeding terga dorsally, although it is still distinctly expanded dorsally compared to its width laterally. In the African *trisetosus* group, tergum 6 is expanded dorsally, but this is difficult to see because it is partially covered by the more strongly expanded tergum 5.

A third potential synapomorphy of *Paramblynotus* discussed by Ronquist (1995a) is the internalization of abdominal sterna 4–6, a feature present in all species except the clade of *P. yangambiculus* and *P. alveolatus*. According to the phylogenetic analysis presented here, the exposed sterna in the latter clade are most probably due to secondary reversal. However, the interpretation of this character is still complicated because all other members of Liopteridae, except species of *Kiefferiella*, share the *Paramblynotus* state of having sterna 4–6 entirely covered by sternum 3. Thus, it is possible that internalization happened twice, once in the ancestor of *Paramblynotus* and once in the ancestor of all liopterids except the Mayrellinae, making this character a *Paramblynotus* synapomorphy. However, an equally parsimonious explanation, given that forward and backward changes carry the same cost, is that the internalization is a ground-plan feature of liopterids and that the sterna became secondarily exposed in *Kiefferiella* and in some *Paramblynotus*. Dissection of a few liopterids with concealed sterna (species of *Pseudibalia* and *Paramblynotus*) revealed that the sterna

are still independent, free, and well-pigmented sclerites even though they are covered by abdominal sternum 3 in normal repose. The presence of free sclerites presumably facilitates repeated reversal to the primitive condition.

The genus *Paramblynotus* was originally placed in the Figitinae (Cameron, 1908) but was later moved to the Liopterinae (Weld, 1930). Hedicke and Kerrich (1940) promoted the subfamily Liopterinae to family status and, in the same paper, Kerrich established a new subfamily Mesocynipinae including five genera, namely *Mesocynips* Cameron, 1903, *Paramblynotus* Cameron, 1908, *Dallatorrella* Kieffer, 1911, *Mayrella* Hedicke, 1922, and *Paribalia* Weld, 1922. Before that, Kieffer (1911) had established a subfamily Dallatorellinae for his new genus *Dallatorrella*, and Hedicke (1922) had proposed another subfamily, Mayrellinae, to include his genus *Mayrella*. In abandoning the two existing subfamily names, Hedicke and Kerrich (1940) apparently recognized Cameron (1903) as the author of Mesocynipinae. However, Cameron had only mentioned in the description of *Mesocynips* that it deserved to be placed in a separate subfamily; the complete lack of a description of the new subfamily or even mention of its name makes it impossible to attribute the subfamily to him.

The arrangement of Hedicke and Kerrich essentially remained unchanged until the recent phylogenetic studies of Ronquist (1995a, 1995b). According to Ronquist (1995a, 1995b), the Liopteridae is monophyletic, constituting the sister group of all other cynipoids excluding Austrocynipidae and Ibaliidae (fig. 3). Ronquist (1995a) divided the liopterids into four monophyletic subfamilies: Liopterinae, Oberthuerellinae, Dallatorrellinae, and Mayrellinae. Of the Mesocynipinae genera of Hedicke and Kerrich (1940), *Mesocynips* and *Dallatorrella* were placed in Mesocynipinae and the others were all grouped into the more widely circumscribed genus *Paramblynotus* and placed in the Mayrellinae together with *Kiefferiella* and *Decellea*. Ronquist also showed that the Mayrellinae are the sister group of all the remaining liopterids and suggested that *Kiefferiella* forms the sister

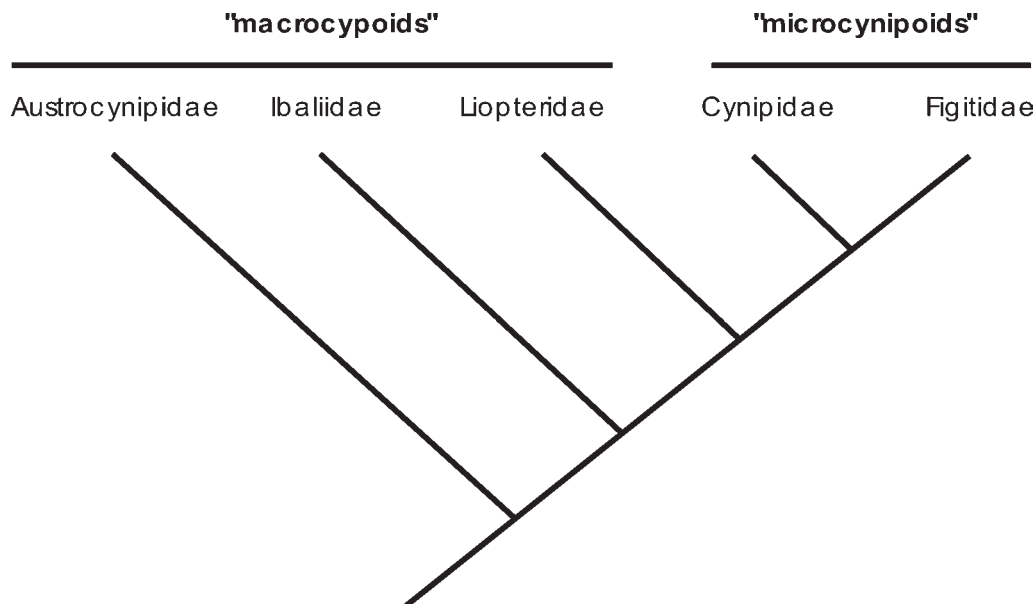


Fig. 3. Phylogenetic relationships among families of Cynipoidea (after Ronquist, 1995b).

group of *Decellea* and *Paramblynotus* within the Mayrellinae (fig. 4).

Here we present a monographic revision of the genus *Paramblynotus* based on a large material assembled from many insect collections around the world. Included in our study is also the genus *Decellea* Benoit, 1956, whose status as a genus distinct from *Paramblynotus* has been controversial, as mentioned above (Benoit, 1956; Weld, 1962; Ronquist, 1995a). In total, the studied material comprised 90 species, and it included 18 of the 20 previously described species of *Paramblynotus* and *Decellea*.

The relationships among the *Paramblynotus* and *Decellea* species were studied based on qualitative and quantitative characters of adult morphology. The quantitative characters were analyzed using a novel implementation of Finite Mixture Coding (FMC; Strait et al., 1996) described here for the first time. We refer to the new method as FMC with  $k$ -means cluster analysis, or FMCK. The resulting character matrix was analyzed using standard parsimony methods. Two undescribed species of *Kiefferiella*, which is the sister group of *Paramblynotus* + *Decellea* (Ronquist, 1995a), were used as outgroups.

The cladistic results showed that *Decellea* is deeply nested within *Paramblynotus* and we

therefore synonymize the former with the latter. Furthermore, based on the cladistic results, we propose a division of *Paramblynotus* into seven monophyletic species groups, only partly matching the tentative species groups recognized previously by Ronquist (1995a). The historical biogeography of the subfamily Mayrellinae was reconstructed based on a synthesis of the *Paramblynotus* phylogeny and the previous genus-level Mayrellinae phylogeny presented by Ronquist (1995a). The data were analyzed using dispersal-vicariance analysis (Ronquist, 1997), and paleoenvironmental data were used to separate alternative, equally parsimonious reconstructions.

The monograph ends with a taxonomic revision of the genus *Paramblynotus*. This part includes keys to species groups and species, descriptions or redescrptions of all the studied species, and summaries of the available distributional and biological information.

## MATERIALS

### SPECIMENS EXAMINED

The study is based on 721 adult specimens borrowed from the insect collections listed

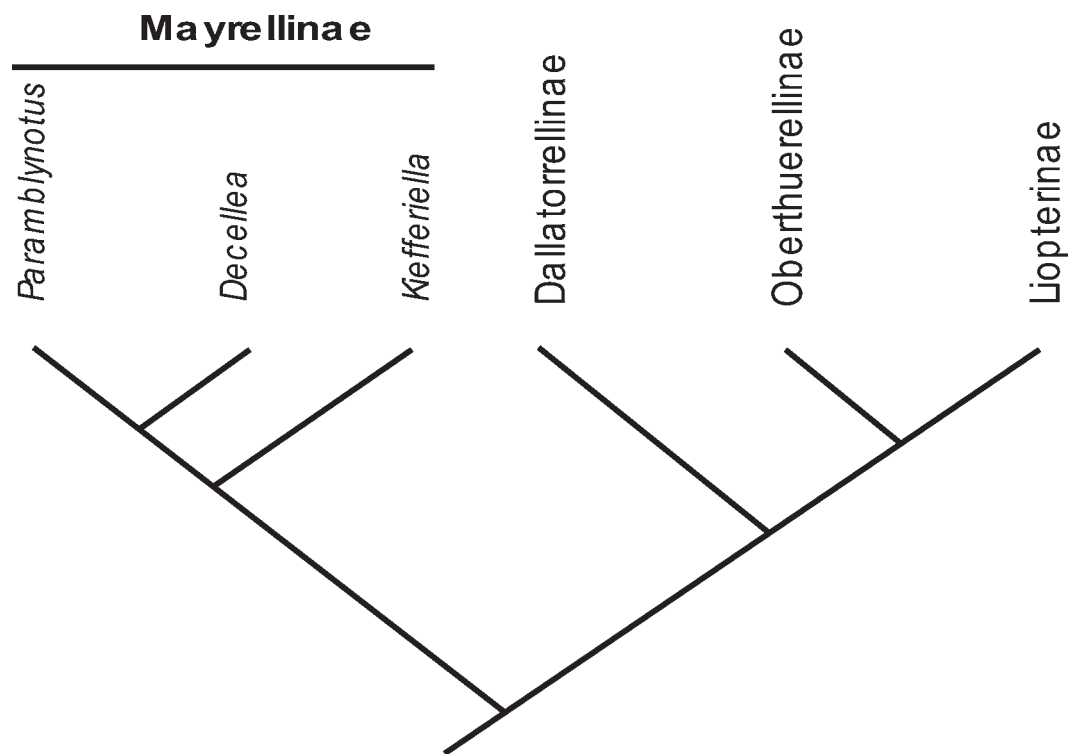


Fig. 4. Phylogenetic relationships among subfamilies of Liopteridae and genera of Mayrellinae (after Ronquist, 1995a).

below. The specimens examined should represent the entire culled material of the study taxa in these collections. The entire material consisted of 92 species, two of which belonged to *Kiefferiella* (outgroup) and 90 of which belonged to *Paramblynotus* and *Decellea* (the latter is synonymized with *Paramblynotus* in the present paper). A detailed list of the examined material is given in appendix 1. Throughout the paper, HT and PT represent Holotype and Paratype, respectively.

LIST OF DEPOSITORIES

|      |  |
|------|--|
| AEI  | American Entomological Institute, Gainesville, FL (D. Wahl)                  |
| BPBM | Bernice P. Bishop Museum, Honolulu, HI (S. Miller)                           |
| CAU  | Entomological Museum, China Agricultural University, Beijing, China (W. Cai) |

|      |   |
|------|---|
| CFR  | F. Ronquist collection, Uppsala University, Sweden                            |
| CMS  | M. Sporrang, private collection, Göteborg, Sweden                             |
| CNCI | Canadian National Collections of Insects, Ottawa, ON, Canada (J. Read)        |
| CSFU | Insect Collection, Central South Forestry University, Zhuzhou, China (M. Wei) |
| EIHU | Hokkaido University, Sapporo, Japan (M. Suwa)                                 |
| MRAC | Musée Royal de l'Afrique Centrale, Tervuren, Belgium (E. De Coninck)          |
| MZLU | Museum of Zoology, Lund University, Lund, Sweden (R. Danielsson)              |
| NHML | The Natural History Museum, London, UK (Tom Huddleston)                       |
| NHRS | Naturhistoriska Riksmuseet, Stockholm, Sweden (T. Pape)                       |

|      |  |
|------|--|
| NNMN | Nationaal Natuurhistorisch Museum, Naturalis, Leiden, The Netherlands (C. van Archterberg)                   |
| NWCF | Natural Enemy Insects Research Laboratory, Northwest College of Forestry, Yangling, Shan'xi, China (Z. Yang) |
| PPRI | Plant Protection Research Institute, Pretoria, South Africa (G. L. Prinsloo)                                 |
| ROME | Royal Ontario Museum, Toronto, ON, Canada (C. Darling).  |
| SAM  | South African Museum, Cape Town, South Africa (S. von Noort, M. Cochrane)                                    |
| UCDC | University of California at Davis, Davis, CA (S. Heydon)   |
| USNM | United States National Museum, Washington, DC (A. Menke).  |
| ZICA | Zoological Institute, Chinese Academy of Sciences, Beijing, China (D. Huang)                                 |
| ZMHB | Zoologisches Museum, Humboldtuniversität, Berlin, Germany (F. Koch)  |
| ZMSP | Zoological Museum, Academy of Sciences, St. Petersburg, Russia (O. V. Kovalev)                               |

## METHODS

The study is entirely based on adult external morphology. Terms for skeletal structures follow Ronquist and Nordlander (1989) and Ronquist (1995a, figs. 5–9). Terms for surface sculpture follow Harris (1979).

### CODING OF QUALITATIVE CHARACTERS

Multistate characters were treated as ordered (additive) characters when it was possible to order the states unambiguously using morphological evidence alone. When a large sample of specimens of a species was available, polymorphism was coded either as the majority state or as all observed states when no absolute majority was observed for any of the involved states (Wiens, 1995). In cases when one of the states of a main character was more finely divided into one or

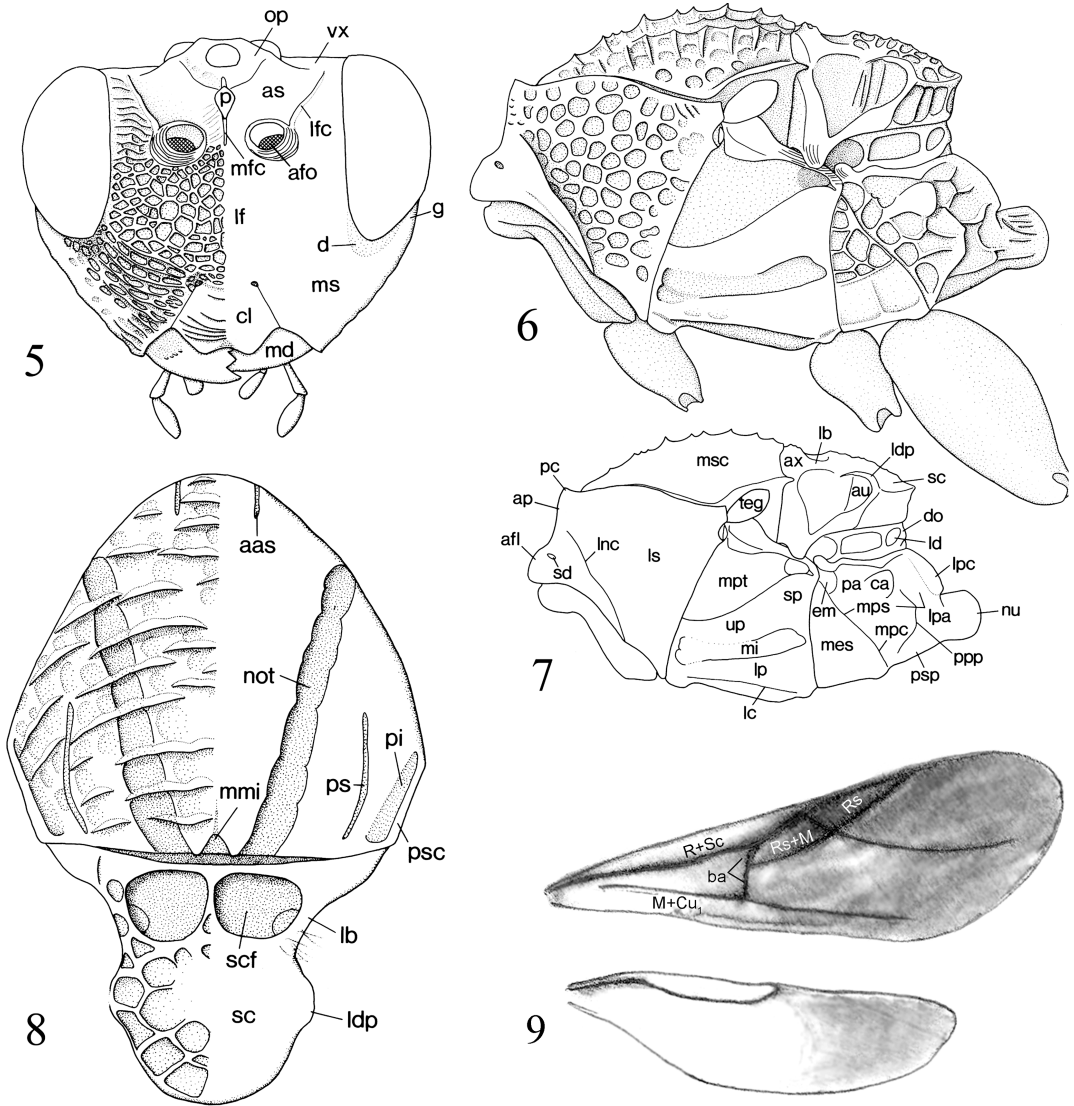
more subsidiary character(s), taxa with other states of the main characters were coded as having state unknown (character not applicable) in the subsidiary character (Maddison, 1993). This coding method is commonly used and is further discussed in Nordlander et al. (1996). The main and subsidiary characters were weighted equally.

### CODING OF QUANTITATIVE CHARACTERS: THE FMCK METHOD

Quantitative characters have frequently been neglected in phylogenetic analysis, mostly because of the difficulties of incorporating such data in character matrices requiring characters represented by discrete values (Chappill, 1989; Thiele, 1993). However, rejection of quantitative characters in favor of qualitative data can only be justified if “quantitative” and “qualitative” data differ in type and if qualitative data can a priori be determined to have more phylogenetic information than do quantitative data. Such an assumption, and hence the rejection of quantitative characters, is unfounded (Thiele, 1993). Quantitative characters are particularly important in lower level phylogenetic studies of taxa with high diversity, such as *Paramblynotus*, where a large number of potentially phylogenetically informative characters are needed to properly resolve the phylogeny. In the present study, 23 quantitative characters were recorded as measurement ratios. The raw data were then analyzed using the FMCK procedure developed by Z.L., and the measurement values were then classified into discrete states.

The FMCK method is similar to the FMC method of Strait et al. (1996). Like FMC, the new method avoids arbitrary criteria of dividing quantitative data into discrete states by producing codes, or character states, as the direct output of a statistical procedure. Therefore, it is different from other available coding methods (Strait et al., 1996), such as gap coding (Mickevich and Johnson, 1976), segment coding (Simon, 1983; Thorpe, 1984; Chappill, 1989), divergence coding (Thorpe, 1984), homogeneous subset coding (Simon, 1983), generalized gap coding (Archie, 1985), and gap weighting (Thiele, 1993). Both the FMC and FMCK methods adopt the con-





Figs. 5–9. Body parts with pubescence removed and associated terminology (figs. 5–8 after Ronquist, 1995a, abbreviations are listed in appendix 5). 5–7, *P. braziliensis*, head in front view (fig. 5), and mesosoma in lateral view (figs. 6, 7); 8, *Kiefferiella* sp., mesosoma in dorsal view; 9, *P. trisectus*, fore- and hindwings. Abbreviations for morphology are listed in appendix 5 and abbreviations for venation follow Ross (1936).

ventional assumption of statistical inference that groups are significantly different if the probability is low that their observed distributions could have been sampled from a single population. If the distribution of taxa with respect to a particular measurement is such that these taxa are probably sampled from a single theoretical statistical (not biological) population, they are not consid-

ered discernible and are assigned the same code. The number of codes for a set of taxa is equal to the number of discernible statistical populations identified by finite mixture analysis and likelihood methods (Strait et al., 1996).

In FMC methods, a dataset of a particular measurement is regarded as a random sample of a mixture distribution with a finite number

of component distributions. The form of each component contribution can be described by an equation, the component density function. Likewise, the form of the mixture can be described by a mixture density function. The number of component populations (hence the number of codes) is found by fitting mixture density functions with various numbers of component distributions to the observed dataset. The FMC procedure of Strait et al. (1996) has three steps. First, using likelihood estimation methods, several mixture density functions are fitted to the dataset. Specific parameters (mixing proportion, mean, and variance) are estimated for each of the component distributions in a mixture. The component distributions are assumed to be normal for species means (Strait et al., 1996). The best parameters are those that maximize the likelihood statistic,  $L$ . The number of mixture models to be examined is specified by the researcher. In the second step, the mixture that provides the best fit with the dataset is identified using the Akaike information index (AIC) (Akaike, 1974). The mixture model with the lowest AIC value describes the dataset best and is thus preferred. Finally, individual species are assigned codes by calculating the probability of a species mean being drawn from any given component distribution in the optimal mixture model.

Finite mixture modeling is usually computationally expensive. Some programs are available for likelihood estimation of finite mixture models, as required by the FMC method (Pearson et al., 1992, Strait et al., 1996). These programs, however, are expensive and limited to the PC platform. Although program source code is also available, most of the people likely to use the method will not find it comfortable to use. Therefore, we took a different approach, using the FMCK method. Though applying finite mixture analysis and likelihood estimation as in FMC, the FMCK method approaches the goal from a different direction by means of  $k$ -mean cluster analysis for a priori statistical modeling of component distributions. This modification enables FMCK to be implemented using readily available statistical programs with  $k$ -mean cluster analysis, such as STATISTICA, MINITAB, or SYSTAT,

available on both PC and Macintosh platforms.

Computationally, both  $k$ -mean cluster analysis and maximum likelihood estimation for finite mixture analysis are iterative procedures that attempt to classify observations into groups that are as distinct as possible. Maximum likelihood estimation classifies observations into groups so that the likelihood statistic  $L$  of the mixture model under investigation is maximized. The  $k$ -mean cluster analysis is like an analysis of variance (ANOVA) "in reverse". The procedure starts with  $k$  random groups (clusters) as arbitrarily set by the researcher and then moves objects between those groups with the goal of (1) minimizing variability within groups and (2) maximizing variability between groups (Statsoft, 1995). Since the likelihood value  $L$  is needed to calculate the AIC, the  $L$  value of the mixture model under investigation is calculated using the resulting group parameters after the cluster analysis is completed. The resulting  $L$  value should be the same or very close to what is expected from maximum likelihood analysis. Empirical comparisons over a range of datasets showed that FMC and FMCK analysis give very similar results (Strait, personal commun.).

In the following, we provide a brief description of the FMCK. For references on statistical details, Akaike (1974), Everit and Hand (1981), Everit (1985), McLachlan and Basford (1988), and, in particular, Pearson et al. (1992) and Strait et al. (1996) should be consulted.

First, the measurement ratios were transformed into logarithmic values. The values for each character were then divided into one, two, three, and four groups using  $k$ -mean cluster analysis as implemented in the Cluster Analysis module of STATISTICA version 5.1. The distribution parameters (i.e., mixing proportion, mean, and variance) were calculated for each component distribution (group) of each mixture model (e.g., four-component mixture).

Small programs were written in STATISTICA BASIC language to calculate the density function of each of the mixture models of a particular dataset (character measurements) using the equations provided

by Pearson et al. (1992) and Strait et al. (1996). For each model,  $L$  was calculated as the product of mixture density functions  $f(\chi)$ , and AIC, Akaike Information Criterion, was then obtained through the equation  $AIC = -2(\ln L) + 2K$ , where  $K$  is the number of independent parameters estimated by the mixture model (Akaike, 1974; Pearson et al., 1992; Strait et al., 1996). The mixture model with the lowest AIC was favored. Characters for which the one-group model was favored were abandoned because they were uninformative about phylogenetic relationship.

Once a mixture model was decided on, the Discriminant Analysis module of STATISTICA was used to calculate posterior probabilities in order to correct possible misclassifications resulting from  $k$ -mean cluster analysis. Based on these results, raw measurements were classified into discrete states for use in phylogenetic analysis, and the states were ordered according to the means of the associated component distributions. The states of the quantitative characters were described using group means, standard deviations, and maximum and minimum values (appendix 3).  $G$ -tests (cf. Pearson et al., 1992; Strait et al., 1996) were not carried out, since the distribution hypotheses with the lowest AIC would be favored anyway.

#### CLADISTIC ANALYSIS

PAUP version 3.1.1 (Swofford, 1993) and PAUP version 4.0 betas (d54 or later) (Swofford, 1997–1998) were used for the phylogenetic analysis. Because of the considerable amount of time and resources needed to carry out phylogenetic analysis of the large data matrix, two strategies were adopted after several “pilot” heuristic searches were finished, each employing one random addition sequence followed by tree bisection-reconnection swapping. For both strategies, heuristic search was used. In the first strategy, more intense searching was used for each random addition sequence, using the same options as in the pilot search except that no more than 10,000 trees longer or equal to the length of 1,215 were saved. The chucking option was used because the length

of the shortest trees found in the 10 completed runs of pilot searches were 1,214 steps, and swapping on more trees longer than 1,214 steps was impractical. In the second strategy, or “shortcut search”, a less intensive search was first performed (options: 1,000 random addition sequences, each followed by nearest neighbor interchange swapping, saving no more than one tree equal to or longer than 1,220 steps), and the resulting single tree was subjected to bisection-reconnection swapping. In total, 192 and 50 runs were carried out using the first and the second strategies, respectively. The shortest trees found in each run were saved in a separate file temporarily, and data on the number and the length of trees of the resulting islands were collected. Only the islands of trees of the shortest length were retained.

#### BIOGEOGRAPHICAL ANALYSIS

The biogeographical study covers the whole subfamily of Mayrellinae. *Kiefferiella* is the sister group to the rest of the Mayrellinae, and all known species of the genus are from the same biogeographical region. *Kiefferiella* was therefore included as one single terminal unit in the biogeographical analysis.

The historical biogeography was reconstructed with DIVA 1.1a (Ronquist, 1996) according to the dispersal-vicariance optimization method proposed by Ronquist (1997). Dispersal-vicariance analysis reconstructs the ancestral distribution in a given phylogeny without any prior assumptions about the form of area relationships. Speciation is assumed to subdivide the ranges of widespread species into vicariant components; the optimal ancestral distributions are those that minimize the number of implied dispersal and extinction events (Ronquist, 1997). The DIVA method differs from cladistic biogeography in that it allows nonhierarchical area relationships and is therefore particularly useful when reconstructing the distribution history of groups occurring in areas, such as the Northern Hemisphere, having a reticulate palaeogeographic history (Nordlander et al., 1996 and references therein; Sanmartin et al., 2001).



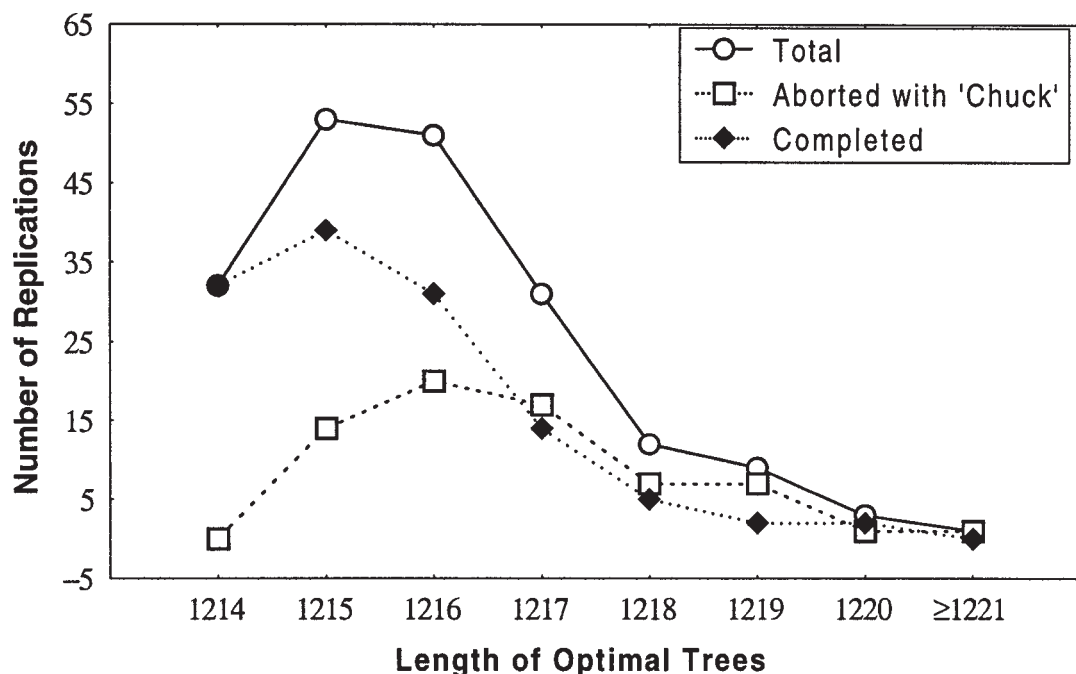


Fig. 10. Length distribution of the shortest trees resulting from 190 replications using the more intensive search strategy, involving random addition sequences and TBR swapping.

## CHARACTERS, PHYLOGENY, AND HISTORICAL BIOGEOGRAPHY

### CHARACTER ANALYSIS

One hundred thirty-two morphological characters were identified and coded as being potentially informative about relationships among species of *Paramblynotus* and *Decellea* (appendices 3, 4). These characters were separated into four categories: main structures (1–76), surface sculpture and pubescence (77–110), colors (111–123), and quantitative characters (124–132). The 8 quantitative characters were identified among 23 as being useful for cladistic analysis using the FMCK coding method (appendix 2). The mean retention index (RI) for the quantitative characters was 0.73, which was not distinctly lower than that for the other characters (main structures 0.82, sculpture and pubescence 0.75, and colors 0.81).

### PHYLOGENETIC ANALYSIS

A total of 252 replications of the heuristic search were completed. An island of trees of

the shortest length was found in 16.27% for all the searches. For the more intensive and the shortcut searches, the results were 16.67% (32/192) and 14% (7/50), respectively. The two options were thus rather similar in terms of efficiency in finding the shortest trees.

More than 70% of all the searches ended on islands falling within one to two steps from the shortest trees found. In addition, the “chuck” option caused abortion of 35.8% of the searches using the more intensive search strategy (fig. 10), and some of these aborted searches might eventually have ended on one of the islands of shortest trees. Thus, a very high proportion of the searches starting with random addition sequences ended on trees of the same length, indicating that it is unlikely that shorter trees exist for this dataset.

### PHYLOGENETIC RELATIONSHIPS

The sum of minimum lengths over all characters in the data matrix (appendix 4) was 247, and the maximum was 3,163. The heuristic searches resulted in 10 islands of shortest trees of the length of 1,214 steps

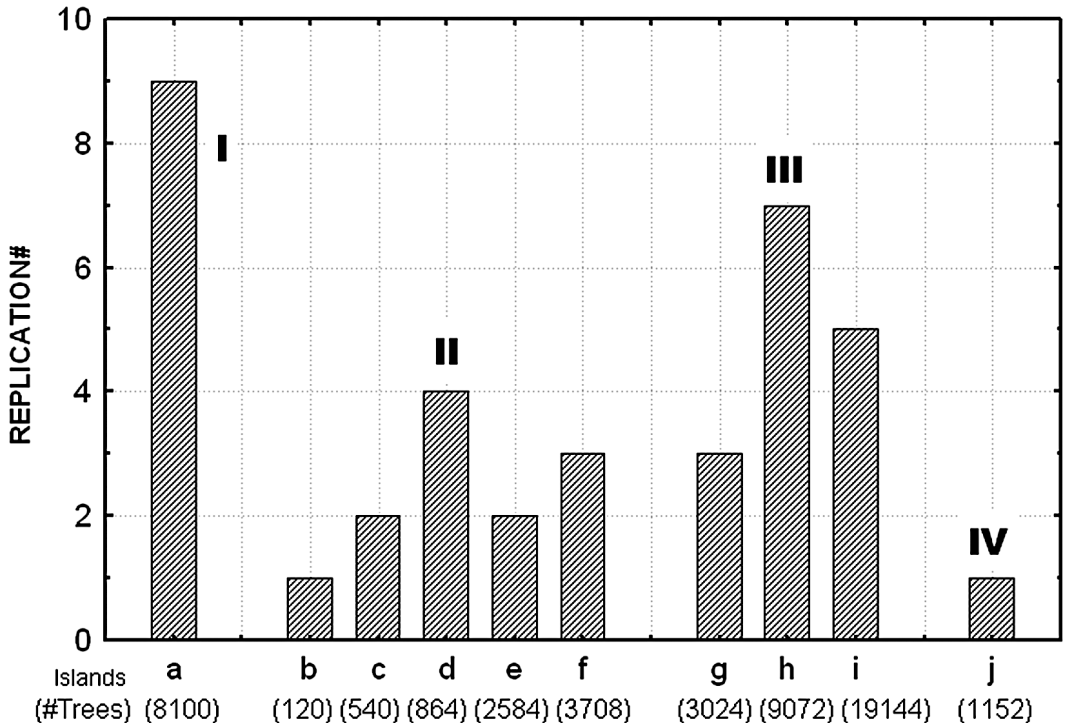


Fig. 11. Types and frequency of islands of shortest trees. The height of a column represents the number of replications found for that island of shortest trees. The islands of shortest trees are grouped into four types (I–IV) based on basal topology of the trees.

(fig. 11). The islands can be classified into four types according to their basal branching (figs. 11, 13a–d).

The strict consensus tree over all the islands of shortest trees (fig. 12) supports the monophyly of *Paramblynotus* + *Decellea* as suggested by Ronquist (1995a). However, *Decellea* is nested within *Paramblynotus* in the clade comprising the African *Paramblynotus* species (figs. 12, 14, 15). The only synapomorphy that unambiguously supported *Paramblynotus* sensu Ronquist was the abdominal sterna 4–6 of the female being entirely covered by the abdominal sternum 3. This synapomorphy no longer held when the newly discovered *P. mixtus* from Kenya was included in the present study. The new species resembles the other species of *Paramblynotus* with respect to this particular character and some others, but it also shares several derived character states with *Decellea*. The monophyly of the group consisting of (*Decellea*, *P. mixtus*) and the remaining African species of *Paramblynotus* is strongly

supported in terms of decay index (fig. 12). *Decellea*, which was reestablished as a separate genus by Ronquist (1995a), is therefore synonymized here, again, with *Paramblynotus*.

Most of the shortest trees strongly support a sister relationship between the North American species *P. virginianus* and the rest of the genus. Six of the islands (type I and II) consistently postulate this relationship (figs. 10, 13a, b), as do a majority (67%) of trees in three other islands of shortest trees (type III) (figs. 11, 13c). In all, this relationship is supported by 90% of the islands of shortest trees (fig. 10) and 77% of all the shortest trees (fig. 14). Only one island (type IV) does not support the sister relationship at all (figs. 10, 13d). Since the number of trees of this island (1,152) makes up only 2.4% of all the shortest trees, the aberrant phylogenetic relationship postulated by this island seems less likely.

Previously, Ronquist (1995a) had tentatively separated the species of *Paramblynotus*

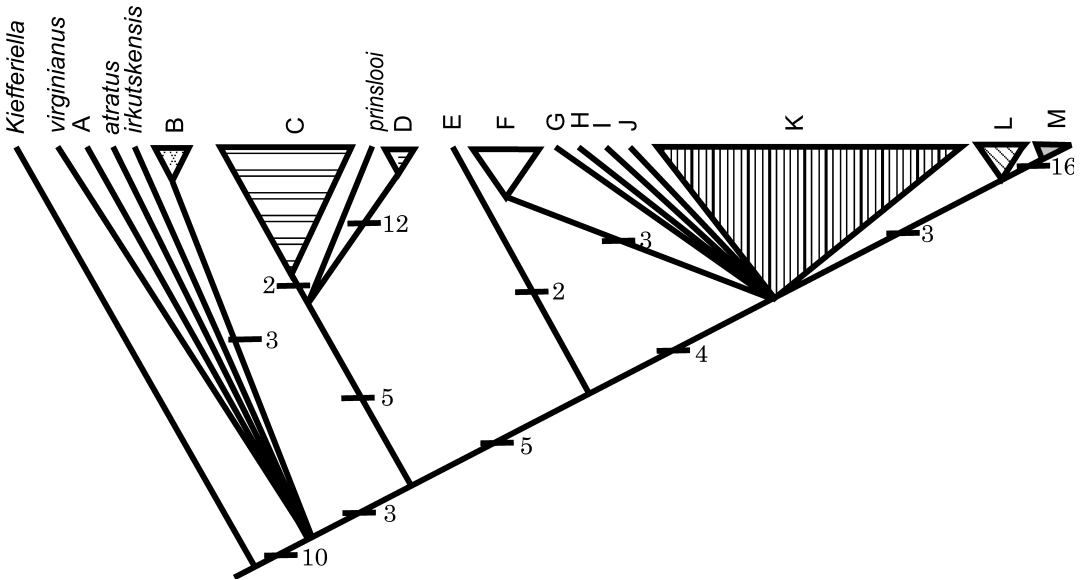


Fig. 12. Strict consensus tree over all islands of shortest trees. Terminals labeled with a species name are single species, and terminals with a capital letter represent two species. Triangles at the ends of internodes and on internodes represent monophyletic clades with three or more species and polytomy, respectively. The size of the triangles roughly reflects the number of species involved. Species involved in these clades or polytomies are listed in appendix 1. The monophyletic clades and polytomies are represented by the same capital letters in figures 5–7 and 9–12.

into supposedly monophyletic species groups, and his groupings are partly supported by the present study. However, there are also some major differences necessitating changes. Based on the phylogeny of the present study (fig. 14), we divide the genus into seven monophyletic species groups, that is, the *virginianus*, *scaber*, *yangambiculus*, *nigricornis*, *apeosus*, *ruficollis*, and *punctulatus* groups.

A sister relationship between the only North American species *P. virginianus* and the remaining species of the genus is supported by a majority (77%) of all shortest trees, and thus a monotypic *virginianus* group is created to accommodate *P. virginianus*. The *scaber* group, consisting primarily of species from the Far East, is the next most basal clade of *Paramblynotus*. This group is basically the same as Ronquist (1995a) proposed. The monophyly of the *scaber* group is supported by 73% of the shortest trees. The monophyly of the remaining species of the genus, as proposed by Ronquist (1995a), is supported by the present analysis (100% of the shortest trees). Other Ronquist (1995a) groups that are also supported by the present

analysis include the *borneanus* group (64%), the *punctulatus* group (except three outliers) (72%), the *zonatus* group (100%), the *trisetosus* group (100%), and the suggested clade comprising the *zonatus* and *ruficollis* groups (100%).

As discussed above, the African species form a monophyletic clade in the present analysis. This means that the *borneanus*, *punctulatus*, and *trisetosus* groups, suggested by Ronquist (1995a) to be closely related, do not form a monophyletic group. Species of *Decellea* sensu Ronquist forms the well-defined, monophyletic *yangambiculus* group, which is the sister group to all other species within the African clade. Although all the African species could have been combined in a single species group, the *yangambiculus* group is separated here because they are morphologically distinct. Its sister clade includes all the species of Ronquist's (1995a) groups *trisetosus* and *nigricornis*, and an additional newly discovered species, *P. prinslooii*, at the base of the clade. The *nigricornis* group sensu Ronquist consists of two monophyletic clades that are paraphy-

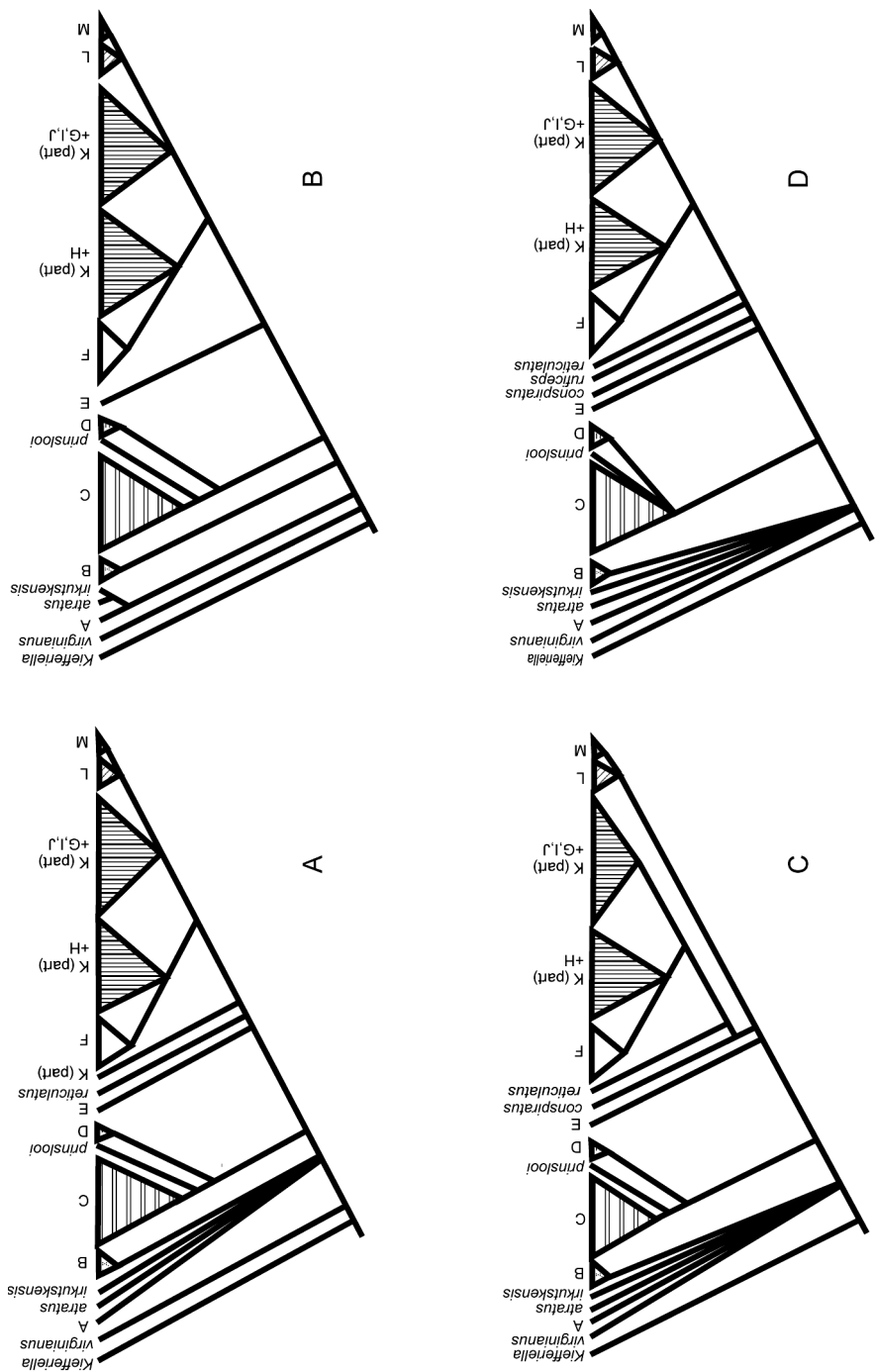


Fig. 13. Strict consensus tree of the shortest tree island types: A, type I; B, type II; C, type III; and D, type IV.

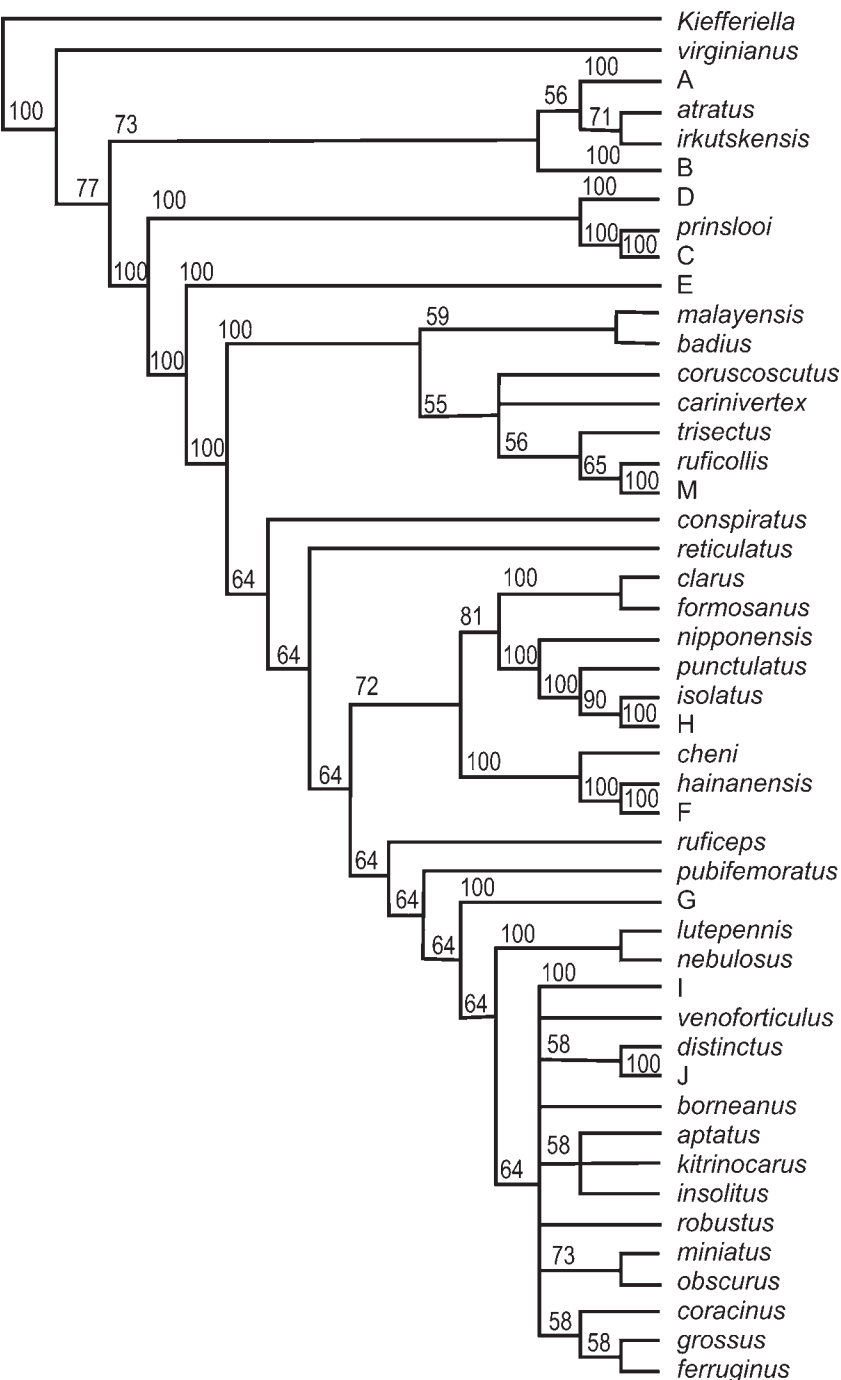


Fig. 14. Majority-rule consensus tree over all shortest trees. Above each branch is the percentage with which that particular branch occurred among the shortest trees. Terminals represented by a capital letter are those resolved in the strict consensus tree (see appendix 1 for information on taxa included in each collapsed clade and polytomy).

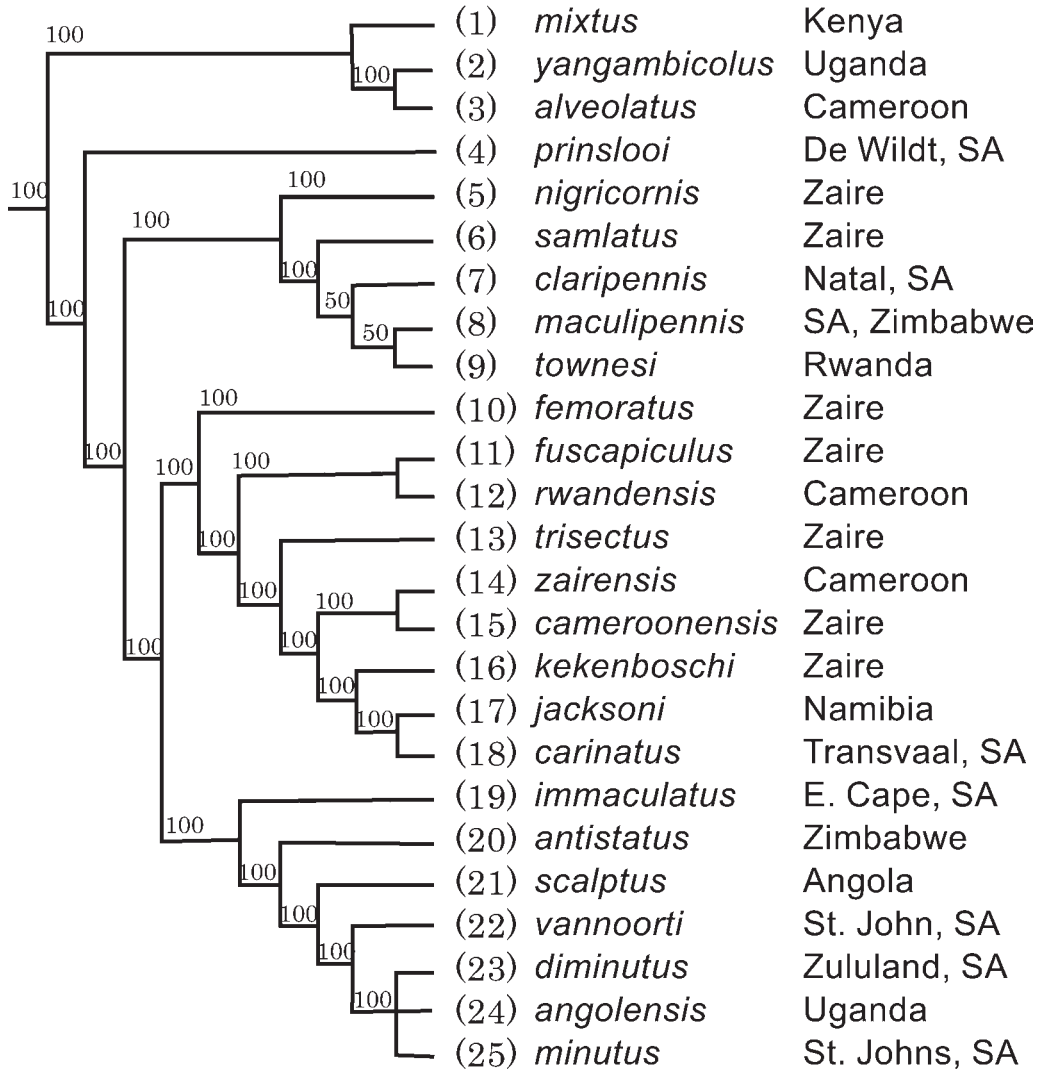


Fig. 15. Strict consensus tree over all islands of the shortest trees: expansion of the clade of African species with distribution records. Numbers within parenthesis following each species name represent the species on the distribution map (fig. 13).

letic with respect to his *trisetosus* group (fig. 15). To avoid unnecessary multiplication of species groups, we propose to group all of the lineages in the sister group of *Decellea* into a more widely circumscribed *trisetosus* species group.

In the new scheme, two very distinct species from the Far East form the small *apeosus* group, while its sister clade is subdivided into two groups, the *ruficollis* and the *punctulatus* groups. The species groups *ruficollis* and *zonatus* sensu Ronquist

make up the *ruficollis* group of the present study. Although the *zonatus* group sensu Ronquist still holds as a monophyletic clade in the present phylogeny, it nests within the *ruficollis* group and we prefer letting the *zonatus* species be subsumed into the *ruficollis* group over splitting the relatively few species in the latter group.

Finally, species of the groups *borneanus* and *punctulatus* sensu Ronquist are united here into the large, yet morphologically homogeneous and geographically restricted

*punctulatus* group. Although most of the species of the *punctulatus* group sensu lato can be assigned into the two groups defined by Ronquist, the few species that cannot be so classified will require the creation of several new monotypic groups if Ronquist's scheme is followed. This would make the groupings less meaningful. Moreover, the relationships among the species of this clade are generally uncertain, and finally the species of the clade are all restricted to the Oriental region. Therefore, in the light of the present analysis, we consider it appropriate to include all the species of this clade into a single species group.

#### BIOGEOGRAPHY

The historical biogeography of the Mayrellinae was analyzed in terms of five main distribution areas: Nearctic, Neotropical, eastern Palearctic, Oriental, and Ethiopian. Because the only two species of *Paramblynotus* that occur in New Guinea are deeply nested within a clade otherwise consisting of Oriental species, and one of the two New Guinean species occurs in the Oriental region, they have apparently dispersed there from the Oriental region rather recently. New Guinea was therefore included in the Oriental region in the biogeographical analysis. Clades with all included species occurring in the same distribution area were treated as single terminal units. Majority rule consensus trees, instead of strict consensus trees, were used as the basis for DIVA analysis, because the resolution of the latter was rather low and DIVA 1.1a does not allow polytomy. The analyses were performed based on the majority rule consensus tree of three of the four types of islands (i.e., type I, II, III). The topology of the majority rule consensus tree over all shortest trees was the same for all three island types when clades including species from the same geographical area were collapsed as terminal entries. The fourth type of island was not taken into account because the phylogenetic relationship depicted by this island, as discussed above, seems less likely.

Initial, exact searches with DIVA based on type I and III islands, respectively, resulted in optimal reconstructions that require four

dispersals, whereas the reconstructions based on type II islands required five dispersals. Depending on the range of the assumed ancestral distributions of the subfamily Mayrellinae and the genus *Paramblynotus*, the reconstructions can be classified into two categories. Most of the reconstructions suggest a widespread ancestral distribution of the Mayrellinae and of *Paramblynotus* in both the Gondwanian and Laurasian areas (see fig. 18). Two of the four reconstructions based on type II island trees suggest a narrow ancestral distribution of the Mayrellinae and of *Paramblynotus* in one or two areas within Laurasia.

Because a widespread ancestral distribution for either the Mayrellinae or *Paramblynotus* is, as discussed below, unlikely, more DIVA searches were performed using the OPTIMIZE option of MAXAREAS = 3. This constrained the distribution areas of any single node to no more than three areas, that is, the maximum number of defined areas within Laurasia. The constraint only had a direct effect on the nodes representing the ancestor of the Mayrellinae and the ancestor of *Paramblynotus* because no other nodes had previously been postulated to have a distribution in more than three areas. The results of the new search based on type II island trees did not differ from the earlier ones, except that the widespread ancestral distribution alternatives were excluded. All the resulting optimal reconstructions of searches based on trees from other island types required five dispersals, which is the same number as that required by reconstructions based on type II island trees. The reconstruction alternatives (based on type I and III islands) that still suggested an ancestral distribution in both Gondwana and Laurasia were subsequently excluded. This resulted in eight optimal reconstruction alternatives for type I and III island trees and two for type II island trees. The reconstructions represent three categories depending on the number of assumed ancestral distribution areas of the Mayrellinae. The three categories of reconstructions suggest the ancestral distribution of the Mayrellinae to be Nearctic, Nearctic + East Palearctic, and Nearctic + East Palearctic + Oriental, respectively. Figures 12–14 summarize the reconstruction



alternatives based on the majority consensus tree of type III island trees. The reconstructions based on type I and II island trees correspond to these reconstructions with only minor differences.

To distinguish the most likely scenario among the competing alternatives, it is necessary to take into account the paleoenvironmental evidence as well as the current distribution pattern.

The latest geological time when Africa was united with the northern land mass of Laurasia was in the Late Triassic (ca. 235–210 Ma) (Axelrod and Raven, 1978; Wing and Sues, 1992). However, the biotas of Gondwana and Laurasia were not biogeographically separated by impassable dispersal barriers until the Middle to early Late Jurassic (180–145 Ma). This is because the rifting of Pangaea was a slow process that continued through the Early Jurassic, and dispersal of major continental areas and separation by ocean basins probably did not occur until then (Wing and Sues, 1992, and references therein). On the other hand, the Triassic biotas were remarkably provincial, and they are commonly divided into northern (Laurasian) and southern (Gondwanan) realms (Wing and Sues, 1992, and references therein). It seems likely that an assumed widespread ancestor of Mayrellinae and *Paramblynotus*, which had been distributed so widely across Pangaea, had also colonized and left some descendants in the other southern continents besides Africa. However, the only Southern Hemisphere elements of the Mayrellinae outside Africa are a few *Paramblynotus* species from Central and South America, which are apparently rather young and have dispersed there recently (Ronquist, 1995a; figs. 12, 16–19). Moreover, species of *Kiefferiella* and *Paramblynotus* are only known to be associated with angiosperm trees, which were generally lacking in the earliest Cretaceous (Doyle and Donoghue, 1986; Wing and Sue, 1992; Crane et al., 1995). Thus, the Mayrellinae (*Kiefferiella* and *Paramblynotus*) are unlikely to have originated in a biogeographically united Pangaea before the Middle to early Late Jurassic. Therefore, a widespread ancestral distribution of the Mayrellinae and/or *Paramblynotus* is not plausible.

Ronquist (1995a) indicated an ancestral distribution of *Paramblynotus* somewhat narrower than the previous scenario of a widespread ancestral distribution. According to Ronquist, the split between *Kiefferiella* and the stem species of *Decellea* + *Paramblynotus* (i.e., the genus *Paramblynotus* sensu lato) might correlate with the separation of North America from western Africa in the middle Jurassic (ca. 180 Ma). That scenario is not supported by the DIVA analysis of the present study because it postulates the origination of *Paramblynotus* either in Africa or in Gondwanaland including Africa. With the changed placement of *Decellea*, deeply nested within *Paramblynotus*, Africa is not likely to be part of the ancestral area of *Paramblynotus*. Instead, it appears that the Mayrellinae originally were in the Holarctic or the whole Northern Hemisphere, and that some of the basal splits in the subfamily were due to vicariance between elements of the Nearctic and East Palearctic or East Palearctic + Oriental. These early vicariance events could have resulted from biotic exchanges between the Nearctic and East Palearctic either by way of Europe or by way of the Bering land bridge.

The European route appears less likely than the Bering route. Many of the lineages close to the base of the phylogeny of the Mayrellinae are restricted to or are at least most diverse in the eastern Palearctic. In contrast, no species of the subfamily has ever been found in Europe. The thermophilic elements of the boreotropical flora and the succeeding mixed mesophytic forest, with which the early Mayrellinae were probably associated, extended to high latitudes of the Northern Hemisphere in the late Cretaceous and in the Tertiary when the global climate was warmer and more equitable. It is generally accepted that the adverse effects of the advancing Pleistocene glaciers (Wolfe, 1978, 1985; Tiffney, 1985) on these elements were more pronounced in Europe than in other northern continents. However, remnants of these thermophilic elements survived in the so-called Tertiary refugia, particularly in topographically complex areas such as the Balkans and Caucasus (Tiffney, 1985). Nonetheless, no Mayrellinae is known from these areas.



Another possibility is that the Mayrellinae might have dispersed along the coasts of the Tethy Seaway during the early to middle Eocene. The Tethy Seaway was an important avenue of dispersal for the boreotropical flora across Eurasia, connecting eastern North America through western Europe to southeastern Asia (Tiffney, 1985). Paleontological evidence reveals an Indomalaysian affinity of early Eocene to Oligocene floras of eastern Europe, Egypt, and England (London Clay) (Tiffney, 1985; Taylor, 1990, and references therein). However, the existence of basal lineages of the Mayrellinae and *Paramblynotus* in the eastern Palearctic but not in the southeastern Asia indicates that the Tethy Seaway was not the route of dispersal in this case.

That the Bering land bridge is more likely to be the dispersal route for Mayrellinae between North America and eastern Palearctic/oriental is also supported by biogeographical reconstructions based on paleoclimatology and paleogeology. The Holarctic has been split and reconnected by various barriers at different locations since the early breakup of Pangaea in the Late Jurassic (e.g., Hallam, 1981; McKenna, 1983; Briggs, 1987). These events have profoundly affected the evolution of organisms of the Northern Hemisphere (McKenna, 1983) as well as the present distribution patterns of these organisms. These barriers are (1) the Turgai Sea, (2) the North American mid-continental seaway, (3) the northern Atlantic Ocean, and (4) the Bering area (e.g., Noonan, 1986; Briggs, 1987; Engghoff, 1995).

The Turgai Sea was formed in the Middle Jurassic (160 Ma) and separated Asia from Europe (Hallam, 1981; Briggs, 1987). Species of *Kiefferiella* and *Paramblynotus* are only known to be associated with angiosperm trees. Although the angiosperms could have diverged before the Cretaceous (145 Ma) (Doyle and Donoghue, 1986; Crane et al., 1995), and the earliest angiosperm fossils are from the Valanginian (140–130 Ma) (Crane et al., 1995), angiosperms were generally lacking in the early Cretaceous (Wing and Sue, 1992). Therefore, early connections between North American and Asian elements of the Mayrellinae through Europe should have occurred after the formation of the

Turgai Sea. By the Oligocene (30 Ma), when the Turgai Sea retreated (Hallam, 1981; Briggs, 1987), no land connection existed between Europe and North America (Hallam, 1981; Scrivastava and Tapscott, 1986). Therefore, the early connections between eastern Asian and North American elements of the Mayrellinae are more likely to have been by way of the Bering land bridge than by way of Europe.

In the northern Pacific, the Bering land bridge connected Asia and North America continuously since at least the Late Cretaceous (Briggs, 1987), possibly earlier (Hallam, 1981; Hickey, 1981). However, the Bering area as a route of biotic exchanges was severely constrained by climate and daylight length because the area was then situated closer to the North Pole than it is today, and it has since slowly and gradually moved southward to its current position (McKenna, 1983). Nonetheless, the global climates were much warmer and equitable during the late Cretaceous and early to middle Tertiary than they are today (Wolfe, 1978, 1980, 1987; Tiffney, 1985; Wing and Sues, 1992). Climates became particularly favorable during the early Tertiary warm intervals, when the Bering land bridge was primarily covered with broadleaved, deciduous forest, perhaps with a thin southern fringe of evergreen, megathermal communities (Tiffney, 1985; Wolfe, 1985). This definitely made it possible for the early Mayrellinae to disperse between the two sides of the land bridge.

Within the historical framework laid out above, plausible reconstructions of the early biogeography of the Mayrellinae based on the three competing alternative hypotheses can be presented as outlined below.

The first two reconstructions (figs. 16, 17) suggest that the ancestral species of Mayrellinae was distributed both in the Nearctic and in East Asia, and it was divided into disjunct populations when a geographical barrier separated these two regions, giving rise to the genera *Paramblynotus* and *Kiefferiella*. The stem species of *Paramblynotus* expanded its distribution by dispersal into the Nearctic and became split by a subsequent vicariance event, leading to the origination of the *P. virginianus* clade and the clade

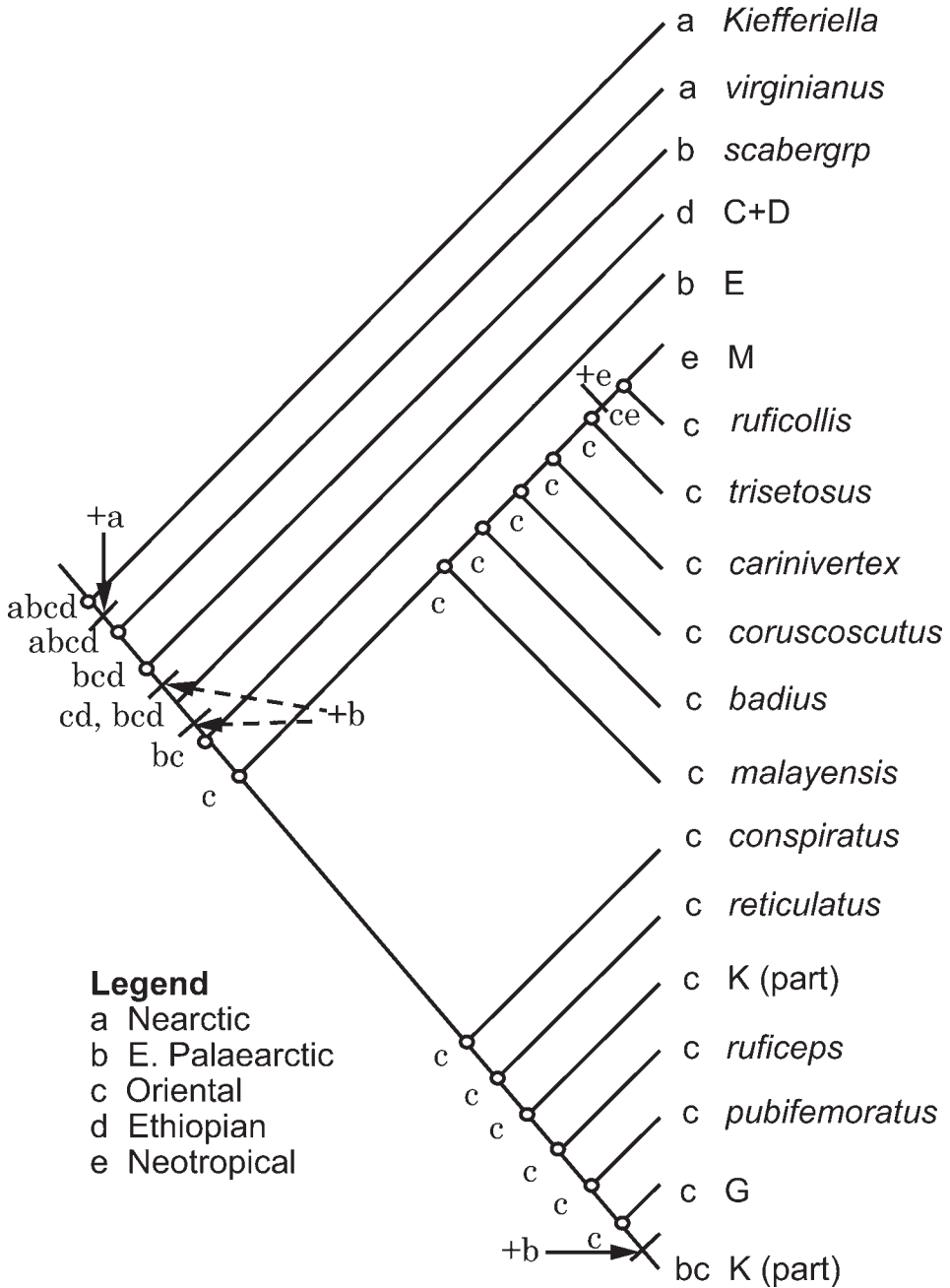


Fig. 16. Summary of the DIVA reconstructions of historical biogeography based on the majority-rule consensus tree of type III islands that postulate a widespread ancestor of the Mayrellinae distributed in both Gondwana and Laurasia. With clades collapsed when the species included are endemic to a single biogeographical area as defined in the present study, the majority-consensus tree over all shortest trees is identical to that of type III islands. Results based on type I and type II islands are similar to the one presented here with minor differences. Dispersal events are indicated on the branches. Arrows with dashed tails indicate alternative positions of dispersal events. These explanations also apply to figures 10–12, except as stated.

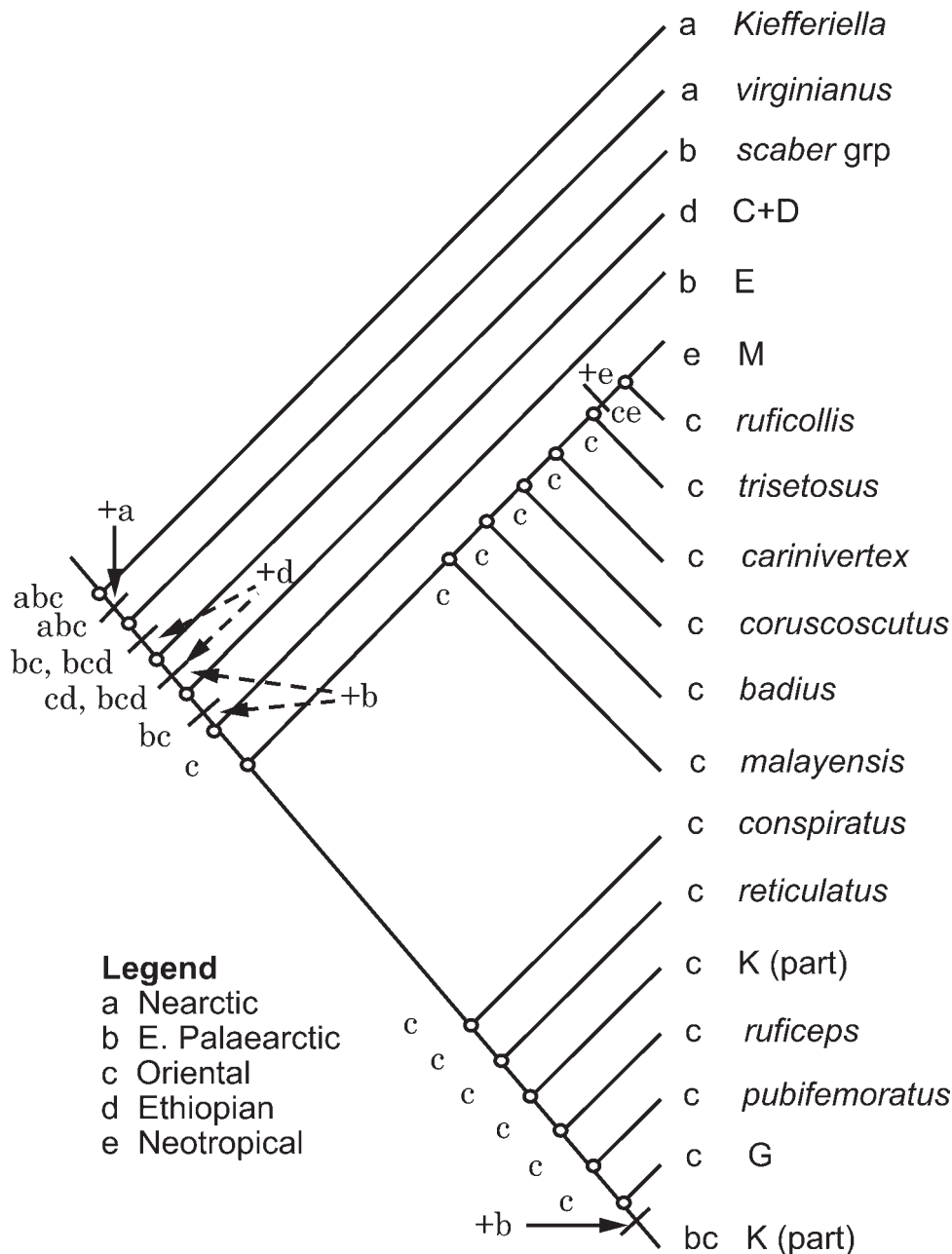


Fig. 17. Summary of the DIVA reconstructions of historical biogeography that postulate an ancestor of the Mayrellinae with a distribution limited to the Nearctic, eastern Palearctic, and Oriental region. Based on the majority-rule consensus tree of type III islands.

comprising the rest of *Paramblynotus*. The ancestral species of the Mayrellinae might have appeared first in either East Asia or the Nearctic and have expanded its distribution across the Bering land bridge during the

warm intervals from the late Cretaceous to the middle Tertiary. Rather than being the result of a vicariance event separating East Asia and Nearctic as indicated by the DIVA analysis, the divergence between *Parambly-*

*notus* and *Kiefferiella* may have been caused by the formation of the Rocky Mountains in western North America. The Rocky Mountains were mainly formed during the latest Paleocene to early Eocene (ca. 56–40 Ma) (Leopold and MacGinitie, 1972), and they created direct topographic barriers to plant movement between southwestern North America and the rest of the then continuous land mass Asiamerica (Briggs, 1987).

The endemic distribution of *Kiefferiella* in western and southwestern North America (Idaho, California, and Texas) is apparently also due to the formation of the Rocky Mountains, which caused the interior of North America to become increasingly drier. The remnants of the earlier, moisture-adapted boreotropical flora were largely confined to the western slopes or retreated southward (Leopold and MacGinitie, 1972; Tiffney, 1985). *Kiefferiella* might have been associated with the earlier boreotropical flora and represents a relic taxon that has retreated to the south. The fossil species *K. connexiva* from Upper Eocene beds in Colorado (34.1 Ma) (Ronquist, 1995a) indicates that the genus was once more widespread in interior North America than it is today.

The disjunction within *Paramblynotus* between the Nearctic and East Asia, that is, between *P. virginianus* and the rest of the genus, probably resulted from the Terminal Eocene Event (34–33 Ma), when the global temperature dropped drastically (Wolfe, 1978, 1980, 1987; Potts and Behrensmeyer, 1992) and the climatic seasonality increased (Wolfe 1978, 1980, Tiffney, 1985). This disrupted the warm-temperate to subtropical broadleaved evergreen forests that had stretched from Asia to North America and replaced them in the Bering area with a cool-temperate deciduous forest (Wolfe, 1980; Tiffney, 1985). Following the Terminal Eocene Event, the climate continued to deteriorate with short, warmer intervals in the Oligocene and Miocene, and this trend of climate deterioration gradually led to the extreme cold of the Pleistocene (Wolfe, 1978; Tiffney, 1985). Thus, suitable habitats for hardwood-associated organisms like *Paramblynotus* were generally lacking in the Bering area after the Terminal Eocene Event (Nordlander et al., 1996, and references

therein), making dispersal of such organisms across the land bridge difficult.

According to the third alternative hypothesis (fig. 18), the stem species of the Mayrellinae was limited to the Nearctic. After a vicariance event within the Nearctic, the ancestral species of *Paramblynotus* expanded its distribution by dispersal into the eastern Palearctic, and a subsequent vicariance event gave rise to *P. virginianus* and the clade comprising the rest of *Paramblynotus*. In this scenario, the formation of the Mid-continental Seaway in North America in the mid-Albian (ca. 100 Ma) (Hallam, 1981; Crabtree, 1987) might correlate with the splitting between *Paramblynotus* and *Kiefferiella*. The retreat of the seaway and reconnection of the two parts of the continent shortly before the end of the Cretaceous (70 Ma) (Hallam, 1981) allowed dispersal of *Paramblynotus* from eastern North America to the eastern Palearctic by way of Beringia. Alternatively, as suggested in the previous scenario, the event was caused by the formation of the Rocky Mountains during latest Paleocene to early Eocene, and the newly evolved *Paramblynotus* then dispersed to eastern Palearctic by way of Beringia. In either case, the dispersal, as suggested earlier, most likely took place before the Terminal Eocene Event.

The genus *Paramblynotus* was probably widely distributed in East Asia, and its species may have differentiated in response to the differentiation of the forest vegetations of the region into temperate elements of the north and subtropical to tropical elements in the south. Currently, the terrestrial ecosystems in continental East Asia stretch from above the polar circle well into the tropics. This large expanse of continuous inland has existed since the latest Triassic (Metcalf, 1988). Within this region, there has been no major physical barrier impeding the migration of plants (Latham and Ricklefs, 1993) or associated organisms, such as *Paramblynotus*. The cooling trend since the Oligocene led to the selection of cool-adapted taxa from the boreotropical flora and their addition to the mixed mesophytic forest of the middle latitudes (Wolfe, 1978; Tiffney, 1985). The continued cooling of climates of later times, which gradually led to the extreme cold of the

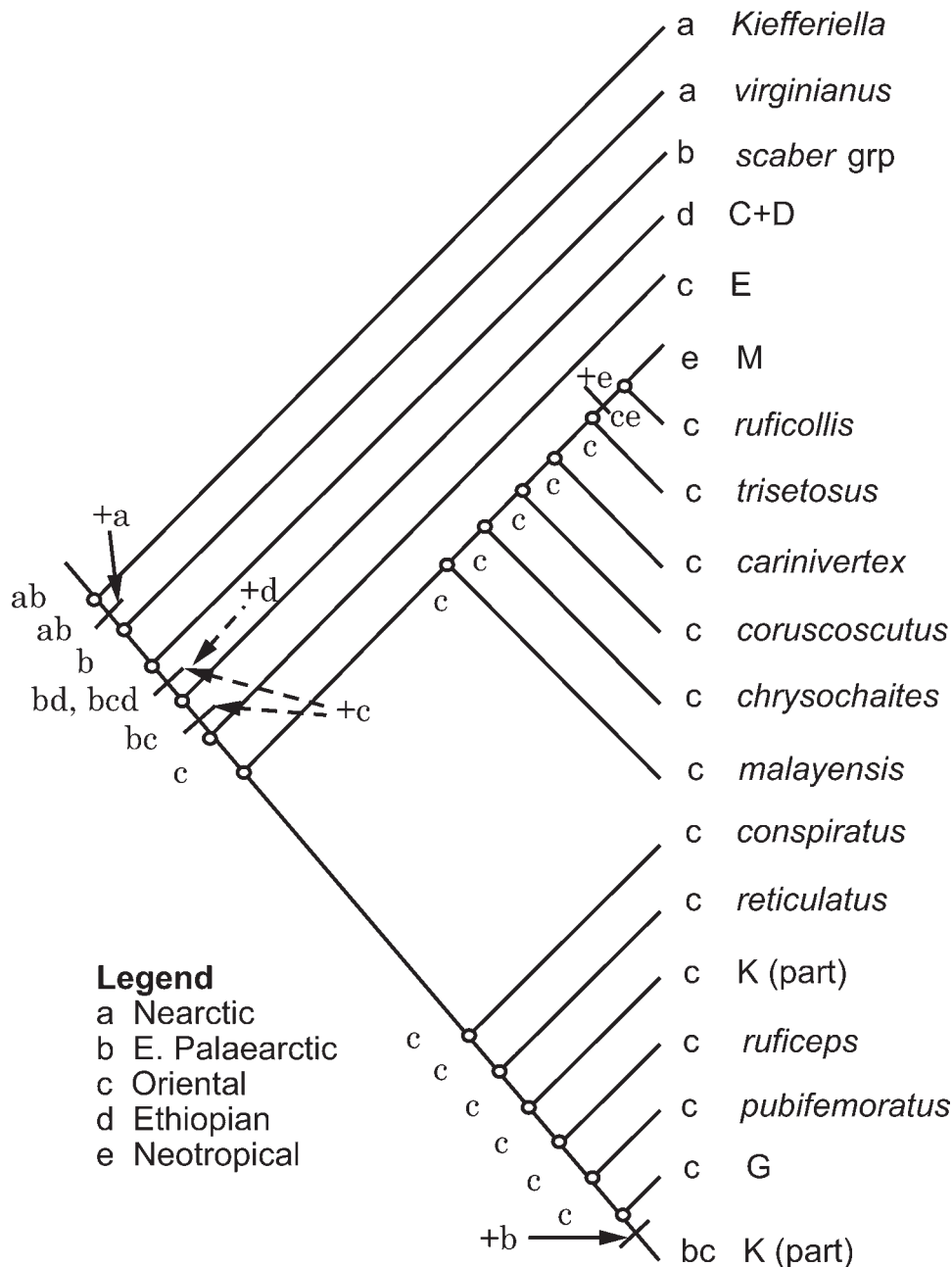


Fig. 18. Summary of the DIVA reconstructions of historical biogeography that postulate an ancestor of the Mayrellinae with a distribution limited to the Nearctic and the eastern Palearctic. Based on the majority-rule consensus tree of type III islands.

Pleistocene, resulted in thermal segregation of the descendants of the boreotropical flora. The evergreen and cold-intolerant elements of the widespread Paleogene forests retreated

to protected southerly refugia or became extinct. The more recently segregated warm-temperate forests were likewise affected, but to a lesser extent (Tiffney, 1985). The effect of

this floral segregation on *Paramblynotus* was a division of the distribution of the genus in East Asia, with the *scaber* group occurring in the eastern Palearctic and its sister clade, excluding the African species, in the Oriental region.

In comparison with the poor representation of *Paramblynotus* in eastern North America with only one species, the genus is represented by 15 species in the eastern part of continental Asia. Similar asymmetric diversification patterns also occur in other taxa with eastern North America and eastern Asia disjunction, including plants (Li, 1952; Latham and Ricklefs, 1993; Qiu et al., 1995; Wen and Zimmer, 1996; Wen et al., 1996) as well as insects (Tangelder, 1988, Nordlander et al., 1996), therefore requiring a general explanation. It has been recognized for a long time that the floras of eastern North America and eastern Asia share many taxa (reviewed by Graham, 1972; Boufford and Spongberg, 1983), primarily at the generic level (Li, 1952). It is also well known that the diversity of plant species of eastern Asia is three times as great as that of eastern North America (Tiffney, 1985; Latham and Ricklefs, 1993). This is at least partly due to the fact that the genera shared between the two regions tend to be more species-rich in eastern Asia (Li, 1952; Latham and Ricklefs, 1993). Tiffney (1985) suggested that the greater plant species diversity in eastern Asia occurred because this region had suffered less extinction in the Quaternary. If this applies to *Paramblynotus*, we would expect to find some of the Asian species near the base of the phylogenetic tree of the genus. Instead, the genus is disjunct at the very base of its phylogenetic tree, with all the Asian species belonging to a monophyletic clade. This distribution pattern strongly indicates considerable diversification in eastern Asia after the disjunction. Similar patterns have also been found in several phylogenetic studies on plants (Qiu et al., 1995; Wen and Zimmer, 1996; Wen et al., 1996). Therefore, the greater species diversity in eastern Asia cannot be solely explained as a refuge effect. Latham and Ricklefs (1993) observed that the existing continuous corridor of mesic forests connecting tropical and temperate latitudes in eastern Asia might have been continuously present since before

the Tertiary. Therefore, they suggested that colonization of temperate biomes in Asia from the tropics played an important role in the development of biotic diversity in the temperate forest communities there over long periods. This is apparently supported by the floral data from the two regions; genera with tropical affinity have distinctly more species in eastern Asia than in eastern North America (Li, 1952; Latham and Ricklefs, 1993). The genus *Paramblynotus* provides an additional example of this type. Similarly, colonization of tropical biomes by temperate elements has probably also occurred. Such biotic exchanges between the tropical and the temperate latitudes may have been augmented by the rather frequent climatic oscillations in the area since the Terminal Eocene Event, particularly in the late Neogene and the Quaternary (P. Wang, 1984; X. Wang, 1984). Several monophyletic, predominantly tropical Southeast Asian branches of *Paramblynotus* have apparently secondarily recolonized temperate eastern Asia. These include (*P. fretus*, *P. apeosus*), (*P. kosugii*, *P. fraxinii*), and certainly *P. shimenensis*, which is the only known northern subtropical continental species of a monophyletic group that is otherwise exclusively found on Southeast Asian islands (represented by F in figs. 12–14 and in appendix 1).

All the *Paramblynotus* species from tropical Southeast Asia constitute a monophyletic group, together with some species from other geographical regions (the *punctulatus* group; figs. 12, 14, and appendix 1). The high diversity of the genus in this part of the Oriental realm might be due to the sea level changes occurring there since the late Oligocene. According to Hutchison (1989, and references therein), the global sea levels remained high from the Palaeocene through Oligocene (65–30 Ma). By the late Oligocene (29 Ma), sea levels fell spectacularly to about 250 m below the present level, and from then onwards the sea levels progressively rose to about 220 m above the present level in the middle Miocene (13 Ma). The sea level then fell again to 220 m below the present level in late Upper Miocene (6.6 Ma), and rose once again to 140 m above the present level at the Miocene-Pliocene boundary (5.2 Ma). This was followed by several cycles of rapidly



fluctuating sea levels. These sea level fluctuations had relatively little effect on the land area of Africa or South America, but they drastically altered the land area configuration in Southeast Asia (Heaney, 1991). During times of low sea levels, Sumatra, Java, and Borneo were part of a peninsula projecting south from continental Asia (often referred to as Sundaland) (Morley and Flenley, 1987; Heaney, 1991), facilitating the dispersal of plants and animals. At times when sea levels became high, large land areas were inundated by water and topological elevations became isolated islands. The many cycles of sea level fluctuations since the late Oligocene presumably repeatedly caused plant and animal species to expand their distributions to newly connected areas and then become isolated in subpopulations, giving rise to new taxa. These cycles of land connection and island isolation have probably caused the high level of endemism and complicated phylogeny of the Southeast Asian and East Asian faunas of *Paramblynotus*, with sister relationships at different levels (figs. 12–14). The apical phylogenetic position, low phylogenetic resolution, and relatively high species diversity of the monophyletic clade comprising predominantly species from the two areas indicate rather recent and rapid diversification.

The few *Paramblynotus* species occurring in southern North America and South America are apparently the result of quite recent dispersal. They form a monophyletic clade nested within the diverse Southeast Asian and eastern Palearctic branch of *Paramblynotus* (figs. 12, 14). It is currently difficult to understand how they reached the New World. Probably a few colonizers accidentally dispersed from Southeast Asia, perhaps in a floating log, giving rise to the stem species of the group, which subsequently radiated.

The dispersal of the ancestral species of the African clade from the eastern Palearctic, as suggested by the biogeographic reconstructions (figs. 17–19), probably occurred rather early because of the basal position of this clade. The route of dispersal could have been either by way of Arabia or by way of the Iberian Peninsula. However, the latter was connected to Morocco in Africa only briefly during the Messinian (6.0–5.5 Ma) (Rögl and

Steininger, 1984; Rage, 1988), and the dispersal event probably occurred earlier.

Thus, the dispersal of *Paramblynotus* to Africa most plausibly took place by the Arabian Peninsula, more precisely during the latest Oligocene to earliest Miocene (26–23 Ma). Africa had been isolated from Laurasia since the Mesozoic rifting, and it only came into contact with Eurasia again when the Afro-Arabian landmass, due to its northward movement, collided with southern Central Asia in the middle Miocene (18–17 Ma) (Axelrod and Raven, 1978). However, a land bridge between Arabia and Iran had existed at least occasionally during the latest Oligocene and earliest Miocene (26–23 Ma), connecting Africa and Eurasia (Rögl and Steininger, 1984; Potts and Behrensmeyer, 1992). During the latter period, Arabia had scrubland communities with wetter vegetation along waters (Potts and Behrensmeyer, 1992), and northern Africa was covered by Savanna woodland with subtropical laurel forests along the northernmost part (Axelrod and Raven, 1978; Potts and Behrensmeyer, 1992). Subtropical savanna woodland had also developed in southern Eurasia during these periods (Axelrod and Raven, 1978). In the Northern Hemisphere, temperate deciduous forests replaced the previous boreotropical flora from the latest Oligocene to the mid-Miocene, and extended from eastern Asia (Xu, 1984a, 1984b) through western Siberia (Song et al., 1984; Wolfe, 1985) to Central Asia (Song et al., 1984; Zhilin, 1989). It appears very likely that the ancestral species of the African *Paramblynotus* dispersed in these extensive temperate broadleaved deciduous forests to reach Africa via the land bridge between Arabia and Iran during the latest Oligocene to earliest Miocene (26–23 Ma) (Potts and Behrensmeyer, 1992). Later dispersal is less likely because of the development of steppes and semidesert in Central Asia during the late Miocene (Song et al., 1984; X. Wang, 1984; Xu, 1984a, 1984b).

Since the initial dispersal, the ancestral species of the African group probably expanded its distribution along with the montane forest vegetation. The current records of the African species are almost exclusively from mountainous areas, mainly from local-

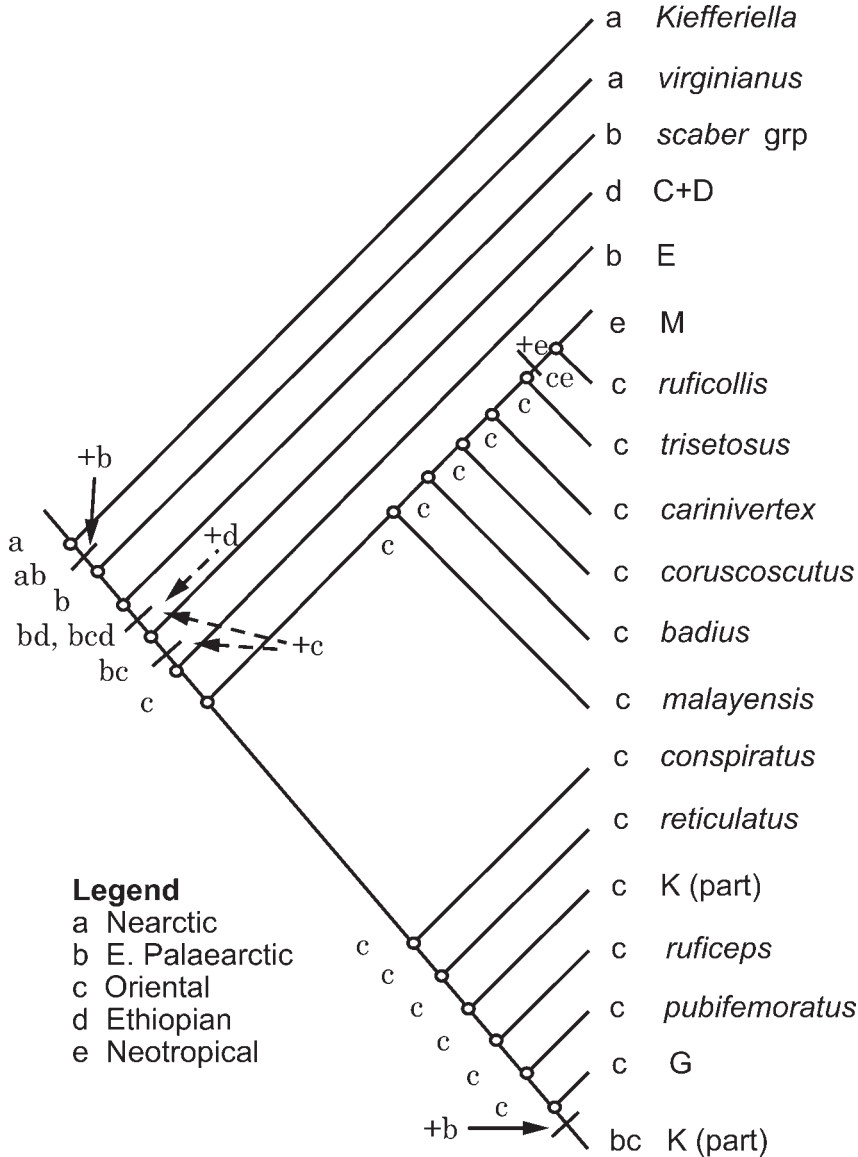


Fig. 19. Summary of the DIVA reconstructions of historical biogeography that postulate an ancestor of the Mayrellinae with a distribution limited to the Nearctic. Based on the majority-rule consensus tree of type III islands.

ities in the mountain ranges of southern Africa along the eastern coast, but with a few species from Cameroon and Angola in the west (fig. 20). This distribution pattern reflects that of the montane forest vegetation. The proportion of plant species shared by montane forests of Mount Cameroon and eastern Africa is as high as 53%. Several typical Afro-montane taxa have been ob-

served in various isolated stations on the southern rim of the Zaire River catchment and along the Guinea Gulf on the ridge of hills connecting Angola to Cameroon. It has been suggested that the montane forests extended to the lowlands during climatic changes, especially during colder periods of the Quaternary, thus facilitating migration between mountain massifs. An important



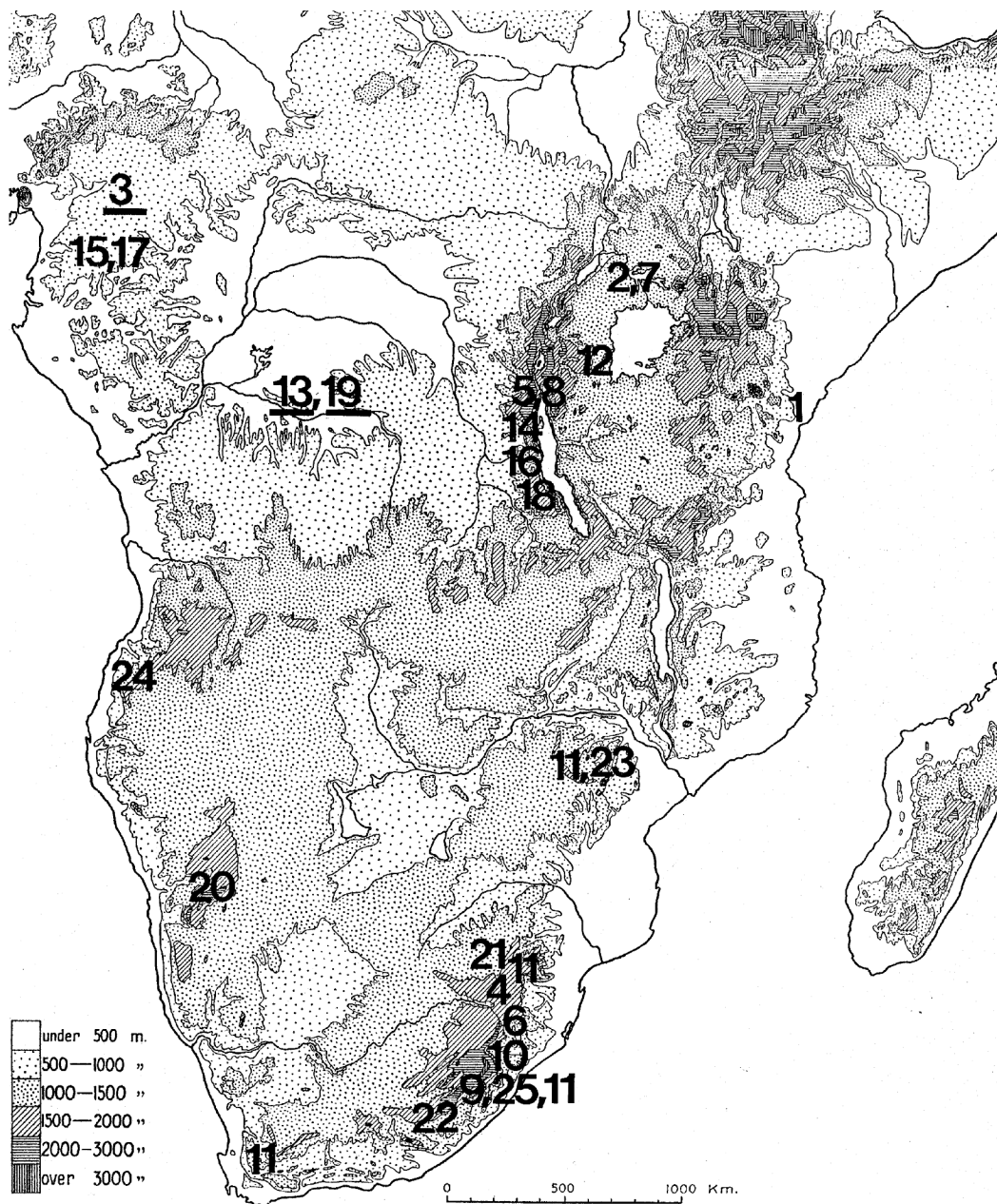


Fig. 20. Distribution records of the *Paramblynotus* species occurring in Africa. Species underlined are those without detailed information on collecting locality; therefore, they are placed in approximately the center of the country where they were collected. Exact collecting localities for three species from Zaire, that is, *P. zairensis* (14), *P. kekenboschi* (16), and *P. carianus* (18), have not been located. However, judging from the altitude records (between 1,800 and 2,300 m), they have certainly been collected from the highlands of eastern Zaire.

migration route, probably existing intermittently during the Quaternary or even before, connected East Africa with Angola and then continued to Cameroon (Maley, 1991, and references therein). The montane forest could either have formed a more-or-less continuous belt connecting the mountains or have formed a series of "stepping stones" in a generally more arid environment (Sosef, 1994, and references therein). The distribution of *Paramblynotus* in Africa apparently supports such a scenario.

The diversity of the genus *Paramblynotus* in the eastern mountain ranges is probably the result of topographic diversity and frequent climatic oscillations. The tectonic uplift and tilting of major portions of the continent from the early Miocene through the Quaternary, especially in eastern and southern Africa, created significant topographic diversity. With global change toward decreasing temperature and moisture, this diverse topography apparently had an increased role in moderating continental climates (Potts and Behrensmeyer, 1992). The effect on the African biota was the fragmentation of closed forests and the subdivision of habitats into complex mosaics of moist and dry zones, including forests, woodlands, grasslands, wetlands, and various montane zones (Potts and Behrensmeyer, 1992). The montane forests occupy the higher parts of the mountain ranges and have probably existed in the east and southeast since the Paleogene, when mountains in the area were sufficiently high and cool to enable certain tropical rainforest taxa to disperse upwards and radiate in the temperate montane zone (Axelrod and Raven, 1978). The climate of Africa has been characterized by frequent oscillations in terms of temperature and moisture since the late Miocene, particularly in the late Neogene and the Quaternary, when glaciations frequently alternated with warmer interglacial periods (Hamilton and Taylor, 1991; Potts and Behrensmeyer, 1992). The climatic oscillations, particularly between the glacial and interglacial periods, would have caused the montane forest to become restricted to the higher mountains during certain periods, causing the local populations of associated taxa to become extinct at relatively low locations and isolated

at higher altitudes. During other periods, these forests invaded the lowlands, facilitating migration between the areas.

Because of the local instability of the montane forest caused by the interaction between climatic oscillations and topographical complexity, most of the current distributions of *Paramblynotus* in Africa are probably rather recent expansions from a few refugia where montane forest persisted. The lack of endemic monophyletic groups in any area strongly supports such a scenario. Refugia for montane forests are found in the Cameroon highlands, the Tanganyika-Malawi highlands, the highlands of eastern Zaire, and in northern Kenya and northern Ethiopia as impoverished islands (Potts and Behrensmeyer, 1992). The basal branch of the African *Paramblynotus* (i.e., members of the former *Decellea*) is distributed in the Cameroon highlands, the highlands of eastern Zaire, and in Kenya. The highlands of eastern Zaire also host the greatest diversity of the group in Africa, comprising one-third of the known *Paramblynotus* species on that continent. Apparently, the area has served as the prime refugium for the African *Paramblynotus*.

The major splits in the Liopteridae phylogeny can be dated by using the historical biogeography reconstruction of the Mayrellinae presented above and data from Ronquist (1995a) (fig. 21). Ronquist (1995a) observed that the historical biogeography of the Liopteridae corresponds fairly closely to the breakup of the Pangaea during the Mesozoic as inferred from geological data, and he dated all other major divergent events within the family except the split between the Mayrellinae and the other subfamilies. The divergence between *Paramblynotus* and *Kiefferiella* has probably been caused, as discussed above, by the formation of the Rocky Mountains in the latest Paleocene and early Eocene (ca. 56–40 Ma), which created a dispersal barrier between southwestern North America and the rest of the continuous Asian landmass. As for the more basal events within the Liopteridae, the Mayrellinae, as discussed above, most probably originated in Laurasia, and its sister clade, consisting of the other subfamilies, apparently originated in Gondwana (Ronquist,

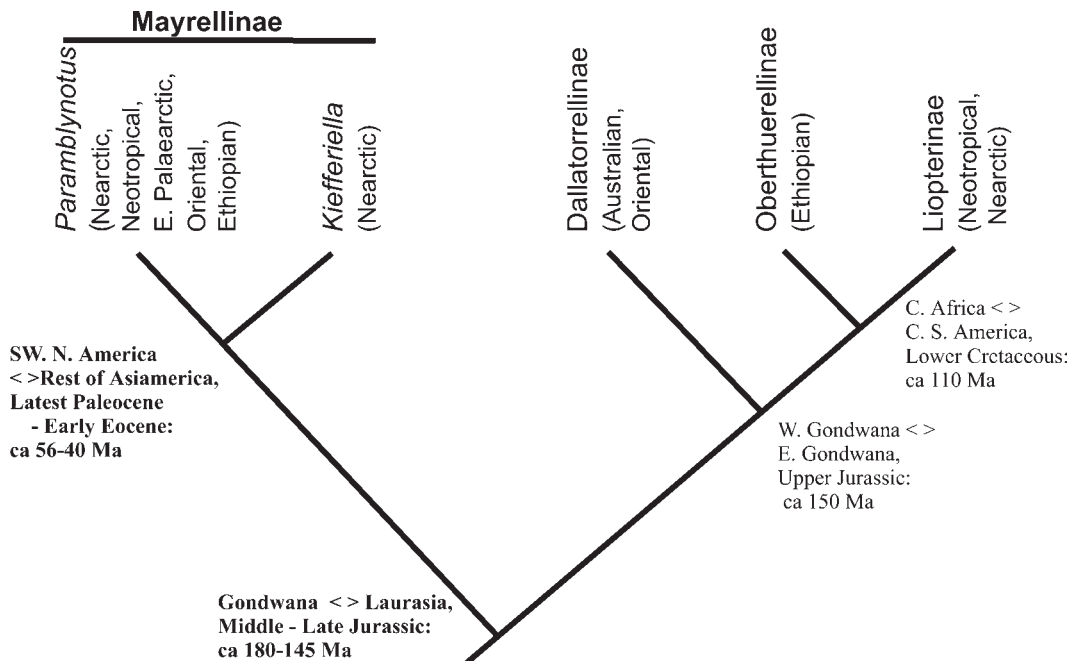


Fig. 21. Suggested ages of major splits in the phylogeny of the Mayrellinae. Ages in bold type are based on the present study, and those in normal font are based on Ronquist (1995a). "< >" represents tectonic split or formation of other geological barrier.

1995a). Therefore, it seems likely that the split between the Mayrellinae and its sister clade is the result of the breakup of Pangaea into Laurasia and Gondwana in the Middle to Late Jurassic (ca. 180–145 Ma).

## REVISION OF THE GENUS *PARAMBLYNOTUS*

THE GENUS *PARAMBLYNOTUS* CAMERON,  
1908

*Paramblynotus* Cameron, 1908: 299. Type species *Paramblynotus punctulatus* Cameron by subsequent designation (Rohwer and Fagan, 1917: 372).

*Paraegilips* Kieffer, 1910b: 335. Type species *Paraegilips reticulata* Kieffer by monotypy. Synonymized with *Paramblynotus* by Hedicke (in Hedicke and Kerrich 1940: 179); resurrected as a valid genus by Weld (1952: 164). Synonymy reestablished by Ronquist (1995).

*Allocynips* Kieffer, 1914: 185. Type species *Allocynips ruficeps* Kieffer (= *Paramblynotus ruficollis* Cameron) by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1930: 137).

*Holocynips* Kieffer, 1916: 284. Type species *Holocynips nigra* Kieffer by original designation and monotypy. Synonymized with *Paraegilips* by Weld (1952: 164). Preoccupied by *Holocynips* Kieffer, 1910a: 114. Synonymized with *Paramblynotus* by Ronquist (1995).

*Diholocynips* Rohwer and Fagan, 1917: 365. Replacement name for *Holocynips* Kieffer, 1916 nec Kieffer, 1910a.

*Mayrella* Hedicke, 1922: 190. Type species *Mayrella formosana* Hedicke by monotypy. Synonymized with *Paramblynotus* by Weld (1952: 158).

*Paribalia* Weld, 1922: 325. Type species *Paribalia borneana* Weld by monotypy. Synonymized with *Paramblynotus* by Ronquist (1995).

*Stylobrachys* Belizin, 1951: 572. Type species *Stylobrachys scaber* Belizin by original designation and monotypy. Synonymized with *Paramblynotus* by Kovalev (1994: 414).

*Baviana* Barbotin, 1954: 125. Type species *Baviana ferruginea* Barbotin by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1962: 279).

*Decellea* Benoit, 1956: 51. Type species *Decellea yangambicola* Benoit by original designation and monotypy. Synonymized with *Paramblynotus* by Weld (1962: 279), and status reestablished by Ronquist (1995). SYNONYMY REESTABLISHED.

**DESCRIPTION:** 1.4–10.0 mm. *Head.* Lower face more or less distinctly foveate/foveolate-reticulate to rugulose, with or without smaller punctures; not keeled medially or, in some species of of *punctulatus* group, with a lamellate median keel (see fig. 5). Median frontal carina usually distinct, not raised to distinctly raised to form a blunt, pyramidal or triangular, lamellate or oval, and dorsally flattened process; the carina is indistinct or almost absent in some species of the *ruficollis* group. Ocellar plate distinctly raised, occasionally indistinctly raised or not discernible. Antennal scrobes indistinctly or distinctly impressed, occasionally not impressed, glabrate with punctures or foveolate, and sometimes with secondary striation. Lateral frontal carina present or absent. Vertex foveate to foveate-areolate; or rugose; occasionally also with some longitudinal costulae; distinctly concave posteriorly, or (in *P. prinslooii*) longitudinally compressed and slightly concave posteriorly. Occiput glabrous or vertically strigate (in some species of *punctulatus* group). Gena glabrous or more or less superficially sculptured, foveate to rugose, occasionally also coriarius; with or without smaller punctures. Occipital carina not angled midlaterally or occasionally weakly angled; not raised or sometimes slightly raised throughout. Malar space distinctly impressed beneath eye or occasionally only slightly so. Clypeus usually glabrate ventrally; glabrate, foveolate to foveate, punctate, foveolate-punctate or rugulose dorsally and medially; with or without some longitudinal strigae; distinctly projecting ventrally; ventral margin straight or slightly incised, occasionally slightly acute. Foveae and punctures on face, gena, and vertex always setigerous, as true also for foveae and punctures of thoracic parts.

*Female antenna.* Flagellum with 11 articles, occasionally with 10; not widened or somewhat widened toward apex; in *P. yangambicolus* and *P. alveolatus* distinctly widened and compressed toward apex.  $F1/F2 = 0.7\text{--}1.2$ ;  $F3$  usually long, occasionally shorter,  $l/w = 1.5\text{--}3.0$ . Placodes start on  $F1$ , occasionally on  $F2$ . Placodes usually dense and cover entire surface of last flagellomere, but can be sparse occasionally (in some species in the *scaber*, *nigricornis*, and *ruficollis* groups).

*Male antenna.* Flagellum with 12 articles, occasionally with 13 articles.  $F1/F2 = 0.7\text{--}1.0$ ;  $F3\ l/w = 2.5\text{--}4.1$ . In the Neotropical species of the *ruficollis* group and *trisetosus* group  $F1$  distinctly swollen and excavated laterally; excavated area glabrate, nude, and without placodes.

*Pronotum.* Anterior flange glabrate, punctate, transversely striolate or longitudinally strigate. Submedian depressions large, deep, open laterally; medially usually more or less connected, but occasionally isolated from each other (see figs. 6, 7). Anterior plate usually glabrous to glabrate and dorsally punctate, or entirely foveolate. Lateral surface foveate, foveate-reticulate, or foveate-areolate, occasionally alveolate; with or without smaller punctures; sometimes with secondary longitudinal carinae. Crest either (1) prominently triangularly raised medially, (2) raised medially to form a more or less distinct triangular process, (3) raised into two separate, submedian, triangular processes, or (4) only slightly raised medially, evenly curved; with or without median emargination. Dorsal pronotal area coriarius, colliculate, or glabrate; secluded or open posteriorly.

*Mesonotum.* Scutum either with foveae and transverse, slightly, but distinctly undulating costae, or entirely distinctly foveate with only indicated or no transverse ridges, or occasionally foveate. Median mesoscutal impression only indicated posteriorly. Notaulus distinct to indistinct; with or without a large depression anteriorly. Parascutal carina conspicuously raised, angulate or slightly produced posteriorly; or not raised, rounded posteriorly. Scuto-scutellar sulcus divided into two foveae by strong median carina, sometimes divided by additional, more or less strong carinae into four or more foveae (*ruficollis* group and several species of *trisetosus* group). Axillula in some species with conspicuous white or yellow pubescence. Dorsal surface of mesoscutellum flat, or somewhat inclined posteriorly with a posterior vertical surface, or strongly inclined posteriorly without a vertical surface; foveate-areolate to slightly asperous, occasionally foveate; laterally and posteriorly margined or not; occasionally projected posteriorly into a short process, with or without a posterior emargination. Lateral and posterior surfaces



of mesoscutellum vertically costulate or rugose. Laterodorsal process small, rounded. Auricula broad, occasionally subdivided.

*Mesopectus*. Mesopleural triangle large, triangular, distinctly impressed; occasionally only slightly impressed; glabrate, densely pubescent, or in some species with conspicuous white or yellow pubescence; ventrally usually distinctly margined but occasionally not margined, margin usually evenly curved but occasionally slightly sinuate. Upper pleuron glabrous to glabrate, occasionally partly foveolate to foveolate-reticulate (*trisetosus* group, *P. mixtus*), or longitudinally carinate (*P. yangambicolus* and *P. alveolatus*). Anterior part of upper pleuron usually with a few foveae/foveolae or larger impressions, with or without punctures. Speculum glabrous; occasionally horizontally costulate. Mesopleural impression percurrent although occasionally very superficial, subdivided by vertical ridges or not. Lower pleuron glabrous to glabrate with more or less sparse hair-punctures, with one to two large anterior impressions, occasionally also with a vertical impression posteriorly, continuous with or separated from median impression. Latero-ventral carina percurrent, more or less strongly curved and occasionally only present posteriorly. Subpleuron transversely costulate. Intercoxal processes peglike or occasionally more rounded, directed obliquely posteriorly.

*Metanotum*. Dorsellum glabrate, punctate, or vertically strigate; lateral depressions distinct, moderately deep to deep, medium-sized to large, with or without vertical carinae (see fig. 8).

*Metapectal-propodeal complex*. Anterior metapleural pit absent except in *scaber* group. Metepisternum rugose, in *ruficollis* group longitudinally strigate in upper half, and in some species of *trisetosus* group medially with an elevated, glabrous patch. Prespiracular area rugose to rugulose; prespiracular process absent or represented by slight to distinct surface convexity. Lateral propodeal area rugose; posterolateral propodeal process absent or present; if present then low to moderately high, ridgelike to slightly raised ventrally and triangular. Median propodeal area carinate, often with median longitudinal carina and a median transverse carina. Lateral propodeal carina percurrent,

sometimes raised, usually not flattened on top, but partly flattened occasionally. When flattened, flattened part of lateral propodeal carina glabrous and nude to punctate and pubescent above. In *yangambicolus* group lateral propodeal carina only present anteriorly and posterior part of median propodeal area alveolate. Postsubpleuron glabrate. Nucha dorsally glabrous to more or less superficially longitudinally costulate, laterally rugose or longitudinally costulate.

*Wings* (see fig. 9). Forewing usually hyaline and occasionally dark brown. Forewing, when hyaline, sometimes with dark brown macula in and around marginal cell and occasionally also with a dark brown transverse band along basalis and an apical infuscate band. Hindwings hyaline with or without an apical infuscate band. In a few species, forewings and Hindwings with wide dark band covering basal half, median one third, or distal one half. Marginal cell with  $Rs/2r = 2.0-3.6$ .  $Rs+M$  arises from middle of basalis, occasionally from upper third, or posterior end. Bulla in  $R_1+Sc$  present or absent.

*Legs*. Protibia apically with one or two teeth. Mesotibial lobe blunt, not margined, with one or two teeth; or absent. Metatibial lobe margined, not produced, with or without three to six teeth, teeth short and blunt or long and pointed. Posterior surface of metatibia with or without longitudinal carina, with two to four spurs, and occasionally also with two to four strong dents. Metatarsomere (as *mt* below) 1 not compressed or slightly to distinctly compressed;  $mt1/mt2-5 = 0.4-1.3$ . Distal margin of *mt1* not produced, or produced into a blunt or tubular process anteroventrally; distal margin of *mt2* not produced.

*Female metasoma*. Petiolar annulus short with length/width =  $0.4-1.0$ , longitudinally costate (sometimes only superficially so dorsally). T3-5 reduced in size, T6 conspicuously expanded dorsally but not ventrally. In a few species in the *trisetosus* group T5 distinctly enlarged, partly covering T6. T7 largely covered by T6. T4-8 keeled medially. Posterior margins of T3-6 dorsally acute, posterior margins of T7 dorsolaterally broadly and deeply incised to expose T8 and sometimes dorsolaterally straight, not incised, entirely covering T8. Terga minutely to coarsely punctate, punctures of anterior

terga only limited to posterior part and punctures of posterior terga coarser and cover larger area. T3 usually has only a few hairs laterally, T4 usually nude and occasionally with a few hairs laterally, T5 almost always nude, and T6–8 usually with hairs in coarse punctures and occasionally densely pubescent. T8 with broad apical impression reaching to or beyond spiracle. Apical impression of T8 obliquely strigate throughout or at least close to spiracle, and rarely entirely punctate. In species with T8 covered by T7, impression and strigation on T8 may be reduced. Eudorsal margin of T8 in lateral view reclivous to vertical and straight or slightly convex. In species with T8 covered by T7, eudorsal margin of T8 may be straight, vertical, and not angled. T9 not or slightly projecting beyond T8. ST4–6 covered by ST3 or (in *P. yangambicolus* and *P. alveolatus*) not. ST7 with one to three rows of submedian hairs and occasionally more broadly pubescent, posterior margin of lateral flap oblique and straight.

**Male metasoma.** Petiolar annulus short to fairly long,  $l/w = 0.6\text{--}1.7$ ; longitudinally costulate, sometimes superficially dorsally. T3–8 subequal in size or T5 slightly to conspicuously enlarged; T4 or T5 largest in lateral view. Posterior margins of terga: T3–4 dorsally straight or acute, T5–7 dorsally broadly incised, T3–7 laterally rounded. T3–8 to T5–8 posteriorly and laterally minutely to more coarsely punctate; punctate area more extensive on posterior terga. T3 with some hairs laterally, T4 nude, sometimes with a few hairs laterally, T5 nude, T6–8 with hairs in coarse punctures. Eudorsal margin of T8 in lateral view almost straight.

**Coloration.** Many species more or less uniformly colored: black, brown, red brown, or yellow brown; *P. luteipennis* bright yellow brown. Other species bicolored: black with postpetiolar metasoma entirely and legs partly red; or black to brownish black with head, antennae, part of mesosoma, and part of legs yellow, red, yellowish brown, or reddish brown. In *P. annulicornis* and several other closely related species flagellum with a median, white band.

**BIOLOGY:** Nine females of *P. trisectus* were collected on tree trunks in Nepal, six females of *P. grossus* on *Syzygium* (Myrtaceae) logs in Papua New Guinea, two males of *P.*

*coruscus* reared from *Dalbergia fusca* (Fabaceae) in Burma, and one female of *P. claripennis* and two females of *P. yangambicolus* from “Coleoptera” in Uganda. Several specimens of *P. fuscipiculus* were reared from Curculionidae in South Africa. All rearing records are associated with angiospermous woody plants.

Diaz (1973) recorded *P. zonatus* from Argentina, collected on *Nectandra* sp. (Lauraceae) attacked by *Oncideres* sp. (Cerambycidae). Judging from Diaz’s description of this material, the record may actually refer to *P. brasiliensis*, which is described in this paper, and not to *P. zonatus*. The type female of *P. zonatus* was taken by beating on *Ulmus crassifolia* (Ulmaceae) in Texas (Weld, 1944). Yang (1994) observed females of *P. fraxinus* ovipositing into the trunk of a recently killed tree of *Fraxinus mandshurica* (Oleaceae) attacked by *Mesosa myops* (Cerambycidae) and *Tremex simulacrum* (Siricidae).

#### CHECKLIST OF SPECIES

Groups are listed according to phylogeny: the most basal is listed first and the most derived is listed last. Within each group, the type species is listed first, followed by the rest in alphabetical order. For convenience of comparison, the species treatments follow the phylogenetic order in the majority rule consensus tree (figs. 14, 15, appendix 1). Synonyms are preceded by an asterisk and are listed under the corresponding valid species. New species not authored by Liu et al. are so indicated.

#### I. VIRGINIANUS GROUP

*virginianus*, new species; USA: Virginia; USNM (HT♀, 15PT♀); ZMLU (M. Sporrang collection, 2PT♀).

#### II. SCABER GROUP

*scaber* (Belizin, 1951: 573, ♀♂); Russia: Primorskiy Kray [Khabarovsk, Irkutsk]; ZMAS (HT♂). As *Stylobrachys*; combination by Kovalev (1994: 414).

*atratus* Liu and Kovalev, new species; ZISP (HT♀, 10PT♀♂)

*belizini*, new species; NHRM (HT♀).  
*irkutensis* Liu and Kovalev, new species; ZISP (HT♀).  
*liaoi*, new species; ZICA (HT♀).  
*marginatus* Liu and Kovalev, new species; ZISP (HT♀).  
*pausatus* Liu and Kovalev, new species; ZISP (HT♀).  
*pronus* Liu and Kovalev, new species; ZISP (HT♀).

### III. *YANGAMBICOLUS* GROUP

*yangambicolus* (Benoit, 1956: 52, ♀; ZAIRE; MRAC (HT♀). Transferred to *Paramblynotus* by Weld (1962: 279) and back to *Decellea* by Ronquist (1995a).  
*alveolatus*, new species; Cameron; MNCN (HT♀).  
*mixtus*, new species; Kenya: Ukunda; USNM (HT♀).

### IV. *TRISSETOSUS* GROUP

*trisetosus* Benoit, 1956: 53, ♀; Zaire; MRAC (HT♀, 3PT♀).  
*angolensis*, new species; NHM (HT♀).  
*antistatus*, new species; NHM (HT♀).  
*cameroonensis*, new species; NHM (HT♀).  
*carinatus*, new species; NHM (HT♀).  
*claripennis*, new species; NHM (HT♀).  
*coxatus*, new species; CNCI (HT♀).  
*diminutus*, new species; NHM (HT♀).  
*fuscapiculus*, new species; PPRI (HT♀, 4PT♀); ZMLU (2PT♀); AEI (4PT♀); NHM (1P).  
*immaculatus*, new species; NHM (HT♀).  
*jacksoni*, new species; NHM (HT♀, 3PT♀♂).  
*kekenboschi*, new species; NHM (HT♀, 1PT♀).  
*minutus*, new species; NHM (HT♀).  
*maculipennis*, new species; IRCT (HT♀).  
*nigricornis* Benoit, 1956: 55, ♀; Zaire; MRAC (HT♀).  
*prinslooii*, new species; PPRI (HT♀).  
*rwandensis*, new species; CNCI (HT ♀).  
*samiatus*, new species; NHM (HT♀).  
*scalptus*, new species; PPRI (HT♀, 1PT♂); CNCI (2PT♂).  
*townesorum*, new species; AEI (HT♀).  
*vannoorti*, new species; SAM (HT♀).  
*zairensis*, new species; NHM (HT♀, 1PT♀).

### V. *APEOSUS* GROUP

*apeosus* Liu and Kovalev, new species; ZISP (HT♀).  
*friatus* Liu and Kovalev, new species; ZISP (HT♀).

### VI. *RUFICOLLIS* GROUP

*ruficollis* Cameron, 1909: 18, ♂; Borneo; BMNH (4T♂, no. 7.9 and in main coll.).  
*\*ruficeps* Kieffer, 1914: 186, ♂; Luzon; USNM (HT♂, not numbered). = *P. ruficollis* Cameron; synonymy by Weld (1930: 137).  
*badius*, new species; NHM (HT♀).  
*braziliensis*, new species; AEI (HT♀, 117PT♀♂).  
*carinivertex*, new species; BMBP (HT♀).  
*coruscus*, new species; BMBP (HT♀); NHM (2PT♂).  
*costaricanus*, new species; NHM (HT♀, 2PT♀); CNCI (1PT♀).  
*malayensis* (Weld, 1922: 329, ♀♂); Borneo; USNM (HT♀, no. 24 377, 1PT♀, 2PT♂). As *Allocynips*; combination by Weld (1930: 137).  
*trisectus* Maa, 1962: 126, ♀; Thailand; BPBM (HT♀).  
*zonatus* Weld, 1944: 56, ♀; USA: TX; USNM (HT♀, no. 56 811).

### VII. *PUNCTULATUS* GROUP

*punctulatus* Cameron, 1908: 300, ♀; Borneo; BMNH (2T♀, in main coll.).  
*\*borneensis* (Weld, 1922: 322, ♀); Borneo; USNM (HT♀, no. 24 380, 2PT♀). As *Allocynips*; combination and synonymy by Weld (1930b: 137).  
*\*rufiventris* Cameron, 1910: 131, ♀; Borneo; BMNH (HT♀, no. 7.8). Synonymy by Ronquist (1995a: 37).  
*annulicornis* Cameron, 1910: 132, ♂; Borneo; BMNH (HT♂, no. 7.11).  
*aptatus*, new species; BPBM (HT♀).  
*asae*, new species; NHM (HT♀, 1PT♀), NNMN (11PT♀).  
*axeli*, new species; ROM (HT♀, 1PT♂).  
*barbarae*, new species; AEI (HT♀, 1PT♀).  
*beckeri*, new species; AEI (HT♀, 6PT♀); CRF (1PT♀).  
*borneanus* (Weld, 1922: 326, ♀♂); Borneo; USNM (HT♀, no. 24 375, PT♂). As *Paribalia*; combination by Ronquist (1995a: 37).  
*cheni*, new species; ZICA (HT♀).  
*chrysochaetes*, new species; AEI (HT♀, 3PT♀).  
*clarus* (Weld, 1922: 330, ♂); Mindanao; USNM (HT♂, no. 24 378). As *Allocynips*; combination by Weld (1930: 137).  
*conspiratus*, new species; AEI (HT♀).  
*coracinus*, new species; AEI (HT♀, 3PT♀).  
*distinctus*, new species; AEI (HT♀).  
*dyak* (Weld, 1922: 329, ♀); Borneo; USNM (HT♀, no. 24 376, PT♀). As *Allocynips*; combination by Weld (1930: 137).  
*ebbae*, new species; ROM (HT♀).

*eriki*, new species, AEI (HT♀).  
*esakii* (Yasumatsu, 1959: 93, ♂); Japan: Honshu; KUEC (HT♂). As *Paribalia*; combination by Ronquist (1995a: 37).  
*ferrugineus* (Barbotin, 1954: 125, ♀); Indochina: Mont Bavi; CFB (HT♀); not seen. As *Baviana*; combination by Weld (1962: 279).  
*filippae*, new species, ROM (HT♀, 1PT♀), RMNH (3PT♀♂).  
*flaviceps* (Kieffer, 1916: 286, ♀); Mindanao; location of type not known, probably lost (cf. Weld, 1952: 164). As *Allocynips*; combination by Weld (1930: 137).  
*formosanus* (Hedicke, 1922: 190, ♀); Taiwan; DEIC (HT♀). As *Mayrella*; combination by Weld (1930: 137).  
*fraxinii* Yang and Gu, 1994; NWCF (HT♀, 2PT♀).  
*fucosus*, new species; NHM (HT♀).  
*glaberus*, new species, AEI (HT♀).  
*grossus*, new species; NHM (HT♀, 11PT♀), BPBM (1PT♀), NNMN (1PT♀), ROM (1PT♀), ZMLU (2PT♀).  
*hainanensis*, new species; USNM (HT♂, 1PT♂).  
*insolitus*, new species; AEI (HT♀).  
*isolatus*, new species; BPBM (HT♀).  
*kitrinocarus*, new species; ZMLU (HT♀).  
*kosugii* Watanabe and Sakagami, 1951; EIHU (HT♂, 3PT♂); NHM (1PT♂).  
*lutepennis*, new species; ZMLU (HT♀).  
*miniatus*, new species; NHM (HT♀).  
*militocephalus*, new species; BMBP (HT♀).  
*nebulosus*, new species; NNMN (HT♀, 4TPT♀); AEI (3PT♀); ZMLU (1PT♀, in MS collection); NHM (1PT♀).  
*niger* (Kieffer, 1916: 285, ♂); Philippines: Palawan; location of type not known, probably lost (Weld, 1952: 164). As *Holocynips* Kieffer, 1916 nec Kieffer, 1910a; transferred to *Paraegilips* by Weld (1952: 164); combination by Ronquist (1995a: 37).  
*nipponensis*, new species; BPBM (HT♀).  
*obscurus*, new species; BPBM (HT♀, 1PT♂), NHM (1PT♀), UCDC (1PT♀).  
*ornatus*, new species; NHRS (HT♀). NHM (3PT♀).  
*pubifemoratus*, new species; AEI (HT♀, 2PT♀); ZMLU (1PT♀).  
*reticulatus* (Kieffer, 1910b: 335, ♂); Indonesia: Bintan; ZMHB (HT♂). As *Paraegilips*; combination by Hedicke in Hedicke and Kerrich (1940: 179) by inference through generic synonymy.  
*robustus*, new species; BPBM (HT♀).*kosugii* Watanabe and Sakagami, 1951: 129, ♂; Japan; EIHU (HT♂, 3PT♂), BMNH (1PT♂).  
*ruficeps* Cameron, 1908: 300, ♂; Borneo; BMNH (HT♂, main coll.).  
*\*isosceles* (Weld, 1922: 331, ♀♂); Singapore; USNM (HT♀, no. 24 379, 3 PT♂). As *Allocy-*

*nips*, = *P. ruficeps* Cameron; combination by Weld (1930: 137), synonymy by Ronquist (1995a: 37).

*rufipes*, new species; BPBM (HT♀).  
*shimenensis*, new species; ZICA (HT♀).  
*stigi*, new species, ROM (HT♀).  
*venoforticulus*, new species; BPBM (HT♀).  
*weiae*, new species, BPBM (HT♀).  
*yuani*, new species, AEI (HT♀).

#### KEY TO SPECIES GROUPS

1. Upper mesopleuron glabrate; speculum with sparse setigerous punctures (fig. 1). Eyes prominent, protruding distinctly beyond genae (fig. 22). Pronotal crest not raised anteromedially. Dorsal surface of mesoscutum convex and predominantly transversely carinate with foveae set in rows. Mesoscutellum convex dorsally, gradually sloped posteriorly (fig. 25). Tergum 8 distinctly exposed. . . . . *virginianus*
- Speculum without setigerous punctures. Other characters vary, but not in combination as above. . . . . 2
2. Antennal flagellum not widened toward apex. Lateral carina of pronotum indistinct; lateral pronotal areas meet medially (fig. 35). Tergum 8 distinctly exposed (fig. 37) . . . . . *scaber* group
- Antennal flagellum usually widened toward apex. Lateral carina of pronotum distinct to prominent; lateral pronotal areas medially separated by the posterior extension of the less sculptured anterior surface. If lateral carina of pronotum indistinct and lateral pronotal areas separated medially, then the antennal flagellum distinctly widened toward apex. . . . . 3
3. Upper mesopleuron at least partially sculptured with dense coarse punctures, foveae, or alveolae. F1 of antenna longer than F2. Lateroventral margin of pronotum evenly curved (fig. 39) . . . . . 4
- Upper mesopleuron glabrous, at most with sparse fine punctures anteriorly. F1 of antenna shorter than F2. Lateroventral margin of pronotum angled where meeting lateral pronotal carina (figs. 49, 57, 66, 76, 88, 97) . . . . . 5
4. Lower face distinctly convex and protruding in lateral view. Pronotal crest gradually raised, anteriorly forming a conspicuous ridge. Speculum longitudinally costate. Median propodeal area not delimited by percurrent lateral propodeal carinae, posteriorly foveate-reticulate. . . . *yangambicohus* group



- Lower face flat (fig. 38), not protruding in lateral view. Pronotal crest not gradually raised anteriorly into a conspicuous ridge (fig. 39). Speculum without longitudinal costae (fig. 39). Median propodeal area distinctly delimited by percurrent lateral propodeal carinae, posteriorly not foveate-reticulate (fig. 41) . . . . . *trisetosus* group
- 5. Occiput distinctly carinate vertically. Pronotal crest not distinctly raised into a conspicuous ridge . . . . . *apeosus* group
- Occiput glabrous or vertically carinate. If occiput distinctly carinate vertically, then pronotal crest always distinctly raised into a conspicuous ridge . . . . . 6
- 6. Pronotal crest always low anteromedially and mesoscutum always convex dorsally (figs. 49, 57). Scutellar foveae divided by strong submedian, longitudinal carinae (figs. 50, 58). Posterior margin of metasomal T7 of female impressed, distinctly exposing T8 (fig. 53) . . . . . *ruficollis* group
- Pronotal crest low (figs. 66, 88, 97) or raised into a conspicuous peak anteromedially (fig. 75) and mesoscutum dorsally convex (fig. 66) or flat (fig. 76). Scutellar foveae usually not divided by strong submedian, longitudinal carinae. Posterior margin of metasomal T7 of female straight or smoothly curved, usually covering T8 entirely (figs. 70, 79, 92, 98). Rarely the scutellar foveae are subdivided and, if so, the pronotal crest always raised into a conspicuous peak anteromedially, T7 always covering T8, and mesoscutum flat dorsally . . . *punctulatus* group

## TAXONOMY OF SPECIES GROUPS

### *VIRGINIANUS* GROUP figures 22–29

This species group currently contains only one species from eastern North America.

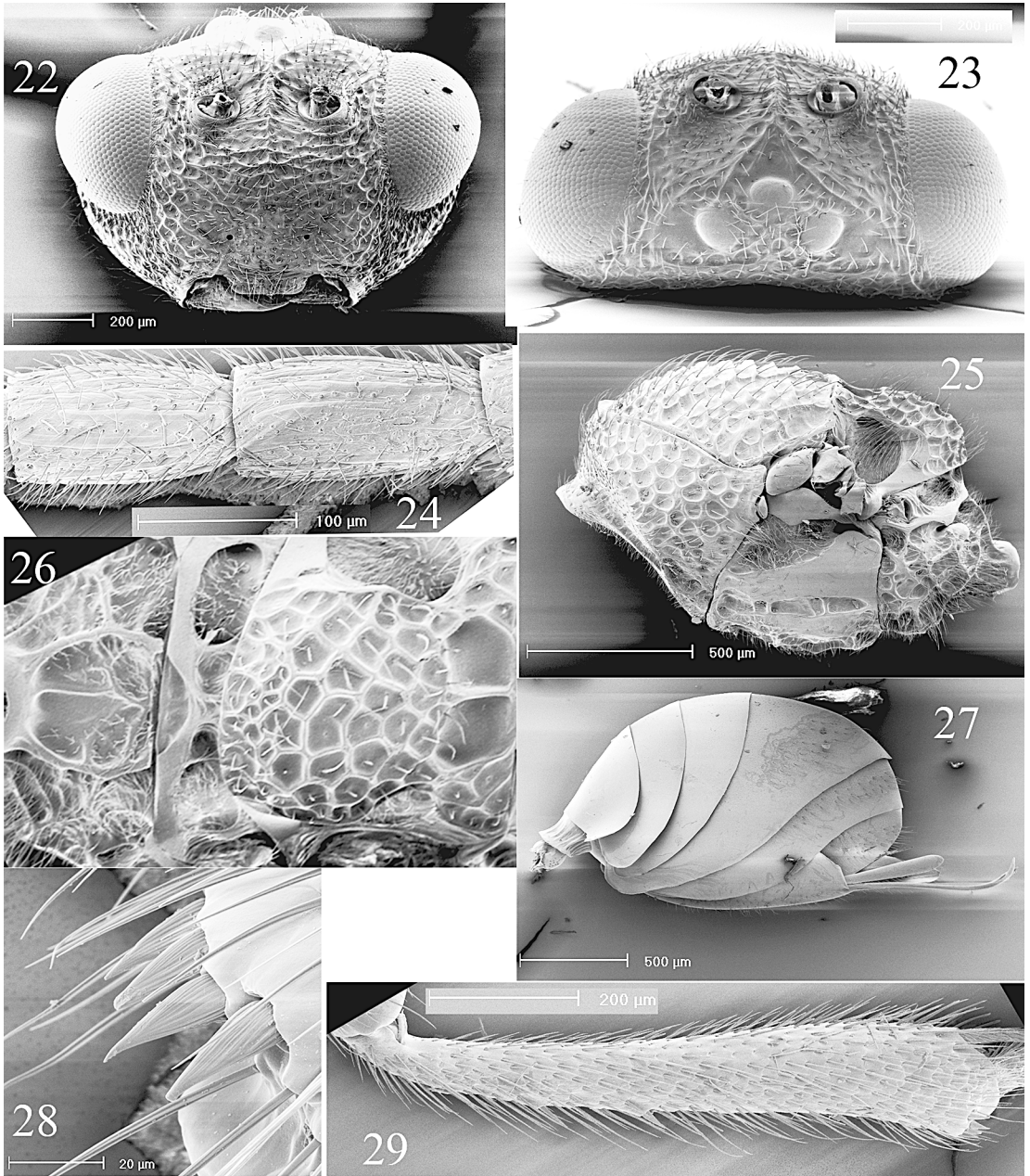
**DIAGNOSTIC CHARACTERS:** Size relatively small. Antenna filiform, not distinctly enlarged apically. Female antenna has 13 segments with F1 distinctly shorter than F2. All flagellomeres have placodes, which are short, not as long as the segments, and are densely distributed on all medial to distal segments (fig. 24). Eye extended laterally, distinctly beyond outer margin of gena. Antennal scrobe defined by apparent lateral carina. Median frontal carina simple, and present only between antennal sockets (figs. 22, 23). Occiput glabrous. Pronotal crest not raised dorsomedially. Dorsal pro-

notal area glabrous. Lateral surfaces of pronotum evenly curved anteroventrally, foveate-reticulate, without secondary transverse costae and punctures, and not separated dorsomedially by an extended, less sculptured anterior area. Lateral pronotal carina distinct, but not reaching pronotal crest dorsomedially. Mesoscutum transversely carinate with distinct foveae set in between (fig. 25). Mesoscutellum sloped posteriorly; posteriorly broadly rounded; dorsally foveate-reticulate. Scutellar sulcus is divided into two foveae by median longitudinal carina. Axillar area without conspicuous pubescence (figs. 25, 26). Mesopleural triangle well defined by a smoothly curved carina. Upper mesopleuron glabrous (fig. 25); speculum with setigerous punctures posterodorsally (fig. 1). Median mesopleural impression straight, narrowed toward ends, and with two to three vertical carinae. Metepisternum alveolate-reticulate in upper half and pubescent ventrally (fig. 25). Wings slightly smoky; Rs-M from middle of basalis. Apical teeth of metatibia long and pointed (fig. 28, 29). First metatarsomere without apical protuberance and shorter than the combined length of the second to fifth metatarsomeres. Lateral propodeal carinae simple, not raised into strong keel or process, and median propodeal area usually with a median longitudinal carina, or two submedian longitudinal carinae, crossed by a modified transverse carina (fig. 26). T6 is at least twice as long as other terga along dorsal margin. T7 of female with posterior margin curved dorsolaterally, distinctly exposing T8 (fig. 27).

### *Paramblynotus virginianus*, new species figures 1, 22–29

**FEMALE:** Length 3.5–5 mm. Body black entirely except tibiae and tarsi of legs, which are yellow to yellowish brown. Wings slightly smoky, somewhat darker across middle.

Face, gena, and vertex foveate-reticulate (figs. 22, 23); foveae on vertex longitudinally set in rows in the spaces between eye and posterior ocelli (figs. 22, 23). Median frontal carina only shortly present between antennal sockets. Anterior tentorial pit small, but distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch; clypeus



Figs. 22–29. *P. virginatus*. 22, Head, front view, ♀; 23, head, dorsal view, ♀; 24, antennal F1–2, lateral view (exterior), ♀; 25, mesosoma, lateral view, ♀; 26, scutellum and propodeum, dorsoposterior view, ♀; 27, metasoma, lateral view, ♀; 28, end of metatibia showing apical teeth, ♀; 29, metatibia, lateral view, ♀.

transversely striate-rugose (fig. 22). Occiput mostly glabrous except foveate laterally.

Lateral pronotal carina distinct, except dorsomedially (fig. 25). Lateral surface of pronotum foveate-reticulate. Dorsal area of pronotum behind pronotal crest glabrous and complete to end of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate with foveae more or less set in rows between transverse costae. Mesoscutellum foveate-reticulate, sloping posteriorly and, viewed from above, rounded posteriorly (fig. 26). Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron anteriorly punctate-rugose, posteriorly glabrous; speculum with several setigerous punctures. Longitudinal mesopleural impression percurrent with unevenly distributed transverse costae. Lower mesopleuron glabrous with setigerous punctures along lower margin. Metanotal-propodeal complex foveate-rugose with dense pubescence (fig. 25). Lateral propodeal carina percurrent, medially somewhat curved laterally. Median propodeal area with one or two irregular longitudinal carinae (fig. 26).

Abdominal petiole slightly shorter than wide, longitudinally carinate. Relative length of T3–8: 2:1:1:3.2:1.3:0.9. T4–8 densely finely punctate. T6–8 also sparsely, coarsely punctate with hairs (fig. 27). All legs densely punctate with pubescence. Metatibia apically with four slender, pointed teeth (figs. 28, 29).  $1\text{mt}/2-5\text{mt} = 0.6$ .

MALE: Unknown.

The species is most similar to species of the *scaber* group, but can be easily separated from the latter by the following characters. Speculum setigerous; median frontal carina branched posteriorly, delimiting a small triangular, glabrous area beneath anterior ocellus; eyes protruding laterally beyond gena; mesoscutum distinctly convex in lateral view; wings smoky.

TYPE MATERIAL: 18♀♀. HOLOTYPE: ♀, USA: Virginia, Essex Co. (1 mi SE Dunnsville, 37°52'N, 76°48'W), 1994-VII-2–15, D. R. Smith coll. (USNM). PARATYPES: 17♀♀. 7♀♀, 1992-VII-8–31 (2), 1994-VII-2–15 (2), and 1995-VII-12–24 (3), other data as holotype; 10♀♀, USA: Virginia, Clarke County, University of Virginia Blandy Experimental Farm (2 mi S Boyce, 39°05'N, 78°10'W),

1995-VII-12–24 (6) and 1994-VI-25–VIII-3 (4) (USNM: 15; ZMLU-MS: 2).

ADDITIONAL MATERIAL EXAMINED: Canada: Ontario (bog in Ancaster) (CNCI: 1♀).

DISTRIBUTION: USA: Virginia; Canada: Ontario.

BIOLOGY: All specimens were collected in Malaise traps. According to Dr. D. Smith (personal commun.), the site in Essex Co., Virginia, was about 120 acres of woodland and open grassy areas. The woods were dominated by pines, mostly *Pinus taeda*, *Quercus* spp., *Hicoria* spp., *Liriodendron tulipifera*, and *Liquidambar styraciflua*. Part of the adjacent property was a tree plantation that had been cut about 15 years earlier and contained considerable underbrush and about 10–15-year-old loblolly pines. Traps were placed at woods edges, along streams, and within woods and the tree plantation. The site in Clarke Co. was an experimental station with about 700 acres and consisted of woodlands, open fields, and ponds surrounded by willows. This site was much more diverse in vegetation than the other site. The woodlands (one about a 110-year-old 70-acre woodlot) were dominated by *Quercus* spp., *Hicoria* spp., and *Ulmus* spp., with a few scattered pines. Traps were placed in many disturbed areas, forest edges, within woods, and around ponds and willows. The 17 specimens of the type series consisted of 7 from the Essex site collected in 3 years and 10 from the Clarke site collected in 2 years. Apparently the species is more abundant in the Clarke site that also had a more deciduous component in the vegetation. Nonetheless, no direct host association can be established.

ETYMOLOGY: Name after type locality.

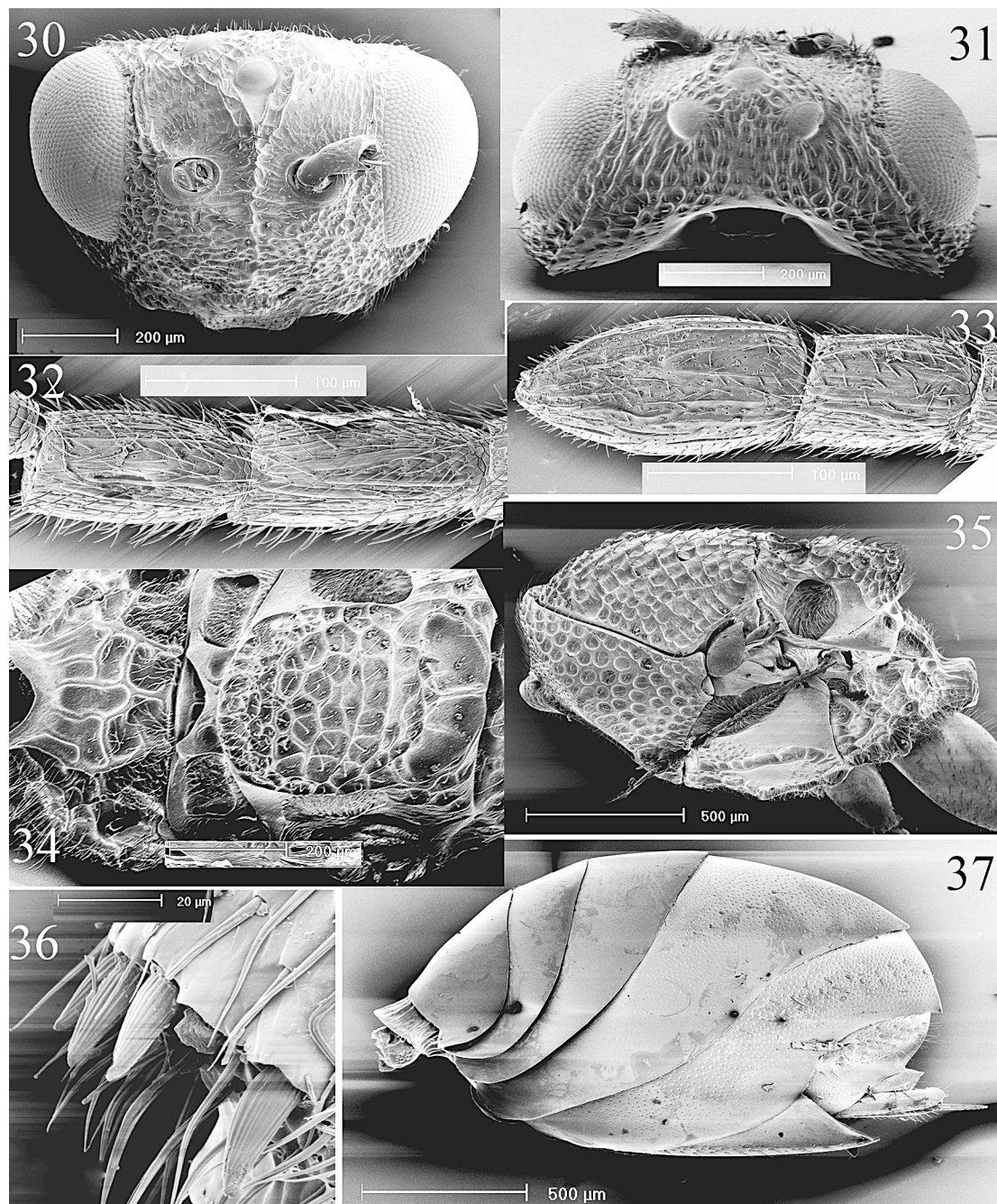
#### SCABER GROUP

figures 30–37

The group is distributed predominantly in the far-eastern Palearctic with one exception from the southwestern Yunnan of China.

DIAGNOSTIC CHARACTERS: Body size relatively small. Antenna filiform. Female antenna has 13 segments with F1 distinctly shorter than F2. Placodes present on all flagellomeres, short, and not as long as the





Figs. 30–37. *P. atratus*. 30, Head, front view, ♀; 31, head, dorsal view, ♀; 32, antennal F6–7, lateral view, ♀; 33, antennal F10–11, dorsal view, ♀; 34, scutellum and propodeum, dorsoposterior view, ♀; 35, mesosoma, lateral view, ♀; 36, end of metatibia showing apical teeth, ♀; 37, metasoma, lateral view, ♀.

segments (figs. 32, 33). Median frontal carina simple and present only between antennal sockets. Antennal scrobes laterally always defined by a weak, but distinct carina (fig. 30). Eye laterally about to reach or slightly extended beyond outer margin of gena (fig. 31). Occiput glabrous. Lateral surfaces of pronotum foveate-reticulate, usually without secondary transverse costae and punctures, and not separated dorsomedially by an extended, less sculptured anterior area. Lateral pronotal carinae distinct, but not reaching pronotal crest dorsomedially (fig. 35). Pronotal crest slightly to strongly raised dorsomedially, with or without a median emargination. Dorsal pronotal area, as defined by dorsal pronotal carina, extended from pronotal crest posteriorly, always sculptured and usually reaching end of dorsal posterior margin of pronotum. Mesoscutum not strongly convex; predominantly transversely carinate with only superficial foveae in between (fig. 35). Mesoscutellum sloped posteriorly, with or without a distinct posterior vertical surface, and foveate-reticulate dorsally. Scutellar sulcus is divided into two foveae by median longitudinal carina. Axillar area with distinct, but not conspicuous pubescence (figs. 34, 35). Mesopleural triangle ventrally well defined by a smoothly curved carina. Upper mesopleural area glabrous; speculum without setigerous punctures. Median mesopleural impression straight, almost continuous posteriorly with the vertical part of the ventral mesopleural impression, and with multiple, equally strong vertical carinae. Metepisternum alveolate-reticulate in upper half and pubescent ventrally (fig. 35). Wings hyaline; Rs-M from middle of basalis. Dorsoapical teeth of metatibia long and bluntly pointed (fig. 36); first metatarsomere without apical protuberance. Lateral propodeal carinae simple, not raised into strong keel or process; median propodeal area usually with a median longitudinal carina, which sometime bifurcates behind the median transverse carina (fig. 34). T7 of female metasoma with posterior margin curved dorsolaterally, distinctly exposing T8, and T6-8 with sparse coarse punctures with hairs (fig. 37). T3-8 of male not modified and subequal in size.

# KEY TO SPECIES OF *SCABER* GROUP

In all keys to species, authors (other than Liu et al.) are indicated.

1. Pronotal crest medially raised into a conspicuous peak. . . . . 2
  - Pronotal crest medially not raised into a conspicuous peak . . . . . 3
2. Gena and malar space strongly vertically carinate-rugose with fused foveae between caninae. Mesoscutellum rounded posteriorly. Length of marginal cell 2.4 times width. . . . . *P. liaoi*, n.sp.
  - Gena mostly foveate to punctate, with some short carinae posteriorly and ventrally. Mesoscutellum truncate posteriorly with a slight emargination. Length of marginal cell 2.0 times width. . . . . *P. pronus* Liu and Kovalev, n.sp.
3. Pronotal crest medially dorsally raised. All antennal flagellomeres with placodes. Surface of mesoscutum almost flat in lateral view. Median propodeal area with a distinctly complete transverse carina . . . . . 4
  - Pronotal crest medially flat. All but first antennal flagellomeres with placodes. Surface of mesoscutum convex in lateral view. Median propodeal area without a complete transverse carina . . . . . 5
4. Pronotal crest medially not emarginate. Gena glabrate posteriorly at lower part, and coarsely punctate elsewhere. T6 about 3.5 times as long as T4 . . . . . *P. marginatus* Liu and Kovalev, n.sp.
  - Pronotal crest medially with a distinct triangular emargination. T6 about 2.5 times as long as T4 . . . . . *P. pausatus* Liu and Kovalev, n.sp.
5. Vertex almost entirely longitudinally carinate . . . . . 6
  - Vertex laterally carinate and punctate medially between lateral ocelli . . . . . 7
6. Gena foveate-rugose. Median emargination of pronotal crest broad and less distinct. Lateral surface of pronotum foveate reticulate with oblique carinae. Median propodeal area glabrate with an almost complete longitudinal median carina. Anterior part of upper mesopleuron foveate-rugose. Rs+M vein of forewing clearly present . . . . . *P. scaber* (Belizin)
  - Gena glabrate-foveate. Median emargination of pronotal crest narrower and distinct. Lateral surface of pronotum foveate reticulate. Median propodeal area areolate-reticulate. Upper mesopleuron almost entirely glabrous. Rs+M vein of forewing reduced to almost invisible. . . . . *P. belizini*, n.sp.



7. Antennal scrobes glabrous. Pronotal crest medially distinctly raised and distinctly emarginated . . . *P. irkutensis* Liu and Kovalev, n.sp.
- Antennal scrobes at least partly carinate posteriorly. Pronotal crest medially not distinctly raised and not distinctly emarginated. . . . . *P. atratus* Liu and Kovalev, n.sp.

*Paramblynotus scaber* Belizin, 1962

*Stylobrachys*; combination by Kovalev (1994: 414).

**FEMALE:** Length 4.3–4.8 mm. Body black entirely except tibiae and tarsi of legs yellow to yellow brown.

Upper face mostly longitudinally carinate except antennal scrobes glabrate-punctate ventrally. Median frontal carina weak, but distinct until one-third of lower face. Lower face mostly radiating-carinate and foveate, except foveate-reticulate medially. Clypeopleurostomal sulcus and epistomal sulcus form a smoothly curved arch; clypeus transversely carinate. Gena foveate-rugose. Vertex longitudinally carinate with obscured foveae. Occiput glabrous, with sparse pubescence.

Anterior flange of pronotum densely carinate longitudinally. Anterior plate of pronotum anterior to lateral pronotal carinae heavily foveate with foveae set in rows between irregular transverse carinae. Lateral pronotal carina distinct except dorsomedially. Lateral surface of pronotum foveate-reticulate with broken oblique carinae. Median pronotal crest low with a broad emargination. Mesoscutum foveate-rugose with irregularly distributed transverse costae. Dorsal area of pronotum behind pronotal crest glabrous or with indistinct carinae and complete to end of dorsal posterior margin of pronotum. Mesoscutellum foveate-reticulate; sloping posterolaterally and posteromedially raised into a hump. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron mostly glabrous except anteriorly foveate-rugose; speculum glabrous. Longitudinal mesopleural impression percurrent with several evenly distributed transverse costae. Lower mesopleuron glabrous with irregular foveae or punctures. Metanotal-propodeal complex glabrous in upper metepisternum and an upper small area of lower metepisternum, otherwise foveate-rugose with dense pubescence. Lat-

eral propodeal carina percurrent and nearly parallel; median longitudinal carina almost percurrent and only diverged posteriorly.

Relative length of T3–T8: 2.3:1:1.2:4:1 0.8. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures. All legs, except metacoxa dorsally glabrous, densely pubescent. Metatibia apically with four stout, pointed teeth.  $1\text{mt}/2\text{--}5\text{mt} = 0.65$ .

**MALE:** Length 3.0–3.8 mm. All abdominal terga of equal length except T5 slightly longer than the rest.

**MATERIAL EXAMINED:** 2♀♀, 7♂♂ (3T): ZISP.

**DISTRIBUTION:** Russia: Primorsk (Usury) and Khabarovsk.

**REMARKS:** The original author recorded six type specimens: two females (one as type) and two males from Usury and two males from Khabarovsk, and one female from Irkusk (Belizin, 1962). However, we found two females and one male from Usury and four males from Khabarovsk, and one female from Irkusk in the type series. All specimens were labeled as “Paratypus” except the two females from Usury were labeled as “Holotypus”. Between the two females that bear holotypus labels, one bears two labels, a white label reading as “*Holotypus Stylobrachys scaber* V. Belizin det” (in handwriting) and a red label (similar to the paratype labels both in size and color) reading as “Holotypus”. The other female specimen bears a larger and redder label reading “*Holotypus* (in print) *Stylobrachys scaber* V. Belizin det ♀” (in handwriting) in one single label. The collection time and collector is the same on both; the locality is slightly different, but not separable based on Belizin’s original information. However, we think that the former “holotype” is an error because the color and size of the label is the same as the other paratypes, and the way the information was recorded onto the two labels is the same as four of the other six paratypes. Therefore, we consider that there is no need for selecting a lectotype. Nonetheless, we still attach an extra label reading “recognized Holotype of Belizin” to avoid confusion for future reference. Also in the original description, the collection date was recorded as 1937-VII-13, but the labels attached to the three types from Usury read “1937-VII-IX” and the

types from Khabalovsk have no collection date.

A female paratype from Irkusk is a misidentification and is described in the present paper as a new species, *Paramblynotus irkutensis*.

*Paramblynotus atratus* Liu and Kovalev,  
new species  
figures 30–37

**FEMALE:** Length 3.5–4.0 mm. Body black entirely except legs dark brown. Wings transparent.

Upper face including antennal scrobes distinctly carinate longitudinally; ocellar plate foveate-reticulate. Median frontal carina present, distinct from below anterior ocellus to somewhat beyond lower margins of antennal sockets, and bifurcated posteriorly to delimit a small glabrous triangular area anterior to anterior ocellus. Lower face entirely foveate-reticulate and slightly rugose (fig. 30). Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch; clypeus foveate-rugose. Gena foveate with sparse pubescence. Vertex distinctly longitudinally carinate with foveae. Occiput glabrous (fig. 31).

Anterior flange of pronotum punctate-foveate. Anterior plate of pronotum before lateral pronotal carinae densely foveate with pubescence. Lateral pronotal carina distinct posteroventrally. Lateral surface of pronotum foveate-reticulate (fig. 35). Median pronotal crest indistinct and medially not or very slightly emarginate. Dorsal pronotal area transversely costate and complete to end of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate with foveae set in rows between distinct transverse costae (fig. 35). Mesoscutellum foveate-reticulate; sloping posterolaterally with a posteromedial hump (figs. 34, 35). Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous except anteriormost part punctate; speculum glabrous. Longitudinal mesopleural impression percurrent with several irregularly distributed transverse costae. Lower mesopleuron glabrous with sparse pubescence. Metanotal-propodeal complex foveate-rugose, glabrous in upper metepisternum and an upper part of lower metepis-

ternum and densely pubescent below. Lateral propodeal carina percurrent and medially distinctly curved laterally; median propodeal area areolate-reticulate, with median longitudinal carina bifurcated posteriorly at anterior third (fig. 34).

Abdominal petiole half as long as wide in lateral view. Relative length of T3–8: 1.8:1:1.3:3:1:0.8. T5–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures. All legs, except metacoxa, dorsally glabrous, densely punctate with pubescence. Metatibia apically with four pointed teeth.  $1\text{mt}/2-5\text{mt} = 0.70$ .

The new species is similar to *P. irkutensis* but it can be easily distinguished by having antennal scrobes at least partly carinate posteriorly and pronotal crest medially not emarginate.

**TYPE MATERIAL:** 6♀♀, 4♂♂: **HOLOTYPE:** ♀: Russia: Primorsk (20 km from Putzilobki Monakino, Forest), 1993-VI-24–28, Belokobylsk leg (ZISP). **PARATYPES:** 10: 5♀♀, 4♂♂, data as holotype (ZISP); 1♀, Russia: Primorsk (10 km from Partizanska Dubniak), 1979-VII-18, Belokobylskij coll. (ZISP).

**DISTRIBUTION:** Russia: Vladivostok.

**BIOLOGY:** Unknown.

*Paramblynotus belizini*, new species

**FEMALE:** Length 5.0 mm. Head and mesosoma black; antenna, legs, and metasoma brown. Wings transparent.

Upper face distinctly longitudinally carinate except lower part of antennal scrobes glabrate. Median frontal carina distinctly present until middle of lower face. Lower face foveate-reticulate except foveate-rugose laterally. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch; clypeus foveate with sparse pubescence. Gena glabrate-foveate. Vertex entirely longitudinally carinate. Occiput glabrous and sparsely punctate with pubescence.

Anterior flange of pronotum glabrous. Anterior plate of pronotum before lateral pronotal carinae glabrate with dense setigerous punctures set in rows. Lateral pronotal carina distinct, except dorsomedially. Lateral surface of pronotum foveate-reticulate. Median pronotal crest slightly raised medially, medially with a small but distinct emargina-

tion. Dorsal pronotal area transversely costate, and complete to end of dorsal posterior margin of pronotum and transversely carinate. Mesoscutum foveate-reticulate with foveae set in rows between distinct, transverse costae. Mesoscutellum foveate-reticulate; sloping posterolaterally and posteromedially raised into a low hump. Mesopleural triangle distinctly impressed and pubescent. Upper mesopleuron glabrous; speculum glabrous. Longitudinal mesopleural impression percurrent with several more or less evenly distributed transverse costae. Lower mesopleuron glabrous. Metanotal-propodeal complex, except upper metepisternum glabrous, foveate-rugose and densely pubescent. Lateral propodeal carina percurrent and slightly curved laterally; median propodeal area areolate-reticulate.

Abdominal petiole half as long as wide in lateral view. Relative length of T3–8: 1.7:1:1:2.3:1:1. T4–8 densely finely punctate. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, pointed teeth.  $1\text{mt}/2-5\text{mt} = 0.75$ .

**DIAGNOSIS:** The new species is similar to *P. scaber* but it can be distinguished by its glabrate-foveate gena, narrow and distinct median emargination of pronotal crest, foveate-reticulate lateral surface of pronotum, areolate-reticulate median propodeal area, and reduced to almost invisible Rs+M vein of forewing. In comparison, the latter has gena foveate-rugose, lower median pronotal crest with a broader and indistinct emargination, lateral surface of pronotum foveate-reticulate with broken oblique carinae, and a distinct Rs+M vein of forewing.

**TYPE MATERIAL:** HOLOTYPE: ♀, Russia: Vladivostok (Sedanka), 1930–VI–29 (NHRM).

**DISTRIBUTION:** Russia: Vladivostok.

**BIOLOGY:** Unknown.

*Paramblynotus irkutensis* Liu and Kovalev,  
new species

**FEMALE:** Length 4.5 mm. Body black entirely, except upper mesopleuron and speculum and legs dark brown. Wings transparent.

Upper face with finely rugose lateral areas separated by distinct longitudinal carinae from the glabrous antennal scrobes. Median frontal carina short, present distinctly between antennal sockets until one-fourth of lower face and continued flattened to clypeus, and bifurcated posteriorly to delimit a small glabrous triangular area anterior to anterior ocellus. Lower face foveate-reticulate. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch; clypeus foveate with pubescence. Gena foveate with sparse pubescence. Vertex foveate-reticulate and laterally with a few secondary longitudinal carinae. Occiput glabrous and sparsely punctate with pubescence.

Anterior flange of pronotum glabrous. Anterior plate of pronotum before lateral pronotal carinae densely punctate with pubescence. Lateral pronotal carina distinct except dorsomedially. Lateral surface of pronotum foveate-reticulate. Pronotal crest distinct and distinctly emarginate medially. Dorsal pronotal area transversely costate and complete to end of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate with foveae set in rows between low transverse costae. Mesoscutellum foveate-reticulate; sloping posterolaterally and posteromedially raised into a low hump. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous mostly and punctate anteriorly; speculum glabrous. Longitudinal mesopleural impression percurrent with several more or less evenly distributed transverse costae. Lower mesopleuron glabrous with sparse pubescence. Metanotal-propodeal complex mostly foveate-rugose with dense pubescence and glabrous in upper metepisternum. Lateral propodeal carina percurrent and distinctly curved laterally; median propodeal area areolate-reticulate.

Abdominal petiole half as long as wide in lateral view. Relative length of T3–8: 1.5:1:1:2:0.8:0.8. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four pointed teeth.  $1\text{mt}/2-5\text{mt} = 0.60$ .

**DIAGNOSIS:** The new species is similar to *P. atratus* but it can be easily distinguished by the following characters: antennal scrobes

glabrous, and pronotal crest medially distinctly raised with a narrow, distinct emargination.

TYPE MATERIAL: HOLOTYPE: ♀, Russia: Irkutsk, B. Yakovlev coll. (ZISP).

DISTRIBUTION: Russia: Irkutsk.

*Paramblynotus marginatus* Liu and Kovalev,  
new species

FEMALE: Length 4.0 mm. Body black almost entirely, only metasoma anteriorly and posteroventrally and legs dark brown. Wings transparent.

Upper face longitudinally carinate laterally; antennal scrobe glabrous and densely punctate. Median frontal carina distinctly present between antennal sockets and diverging posteriorly to delimit a glabrous triangular area anterior to anterior ocellus. Lower face entirely foveate-rugose. Clypeopleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus slightly raised medially, foveate-rugose, and pubescent anteriorly. Anterior tentorial pits distinct. Gena foveate-reticulate with dense pubescence. Vertex foveate-reticulate, and foveae set in rows between longitudinal carinae. Occiput glabrous; sparsely punctate with pubescence.

Anterior flange of pronotum glabrous. Anterior plate of pronotum before lateral pronotal carinae glabrate and sparsely punctate with pubescence anteriorly, and mostly coarsely and densely punctate with pubescence. Pronotum dorsomedially strongly raised, slightly higher than the highest point of mesoscutum in lateral view. Pronotal crest distinctly raised and medially not emarginate. Lateral pronotal carina distinct, extending dorsomedially to nearly meet pronotal crest. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area transversely costate and complete to end of dorsal posterior margin of pronotum, but narrowed distinctly posteriorly. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Mesoscutellum foveate-reticulate; sloping posterolaterally and strongly raised posteromedially, making dorsal surface of mesoscutellum almost flat in lateral view. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous ex-

cept anteriorly punctate with pubescence; speculum glabrous. Longitudinal mesopleural impression percurrent with several more or less evenly distributed transverse costae. Lower mesopleuron glabrous with sparse pubescence. Metanotal-propodeal complex foveate-rugose with dense pubescence, except upper metepisternum glabrous. Lateral propodeal carina strongly curved laterally and medially indistinct; median propodeal area areolate-reticulate.

Abdominal petiole 0.6 times as long as wide in lateral view. Relative length of T3–8: 2:1:1.2:3.5:1:1. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures set in one or two rows. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, pointed teeth.  $1mt/2-5mt = 0.75$ .

DIAGNOSIS: The new species is similar to *P. pausatus*, n.sp. but it can be easily distinguished by the following characters: pronotal crest medially not emarginate, gena glabrate posteriorly at lower part, and coarsely punctate elsewhere, and T6 about 3.5 times as long as T4.

TYPE MATERIAL: HOLOTYPE: ♀, Russia: Primorsk, Kegrovaya, 1976-VIII-24, Storonsa coll. (ZISP).

DISTRIBUTION: Russia: Primorsk.

*Paramblynotus pausatus* Liu and Kovalev,  
new species

FEMALE: Length 3.4 mm. Body black entirely, except antenna and legs dark brown. Wings transparent, slightly tinted yellow and more so in marginal and submarginal cells.

Upper face asperous laterally; antennal scrobe densely punctate with scarce longitudinal carinae posteriorly. Median frontal carina distinctly present between antennal sockets and bifurcated posteriorly to delimit a glabrous triangular area anterior to anterior ocellus. A second carina parallel and laterad to the divergent carina is also present. Vertex foveate-reticulate. Lower face and clypeus entirely foveate-rugose. Clypeopleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Anterior tentorial pits distinct. Gena foveate-rugose.



Occiput glabrous; sparsely punctate with pubescence.

Anterior flange of pronotum irregularly carinate longitudinally. Anterior plate of pronotum before lateral pronotal carinae glabrous and densely punctate with pubescence. Pronotum dorsomedially strongly raised, in lateral view slightly higher than the highest point of mesoscutum. Pronotal crest distinctly raised and medially with a distinct triangular emargination. Lateral pronotal carina distinct, almost meeting pronotal crest dorsomedially. Lateral surface of pronotum coarsely foveate-reticulate. Dorsal pronotal area complete to end of dorsal posterior margin of pronotum and narrowed toward the rear, transversely costate with foveae throughout. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Mesoscutellum foveate-reticulate; sloping posterolaterally and strongly raised posteromedially so that dorsal surface of mesoscutellum is almost flat in lateral view. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous except foveate most anteriorly; speculum glabrous. Longitudinal mesopleural impression percurrent with several more or less evenly distributed transverse costae. Lower mesopleuron glabrous. Metanotal-propodeal complex foveate-rugose and densely pubescent, except upper metepisternum largely glabrous. Lateral propodeal carina strongly curved laterally; median propodeal area with two transverse carinae and one longitudinal carina in anterior half, and with two longitudinal carinae posteriorly.

Abdominal petiole 0.5 times as long as wide in lateral view. Relative length of T3–8: 1.8:1:1.2:2.5:0.8:0.8. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures set in one or two rows. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four pointed teeth.  $1\text{mt}/2\text{--}5\text{mt} = 0.75$ .

**DIAGNOSIS:** The new species is similar to *P. marginatus*, n.sp., but can be easily distinguished by the following characters: pronotal crest medially with a distinct triangular emargination; T6 about 2.5 times as long as T4; wings slightly tinted yellow. The

species is also distinguished from all other species of the *scaber* group by the shape of the T6 and T7; lateroposterior margin of T6 and T7 is almost straight in *P. pausatus*, but it is distinctly curved in the other species.

**TYPE MATERIAL:** HOLOTYPE: ♀, Russia: Primorsk, Partizansk, 1975-VII-24, Krivagutzkaya coll. (ZISP).

**DISTRIBUTION:** Russia: Primorsk.

*Paramblynotus pronus* Liu and Kovalev,  
new species

**FEMALE:** Length 4.2 mm. Body black entirely except antenna and legs dark brown, T3 ventrally brown. Wings transparent, slightly tinted yellow and more so in marginal and submarginal cells.

Upper face longitudinally carinate laterally; antennal scrobe densely punctate and scarcely carinate posteriorly. Median frontal carina present between antennal sockets and bifurcated posteriorly to delimit a glabrous triangular area anterior to anterior ocellus. Antennal scrobes densely punctate and longitudinally carinate posteriorly. Lower face and clypeus entirely foveate- to punctate-rugose. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Gena glabrate and mostly densely foveate, and foveate-rugose in lower part. Vertex foveate-reticulate; foveae often partially fused with each other longitudinally. Occiput glabrous; sparsely punctate with pubescence.

Anterior flange of pronotum carinate longitudinally. Anterior plate of pronotum before lateral pronotal carinae glabrous and densely punctate with pubescence. Pronotum dorsomedially prominently raised into a peak, in lateral view distinctly higher than the highest point of mesoscutum. Pronotal crest distinctly raised and medially with a distinct triangular emargination. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area transversely costate, reaching to end of dorsal posterior margin of pronotum, but become almost indistinguishable from lateral surface as dorsal pronotal carina diminishes posteriorly. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae.



Scutellar foveae further divided by submedian longitudinal carinae weaker than median carina. Mesoscutellum foveate-reticulate, sloping slowly posteriorly with dorsal surface oblique in lateral view. Posterior margin of mesoscutellum truncate with a slight emargination in dorsal view. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous except foveate most anteriorly; speculum glabrous. Longitudinal mesopleural impression percurrent with several transverse costae distributed more or less evenly. Lower mesopleuron glabrous. Metanotal-propodeal complex foveate-rugose and densely pubescent, except upper metepisternum largely glabrous. Lateral propodeal carina strongly curved laterally; transverse carina of median propodeal area bifurcated laterally to form on each side one large fovea with the lateral propodeal carina; median longitudinal carina only present prior to the transverse carina.

Abdominal petiole 0.5 times as long as wide in lateral view. Relative length of T3–8: 1.6:1.1:2.0:0.8:0.6. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures set in one or two rows. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, pointed teeth.  $1mt/2-5mt = 0.75$ .

**DIAGNOSIS:** The new species is similar to *P. liaoi*, n.sp. They differ from the other species of the *scaber* group by pronotum being prominently raised dorsomedially and scutellar foveae further divided by submedian longitudinal carinae weaker than median carina. The new species can be further distinguished from *P. liaoi* by the following characters: genae mostly foveate to punctate, with some short carinae posteriorly and ventrally; mesoscutellum truncate posteriorly with a slight emargination; length of marginal cell 2.0 times width.

**TYPE MATERIAL:** HOLOTYPE: ♀, Russia: Primorsk, Shkotovsk, 1975-VII-22, Krivagutzkaya coll. (ZISP).

**DISTRIBUTION:** Russia: Primorsk.

*Paramblynotus liaoi*, new species

**FEMALE:** Length 4.5 mm. Body black entirely except antenna and legs dark brown,

T3 ventrally brown. Wings transparent, slightly tinted yellow and more so in marginal and submarginal cells.

Upper face asperous laterally; antennal scrobe densely punctate and lightly longitudinally carinate posteriorly. Median frontal carina present between antennal sockets and bifurcated posteriorly to delimit a glabrous triangular area beneath anterior ocellus. Lower face and clypeus entirely foveate- to punctate-rugose. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Gena foveate-rugose. Vertex foveate-reticulate; foveae often partially fused with each other longitudinally. Occiput glabrous; sparsely punctate with pubescence.

Anterior flange of pronotum carinate longitudinally. Anterior plate of pronotum before lateral pronotal carinae coarsely and densely punctate with pubescence. Pronotum dorsomedially prominently raised into a peak, in lateral view distinctly higher than the highest point of mesoscutum. Pronotal crest distinctly raised and medially with a distinct triangular emargination. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area transversely costate, reaching to end of dorsal posterior margin of pronotum, but becoming almost indistinguishable from lateral surface as dorsal pronotal carina diminishes posteriorly. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Scutellar foveae divided by submedian longitudinal carinae weaker than median carina. Mesoscutellum foveate-reticulate; sloping posteriorly; dorsal surface of mesoscutellum obliquely flat in lateral view. Posterior margin of mesoscutellum rounded in dorsal view. Mesopleural triangle distinctly depressed and pubescent. Upper mesopleuron glabrous except foveate at most anterior part; speculum glabrous. Longitudinal mesopleural impression percurrent with several more or less evenly distributed transverse costae. Lower mesopleuron glabrous. Metanotal-propodeal complex foveate-rugose with dense pubescence except upper metepisternum glabrous. Lateral propodeal carina curved laterally; median propodeal area with two transverse carinae; median longitudinal

carina bifurcated posteriorly (behind the 2nd transverse carina).

Abdominal petiole 0.6 times as long as wide in lateral view. Relative length of T3–8: 1.8:1:1:2.5:1:0.8. T4–8 densely finely punctate; T6–8 also with a few slightly larger setigerous punctures set in one or two rows. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, pointed teeth.  $1\text{mt}/2-5\text{mt} = 0.75$ .

**DIAGNOSIS:** The new species is similar to *P. pronus*, n.sp. but can be distinguished by the following characters: genae mostly foveate-rugose; mesoscutellum rounded posteriorly and without emargination; length of marginal cell 2.4 times width.

**TYPE MATERIAL:** HOLOTYPE: ♀, China: Yunnan, Diqing, Chongjianghe (2300 m), 19984-VIII-4, D. Liao coll. (ZICA).

**DISTRIBUTION:** China: Yunnan.

#### *YANGAMBICOLUS* GROUP

The species group is endemic to southern Africa.

**DIAGNOSTIC CHARACTERS:** Body size large to relatively small. Antenna filiform, distinctly enlarged toward apex, and sometimes with the apical segment compressed. Female antenna has 13 segments with F1 distinctly longer than F2. All flagellomeres have placodes, which are short, not as long as the segments, and are densely distributed on each medial to distal segment. Median frontal carina varies in strength. Ocellar plate not well defined laterally by a carina and hardly raised. Eyes not or moderately protruding laterally beyond genae. Occiput glabrous. Pronotal crest moderately raised dorsomedially into broad process. Lateral surfaces of pronotum evenly curved anteroventrally, foveate-reticulate without secondary transverse costae and punctures, and not separated dorsomedially by an extended, less sculptured anterior area. Lateral pronotal carinae weak, present only in ventral two-thirds. Mesoscutum coarsely foveate-reticulate with rough and discontinuous transverse carinae. Mesoscutellum either raised posteriorly and forming a flat dorsal surface and a vertical posterior surface or sloped posteriorly without a distinct pos-

terior vertical surface. Scutellar sulcus divided into two foveae by median longitudinal carina. Axillar area without conspicuous hair tuft. Mesopleural triangle ventrally marked by a smoothly curved or slightly sinuated carina. Upper mesopleural area areolate-reticulate to strongly carinate; speculum strongly or finely longitudinally carinate. Median mesopleural impression absent or present with multiple, equally strong vertical carinae in posterior half. Metepisternum irregularly foveate to areolate in upper half and pubescent ventrally. Dorsoapical dents of metatibia short and blunt; first metatarsomere without apical protuberance. Lateral propodeal carinae incomplete and not raised into strong keel or process; posterior half of propodeum including median propodeal area alveolate-reticulate. Metatarsomere 1 longer than the combined length of mt2–5. Metasoma strongly to moderately compressed laterally. Tergum 7 of female with posterior margin curved dorsolaterally, distinctly exposing T8, and T8 with sparse coarse punctures with hairs.

#### KEY TO SPECIES OF *YANGAMBICOLUS* GROUP

1. Body length about 4 mm. Body color entirely dark. Eyes prominent, protruding distinctly beyond genae. Median frontal carina percurrent in lower face and almost reaching to clypeus. Antennal scrobes rugose. Speculum distinctly longitudinally carinate. Upper mesopleuron foveate-reticulate. Mesoscutellum sloped posteriorly. Wings entirely transparent. Metasoma somewhat, but not strongly, compressed laterally. Metasomal T6 almost about the same size as the three preceding ones. Metasomal sterna 4–6 entirely covered by sternum 3 . . . . . *P. mixtus*, n.sp.
- Body length about 6–10 mm. Body not entirely dark; head and thorax dark and metasoma yellow to brown. Median frontal carina absent in lower face. Antennal scrobes longitudinally carinate entirely. Speculum very finely and superficially carinate. Upper mesopleuron entirely longitudinally costate. Mesoscutellum raised posteriorly, forming a flat dorsal surface. Forewing evenly ferruginous with darker marginal cell and a dark narrow strip along anterior-interior margin of the first submarginal cell. Metasoma strongly compressed laterally. Metasomal T6 distinctly larger than any of the 3 preceding ones.

- Metasomal sterna 4–6 not covered by sternum 3 and exposed . . . . . 2
2. Face evenly curved in lateral view. Genae ventrally strongly expanded posteriorly. Median mesopleural impression distinct. Lower mesopleuron densely punctate with pubescence. Apical teeth of metatibia rounded apically;  $1mt/2-5mt = 2.0$  . . . *P. alveolatus*, n.sp.
- Face distinctly raised medially and curved inward ventrally in lateral view. Median mesopleural impression usually obscured by extension of longitudinal carinae in upper mesopleuron. Lower mesopleuron glabrate and sparsely punctate with sparse pubescence. Apical teeth of metatibia pointed apically;  $1mt/2-5mt = 1.5$  . . . . . *P. yangambicolus*

*Paramblynotus mixtus*, new species

FEMALE: Length 4 mm. Body entirely dark; antennae and legs dark brown. Wings clear.  $1tm/2-5tm = 1.1$ .

Head, in profile, medially not distinctly raised anteriorly. Vertex foveate-reticulate. Median frontal carina low, dorsally slightly flattened, bifurcated posteriorly to delimit a glabrous triangular area below anterior ocellus, and ventrally extended in lower face to the level of lower margin of eye. Eye extended laterally beyond outer margin of gena. Upper face foveate laterally; antennal scrobe foveate rugose. Lower face and clypeus entirely foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus straight, not forming smoothly curved arch. Gena foveate-reticulate. Occiput glabrous.

Anterior plate of pronotum before lateral pronotal carinae densely punctate with pubescence. Pronotum dorsomedially distinctly raised, in lateral view height as highest point of mesoscutum. Pronotal crest distinct and medially without emargination. Lateral pronotal carina distinct, nearly meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area foveate, reaching only to middle of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Scutellar foveae subdivided by submedian longitudinal carinae weaker than median carina. Mesoscutellum foveate-reticulate; sloping posteriorly in lateral view; posterior margin round-

ed in dorsal view. Mesopleural triangle ventrally defined by a smoothly curved carina; upper mesopleuron irregularly foveolate-reticulate; median impression percurrent with several vertical carinae; speculum with distinct longitudinal carinae. Metanotal-propodeal complex coarsely foveate-rugose with dense pubescence except nude in upper metepisternum. Lateral propodeal carina indistinguishable except anteriorly; median propodeal area areolate/foveate-reticulate. Rs+M of forewing arising from basal vein at posterior third.

Abdominal petiole 0.4 times as long as wide in lateral view. Relative length of T3–8: 1.7:1:1:0.9:0.15:0.4. T4–8 densely finely punctate; T8 also with a few slightly larger setigerous punctures set in one row. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, pointed teeth.  $1mt/2-5mt = 1.0$ .

MALE: Unknown.

*Paramblynotus mixtus* is distinctly different from the other two species of *yangambicolus* group in a number of characters. Antennae are not laterally compressed distally though enlarged toward apex; median frontal carina ventrally extended almost to clypeus in lower face. Antennal scrobe coarsely rugose. Eye prominent, protruding beyond gena. Mesoscutum anteriorly curved in lateral view; mesoscutellum sloped strongly posteriorly; mesopleural triangle ventrally well defined by a smoothly curved carina; upper mesopleuron irregularly foveolate-reticulate; speculum with distinct and rather strong longitudinal carinae. Wings clear; marginal cell of forewing only slightly longer than submarginal cell. Metasoma oval in profile, almost as long as head and mesosoma combined; terga 3–6 subequal in size dorsally; metasomal sterna 4–6 entirely covered by sternum 3.

TYPE MATERIAL: HOLOTYPE: ♀, Kenya, Ukunda, 1968-I-24, K.V. Krombein coll. (USNM).

DISTRIBUTION: Kenya: Ukunda.

ETYMOLOGY: From Latin, *mixtus*, mingled. The name describes the species' possession of a number of obviously plesiomorphic characters that are more frequently found in the other species groups.

*Paramblynotus yangambicolus* (Benoit, 1956)

**FEMALE:** Length 6–9 mm. Head, antennae, mesosoma, and legs black; metasoma pale yellow. Wings ferruginous with marginal cell somewhat darker.  $1\text{mt}/2\text{--}5\text{mt} = 1.4$ .

Head, in profile, medially distinctly raised anteriorly. Vertex foveate-reticulate. Median frontal carina simple and present only between upper margin of antennal sockets to anterior ocellus. Eye laterally not extended beyond outer margin of gena. Upper face glabrous-punctate laterally; antennal scrobe longitudinally carinate. Lower face entirely foveate-reticulate with pubescence. Anterior tentorial pits indistinct. Clypeo-pleurostomal sulcus and epistomal sulcus straight, not forming smoothly curved arch. Clypeus rugose. Gena foveate-reticulate and vertically rugose. Occiput glabrous.

Anterior flange of pronotum longitudinally carinate; anterior plate of pronotum glabrate anteriorly and punctate/foveate with pubescence posteriorly. Pronotum dorsomedially distinctly raised, in lateral view distinctly higher than highest point of mesoscutum. Pronotal crest prominent and medially without emargination. Lateral pronotal carina distinct, not reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate, with slightly glabrate posterior area. Dorsal pronotal area distinctly present only to posterior two-thirds of dorsal posterior margin of pronotum and distinctly transversely carinate anteriorly (carination faint posteriorly). Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Scutellar foveae not subdivided by submedian longitudinal carinae. Mesoscutellum foveate-reticulate; posteriorly raised and projected into a truncate lamella with a slight emargination in dorsal view. Mesopleural triangle ventrally defined by a rather smoothly curved carina; upper mesopleuron longitudinally carinate; median impression at least partly absent; speculum finely longitudinally carinate. Metanotal-propodeal complex coarsely foveate-rugose with dense pubescence. Lateral propodeal carina distinct anteriorly and inseparable from the longitudinal carinae posteriorly; median propodeal area areolate-reticulate, with a distinct transverse carina across mid-

dle.  $\text{Rs}+\text{M}$  of forewing arising from basal vein at middle.

Abdominal petiole 0.3 times as long as wide in lateral view. Relative length of  $\text{T3--8}$ :  $1.5:1:1:1.8:0.5:0.25$ .  $\text{T4--8}$  densely finely punctate;  $\text{T8}$  also with a few slightly larger setigerous punctures set in one row. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four stout, pointed teeth.  $1\text{mt}/2\text{--}5\text{mt} = 1.5$ .

**MATERIALS EXAMINED:** 6♀♀: MRAC, 1♂(T); NHM, 5♀♀.

**DISTRIBUTION:** Zaire: Yangambi; Uganda: Mpanga, Itwala Forest, and Kawanda.

**BIOLOGY:** Benoit (1956) stated in his original description of the species that the holotype was captured on a dead tree trunk of *Drypetes gossweileri*, which belongs to Euphorbiaceae. The two specimens from Mpanga, Uganda, bear labels reading “Lepidoptera”; the two specimens from Itwala Forest, Uganda, bear labels reading “ex. Coleoptera”.

*Paramblynotus alveolatus*, new species

**FEMALE:** Length 10 mm. Head, antennae, mesosoma, and legs black; metasoma brown. Wings ferruginous with marginal cell somewhat darker.  $1\text{mt}/2\text{--}5\text{mt} = 1.62$ .

Head, in profile, medially not distinctly raised anteriorly. Vertex foveate-reticulate; some foveae fused with each other longitudinally. Median frontal carina simple and present only between antennal sockets and anterior ocellus. Eye laterally not extended beyond outer margin of gena. Upper face including antennal scrobe longitudinally carinate. Lower face entirely foveate-rugose with pubescence. Anterior tentorial pits indistinct. Clypeo-pleurostomal sulcus and epistomal sulcus straight, not forming smoothly curved arch. Clypeus foveate-rugose. Gena finely vertically carinate-foveate and otherwise glabrate foveate-reticulate. Occiput glabrous with setigerous punctures.

Anterior flange of pronotum longitudinally carinate; anterior plate of pronotum glabrate anteriorly and punctate/foveate with pubescence posteriorly. Pronotum dorsomedially distinctly raised, in lateral view distinctly higher than highest point of mesoscu-



tum. Pronotal crest prominent and medially without emargination. Lateral pronotal carina distinct, not reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate, and also slightly glabrate posteriorly. Dorsal pronotal area complete to end of dorsal posterior margin of pronotum and distinctly transversely carinate; carination fine anteriorly and coarser posteriorly. Mesoscutum foveate-reticulate with foveae set in rows between transverse costae. Scutellar foveae not subdivided by submedian longitudinal carinae. Dorsal surface of mesoscutellum foveate-reticulate; posteriorly raised and projected into a truncate lamella. Mesopleural triangle ventrally not well defined by smoothly curved carina; upper mesopleuron longitudinally carinate; median impression percurrent; speculum with distinct longitudinal carinae; lower mesopleuron densely punctate and pubescent. Metanotal-propodeal complex coarsely foveate-rugose with dense pubescence. Lateral propodeal carina distinct anteriorly and inseparable from the longitudinal carinae posteriorly; median propodeal area areolate-reticulate. Rs+M of forewing arising from basal vein at middle.

Abdominal petiole 0.3 times as long as wide in lateral view. Relative length of T3–8: 2:1:1:3:0.5:0.2; T4–8 densely finely punctate; T8 also with a few slightly larger setigerous punctures. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four stout, apically round teeth.  $1mt/2-5mt = 2.0$ .

MALE: Unknown.

*Paramblynotus alveolatus* is most similar to *P. yangambiculus*, but it can be distinguished from the latter by the following characters: head in profile medially not distinctly raised anteriorly; median impression of mesopleuron distinct, not obscured by the extension of the longitudinal carinae of upper pleuron; apical teeth of metatibia stout and apically rounded;  $1mt/2-5mt = 2.0$ .

TYPE MATERIAL: HOLOTYPE: ♀, Cameroon, 1898–1899, La Conradt coll. (MNCN).

DISTRIBUTION: Cameroon.

ETYMOLOGY: From Latin, *alveus*, cavity. The name refers to the alveolate sculpture on dorsal surface of the propleuron, which is characteristic of the *yangambiculus* group.

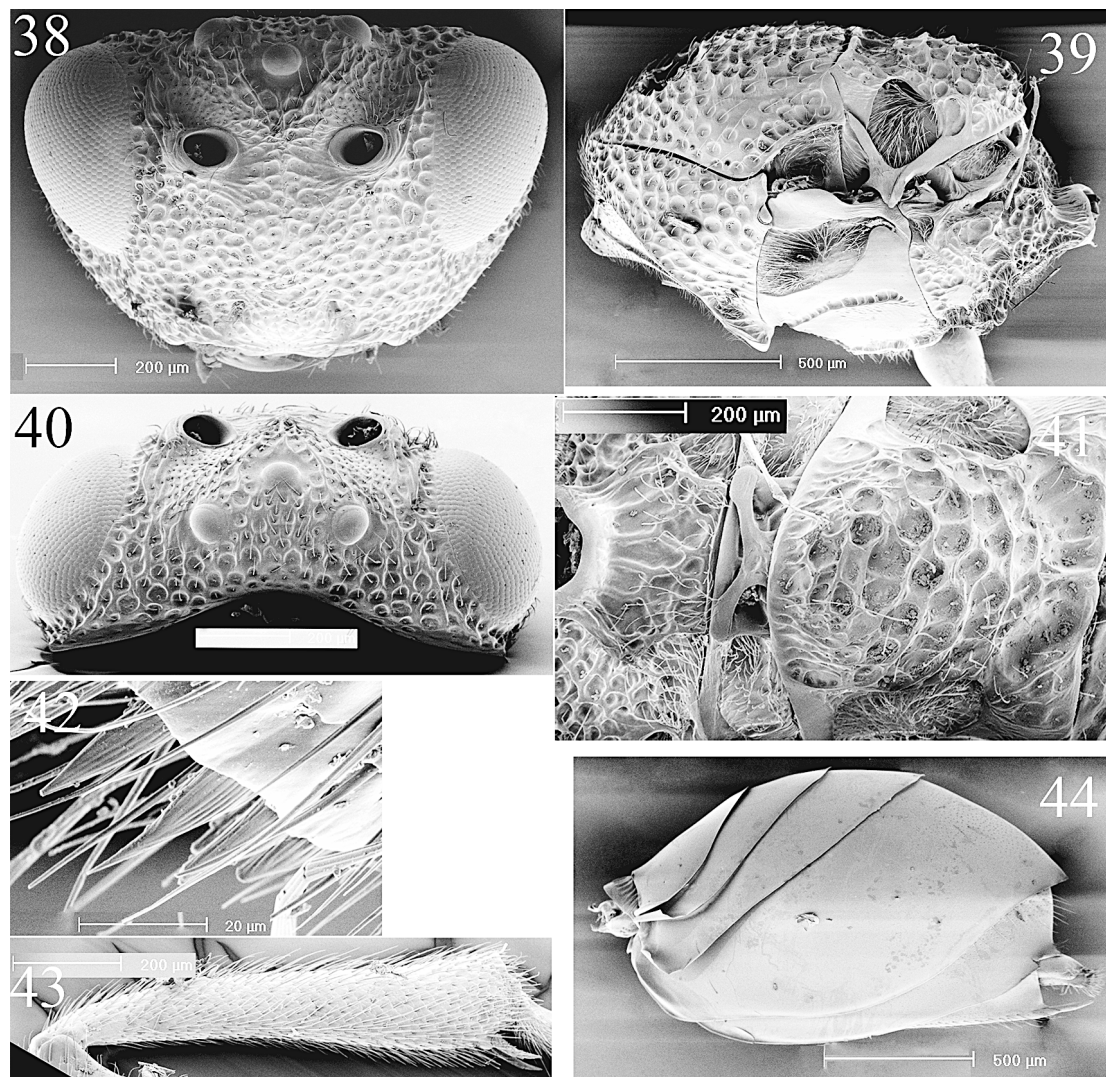
### TRISETOSUS GROUP

figures 38–44

The species group is endemic to southern Africa and is distributed predominantly in mountainous areas, particularly in the east of the continent.

DIAGNOSTIC CHARACTERS: Body relatively small. Antenna cylindrical, usually enlarged toward apex. Female antenna 12- or 13-segmented with F1 shorter than or equal to F2. Placodes of antennal flagellomeres are as long as the segments, relatively evenly spaced, and roughly parallel with each other. Male antennae 14-segmented with 1st flagellomere sinuate laterally. Antennal scrobes are usually defined by distinct lateral carinae. Median frontal carina usually present but sometimes absent. Eyes moderately protruding, laterally always beyond genae (fig. 38). Occiput glabrous. Submedian depression of pronotum laterally open. Pronotal crest not raised dorsomedially (fig. 39), only occasionally raised into a very small but distinct triangular process. Lateral surfaces of pronotum evenly curved anteroventrally, foveate-reticulate without secondary transverse costae and punctures, and dorsomedially separated or not by an extended, less sculptured anterior area (fig. 39). Lateral pronotal carinae weak, not extended to meet pronotal crest. Mesoscutum strongly convex dorsally, foveate-reticulate or transversely carinate with foveae set in rows (fig. 39). Mesoscutellum strongly sloped posteriorly without a distinct posterior vertical surface and foveate-reticulate dorsally. Scutellar sulcus divided into two foveae by median longitudinal carina, or less frequently, divided into several foveae by several submedian longitudinal carinae. Axillar area distinct, but no conspicuous hair tuft. Mesopleural triangle ventrally well defined by a smoothly curved carina. Upper mesopleural area glabrous or sculptured; speculum usually glabrous but sometimes longitudinally carinate. Median mesopleural impression present with multiple, equally strong vertical carinae. Metepisternum foveate to areolate in upper half, pubescent in lower part, and more often than not with a medial elevated glabrous area (fig. 39). Lateral propodeal carinae percurrent and not





Figs. 38–44. *P. fuscipiculus*. 38, Head, front view, ♀; 39, mesosoma, lateral view, ♀; 40, head, dorsal view, ♀; 41, scutellum and propodeum, dorsoposterior view, ♀; 42, end of metatibia showing apical teeth, ♀; 43, metatibia, lateral view, ♀; 44, metasoma, lateral view, ♀.

raised into strong keel or process; median propodeal carina distinctly percurrent (sometimes indistinct) (fig. 41). Metasoma of female moderately compressed laterally; oval in lateral view and about the same length as head and mesosoma combined. Tergum 6 usually much larger than previous ones dorsally. Tergum 7 of female with posterior margin curved or not dorsolaterally, hence exposing or covering T8 (fig. 44).

Sometimes T5 conspicuously expanded dorsally to become larger than T6 dorsally, pushing T6 backward to cover T7 entirely. T6–8 with or without sparse coarse punctures with hairs. Metasomal T5 of male conspicuously enlarged and by far largest among all. Apical teeth of metatibia long and pointed (fig. 42). First metatarsomere without apical protuberance and shorter than the combined length of the

mt2–5. First metatarsomere without apical protuberance.

#### KEY TO SPECIES OF *TRISETOSUS* GROUP

1. Head compressed longitudinally; occiput not concave in dorsal view. Mesoscutum densely foveate, without transverse carinae . . . . . *P. prinslooii*, n.sp.
- Head not compressed longitudinally; occiput distinctly concave in dorsal view (fig. 40). Mesoscutum more or less foveate-reticulate, but always with transverse carinae (fig. 39). .2
2. Median frontal carina absent (fig. 38). T6 of female metasoma the largest and T8 distinctly exposed (fig. 44). Median propodeal area without a strong transverse carina (fig. 41) . . . . . 3
- Median frontal carina present. T6 of female metasoma not always the largest; if T6 the largest, then T8 is not exposed. Median propodeal area with a strong transverse carina. Occasionally variations occur, but never come in combination of features as the above collate. . . . . 7
3. Forewing entirely clear . . . . . 4
- Forewing at least ferruginous in marginal cell. . . . . 5
4. Antennae of female with 11 flagellomeres; apical flagellomere less than twice as long as subapical flagellomere. Pronotal crest medially not raised into a triangular process. Metasoma black . . . . . *P. nigricornis* Benoit, 1956
- Antennae of female with 10 flagellomeres; apical flagellomere longer than twice as long as subapical flagellomere. Pronotal crest medially raised into a small but distinct triangular process. Metasoma brown. . . . . *P. claripennis*, n.sp.
5. Antennal scrobes longitudinally carinate in upper part and glabrous in lower part. Upper mesopleuron glabrous. Metasoma black . . . . . *P. samiatius*, n.sp.
- Antennal scrobes longitudinally carinate entirely. Upper mesopleuron foveate to rugose. Metasoma brown . . . . . 6
6. Vertex longitudinally carinate laterally. Pronotal crest medially raised into a small, distinct rounded triangular process. Scutellar foveae without submedian carina . . . . . *P. maculipennis*, n.sp.
- Vertex foveate-reticulate entirely without longitudinal carination. Pronotal crest smoothly flat, without triangular process. Scutellar foveae subdivided by distinct submedian carinae . . . . . *P. townesorum*, n.sp.
7. Distance between posterior ocelli at most twice as large as the distance between posterior ocellus and eye. Wings clear; Rs+M vein of forewing arising from middle of basalis. Metasomal T5 of female normal, T6 the largest; T7 exposed, almost entirely covering T8 . . . . . 8
- Distance between posterior ocelli at least three times the distance between posterior ocellus and eye. Wings with different color patterns; Rs+M vein of forewing arising from posterior end of basalis. Metasomal T5 of female dorsally expanded, being the largest (at least so dorsally); T7 is largely or entirely covered by T6; T8 exposed. . . . . 16
8. Flagellum distinctly thicker toward apex; median flagellomeres not or slightly constricted toward ends. Antennae with distal flagellomeres 1–3 black, contrasting to the rest, which is yellow . . . . . 9
- Flagellum not distinctly thicker toward apex; median flagellomeres distinctly constricted toward ends. Antennae yellow or gradually becoming somewhat darker toward apex, but never with contrasting colors between distal and proximal flagellomeres. . . . . 10
9. Antennae with distal flagellomeres 1–2 brown. Antennal scrobes finely punctate and without longitudinal carinae posteriorly. Metacoxa ventrally expanded to form a triangular lobular process . . . . . *P. coxatus*, n.sp.
- Antennae with distal flagellomeres 1–2 black. Antennal scrobes heavily and densely punctate and with longitudinal carinae posteriorly. Metacoxa ventrally not expanded to form a triangular lobular process. . . . . *P. fuscipiculus*, n.sp.
10. Ocellar plate of head not defined by lateral carinae, and without a small, triangular glabrous area beneath anterior ocellus. . . . . *P. trisetosus* Benoit, 1956
- Ocellar plate of head well defined by lateral carinae, with a small, triangular glabrous area beneath anterior ocellus. . . . . 11
11. Vertex with distinct longitudinal carination . . . . . 12
- Vertex without distinct longitudinal carination . . . . . 14
12. Median frontal carina almost extending to clypeus. Ocellar plate with a row of relatively uniform, large foveae along the lateral carinae delimiting the plate . . . . . *P. carinatus*, n.sp.
- Median frontal carina not or slightly extending in lower face. Ocellar plate delimited only by a simple lateral carina. . . . . 13
13. Lateral surface of pronotum longitudinally costate in lower part. Lateral propodeal carinae medially strongly curved. Nucha

- dorsally longitudinally carinate. . . . .  
 . . . . . *P. kekenboschi*, n.sp.
- Lateral surface of pronotum without longitudinal costa in lower part. Lateral propodeal carinae nearly parallel. Nucha dorsally glabrate. . . . . *P. zairensis*, n.sp.
14. Median frontal carina not distinctly extending in lower face. Head and mesosoma black. Rs and Rs+M veins of forewing distinct and brown in color. . . . . *P. jacksoni*, n.sp.
- Median frontal carina distinctly extending to middle of lower face. Head and mesosoma brown to dark brown. Rs and Rs+M veins of forewing reduced and pale in color. . . . . 15
15. Antennal scrobes not distinctly depressed. Mesoscutum foveate-reticulate. Head, pronotum, mesoscutum, and mesoscutellum dark brown. Antenna yellow. Lateral occipital carinae well developed and crestlike. Median propodeal area glabrate. . . . .  
 . . . . . *P. cameroonensis*, n.sp.
- Antennal scrobes distinctly depressed. Mesoscutum transversely costate with foveae set in between. Head, pronotum, mesonotum, and mesoscutellum reddish brown. Antenna black except basal two segments yellow. Lateral occipital carinae not crestlike. Median propodeal area areolate-reticulate. . . . .  
 . . . . . *P. rwandensis*, n.sp.
16. Wings slightly and evenly tinted. . . . .  
 . . . . . *P. immaculatus*, n.sp.
- Wings with large brown to dark brown macula. . . . . 17
17. Upper mesopleuron foveate-rugose. . . . .  
 . . . . . *P. minutus*, n.sp.
- Upper mesopleuron glabrous. . . . . 18
18. Vertex diagonally carinate entirely or heavily punctate medially and diagonally carinate laterally. . . . . 19
- Vertex generally glabrate to glabrous with sparse punctures, and sometimes slightly rugose laterally. . . . . 20
19. Vertex entirely diagonally carinate. Forewing clear basally and distally with a broad medial smoky band across the marginal and submarginal cells. Metasomal T7 of female almost covered by T6. . . . . *P. vannoorti*, n.sp.
- Vertex heavily punctate medially and diagonally carinate laterally. Forewing clear in distal two-fifths and ferruginous basally. Metasomal T7 of female distinctly exposed. . . . . *P. sculptus*, n.sp.
20. Lateral propodeal carinae straight and percurrent; medial propodeal area with one straight and percurrent longitudinal carina. . . . .  
 . . . . . *P. diminutus*, n.sp.
- Lateral propodeal carinae discontinuous, medially interrupted by a large fovea; medial propodeal area with more than one nonpercurrent longitudinal carinae. . . . . 21
21. Forewing ferruginous only medially, and clear both proximally and distally. Metasomal T7 of female only slightly exposed, only 1:15 as long as T6 as measured medially on lateral sides. . . . . *P. angolensis*, n.sp.
- Forewing clear only distally, and ferruginous in basal two-thirds. Metasomal T7 distinctly visible, about 1:2.5 as long as T6 as measured along middle of lateral sides. . . . .  
 . . . . . *P. antistatus*, n.sp.

### *Paramblynotus prinsloo*, new species

**FEMALE:** Length 4.5 mm. Head, antennae, and mesosoma mostly black; mandibles, upper part of lateral surface of pronotum, propodeum, metasoma, and legs red brown. Wings clear.

Head strongly compressed longitudinally, occiput only slightly concave in dorsal view. Ocellar plate not obviously raised and not defined laterally by carinae. Antennal scrobe not defined by lateral carinae. Upper face glabrous and punctate-foveate entirely. Median frontal carina only shortly present between antennal sockets and two lateral carinae branching from it at level of upper margin of antennal socket toward (reaching or not) posterior ocellus. Vertex glabrous; sparsely punctate anteriorly and rather densely foveate posteriorly. Eye prominent, laterally extended much beyond outer margin of gena. Lower face entirely punctate-foveate-rugose with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus foveate-reticulate. Gena glabrous and moderately densely foveate/punctate. Occiput glabrous with setigerous punctures.

Anterior flange of pronotum glabrate; anterior plate of pronotum foveate-reticulate with pubescence, and posteriorly also longitudinally carinate. Pronotum dorsomedially not distinctly raised. Pronotal crest medially without emargination. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate, and also somewhat glabrate posteriorly and ventrally. Dorsal pronotal area glabrous and complete to end of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate, not transversely costate.



Scutellar sulcus divided by several submedian longitudinal carinae. Dorsal surface of mesoscutellum foveate-reticulate; posteriorly sloping gradually. Mesopleural triangle ventrally well defined by smoothly curved carina; upper mesopleuron foveate-reticulate; median impression percurrent with evenly spaced transverse carinae; speculum elevated and glabrous. Metanotal-propodeal complex coarsely foveate-rugose with dense pubescence. Propodeum not protruding posteriorly; postsubpleuron short. Lateral propodeal carina percurrent, distinctly curved medially, and forming a right angle with dorsal surface of nucha in lateral view; median propodeal carina percurrent and crossed by two transverse carinae. Rs+M of forewing nebulous, arising from basal vein at posterior two-thirds. Marginal and submarginal cells of forewing short; marginal cell 1.65 times as long as wide. Bulla on Sc+R<sub>1</sub> distinct.

Abdominal petiole 0.3 times as long as wide in lateral view. Posterior margin of T7 of metasoma concave, exposing T8. Relative length of T3–8: 1.8:1:1.4:4.2:0.8:0.8; T4–8 densely finely punctate; T6–8 also with a band of larger setigerous punctures. All legs densely punctate with pubescence except femora sparsely so and metacoxa dorsally glabrous. Metatibia apically with four long, slender, apically pointed teeth.  $1mt/2-5mt = 0.45$ .

MALE: Unknown.

*Paramblynotus prinsloo* is unique among all species of *Paramblynotus* in (1) head strongly compressed longitudinally, occiput only slightly concave in dorsal view, and (2) propodeum not protruding posteriorly with lateral propodeal carinae forming a right angle with dorsal surface of nucha in lateral view; postsubpleuron short. This species is also unique among other species of the *trisetosus* group in (1) vertex, upper face, and genae glabrate-punctate with hairs; (2) mesoscutum foveate, without transverse costae; and (3) upper mesopleuron densely punctate with hairs in anterior half.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa, De Wildt, 1979-iv, G.L. Prinsloo coll. (PPRI).

DISTRIBUTION: South Africa.

ETYMOLOGY: The species is named after its collector Gerhard Prinsloo.

*Paramblynotus nigricornis* Benoit, 1956

FEMALE: Length 3 mm. Head and mesosoma black; antenna, legs, and metasoma brown. Wings clear.

Antenna 13-segmented with apical flagellomere less than twice the length of the subapical flagellomere. Ocellar plate distinctly raised. Vertex foveate-reticulate. Antennal scrobes longitudinally carinate above and glabrous below. Gena coarsely sculptured, rugose to rugulose. Clypeus diagonally carinate. Pronotal crest medially not raised into a triangular process. Upper mesopleuron foveate. Scutellar sulcus divided by a several longitudinal carinae. Metepisternum alveolate to rugose with dense pubescence in lower part, without elevated glabrous area. T6 of female metasoma the largest among all terga, lateral margin of T7 concave, T8 distinctly exposed.  $1mt/2-5mt = 0.65$ .

MALE: Unknown.

*Paramblynotus nigricornis* forms a distinct, monophyletic clade with *P. samiat*, *P. claripennis*, *P. maculipennis*, and *P. townesorum* within the *trisetosus* group. They are easily separated from the rest of the species group by (1) ocellar plate distinctly raised; (2) T6 of female metasoma the largest, lateral margin of T7 concave, T8 distinctly exposed; (3) gena coarsely sculptured, rugose to rugulose; and (4) metepisternum without elevated nude area. Among the five species, *P. nigricornis* and *P. claripennis* are separated from the rest by having clear wings. In addition, *P. nigricornis* is unique among the five species in that it has 13-segmented antenna with apical flagellomere less than twice the length of the subapical one.

MATERIAL EXAMINED: MRAC: 1♀ (holotype, one antenna and wings from one side are mounted on separate slide).

DISTRIBUTION: Zaire: Kivu.

*Paramblynotus samiat*, new species

FEMALE: Length 2.8 mm. Head and mesosoma dark; antenna, legs, and metasoma dark brown. Wings transparent; forewing with marginal and submarginal cells ferruginous.

Vertex foveate-reticulate and longitudinally carinate. Eye prominent, laterally extended

much beyond outer margin of gena. Ocellar plate raised and defined laterally by an irregular carina lined along interior side by a row of irregular foveae. Upper face punctate-rugose laterally; antennal scrobe mostly longitudinally carinate and glabrous anteriorly, and laterally defined by a carina. Median frontal carina absent. Lower face entirely foveate-reticulate with pubescence and longitudinally carinate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus diagonally carinate. Gena glabrate-foveate and horizontally rugose in middle third. Occiput glabrous.

Anterior plate of pronotum foveate-reticulate with pubescence. Pronotum dorsomedially not distinctly raised; pronotal crest medially raised into a small, triangular process. Lateral pronotal carina distinct, continuous dorsomedially, but not reaching pronotal crest. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area weakly carinate diagonally, narrowing posteriorly to reach to about two-thirds of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate, foveae set in rows between transverse costae. Scutellar sulcus divided by a median and two submedian longitudinal carinae. Dorsal surface of mesoscutellum foveate-reticulate; sloping gradually posteriorly. Mesopleural triangle ventrally well defined by smoothly curved carina; upper mesopleuron glabrous; median longitudinal impression percurrent with evenly spaced transverse carinae; speculum glabrous. Metanotal-propodeal complex areolate-punctate-rugose with metepisternum distinctly longitudinally rugose in upper part. Lateral propodeal carina percurrent, smoothly curved medially; median longitudinal propodeal carina percurrent and crossed by two transverse carinae. Rs+M of forewing nebulous, arising from basal vein at anterior third. Marginal cell 2.0 times as long as wide. Bulla on Sc+R<sub>1</sub> present.

Abdominal petiole 0.5 times as long as wide in lateral view. Posterior margin of T7 of metasoma only slightly concave, exposing T8 as a small triangle. Relative length of T3–8: 1.5:1:1.3:3.0:0.6:0.4; T4 sparsely finely punctate; T5–8 densely finely punctate; T6–8 also with a band of larger setigerous punctu-

res. All legs densely punctate with pubescence except femora sparsely so and metacoxa dorsally glabrous. Metatibia apically with four slender, apically pointed teeth.  $1\text{mt}/2-5\text{mt} = 0.65$ .

MALE: Unknown.

*Paramblynotus samiatu*s differs from all other species of the *P. nigricornis* clade in that its upper mesopleuron is entirely glabrous.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa, Zululand, Eshowe, 1925-IV-1–22, R.E. Turner coll. (NHM).

DISTRIBUTION: South Africa: Zululand.

ETYMOLOGY: From Latin, *samio*, to polish. The name is coined to describe the glabrous nature of its upper mesopleuron.

#### *Paramblynotus claripennis*, new species

FEMALE: Length 3.0 mm. Head and mesosoma black; antenna and metasoma light brown; legs dark brown. Wings entirely transparent with marginal cell slightly ferruginous.

Antenna 12-segmented. Vertex entirely longitudinally carinate with foveae set between the carinae. Eye prominent, laterally extended much beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina lined along interior side by a row of irregular foveae. Upper face asperous laterally; antennal scrobe longitudinally carinate posteriorly and glabrous anteriorly, and laterally defined by lateral carinae; lateral carinae delimiting ocellar plate extended beyond lower margin of antennal sockets. Median frontal carina present briefly. Lower face roughly foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus longitudinally rugose. Gena horizontally carinate-rugose with foveae. Occiput glabrous.

Anterior plate of pronotum coarsely punctate with pubescence. Pronotum dorsomedially not distinctly raised; pronotal crest medially raised into a small, triangular process. Lateral pronotal carina distinct, not reaching pronotal crest. Lateral surface of pronotum foveate-reticulate with secondary



transverse carination. Dorsal pronotal area foveate, narrowing posteriorly and present along whole length of dorsal posterior margin of pronotum. Mesoscutum foveate-reticulate, foveae set in rows between irregular transverse costae. Scutellar sulcus divided by a median and several submedian longitudinal carinae. Dorsal surface of mesoscutellum areolate-reticulate; sloping gradually posteriorly, but less so posteromedially. Mesopleural triangle ventrally well defined by smoothly curved carina; upper mesopleuron coarsely punctate in anterior half; median longitudinal impression percurrent with evenly spaced transverse carinae; speculum glabrous. Metanotal-propodeal complex areolate-punctate-rugose with metepisternum largely areolate-reticulate, and densely pubescent in lower part. Lateral propodeal carina percurrent, slightly curved medially; median propodeal carina percurrent; median propodeal area otherwise areolate-reticulate. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.5 times as long as wide in lateral view. Posterior margin of T7 of metasoma only slightly concave, only exposing T8 as a small triangle. Relative length of T3-8: 2.0:1.0:1.0:4.0:1.0:0.8; T3-5 glabrous; T6 very finely punctate posterior on half and glabrous anteriorly; T7-8 densely punctate; T6-8 also with small cluster of larger setigerous punctures. All legs densely punctate with pubescence except femora sparsely so and metacoxa dorsally glabrous.

MALE: Unknown.

*Paramblynotus claripennis* differs from all the other species of the *P. nigricornis* clade except *P. nigricornis* by its entirely clear wings. It can be further distinguished from *P. nigricornis* by its entirely carinate vertex, 12-segmented antenna with apical flagellomere more than twice as long as the subapical, and median triangular process raised from pronotal crest.

TYPE MATERIAL: HOLOTYPE: ♀, Uganda, Mpanga, 1960-V-20, K.W. Brown coll. (NHM).

DISTRIBUTION: Uganda: Mpanga.

BIOLOGY: Collection label with the holotype reads "ex Coleoptera".

ETYMOLOGY: From Latin, *claro*, bright, and *penna*, wing. The name describes its entirely transparent wings.

*Paramblynotus maculipennis*, new species

FEMALE: Length 3.5 mm. Head, antenna, and mesosoma black; metasoma brown; legs dark brown. Wings lightly smoky with marginal and submarginal cells deeply ferruginous.

Antenna 12-segmented. Vertex foveate-reticulate with subordinate longitudinal carinate component. Eye prominent, laterally extended much beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina delimiting ocellar plate extended beyond lower margin of antennal sockets; ocellar plate longitudinally carinate anterior to anterior ocellus. Upper face longitudinally carinate laterally; antennal scrobe longitudinally carinate posteriorly and glabrous anteriorly, and laterally defined by lateral carinae. Median frontal carina present from anterior ocellus to slightly beyond lower margin of antennal sockets. Lower face coarsely foveate-reticulate with pubescence. Anterior tentorial pits indistinct. Clypeo-pleurostomal sulcus and epistomal sulcus straight. Clypeus longitudinally carinate. Gena asperous and punctate, with short horizontal carinae close to eye. Occiput glabrous.

Anterior plate of pronotum coarsely punctate with pubescence. Pronotum dorsomedially not distinctly raised; pronotal crest medially raised into a small, triangular process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area foveate, indistinctly transversely carinate, complete along whole length of dorsal posterior margin of pronotum, narrowing posteriorly. Mesoscutum foveate-reticulate with short, indistinct transverse costae. Scutellar sulcus divided only by median longitudinal carinae. Dorsal surface of mesoscutellum areolate-reticulate, slightly sloping posteriorly; posterior margin of mesoscutellum truncate. Mesopleural triangle ventrally well defined by smoothly curved carina. Upper mesopleuron almost entirely coarsely foveate-reticulate except speculum

glabrous; median impression percurrent with evenly spaced transverse carinae. Metanotal-propodeal complex areolate-punctate-rugose with metepisternum largely areolate-reticulate and densely pubescent ventrally. Lateral propodeal carina percurrent, slightly curved medially; median propodeal area with a percurrent median longitudinal carina crossed by a transverse carina. Rs+M of forewing distinct, arising from middle of basal vein. Marginal cell 2.3 times as long as wide. Bulla on Sc+R<sub>1</sub> present.

Abdominal petiole 0.7 times as long as wide in lateral view. Posterior margin of T7 of metasoma only slightly concave, exposing T8 as a small triangle. Relative length of T3–8: 1.7:1.0:1.0:4.0:0.8:0.6; T3–5 glabrous; T6 very finely punctate on posterior half and glabrous anteriorly; T7–8 densely punctate; T6–8 also with small cluster of larger setigerous punctures. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, apically pointed teeth. 1mt/2–5mt = 0.7.

MALE: Unknown.

*Paramblynotus maculipennis* can be easily separated from *P. nigricornis* by its maculate forewings and 12-segmented antennae, from *P. samiatu*s by its foveate-rugose upper mesopleuron, and from *P. townesorum* by its small triangular process raised from pronotal process and scutellar sulcus divided by only median longitudinal carina.

TYPE MATERIAL: HOLOTYPE: ♀, Zaire, Kivu (Goma Borob lac Kiou), 1987-IX-20–22, Ph. Bruneau de Mire coll. (IRCT).

DISTRIBUTION: Zaire: Kivu.

ETYMOLOGY: From Latin, *macula*, mark, and *penna*, wing. The name describes the species' maculate forewing.

#### *Paramblynotus townesorum*, new species

FEMALE: Length 3.0 mm. Head and mesosoma black; antenna dark brown; legs and metasoma brown. Wings transparent, forewing with marginal cell ferruginous.

Antenna 12-segmented. Vertex foveate-reticulate with indistinct subordinate longitudinal carinate component. Eye prominent, laterally extended beyond outer margin of gena. Ocellar plate raised and defined later-

ally by a carina; lateral carina delimiting ocellar plate extended to lower margin of antennal sockets and lined by a row of foveae along interior side; ocellar plate longitudinally carinate with a few scattered foveae before to anterior ocellus and foveate posteriorly. Upper face shagreened laterally; antennal scrobe longitudinally carinate posteriorly and glabrate anteriorly, and defined laterally by a carina. Median frontal carina present very briefly below lower margin of antennal sockets and posteriorly bifurcated to seclude a small, glabrous triangular area beneath anterior ocellus. Lower face coarsely foveate-punctate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus transversely carinate and punctate. Gena longitudinally rugose and densely punctate-foveate. Occiput mostly obliquely carinate and glabrous only medially.

Anterior flange of pronotum very finely transversely carinate. Submedian pronotal depressions large, medially partially fused. Anterior plate of pronotum coarsely punctate with pubescence; punctures set in rows. Pronotum dorsomedially not distinctly raised; pronotal crest medially raised into a small, apically rounded triangular process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area coarsely foveate, indistinctly transversely carinate; complete along whole length of dorsal posterior margin of pronotum, narrowing posteriorly; delimited from lateral surface by a distinct carina only in posterior half. Mesoscutum foveate-reticulate, with short, indistinct transverse costae. Scutellar sulcus divided by several longitudinal carinae. Dorsal surface of mesoscutellum areolate-reticulate and transversely costate; sloping posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina. Upper mesopleuron foveate anteriorly and glabrous posteriorly; speculum glabrous; median impression percurrent with evenly spaced transverse carinae. Metanotal-propodeal complex areolate-rugose; metepisternum areolate-reticulate and nude above and densely pubescent ventrally; propodeum

densely pubescent. Lateral propodeal carina percurrent, slightly curved medially; median propodeal area foveate-punctate with a percurrent median longitudinal carina. Rs+M of forewing distinct, arising from posterior two-fifths of basal vein. Marginal cell 2.4 times as long as wide. Bulla on Sc+R<sub>1</sub> present.

Abdominal petiole 0.8 times as long as wide in lateral view. Posterior margin of T7 of metasoma slightly concave, exposing T8 as a small triangle. Relative length of T3–8: 2.2:1.0:1.0:3.0:0.8:0.3; T3–4 glabrous; T5–7 very finely punctate; T6 also with a row of sparse pubescence; T7–8 sparsely pubescent entirely. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four slender, apically pointed teeth.  $1mt/2-5mt = 0.75$ .

MALE: Unknown.

*Paramblynotus townesorum* is unique among the species of the *trisetosus* group in having occiput mostly obliquely carinate. It is similar to *P. nigricornis*, but it can be further separated from the latter by having 12-segmented antenna in female and ferruginous marginal cell in forewing.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa: Port St. Johns, 1970-XII-12, H. and M. Townes, deposited in the American Entomological Institute, Gainesville, FL (AEI).

DISTRIBUTION: South Africa: Port St. Johns.

ETYMOLOGY: The species is named after the collectors of the species, the late Hymenoptera taxonomist Henry Townes and M. Townes.

*Paramblynotus coxatus*, new species

FEMALE: Length 3.6 mm. Body entirely dark brown to black, legs dark brown. Antenna yellow with apical three flagellomeres black.  $1mt/2-5mt = 0.6$ .

Antenna 13-segmented; flagellum distinctly thicker apically; median flagellomeres slightly constricted toward ends. Vertex foveate reticulate; with only very weak longitudinal carinate component. Eye laterally slightly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina delimiting ocellar plate extended to lower margin of

antennal sockets and lined by a row of foveae along interior side; ocellar plate foveate-reticulate. Upper face densely punctate and longitudinally rugose laterally; antennal scrobe densely punctate and laterally defined by lateral carina. Median frontal carina present from anterior ocellus and upper fourth of lower face. Lower face roughly foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form a rectangle. Clypeus longitudinally carinate and punctate. Gena foveate-reticulate and slightly longitudinally rugose. Occiput glabrous with sparse pubescence.

Anterior flange of pronotum obliquely carinate. Submedian pronotal depressions large, medially partially fused. Anterior plate of pronotum densely punctate with pubescence. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, not meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrous; only present to middle of dorsal posterior margin of pronotum and becoming narrower posteriorly; delimited from lateral surface by a distinct carina. Mesoscutum distinctly arched dorsally, foveate-reticulate, foveae set in rows between transverse costae. Scutellar sulcus divided by a single longitudinal median carina. Dorsal surface of mesoscutellum areolate-reticulate and transversely rugose; sloping posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle defined ventrally by smoothly curved carina. Upper mesopleuron, including speculum, glabrous with a few shallow setigerous punctures anteriorly; median longitudinal impression percurrent with evenly spaced transverse carinae. Metepisternum foveate-reticulate, nude above, with a small elevated glabrous area medially, and pubescent ventrally. Lateral area of propodeum without pubescence, areolate-reticulate anteriorly, and longitudinally rugose posteriorly; lateral propodeal carina percurrent, distinctly curved medially; median propodeal area foveate-punctate with a percurrent median propodeal carina and a weaker parallel submedian carina on each side crossed by a transverse carina. Rs+M of forewing

distinct, arising from posterior two-thirds of basal vein. Marginal cell 2.3 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.5 times as long as wide in lateral view. Relative length of T3–7: 1.6:1.0:1.3:3.0:1.4; T3–5 glabrous; T6 with a row of setigerous punctures; T7 entirely finely punctate with a row of setigerous punctures. T8 completely covered by T7. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metacoxa prominently expanded anteroventrally into a lobular process. Metatibia apically with four small, thin, apically pointed teeth.  $1\text{mt}/2\text{--}5\text{mt} = 0.62$ .

MALE: Unknown.

Within the *trisetosus* group, *P. coxatus* forms a distinct monophyletic clade, the trisetosus clade, with *P. fuscipiculus*, *rwandensis*, *trisetosus*, *zairensis*, *cameroonensis*, *kekenboschi*, *jacksoni*, and *carinatus*. This clade differs from the other species of the trisetosus species group in that (1) upper mesopleuron and speculum glabrous; (2) posterior margin of T7 of female metasoma not emarginate, covering T8 entirely; and (3) metepisternum with a median nude, glabrous area. *P. coxatus* differs from all other *Paramblynotus* species by the presence of anteroventral lobular expansion on its metacoxa and a vertical impression along the posterior margin of the lower mesopleuron. Otherwise, this species is very close to *P. fuscipiculus*.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa: Natal, 1982-I-10–15, J. Londt coll. (CNCI).

DISTRIBUTION: South Africa: Natal.

ETYMOLOGY: From Latin, *coxa*, coxa. The name coined for its unique coxa feature of anteroventral lobular expansion.

***Paramblynotus fuscipiculus*, new species**  
figures 38–44

FEMALE: Length 2.8–4.0 mm. Body entirely black except antennae and legs. Antennae yellow with the apical, sometimes also the subapical flagellomeres, black. Legs yellow.  $1\text{mt}/2\text{--}5\text{mt} = 0.61$ .

Antenna 13-segmented; flagellum distinctly thicker apically. Vertex foveate-reticulate; with very weak longitudinal carinate compo-

nent. Eye laterally slightly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting median frontal carina above antennal sockets and lined by a row of irregular foveae along interior side; ocellar plate foveate-reticulate; median frontal carina present from anterior ocellus and antennal sockets. Upper face foveate laterally; antennal scrobe densely punctate and laterally defined by lateral carina. Lower face foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form a rectangle. Clypeus foveate. Gena foveate-reticulate (figs. 38, 40). Occiput glabrous with sparse pubescence (fig. 40).

Anterior flange of pronotum finely obliquely carinate. Anterior plate of pronotum glabrous anteriorly and densely punctate with pubescence posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, almost meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate (fig. 39). Dorsal pronotal area glabrous, complete to end of posterior margin of pronotum, but very narrow posteriorly, and separated from lateral surface by a distinct carina throughout. Mesoscutum dorsally distinctly arched, foveate-reticulate, foveae set in rows between transverse costae. Scutellar sulcus divided by three parallel, longitudinal carinae. Dorsal surface of mesoscutellum areolate-reticulate and transversely costate; sloping posteriorly; posterior margin rounded in dorsal view (fig. 41). Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous white pubescence. Upper mesopleuron, including speculum glabrous; median longitudinal impression percurrent with evenly spaced transverse carinae. Metepisternum foveate-reticulate and nude above, with a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and strongly curved medially; median propodeal area areolate-reticulate (fig. 41). Rs+M of forewing nebulous, arising from posterior three-fifths of basal vein. Marginal cell 2.4 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.



Abdominal petiole 0.3 times as long as wide in lateral view. Relative length of T3–7: 1.6:1.0:1.0:2.0:0.6; T3–4 glabrous; T5 with very finely punctate; T6 entirely finely punctate except anteriorly and with a row of setigerous punctures; T7 entirely punctate with narrow band of pubescence. T8 completely covered by T7 (fig. 44). All legs densely punctate with pubescence except metacoxa dorsally glabrous. Metatibia apically with four small, thin, apically pointed teeth (figs. 42, 43).  $1\text{mt}/2-5\text{mt} = 0.8$ .

MALE: Unknown.

*Paramblynotus fuscipiculus* is very similar to *P. coxatus* and differs from the latter in (1) metacoxa not expanded anteroventrolly and (2) scutellar sulcus with submedian longitudinal carinae. *P. fuscipiculus* differs from all other species of the *trisetosus* clade except *P. coxatus* by its antennal flagellum of female being distinctly thicker apically and median flagellomeres not constricted toward ends.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa, Cape Province, Alexandria, 1962-II-22 (Acc. P.E. 857) (PPRI). PARATYPES: 4♀♀ (PPRI), collection data as holotype; 2♀♀, collection data as holotype (ZMLU-MS).

ADDITIONAL MATERIAL: 2♀♀, South Africa, Royal Natal National Park, 1971-I-30, H. and M. Townes coll.; 2♀♀, South Africa: Pretoria (Transval), 1971-I-9, H. and M. Townes coll. (AED); 1♀, South Africa, Clarens (28.34S, 28.28E), 1986-I-15–18, J.S. Donaldson coll. (PPRI); 1♀, South Africa, Port St. John, Bondoland, 1923-XI, and 1♀, Zimbabwe, Salisbury (Chishawasha), 1979-IX, A. Watsham coll. (NHM).

DISTRIBUTION: South Africa; Zimbabwe: Salisbury.

ETYMOLOGY: From Latin, *fuscus*, dark, and *apex*, tip. The name describes the species' yellow antenna with black apex.

***Paramblynotus rwandensis*, new species**

FEMALE: Length 3.0 mm. Head, pronotum, mesoscutum, and mesoscutellum yellow brown; other part of mesosoma and metasoma dark brown to black. Antennal flagellum black; scape and pedicel yellow. Legs light yellow except metacoxa and femur dark. Wings completely clear. Head, mesosoma

except mesopleuron, and legs except metafemoral grooves with rather dense silver hairs.

Antenna 13-segmented; flagellum slightly thicker apically; median flagellomeres constricted both proximally and apically. Vertex foveate-reticulate. Eye laterally distinctly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina lined by a row of foveae along interior side; ocellar plate foveate-reticulate. Upper face foveate/punctate laterally; antennal scrobe laterally defined by lateral carina, and mostly densely punctate and longitudinally carinate laterally and posteriorly. Median frontal carina absent. Lower face foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus foveate. Gena foveate-reticulate mostly and rugose vertically. Occiput glabrous with sparse pubescence.

Anterior flange of pronotum finely longitudinally carinate. Anterior plate of pronotum glabrous anteriorly and densely punctate with pubescence posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially raised into a small triangular, apically rounded process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrate; only distinctly present to anterior one-eighth of posterior margin of pronotum. Mesoscutum dorsally distinctly arched, foveate, and with foveae set in rows between transverse costae. Scutellar sulcus divided by a median longitudinal carina and two weaker submedian carinae. Dorsal surface of mesoscutellum areolate-reticulate; sloping posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous gold-tinted pubescence. Upper mesopleuron, including speculum, glabrous with a few shallow setigerous punctures anteriorly; median impression percurrent, glabrous anteriorly, and with evenly spaced transverse carinae in posterior half. Metepisternum foveate-reticulate and nude above, with a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and strongly curved medially; median



propodeal area areolate-reticulate. Rs+M of forewing nebulous proximally, arising from middle of basal vein. Marginal cell 3.0 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.8 times as long as wide in lateral view. Relative length of T3–7: 1.8:1.0:1.2:3.0:1.2; T3–5 glabrous; T6 entirely finely punctate except anteriorly and with a row of setigerous punctures; T7 entirely punctate with narrow band of pubescence. T8 completely covered by T7. All legs densely punctate with pubescence except metacoxa glabrous dorsally. Metatibia apically with four small, thin, apically pointed teeth. 1mt/2–5mt = 0.85.

MALE: Unknown.

*Paramblynotus rwandensis* is similar to *P. cameroonensis*, but it can be distinguished from the latter by the following characters: antennal scrobes distinctly depressed; mesoscutum transversely costate with foveae set in between; head, pronotum, mesonotum, and mesoscutellum red brown; antenna black except basal two segments yellow; lateral occipital carinae not crestlike; and median propodeal area areolate-reticulate.

TYPE MATERIAL: HOLOTYPE: ♀, Rwanda, Nyungwe Forest (2°46'10"S, 29°21'09"E, primary rainforest), 1993-IX-22–24, T. Munyampiwa coll. (CNCI).

DISTRIBUTION: Rwanda.

ETYMOLOGY: The species is named after type locality.

***Paramblynotus trisetosus* Benoit, 1956**

FEMALE: Length 2.1 mm. Body entirely dark brown, antenna and legs yellow brown. Wings clear; marginal and submarginal cells of forewing slightly smoky.

Antenna 13-segmented. Vertex foveate-reticulate with distinct longitudinal carinate component. Antennal scrobes glabrate. Median frontal carina weakly present in upper part of lower face. Anterior tentorial pits invisible. Marginal cell of forewing 2.2 times as long as wide; Rs+M of forewing nebulous, arising from middle of basal vein. Relative length of T3–7: 1.8:1.0:1.1:3.0:1.0. 1mt/2–5mt = 0.53.

*Paramblynotus trisetosus* differs from the other species of the *trisetosus* clade by its ocellar plate laterally not defined by a distinct carina.

MATERIAL EXAMINED: 1♀, Zaire, Bambesa, 1947-I, P.L.G. Benoit coll. (holotype, MRAC). One antenna and wings from one side are mounted on separate slides.

DISTRIBUTION: Zaire.

***Paramblynotus zairensis*, new species**

FEMALE: Length 2.5 mm. Body entirely dark brown, except legs yellow to yellow brown. Wings clear.

Antenna 13-segmented; flagellum thicker apically; median flagellomeres constricted both proximally and apically. Vertex entirely longitudinally carinate. Eye laterally distinctly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting median frontal carina above antennal sockets and lined by a row of irregular foveae along interior side; ocellar plate glabrate anteriorly except for the foveae along lateral carinae and longitudinally carinate posteriorly. Upper face, including antennal scrobes, glarous; antennal scrobe laterally defined by lateral carina. Median frontal carina present weakly from between antennal sockets to upper third of lower face. Lower face foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus foveate. Gena areolate-rugose. Occiput glabrous.

Anterior flange of pronotum glabrous. Anterior plate of pronotum mostly glabrous except densely punctate with pubescence posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area transversely costate; almost complete to end of posterior margin of pronotum. Mesoscutum foveate-reticulate with indistinct transverse costae posteriorly. Mesoscutum dorsally distinctly arched, areolate-reticulate with indistinct transverse costae. Scutellar sulcus divided by a single median longitudinal carina. Dorsal surface of mesoscutellum areolate-reticulate; sloping posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly

curved carina and with white pubescence. Upper mesopleuron, including speculum, glabrous; median longitudinal impression present with transverse carinae posteriorly and reduced anteriorly. Metepisternum foveate-reticulate and nude above, with a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and distinctly curved medially; median propodeal area areolate-reticulate with a percurrent median longitudinal carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide. Bulla on Sc+R<sub>1</sub> weakly present.

Abdominal petiole 0.8 times as long as wide in lateral view. Relative length of T3–7: 1.5:1.0:1.0:3.5:1.0; T3–6 glabrous; T7 sparsely punctate with a few setigerous punctures. T8 completely covered by T7. Front and middle legs sparsely punctate with pubescence; hindleg rather densely punctate with pubescence except metacoxa sparsely punctate with pubescence. Metatibia apically with four small, thin, apically pointed teeth. 1mt/2–5mt = 0.60.

MALE: Unknown.

*Paramblynotus zairensis* is similar to *P. carinatus* and *P. kekenboschi* in vertex with longitudinal carination as the dominant sculpture. *P. zairensis* and *P. kekenboschi* are further separated from *P. carinatus* by (1) median frontal carina extended only to upper third of lower face and (2) ocellar plate laterally defined by simple carinae. *P. zairensis* is distinguished from *P. kekenboschi* by (1) lateral propodeal carinae nearly parallel and (2) nucha dorsally glabrate.

TYPE MATERIAL: HOLOTYPE: ♀, Zaire, P.N.A., Massif Ruwenzori Kalonge (2,210 m), 1952-VIII-26–28, P. Vanschuytbroeck and J. Kekenbosch coll. (NHM).

ADDITIONAL MATERIAL: 1♀, Zaire, P.N.U., R. Kenia (affl. dr. Lusinga, 1,585 m), 1947-XII-19, G.F. de Witte coll. (NHM).

DISTRIBUTION: Zaire.

ETYMOLOGY: The species is named after the type locality.

*Paramblynotus cameroonensis*, new species

FEMALE: Length 2.0 mm. Body brown. Antennae and legs yellow. Head, mesosoma

except mesopleuron, and legs except metapleural grooves with rather dense silver hairs. Wings clear.

Antenna 13-segmented; flagellum thicker apically; median flagellomeres constricted both proximally and apically. Vertex foveate-reticulate with longitudinal carinate component. Eye laterally distinctly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting median frontal carina above antennal sockets and lined by a row of irregular foveae at interior side; ocellar plate foveate-reticulate. Upper face, including antennal scrobes, glabrate and weakly foveate-reticulate; antennal scrobe indistinctly depressed and laterally defined by lateral carina. Median frontal carina present weakly from between antennal sockets to level of lower margin of eyes. Lower face irregularly foveate-reticulate with long pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus punctate. Gena foveate-reticulate anteriorly and longitudinally costate posteriorly. Lateral occipital carina very developed, crestlike. Occiput glabrous.

Anterior flange of pronotum glabrate with faint transverse striation. Anterior plate of pronotum glabrous mostly and punctate with pubescence posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrous, narrow, and complete to end of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and nearly foveate-reticulate with indistinct transverse costae. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate and sloped posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with white pubescence. Upper mesopleuron, including speculum, glabrous; median longitudinal impression percurrent with evenly distributed transverse carinae; lower mesopleuron glabrous and pubescent ventrally. Metepisternum foveate-reticulate and nude above, with

a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and strongly curved medially; median propodeal area glabrate with a percurrent median longitudinal carina. Rs+M of forewing nebulous, arising from posterior middle of basal vein. Marginal cell 3.5 times as long as wide. Bulla on Sc+R<sub>1</sub> weakly present.

Abdominal petiole 0.4 times as long as wide in lateral view and glabrate dorsally. Relative length of T3–7: 1.5:1.0:1.0:4.0:1.0; T3–5 glabrous; T6 glabrous except for a row of setigerous punctures; T7 punctate with a few setigerous punctures. T8 completely covered by T7. Front and middle legs sparsely punctate with pubescence; hindlegs sparsely punctate with pubescence except metacoxa glabrous dorsally and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia small, thin, and pointed apically.  $1\text{mt}/2-5\text{mt} = 0.50$ .

MALE: Unknown.

The new species is similar to *P. rwandensis*, but it differs from the latter in the following characters: antennal scrobes not distinctly depressed; mesoscutum foveate-reticulate; head, pronotum, mesoscutum, and mesoscutellum dark brown; antenna yellow; lateral occipital carinae well developed and crestlike; and median propodeal area glabrate.

TYPE MATERIAL: HOLOTYPE: ♀, Cameroon: Nkoemvon, 1979-XI-19–30, D. Jackson coll. (NHM).

DISTRIBUTION: Cameroon.

ETYMOLOGY: The species is named after the type locality.

*Paramblynotus kekenboschi*, new species

FEMALE: Length 2.5 mm. Body dark brown to black except antenna and legs. Antenna yellow at base and becoming gradually black. Legs yellow.

Antenna 13-segmented; flagellum distinctly thicker apically; median flagellomeres constricted proximally and apically. Vertex foveate-reticulate with distinct longitudinal carinate component. Eye laterally distinctly extended beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting median frontal carina above anten-

nal sockets and lined by a row of irregular foveae along interior side; ocellar plate foveate. Upper face, including antennal scrobes, glabrate with fine punctures and weakly longitudinally carinate posteriorly; antennal scrobe defined by carina laterally. Median frontal carina present weakly from between antennal sockets to clypeus. Lower face foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurosomal sulcus and epistomal sulcus almost form an arch. Clypeus longitudinally carinate with punctures. Gena foveate-rugose. Lateral occipital carina very developed, crestlike. Occiput glabrous.

Anterior plate of pronotum mostly glabrous except punctate with pubescence posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum largely foveate-reticulate, and longitudinally carinate ventrally. Dorsal pronotal area glabrous, narrow, and complete to end of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and foveate-reticulate with foveae set in rows between indistinct transverse costae medially. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate and sloped posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with white pubescence. Upper mesopleuron, including speculum, glabrous; median impression percurrent with evenly distributed transverse carinae; lower mesopleuron glabrous and pubescent ventrally. Metepisternum foveate-reticulate and nude above, with a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral and median propodeal carina distinct only in anterior half before a transverse carina; median propodeal area entirely longitudinally carinate posteriorly. Rs+M of forewing nebulous, arising from posterior middle of basal vein. Marginal cell 2.7 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.75 times as long as wide in lateral view and glabrate dorsally. Relative length of T3–7: 1.4:1.0:1.2:3.6:1.0; T3–4 glabrous; T5 only with a few scattered

punctures; T6 glabrous with a few punctures anteriorly and finely punctate posteriorly; T7 punctate with a row of sparse setigerous punctures. T8 completely covered by T7. Front and middle legs sparsely punctate with pubescence; hindlegs sparsely punctate with pubescence except metacoxa glabrous dorsally and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia small, thin, and pointed apically.  $1mt/2-5mt = 0.56$ .

MALE: Unknown.

*Paramblynotus kekenboschi* is similar to *P. zairensis*, but it can be easily separated from the latter by (1) lateral surface of pronotum longitudinally costate in lower part; (2) lateral propodeal carina distinctly present anteriorly, posterior half of median propodeal area entirely longitudinally carinate; and (3) nucha dorsally longitudinally carinate.

TYPE MATERIAL: HOLOTYPE: ♀, Zaire (P.N.A.): Massif Ruwenzori Kalonge (2,130 m), River Kiondo, aff. Butahu, 1952-VII-31, P. Vanschuytbroeck and J. Kekenbosch coll. (NHM). PARATYPE: 1♀, Zaire (P.N.A.): Massif Ruwenzori Kalonge (2,010 m), River Nyamwamba, aff. Butahu, 1953-II-2, P. Vanschuytbroeck and J. Kekenbosch coll. (NHM).

DISTRIBUTION: Zaire.

ETYMOLOGY: The species is named after one of the two collectors with the simpler last name.

*Paramblynotus jacksoni*, new species

FEMALE: Length 2.5–3.3 mm. Body entirely black except antenna dark brown and legs yellow.

Antenna 13-segmented; flagellum not distinctly thicker apically; median flagellomeres constricted proximally and apically. Vertex foveate-reticulate with distinct longitudinal carinate component. Eye prominent, distinctly extended laterally beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting medially above antennal sockets and lined by a row of irregular foveae along interior side; ocellar plate foveate. Upper face, including antennal scrobes, glabrate and finely punctate, weakly carinate in upper

part; antennal scrobe defined by carina laterally. Median frontal carina absent or weakly present in upper half of lower face. Lower face heavily foveate-reticulate with pubescence. Anterior tentorial pits indistinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus rugose anteriorly and foveate-reticulate posteriorly. Gena foveate-rugose with long pubescence. Lateral occipital carina very developed. Occiput glabrous.

Anterior flange of pronotum finely longitudinally carinate. Anterior plate of pronotum glabrous and sparsely punctate anteriorly, and coarsely punctate posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate except ventral one-fourth longitudinally carinate. Dorsal pronotal area glabrous, only visible until anterior fourth of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and strongly foveate-reticulate with indistinct transverse costae. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate and sloped posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with white pubescence. Upper mesopleuron, including speculum, glabrous; median longitudinal impression percurrent with evenly distributed, reduced transverse carinae; lower mesopleuron glabrous and pubescent ventrally. Metepisternum foveate-reticulate and nude above, with a small elevated glabrous area medially, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and not obviously curved. Median propodeal area glabrate and sparsely punctate; median longitudinal carina percurrent and with a transverse carina anteriorly. Rs+M of forewing distinct and yellow, arising from middle of basal vein. Marginal cell 2.7 times as long as wide. Bulla on Sc+R<sub>1</sub> weakly present.

Abdominal petiole 0.7 times as long as wide in lateral view and glabrate dorsally. Relative length of T3–7: 1.6:1.0:1.0:4.0:1.1; T3–5 glabrous; T6 glabrous except for



setigerous punctures in a row; T7 punctate with a few setigerous punctures in a row. T8 slightly exposed beneath T7. Front and middle legs sparsely punctate with pubescence; hindlegs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia small, thin, and pointed apically.  $1\text{mt}/2-5\text{mt} = 0.55$ .

**MALE:** Length 2.2–3.0 mm. Antenna 14-segmented. Tergum 5 expanded both dorsally and ventrally, but more so ventrally.

*Paramblynotus jacksoni* is similar to *P. cameroonensis* and *P. rwandensis*, but it differs from the latter two species in (1) median frontal carina not distinctly extending in lower face, (2) head and mesosoma black, and (3) Rs and Rs+M veins of forewing distinct and brown. It further differs from *P. cameroonensis* in having longer petiole, and from *P. rwandensis* in having median propodeal area glabrate.

**TYPE MATERIAL:** HOLOTYPE: ♀, Cameroon: Nkoemvon, 1980-XI-2–XII-13, D. Jackson coll. (NHM). PARATYPES: 4♀♀, 2♂♂: 1♂, 1978-IX–XI, other data same as holotype (NHM); 1♀, 1979-VII–VIII, and 3♀♀, 1♂, 1980-XI–XII, other data same as holotype (NHM).

**DISTRIBUTION:** Cameroon.

**BIOLOGY:** Collection label reads (collected along) “forest path”, otherwise unknown.

**ETYMOLOGY:** The species is named after the collector.

*Paramblynotus carinatus*, new species

**FEMALE:** Length 3.2 mm. Body entirely dark brown; legs yellow. Wings clear.

Antenna 13-segmented; flagellum not distinctly thicker apically; median flagellomeres constricted proximally and apically. Vertex foveate-reticulate with distinct longitudinal carinate component. Eye prominent, distinctly extended laterally beyond outer margin of gena. Ocellar plate raised and defined laterally by a carina; lateral carina of ocellar plate meeting medially above antennal sockets and lined by a row of irregular foveae along interior side; ocellar plate foveate; median frontal carina distinct in lower face, reaching to epistomal sulcus and bifurcated poster-

iorly to delimit a glabrous triangular area beneath anterior ocellus. Upper face glabrate laterally and antennal scrobes glabrous; antennal scrobe defined by carina laterally. Lower face coarsely foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form a smoothly curved arch. Clypeus longitudinally carinate anteriorly, glabrous in the middle, and foveate-rugose posteriorly. Gena coarsely foveate-rugose. Lateral occipital carina almost meeting eye dorsally. Occiput glabrous.

Anterior flange of pronotum glabrate. Anterior plate of pronotum glabrous and sparsely punctate anteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate dorsolaterally and longitudinally carinate lateroventrally. Dorsal pronotal area glabrous, reaching end of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and foveate-reticulate with indistinct transverse costae. Scutellar sulcus divided by a median longitudinal carina and two submedian longitudinal carinae; mesoscutellum foveate-reticulate and sloped posteriorly; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with white pubescence. Upper mesopleuron, including speculum, glabrous; median longitudinal impression percurrent with evenly distributed transverse carinae; lower mesopleuron glabrous and pubescent ventrally. Metepisternum foveate-reticulate and nude above, with an elevated glabrous area medially, and conspicuously pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and distinctly curved medially. Median propodeal area glabrate to rugulose; median longitudinal carina percurrent, a transverse carina present anteriorly, and two submedian longitudinal carinae present posterior to transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 2.4 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.6 times as long as wide in lateral view and glabrate dorsally.



Relative length of T3-7: 1.7:1.0:1.0:2.5:1.1; T3-5 glabrous; T6 finely punctate with a few setigerous punctures in a row; T7 punctate with a row of setigerous punctures. T8 entirely covered by T7. Front and middle legs sparsely punctate with pubescence; hind-legs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia long, thin, and pointed apically.  $1\text{mt}/2-5\text{mt} = 0.60$ .

MALE: Unknown.

*Paramblynotus carinatus* is similar to *P. kekenboschi* and *P. zairensis*, but it can be easily separated from them by (1) median frontal carina distinct in lower face, extending beyond lower margin of eyes reaching epistomal sulcus; and (2) ocellar plate with a row of relatively uniform large foveae along lateral carina.

TYPE MATERIAL: HOLOTYPE: ♀, Zaire, P.N.A., Nyasheke, Volley Nyamuragia (1,820 m), 1935-VI-14-26, G.F. de Witte coll. (NHM).

DISTRIBUTION: Zaire.

ETYMOLOGY: From Latin, *carina*, keel. The species name describes the carinate sculpture on the vertex.

*Paramblynotus immaculatus*, new species

FEMALE: Length 1.9 mm. Head and mesosoma black and other body parts dark brown. Wings slightly, evenly ferruginous.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex foveate-reticulate. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli 3.3 times as wide as the distance between posterior ocellus and eye. Ocellar plate slightly raised and not distinctly defined laterally by a carina; the reduced lateral carina of ocellar plate meeting medially above antennal sockets and lined by a row of foveae along interior side; ocellar plate foveate; median frontal carina distinct in lower face, reaching to epistomal sulcus anteriorly and bifurcated posteriorly to delimit a glabrous triangular area beneath anterior ocellus. Upper face glabrate laterally and antennal scrobes glabrous except foveate medially (at the level of anterior ocellus);

antennal scrobe defined by carina laterally. Lower face coarsely foveate-reticulate with pubescence. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus longitudinally carinate. Gena coarsely foveate-rugose. Lateral occipital carina extended dorsally to meet lateral carina of antennal scrobe. Occiput glabrous.

Anterior flange of pronotum finely longitudinally carinate. Submedian pronotal depression fused medially. Anterior plate of pronotum glabrous and punctate. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, meeting pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate dorsolaterally and longitudinally rugose lateroventrally. Dorsal pronotal area glabrate-punctate and reaching to end of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and foveate-reticulate. Scutellar sulcus divided by single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin broadly emarginate in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with white pubescence. Upper mesopleuron glabrous, distinctly depressed; speculum longitudinally carinate; median longitudinal impression percurrent with three unevenly distributed transverse carinae. Lower mesopleuron glabrous; pubescence sparse above and dense ventrally. Metepisternum depressed and nude above, with an oblique, elevated glabrous area across the middle, and conspicuously pubescent ventrally. Propodeum, including median propodeal area, areolate-reticulate; lateral propodeal carina present only anteriorly and median longitudinal carina percurrent. Nucha glabrous. Rs+M of forewing nebulous, arising from posterior end of basal vein. Marginal cell 2.6 times as long as wide. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.36 times as long as wide in lateral view. Relative length of T3-8: 1.3:1.0:2.0:1.2:0:0.4; T3-5 glabrous; T6 finely punctate; T7 almost completely covered by T6 except posterolaterally slightly exposed; T8 punctate with a few foveae. Front and middle legs sparsely punctate with pubescence; hindlegs sparsely punctate with pubes-

cence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia long, thin, and pointed apically.  $1mt/2-5mt = 0.64$ .

MALE: Unknown.

*Paramblynotus immaculatus*, *antistatus*, *scalptus*, *vannoorti*, *diminutus*, *angolensis*, and *minutus* form a very distinct, monophyletic clade within the *trisetosus* group. This clade is characteristic in having (1) very conspicuous anterior tentorial pits; (2) distance between posterior ocelli at least three times as wide as distance between posterior ocellus and eye; (3) speculum longitudinally carinate; (4) T5 of female dorsally expanded and the largest metasomal tergum, T7 largely or entirely covered by T6, T8 exposed; and (5) wings with different color patterns; Rs+M vein of forewing arising from posterior end of basal cell.

*Paramblynotus immaculatus* can be easily separated from the other species of this clade by having (1) wings evenly ferruginous and without darker bands, (2) mesoscutellum posteriorly with a broad emargination, and (3) median frontal carina almost reaching clypeus.

TYPE MATERIAL: HOLOTYPE: ♀, Zaire, Pidigala, 1952-iv-23, H. De Saeger coll. (NHM).

DISTRIBUTION: Zaire.

ETYMOLOGY: From Latin, *im-* not, and *macula*, mark, spot. The name describes the evenly ferruginous wings of the species.

#### *Paramblynotus antistatus*, new species

FEMALE: Length 2.1 mm. Body black to dark brown with antennae and legs yellow to yellow brown. Forewing brown in about basal two-thirds and clear beyond the tip of marginal cell.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex largely glabrous with sparse punctures, slightly rugose laterally. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli 3.0 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised and not defined laterally by a carina; median frontal carina

extended from anterior ocellus to slightly beyond lower margin of antennal sockets. Upper face, including antennal scrobe, coriarius; antennal scrobes only slightly depressed, defined by carina laterally. Lower face coriarius above and transversely rugose with foveae ventrally. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an arch. Clypeus glabrate and weakly longitudinally carinate. Gena coriarius. Lateral occipital carina indistinct beyond vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Submedian pronotal depressions distinctly separated medially. Anterior plate of pronotum glabrate and coarsely punctate. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, not reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrate-punctate and reaching to end of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin round in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and partly with white pubescence. Upper mesopleuron glabrous, distinctly depressed; speculum longitudinally carinate; median impression percurrent with three unevenly distributed transverse carinae. Lower mesopleuron glabrous; pubescence sparse above and dense ventrally. Metepisternum foveate-rugose, nude above and conspicuously pubescent ventrally. Propodeum, including median propodeal area, areolate-reticulate; lateral and median propodeal carinae present only anteriorly; lateral propodeal carina with distinct pubescence dorsally. Nucha glabrous. Rs+M of forewing nebulous, arising from close to posterior end of basal vein. Marginal cell 2.0 times as long as wide, and as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.3 times as long as wide in lateral view. Relative length of T3-8: 1.3:1.0:2.0:1.1:0.4:0.4; T3-4 glabrous; T6-7 punctate; T7 of metasoma distinctly exposed; T8 punctate with a few foveae. Front and

middle legs sparsely punctate with pubescence; hindlegs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely punctate with pubescence. Apical teeth of metatibia long, thin, and pointed apically.  $1mt/2-5mt = 0.55$ .

MALE: Unknown.

*Paramblynotus antistatus* can be divided from the other species of the *immaculatus* clade by its distinctly exposed T7 of female metasoma and its smooth gena, except *P. scalptus*. However, *P. antistatus* differs from *P. scalptus* in having vertex and gena glabrous.

TYPE MATERIAL: HOLOTYPE: ♀, Namibia, Windhoek, Regenstein (15 mi SSW), 1972-IV-9 (NHM).

DISTRIBUTION: Namibia, Windhoek.

ETYMOLOGY: From Latin, *anti-*, against, and *estat*, position, standing. This name was coined because of the glabrous vertex and gena of this species, being in distinct contrast to the sculptured vertex and gena of the most similar species, *P. scalptus*.

#### *Paramblynotus scalptus*, new species

FEMALE: Length 2.8 mm. Head and mesosoma black. Metasoma black with T3 and T4 brown. Antennae yellow with distal three segments dark. Forewing clear in about distal two-fifths, and ferruginous basally. Fore- and middle legs brown to dark brown. Hindlegs dark brown to almost black.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex densely punctate medially and diagonally carinate laterally. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli 3.5 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised and not defined laterally by a carina; median frontal carina only weakly present between antennal sockets. Upper face, including antennal scrobe, coriarius; antennal scrobes only slightly depressed with very slight traces of foveate sculpture, and defined by carina laterally. Lower face foveate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sul-

cus and epistomal sulcus almost form an arch. Clypeus distinctly longitudinally carinate. Gena foveate-punctate. Lateral occipital carina indistinct beyond vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Submedian pronotal depressions distinctly separated medially. Anterior plate of pronotum glabrate anteriorly and coriarius posteriorly, laterally also with setigerous punctures. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, not reaching pronotal crest dorsomedially. Lateral surface of pronotum coarsely foveate-reticulate. Dorsal pronotal area reaching end of posterior margin of pronotum and with closely arranged punctures in a single row. Mesoscutum distinctly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin narrowly rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous white pubescence. Upper mesopleuron glabrous; speculum longitudinally carinate; and median impression percurrent with multiple unevenly distributed transverse carinae. Lower mesopleuron glabrous, conspicuously pubescent ventrally. Metepisternum impressed and nude above, with an elevated, glabrous-punctate area posteromedially, and somewhat depressed and pubescent ventrally. Propodeum mostly areolate-reticulate; lateral and median propodeal carinae present only anteriorly and about same strength as additional longitudinal carinae posteriorly. Nucha glabrous. Rs+M of forewing nebulous, arising from posterior end of basal vein. Marginal cell 2.0 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.5 times as long as wide in lateral view. Relative length of T3-8: 1.4:1.0:2.0:0.8:0.15:0.3; T3-5 glabrous; T6-7 finely punctate; T7 of metasoma slightly exposed; T8 with a few large setigerous punctures. All legs densely punctate with pubescence except metacoxa dorsally glabrous. Apical teeth of metatibia long, thin, and pointed apically.  $1mt/2-5mt = 0.55$ .

MALE: Length 2.5 mm.

*Paramblynotus scalptus*, as stated above, is similar to *P. antistatus*, but it can be distinguished by its sculptured vertex and gena. In addition, its forewing is more extensively ferruginous, extending to cover basal three-fifths, instead of basal two-thirds as *P. antistatus*.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa: Transvaal (Rustenburg Nature Reserve, 25.40S, 27.12E), 1983-XII-8, C.D. Eardley coll. (PPRI). PARATYPES: 1♀, 1♂: 1♀, South Africa, Transvaal, Kruger National Park, Pufuri (22.26S, 31.12E), 1984-I-21, C.D. Eardley coll. (PPRI); 1♂, South Africa, East Transvaal (in woodland 15 km east of Klaserie, Guernsey Farm), 1985-XII-19-31, S. and J. Peck coll. (CNCI).

DISTRIBUTION: South Africa, East Transvaal.

ETYMOLOGY: From Latin, *scalpo*, cut, carve. The name describes the sculptured vertex and gena of the species as compared to *P. antistatus*.

***Paramblynotus vannoorti*, new species**

FEMALE: Length 2.2 mm. Body black except antennae dark yellow. Forewing mostly clear with a wide, medial smoky band covering marginal and submarginal cells and the areas behind; darker in marginal and submarginal cells and lighter behind.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex entirely diagonally carinate. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli nearly 5.0 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised, defined laterally by a carina, radiating carinate anteriorly and foveate-reticulate posterior to anterior ocellus; median frontal carina extended slightly beyond lower margin of antennal sockets. Upper face, including most of antennal scrobe, coriarius with very sparse fine punctures, and defined by carina laterally. Antennal scrobes shallow, glabrous posteriorly. Lower face coarsely coriarius and superficially foveate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus almost form an

arch. Clypeus glabrous. Gena cariarious. Lateral occipital carina indistinct beyond vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Submedian pronotal depressions fused with each other medially. Anterior plate of pronotum glabrous anteriorly and sparsely, coarsely punctate posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, nearly reaching pronotal crest dorsomedially. Lateral surface of pronotum coarsely foveate-reticulate. Dorsal pronotal area reaching to end of posterior margin of pronotum, glabrous anteriorly, and with closely arranged punctures in a single row. Mesoscutum distinctly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous white pubescence. Upper mesopleuron glabrous; speculum longitudinally carinate; and median longitudinal impression percurrent with multiple unevenly distributed transverse carinae. Lower mesopleuron glabrous, pubescent ventrally. Metepisternum coarsely foveate-reticulate and nude above, with a small elevated, glabrous area medially, and pubescent ventrally. Propodeum mostly areolate-reticulate; lateral and median propodeal carinae present only anteriorly and about same strength as the additional longitudinal carinae present posteriorly. Median propodeal area alveolate anteriorly and longitudinally carinate posteriorly. Nucha glabrous. Rs+M of forewing nebulous, arising from close to posterior end of basal vein. Marginal cell 2.0 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.5 times as long as wide in lateral view. Relative length of T3-8: 1.4:1.0:2.0:1.0:0.0:2; T3-4 glabrous; T5 very finely and sparsely punctate, T6-7 finely punctate; T7 completely covered by T6; T8 slightly exposed, with sparse setigerous punctures. All legs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely pu-



bescent. Apical teeth of metatibia long, thin, and pointed apically.  $1mt/2-5mt = 0.56$ .

The new species is similar to *P. sculptus*, but it differs from the latter in the (1) vertex diagonally carinate entirely, (2) forewing clear basally and distally with a broad medial smoky band covering the marginal and submarginal cells and the areas behind, and (3) metasomal T7 of female completely covered by T6.

MALE: Unknown.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa: East Cape, Bathurst, Waters Meeting Nature Reserve, Lookout (33.32S, 26.47E), 1988-III-5, S. von Noort coll. (SAM: SAM-HYM-P002873).

DISTRIBUTION: South Africa, East Cape.

ETYMOLOGY: The species is named after the Hymenoptera expert of South Africa, Simon van Noort.

BIOLOGY: The specimen bears a label reading "collected while feeding on flowers of *Schotia affa*".

*Paramblynotus diminutus*, new species

MALE: Length 1.6 mm. Head and mesothorax black, and the rest of the body brown. Forewings basal to tip of submarginal cell evenly grayish ferruginous and distally clear.

Antenna 14-segmented, filiform, with the third (F1) lateroventrally sinuated; median flagellomeres not constricted. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli nearly 4.5 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised, not defined laterally by a carina; median frontal carina indistinctly present between antennal sockets. Vertex coriarius with sparse punctures and fine pubescence. Upper face, including antennal scrobe and ocellar plate, and lower face coriarius with very fine pubescence. Antennal scrobe only slightly depressed and defined by weak carina laterally. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct, forming an arch. Clypeus glabrous and punctate. Gena cariarious. Malar space horizontally weakly carinate. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Submedian pronotal depressions fused with each other medially. Anterior plate of pronotum coriarius, sparsely punctate posteriorly. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, reaching to pronotal crest dorsomedially. Lateral surface of pronotum coarsely foveate-reticulate. Dorsal pronotal area reaching end of posterior margin of pronotum and with closely arranged punctures in a single row. Mesoscutum distinctly arched dorsally, and foveate-reticulate. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous white pubescence. Upper mesopleuron glabrous; speculum longitudinally carinate; and median longitudinal impression percurrent with reduced transverse carinae. Lower mesopleuron glabrous, pubescent ventrally. Metepisternum irregularly foveate-reticulate, nude above and pubescent ventrally. Propodeum foveate-rugose laterally. Lateral propodeal carinae straight and parallel. Median propodeal area with straight median longitudinal carina crossed by one straight transverse carina. Nucha glabrous. Rs+M of forewing nebulous, arising from close to posterior end of basal vein. Marginal cell 2.4 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent. M vein nebulous.

Abdominal petiole 0.5 times as long as wide in lateral view. T5 of metasoma is the largest tergum, dorsally not much longer than either T4 or T6, but ventrolaterally conspicuously expanded anteriorly and distinctly larger than the other terga. Posterior margin of T3-4 oblique in lateral view, and the same part of T5-7 vertical with slight sinuation medially. All legs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely pubescent. Apical teeth of metatibia long, thin, and pointed apically.  $1mt/2-5mt = 0.54$ .

FEMALE: Unknown.

*Paramblynotus diminutus* is similar to *P. angolensis* and *P. antistatus*, but it differs from the latter two species in (1) lateral



propodeal carinae straight and percurrent, (2) medial propodeal area with one straight and percurrent longitudinal carina, and (3) median frontal carina almost invisible.

TYPE MATERIAL: HOLOTYPE: ♂, Zimbabwe, Salisbury, 1970-X-23, A. Watsham coll. (NHM).

DISTRIBUTION: Zimbabwe, Salisbury.

ETYMOLOGY: From Latin, *deminuo*, lessen, describing the relatively smaller size in comparison with other species of the clade.

*Paramblynotus angolensis*, new species

FEMALE: Length 2.1 mm. Head and mesosoma black and metasoma and hind-legs dark brown. Antennae yellow with distal two segments black. Forewing with a wide ferruginous band across middle third and clear both basally and distally. Hindwing ferruginous across central half. Fore- and middle legs brown to yellow brown.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex glabrate with sparse, fine punctures. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli nearly 4.5 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised, defined laterally by a very weak carina, finely radiating carinae anteriorly and coriaceous posterior to anterior ocellus; median frontal carina distinct, extended slightly beyond lower margin of antennal sockets. Upper face, including antennal scrobe, coriaceous with sparse fine punctures; antennal scrobe defined by carina laterally. Lower face coarsely coriaceous and superficially foveate-reticulate. Anterior tentorial pits conspicuous. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Clypeus glabrate and punctate. Gena coriaceous. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Anterior plate of pronotum glabrous and finely, sparsely punctate. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, nearly reach-

ing pronotal crest dorsomedially. Lateral surface of pronotum coarsely foveate-reticulate. Dorsal pronotal area reaching to end of posterior margin of pronotum and with closely arranged punctures in a single row. Mesoscutum distinctly arched dorsally, and foveate-reticulate with distinct transverse carinate component. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin narrowly rounded in dorsal view. Mesopleural triangle ventrally well defined by smoothly curved carina and with conspicuous white pubescence. Upper mesopleuron glabrous except anteriorly with weak, transverse imbrication; speculum longitudinally carinate; and median longitudinal impression percurrent with multiple transverse carinae. Lower mesopleuron glabrous, pubescent ventrally. Metepisternum almost entirely depressed and punctate with long pubescence, posteromedially with a small area slightly elevated and glabrate with punctures. Propodeum mostly areolate-reticulate; lateral propodeal carina distinct only anteriorly, and interrupted by a large fovea medially. Median propodeal area glabrate with a complete median longitudinal carina crossed by a transverse carina. Nucha glabrous. Rs+M of forewing nebulous, arising from close to posterior end of basal vein. Marginal cell 2.0 times as long as wide, and almost as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.4 times as long as wide in lateral view. Relative length of T3–8: 1.8:1.0:2.0:1.3:0.15:0.0; T3–4 glabrous; T5 glabrous anteriorly and finely, sparsely punctate posteriorly; T6 finely punctate; T8 slightly visible. All legs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely pubescent. Apical teeth of metatibia long, thin, and pointed apically. 1mt/2–5mt = 0.63.

MALE: Unknown.

The new species is similar to *P. antistatus*, but it differs from the latter by (1) forewing ferruginous only medially, and clear both proximally and distally; and (2) metasomal T7 of female slightly exposed; exposed T7 is 1:15 of T6 as measured medially on lateral side.

TYPE MATERIAL: HOLOTYPE: ♀, Angola: Mocamedes (10 mi NE of), 1972-II-27–29, R. Giraul coll. (NHM).

DISTRIBUTION: Angola, Mocamedes.

ETYMOLOGY: The species is named after the type locality.

*Paramblynotus minutus*, new species

FEMALE: Length 2.4 mm. Head and mesosoma black and metasoma and hindlegs dark brown. Antennae yellow and darker toward apex. Fore- and middle legs brown to yellow brown. Forewing with a wide ferruginous band across middle third and clear both basally and distally.

Antenna 13-segmented; flagellum gradually expanded apically; median flagellomeres not constricted. Vertex foveate-rugulose, with longitudinal carinate component. Eye prominent, distinctly extended laterally beyond outer margin of gena. Distance between posterior ocelli nearly 4.5 times as wide as the distance between posterior ocellus and eye. Ocellar plate not raised, not defined laterally by carina, finely rugose and somewhat radiating anteriorly and foveate posterior to anterior ocellus; median frontal carina distinct to upper margin of antennal sockets; short transverse costae present on both sides of median frontal carina. Upper face, including antennal scrobe, coarsely coriarius with sparse superficial foveae; antennal scrobe defined by carina laterally. Lower face foveate-reticulate, superficially carinate laterally. Anterior tentorial pits conspicuous. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Clypeus glabrate with a few longitudinal carinae. Gena imbricate with sparse foveae. Lateral occipital carina reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Anterior plate of pronotum densely punctate with punctures set in rows. Pronotum dorsomedially not distinctly raised; pronotal crest medially not raised into a process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area reaching end of posterior margin of pronotum and with closely arranged punctures in a single row. Mesoscutum distinctly arched dorsally, and foveate-re-

ticulate with distinct transverse carinate component. Scutellar sulcus divided by a single median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin truncate in dorsal view. Mesopleural triangle ventrally well defined by a somewhat sinuated carina and with conspicuous white pubescence. Median mesopleural longitudinal impression percurrent, conspicuously broadened posteriorly, and areolate-reticulate structure; speculum longitudinally carinate; upper mesopleuron glabrate, relatively small because of the expansion of the longitudinal impression, and with sparse punctures. Lower mesopleuron glabrous and pubescent ventrally. Metepisternum depressed in upper part, posteromedially elevated and glabrate, and ventrally with sparse pubescence in a depressed pocket bordered posteriorly by foveae lined in an arch. Propodeum areolate-reticulate; lateral propodeal carina distinct anteriorly, medially disrupted by a large fovea. Median propodeal area glabrate with a complete median longitudinal carina crossed by a transverse carina, and posteriorly also with extra carinae parallel to the median one. Nucha glabrous. Rs+M of forewing nebulous, arising from close to posterior end of basal vein. Marginal cell 2.4 times as long as wide, and 1.2 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.8 times as long as wide in lateral view. Relative length of T3–8: 1.3:1.0:2.2:0.8:0.0:0.1; T3–4 glabrous; T5 glabrous anteriorly and very finely, sparsely punctate posteriorly; T6 finely punctate; T8 slightly visible. All legs sparsely punctate with pubescence except metacoxa dorsally glabrous and metatibia and metatarsomeres densely pubescent. 1mt/2–5mt = 0.7.

MALE: Unknown.

The species is different from all other species of the *P. immaculatus* clade by the conspicuously broadened median mesopleural impression and the surface sculpture of the impression.

TYPE MATERIAL: HOLOTYPE: ♀, South Africa: Port St. John (Pondoland), 1924-I, R.E. Turner coll. (NHM).

DISTRIBUTION: South Africa: Port St. John.

ETYMOLOGY: From Latin, *minutus*, small. The name describes the small size of the species.

#### *APEOSUS* GROUP

Both species of the *apeosus* group described here are from the Far East Russia.

DIAGNOSTIC CHARACTERS: Body size medium. Antenna filiform; median flagellomeres not constricted. Female antenna 13-segmented with F1 distinctly shorter than F2. All flagellomeres with placodes; placodes short, not as long as the flagellomeres, and densely distributed on each medial to distal flagellomere. Distance between posterior ocelli about as wide as distance between posterior ocellus and eye. Median frontal carina only weakly present between antennal sockets or extending shortly into lower face. Occiput longitudinally carinate. Submedian depressions of pronotum separated medially. Lateral pronotal carinae reaching pronotal crest dorsomedially. Lateral surfaces of pronotum foveate-reticulate, with secondary punctures, and medially separated by the less sculptured anterior pronotal plate. Pronotal crest not raised dorsomedially. Mesoscutum mostly flat and bent anteriorly in lateral view, and dorsally foveate-reticulate with more or less distinct, secondary transverse carinae. Mesoscutellum foveate-reticulate and sloped posteriorly. Scutellar sulcus is divided into two foveae by the median longitudinal carina, with or without somewhat weaker, submedian longitudinal carinae. Axillar area without conspicuous hair tuft. Upper mesopleural area glabrous. Median mesopleural impression narrow with many vertical carinae, posteriorly curved downwards and continuous with a vertical impression along posterior margin of lower mesopleuron. Metepisternum alveolate above and pubescent below. First metatarsomere without apical protuberance. T7 of female not curved dorsolaterally at posterior margin, T8 entirely covered. Terga 6–8 with sparse coarse punctures with hairs. Male unknown.

#### KEY TO SPECIES OF *APEOSUS* GROUP

1. Median frontal carina present between antennal sockets. Gena glabrous posteriorly. Pro-

notal crest smooth. Mesoscutellar foveae with several submedian longitudinal carinae weaker than the median carina. . . . .

- . . . . . *P. apeosus* Liu and Kovalev, n.sp.
- Median frontal carina absent. Gena entirely punctate and rugulose. Pronotal crest raised medially into a small triangular process. Mesoscutellar foveae without submedian longitudinal carinae. . . . .
- . . . . . *P. friatus* Liu and Kovalev, n.sp.

#### *Paramblynotus apeosus* Liu and Kovalev, new species

FEMALE: Length 4.4 mm. Body entirely black to dark brown except antenna and legs brown. Wings evenly, slightly ferruginous, with marginal cell of forewing somewhat darker.

Antenna 13-segmented; flagellum moderately stout and slightly thickened apically. Vertex foveate-punctate. Eye distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, foveate, and defined laterally by carina lined with a row of foveae lined along interior side. Median frontal carina weakly present between antennal sockets. Upper face foveate laterally; antennal scrobe densely punctate, defined in lower part by a lateral carina. Lower face foveate-reticulate, superficially carinate laterally. Anterior tentorial pits conspicuous. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Clypeus glabrate with a few longitudinal carinae. Gena with vertical carina separating the anterior coarsely punctate area from the posterior glabrous, very finely punctate areas. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate.

Anterior flange of pronotum glabrous. Anterior plate of pronotum glabrate, finely densely punctate with fine pubescence. Pronotum dorsomedially distinctly raised, but with peak distinctly lower than mesoscutum; pronotal crest medially not raised into a process. Lateral pronotal carina distinct and extended to almost reach pronotal crest dorsomedially. Lateral surface of pronotum punctate-foveate. Dorsal pronotal area glabrate and very finely transversely striate, reaching end of posterior margin of pronotum. Mesoscutum almost flat dorsally except slightly depressed anteriorly, and transversely

costate with superficial foveae set in rows between costae. Scutellar sulcus divided by median longitudinal carina and with short submedian longitudinal carinae; mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Mesopleural triangle well defined ventrally by a smoothly curved carina, densely punctate with conspicuous white pubescence in anterior half and sparse pubescence in posterior half. Median mesopleural impression percurrent, turned smoothly to lower mesopleuron posteriorly, and distinctly transversely costate; mesopleuron with a broad transverse depression anteriorly; upper mesopleuron glabrous with a few punctures both anteriorly and posteriorly. Lower mesopleuron glabrous, pubescent ventrally. Metepisternum areolate-reticulate, mostly devoid of pubescence. Propodeum areolate-reticulate; lateral propodeal carina percurrent and distinctly curved medially; median propodeal area glabrate with a complete median longitudinal carina crossed by an anterior transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Bulla on Sc+R<sub>1</sub> absent. Apical teeth of metatibia long and pointed apically. (Abdomen lost.)

MALE: Unknown.

The species can be easily separated from *P. friatus*, the only other species of the species group, using the above key.

TYPE MATERIAL: HOLOTYPE: ♀, Russia: Primorsk (20 km from Spassk), 1984-IX-6, collected by Belokobylskij coll. (ZISP).

DISTRIBUTION: Russia: Primorsk.

ETYMOLOGY: From Greek, *apios*, far away, and *eos*, East. The name is an arbitrarily shortened version of the composite word.

*Paramblynotus friatus* Liu and Kovalev,  
new species

FEMALE: Length 4.0 mm. Body entirely black to dark brown except antenna and legs brown. Wings evenly, slightly ferruginous, except marginal cell of forewing somewhat darker.

Antenna 13-segmented; flagellum moderately stout and slightly thickened apically. Vertex foveate-reticulate. Eye distinctly extended laterally beyond outer margin of

gena. Ocellar plate distinctly raised, foveate, and not defined laterally by carina. Median frontal carina absent. Upper face foveate-reticulate except antennal scrobe densely punctate; antennal scrobe defined by carina laterally in lower part. Lower face and clypeus foveate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Gena entirely punctate, medially more or less vertically rugose. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate.

Anterior flange of pronotum glabrous. Anterior plate of pronotum glabrate, finely densely punctate with fine pubescence. Pronotum dorsomedially distinctly raised, but with peak distinctly lower than mesoscutum; pronotal crest medially raised into a small median process. Lateral pronotal carina distinct and extended to almost reach pronotal crest dorsomedially. Lateral surface of pronotum punctate-foveate. Dorsal pronotal area glabrate, reaching to end of posterior margin of pronotum. Mesoscutum almost flat dorsally except slightly depressed anteriorly, and discontinuously transversely costate with distinct foveae set in between. Scutellar sulcus divided by median longitudinal carina; mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Mesopleural triangle well defined ventrally by a smoothly curved carina, densely punctate with conspicuous white pubescence in anterior half and sparsely pubescent in posterior half. Median mesopleural impression percurrent, turned smoothly to lower mesopleuron posteriorly, and distinctly transversely costate; mesopleuron with a broad transverse depression anteriorly; upper mesopleuron glabrous and with scattered punctures posteriorly. Metepisternum areolate-reticulate, devoid of pubescence in upper part, and densely pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and strongly curved medially; median propodeal area glabrate with a complete median longitudinal carina crossed by an anterior transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide and 1.5 times as long as submarginal cell. Marginal cell 3.0 times as long as wide and



1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.25 times as long as wide in lateral view. Relative length of T3–7: 2.3:1.0:1.5:2.7:1.4; T3–4 glabrous; T5 glabrous anteriorly and very finely punctate posteriorly, T6–7 densely punctate, each with a band of sparse pubescence; T8 completely covered by T7. Apical teeth of metatibia long and pointed apically. 1mt/2–5mt = 0.85.

MALE: Unknown.

TYPE MATERIAL: HOLOTYPE: ♀, Russia: Primorsk (Shkotovsk), 1975–VII–22, collected by Krivagutzkaya coll. (ZISP).

The species can be separated from *P. apeosus*, the only other species of the species group, using the above key.

DISTRIBUTION: Russia: Primorsk.

ETYMOLOGY: From Latin, *fretus*, trusting to. No particular reference, just personal caprice of the authors.

#### *RUFICOLLIS* GROUP

figures 45–63

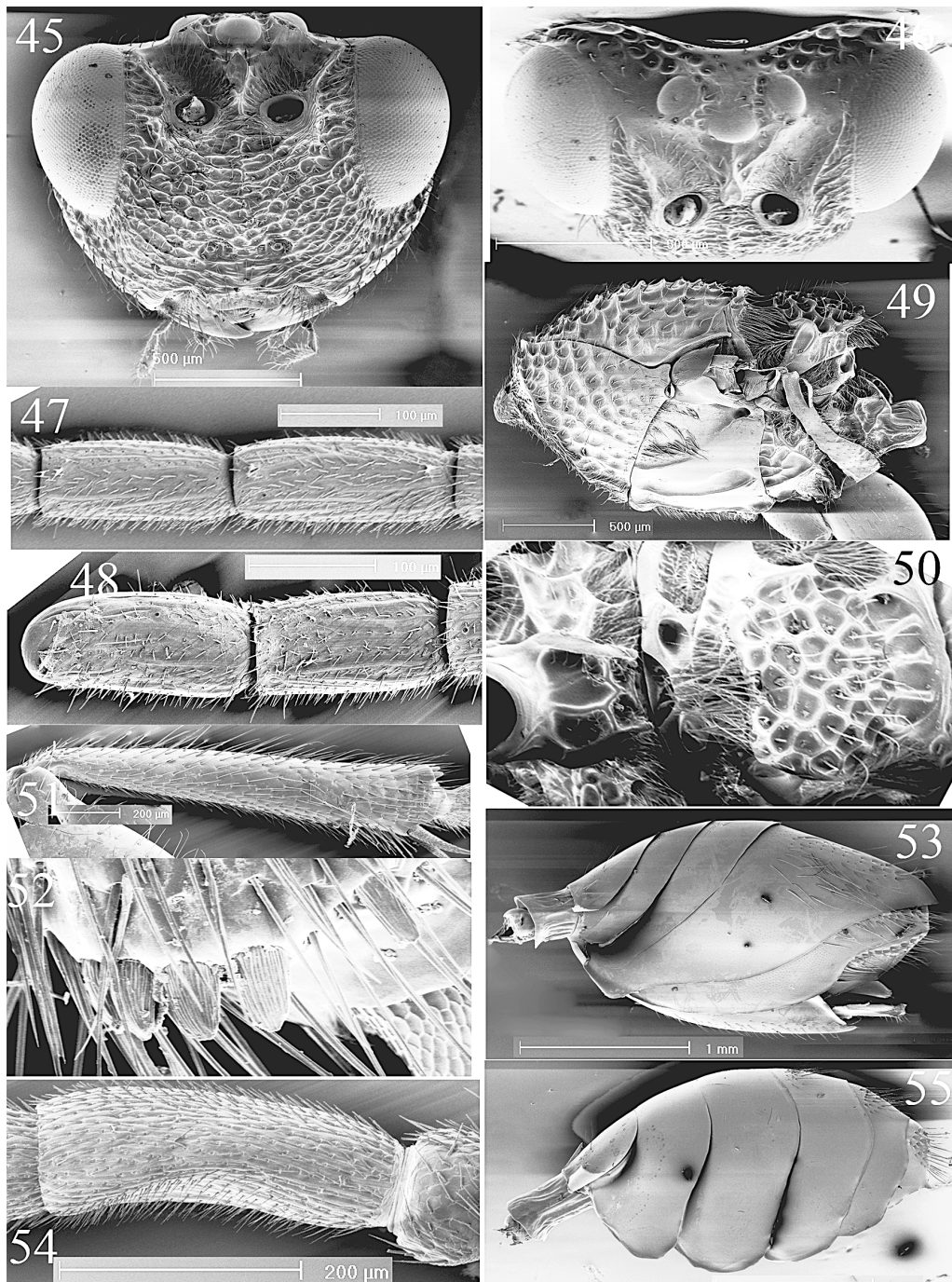
The *ruficollis* group is mainly distributed in the Oriental region with a terminal clade comprising three species from the Neotropical region.

DIAGNOSTIC CHARACTERS: Body size median to relatively large. Antenna filiform. Female antenna has 13 segments with F1 distinctly or slightly shorter than F2. All flagellomeres have placodes; placodes short, not as long as the flagellomeres, and are usually densely, but relatively sparsely in the Neotropical species, distributed on each medial to distal segment. Male antenna has 14 segments, F1 almost cylindrical, only very slightly depressed on ventral side. Median frontal carina generally lacking in lower face. Occiput glabrous, occasionally coriarius. Lateral pronotal carinae not reaching pronotal crest dorsomedially. Lateral sides of pronotum foveate to foveate-reticulate, with or without secondary transverse costae, and not separated by the extended, less sculptured anterior surface. Pronotal crest raised dorsomedially into a small, distinct process or two submedian processes. Mesoscutum predominantly transversely carinate with more or less obvious foveae in between. Mesoscu-

tellum flat or slightly sloped posteriorly, and foveate-reticulate. Scutellar sulcus always divided into more than two foveae by several subequally strong longitudinal carinae. Axillar area with conspicuous hair tuft. Upper mesopleural area glabrous. Median mesopleural impression medially bent, wider and deeper toward ends. Metepisternum divided into several longitudinal impressions by several strong longitudinal carinae. Dorsoapical dents of metatibia short and blunt; first metatarsomere without apical protuberance. T7 of female with posterior margin curved dorsolaterally, distinctly exposing T8. T6–8 with more or less coarse punctures with hairs. Post petiolar terga of male subequal to each other.

#### KEY TO SPECIES OF *RUFICOLLIS* GROUP

1. Apical flagellomere conical, not compressed and broadly rounded apically, and distinctly longer than the subapical one. Forewing evenly colored. . . . . 2
- Apical flagellomere compressed and broadly rounded apically, and almost as long as the subapical one (fig. 48). Forewing with two dark brown maculae: a distal one in marginal cell and basal part of Rs-cell, and a proximal, transverse one along outer side of basal vein 7
2. Mesoscutum and mesoscutellum glabrous with foveae, and laterally also with reduced transverse costae, appearing polished . . . . . *P. coruscus*, n.sp.
- Mesoscutum distinctly transversely costate; mesoscutellum foveate-reticulate. . . . . 3
3. Vertex medially with dense, longitudinal carinae that end before running into occiput. . . . . *P. carinivertex*, n.sp.
- Vertex without longitudinal carinae . . . . . 4
4. Head and pronotum red to orange. Vertex, gena, and lower part of lateral sides of pronotum glabrous. Lower face shallowly foveate-reticulate. Antennal scrobes glabrous. . . . . *P. ruficollis* Cameron, 1909
- Head dark. Vertex, gena, and lower part of pronotum sculptured. . . . . 5
5. Pronotal crest anteromedially flat. Median frontal carinae percurrent to clypeus. . . . . *P. malayensis* (Weld, 1922)
- Pronotal crest anteromedially more or less raised. Median frontal carina only reaching middle of lower face . . . . . 6
6. Pronotum anteromedially raised into a small, triangular process. Pronotum and mesothorax red brown, or largely dark with small red areas . . . . . *P. trisectus* Maa, 1962



Figs. 45–55. *P. braziliensis*. 45, Head, front view, ♀; 46, head, dorsal view, ♀; 47, antennal F6–7, lateral view, ♀; 48, antennal F10–11, dorsal view, ♀; 49, mesosoma, lateral view, ♀; 50, scutellum and propodeum, dorsoposterior view, ♀; 51, metatibia, dorsolateral view, ♀; 52, end of metatibia showing apical teeth, ♀; 53, metasoma, lateral view, ♀; 54, antennal F1, dorsal view, ♂; 55, metasoma, lateral view, ♂.

- Pronotum anteromedially raised into gradual, rather conspicuous peak. Pronotum and mesothorax dark. . . . . *P. badius*, n.sp.
- 7. Vertex, especially medially, coarsely punctate. Pronotal crest raised into two prominent, separate, triangular, submedian processes. Lateral sides of posterior part of mesoscutellum strongly raised, smoothly continuous with dorsal lateral process anteriorly (fig. 50). Petiole almost as long as wide. Forewing with a broad smoky band along outer margin. Tergum 6 of female with tip reaching as far T7 posteriorly, dorsal margin evenly, moderately curved posteriorly and posterior margin distinctly concave (fig. 53) . . . . . *P. braziliensis*, n.sp.
- Vertex glabrous with sparse punctures. Submedian processes of pronotal crest indistinct. Lateral sides of posterior part of mesoscutellum not strongly raised, abruptly narrowed behind dorsal lateral process. Petiole about twice as long as wide. Forewing without smoky band along outer margin. Tergum 6 of female distinctly not reaching as far as T7, dorsal margin abruptly curved posteriorly, and posterior margin almost straight. . . . 8
- 8. Lateral sides of pronotum largely glabrous. Gena glabrous entirely. Mesoscutellum posteriorly with a deep, broad triangular emargination . . . . . *P. costaricanus*, n.sp.
- Lateral sides of pronotum entirely foveate-reticulate. Gena sculptured. Mesoscutellum posteriorly with a shallow, smoothly curved emargination. . . . . *P. zonatus* Weld, 1944

*Paramblynotus ruficollis* Cameron, 1909

*Paramblynotus ruficollis* Cameron, 1909: 18, ♀; Borneo; NHM (4 T♀, no. 7.9 and in main coll.).  
*\*ruficeps* Kieffer, 1914: 186, ; Luzon; USNM (HT♀, not numbered). = *P. ruficollis* Cameron; synonymy by Weld (1930: 137).

FEMALE: Length 6.5–9.0 mm. Head, pronotum, and foreleg orange; antenna and rest of body, and middle and hindlegs black. Wings lightly ferruginous with marginal and submarginal cells of forewings darker.

Vertex foveate; gena glabrous with sparse fine punctures. Ocellar plate well defined by lateral carina. Antennal scrobe glabrous with fine punctures. Median frontal carina absent in lower face. Pronotal crest medially raised into a very distinct, apically rounded triangular process. Lateral surface of pronotum foveate, with sparse punctures. Mesoscutum transversely carinate with foveae in between.

Mesoscutellum raised posteriorly. Lateral propodeal carina raised throughout, right-angled anteriorly in lateral view.  $1mt/2-5mt = 0.96$ .

The species is distinguished from all other species of the *ruficollis* group for its large body size, as well as its red head and pronotum in contrast of the rest of its body, which is shining black. Additional characters to distinguish the species include sculptures on vertex, genae, and lateral sides of pronotum.

MALE: Length 4.0–7.0 mm, otherwise similar to female.

MATERIAL EXAMINED: NHM: 6 (1T); AEI: 1; NNMN: 2; BPBM: 3.

DISTRIBUTION: Malaysia: Borneo; Laos; Philippines: Luzon.

*Paramblynotus malayensis* (Weld, 1922)

*Allocynips malayensis* Weld, 1922: 329, ♂♂; Borneo; USNM (HT♀, no. 24 377, 1 PT♀, 2 PT♂).  
*Paramblynotus malayensis*, combination by Weld (1930: 137).

FEMALE: Length 4.0 mm. Body and legs entirely dark brown except tibiae and tarsomeres of legs yellow to yellow brown. Wings mostly clear except marginal cell of forewing and neighboring areas somewhat ferruginous.

Vertex foveate-reticulate; gena glabrous with foveae and punctures. Ocellar plate laterally not defined by a carina; antennal scrobes fine, densely punctate. Median front carina very distinct, extending to clypeus in lower face. Pronotal crest medially not raised into a triangular process. Mesoscutellum not raised posteriorly. Lateral propodeal carina not distinctly raised in lateral view.  $1mt/2-5mt = 0.76$ .

The species is easily separated from the other species of the group *ruficollis* for its small size and its median frontal carina complete in lower face.

MATERIAL EXAMINED: USNM1 (1T).

DISTRIBUTION: Malaysia: Borneo, Sandakan.

*Paramblynotus badius*, new species

FEMALE: Length 4.5 mm. Body, antenna, and hindleg entirely black to dark brown; fore- and middle legs yellow brown. Wings



slightly ferruginous with marginal and submarginal cells of forewings darker.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent, distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, densely, coarsely punctate, and not defined laterally by carina. Median frontal carina weakly present above antennal sockets. Upper face entirely punctate-foveate except antennal scrobe somewhat longitudinally carinate posteriorly; antennal scrobe slightly depressed and defined by carina laterally. Lower face foveate-punctate with transverse rugosity. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Clypeus longitudinally carinate and punctate posteriorly, transversely carinate medially, and glabrate-punctate anteriorly. Gena glabrate and punctate-foveate. Lateral occipital carina reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous. Anterior plate of pronotum glabrate, densely punctate with fine pubescence. Submedian pronotal depressions separated far apart medially. Pronotum dorsomedially distinctly raised, but lower than mesoscutum; pronotal crest medially gradually raised into median peak. Lateral pronotal carina distinct and extended to reach pronotal crest dorsomedially. Lateral surface of pronotum punctate-foveate with oblique carinate component posteromedially. Dorsal pronotal area glabrate, reaching to one-third of posterior margin of pronotum. Mesoscutum slightly arched dorsally and foveate-reticulate with foveae set in rows between transverse costae. Scutellar sulcus divided by median longitudinal carina and two submedian carinae; mesoscutellum foveate-reticulate, with posterior margin rounded in dorsal view. Mesopleural triangle well defined ventrally by a smoothly curved carina, with conspicuous white pubescence. Median mesopleural impression percurrent, distinctly transversely costate; upper mesopleuron glabrous mostly except finely, densely punctate anteriorly; lower mesopleuron entirely glabrate and pubescent, and bordered by a distinct, straight carina ventrally. Metepisternum longitudinally costate and devoid of pubescence in upper part, conspicuously pubescent ven-

trally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and curved medially; median propodeal area glabrate, median longitudinal carina present only anterior to median transverse carina. Nucha glabrous. Rs+M of forewing arising from middle of basal vein. Marginal cell 3.3 times as long as wide, and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.3 times as long as wide in lateral view, lateroposterior margin broadly angular. Relative length of T3-8: 2.0:1.0:1.0:3.7:1.0:0.7; T3-5 glabrous; T6 glabrous anteriorly with a band of sparse pubescence, T7 with a medial band of sparse pubescence in punctures and densely and finely punctate posteriorly; T8 with a band of dense pubescence. Legs, particularly metatibia and metatarsomeres, densely pubescent. Apical teeth of metatibia short, stout, and blunt apically.  $1mt/2-5mt = 0.80$ .

MALE: Unknown.

*Paramblynotus badius* differs from all other species of the *ruficollis* group in having its pronotum anteromedially raised into gradual, rather conspicuous peak. The species can be further separated from the most similar species, *P. trisectus*, by having pronotum and mesothorax dark.

TYPE MATERIAL: HOLOTYPE: ♀, Sarawak, Mt. Dulit (1,000 ft, Moss Forest), 1932-X-16, native leg. (NHM).

DISTRIBUTION: Indonesia: Borneo.

ETYMOLOGY: From Latin, *coruscus*, *badius*, brown or chestnut-colored. The name refers to its slightly ferruginous wings.

#### *Paramblynotus coruscus*, new species

FEMALE: Length 5.0 mm. Body entirely black; antenna dark brown; legs red brown. Wings clear. Head and lateral pronotum very densely pubescent; anterior two-thirds of mesopleural triangle and lower part of metepisternum with conspicuous, long silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate-foveate, and not defined laterally by carina. Median frontal carina weakly, briefly present posterior to antennal sockets. Upper face,



including antennal scrobe, glabrate-foveate; antennal scrobe defined by carina laterally. Lower face, clypeus, and gena densely punctate and foveate with heavy pubescence. Anterior tentorial pits small. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Lateral occipital carina reaching vertex. Occiput glabrous medially and very finely transversely striate laterally.

Anterior flange of pronotum finely, transversely striate. Submedian pronotal depressions fused with each other medially and punctate. Anterior plate of pronotum densely punctate and pubescent. Pronotum dorsomedially distinctly raised, but lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct and extended to reach pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and punctate. Dorsal pronotal area glabrous, reaching to one-third of posterior margin of pronotum. Mesoscutum slightly arched dorsally, transversely costate with foveae set in rows, and glabrate medially and lateroposteriorly with the appearance of polished metal surface. Scutellar sulcus divided by median longitudinal carina and four submedian equally strong carinae; mesoscutellum glabrous-foveate, with posterior margin rounded in dorsal view. Mesopleural triangle well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, without transverse costae; upper mesopleuron glabrous, with setigerous punctures in anterior half; lower mesopleuron glabrous, and bordered by a distinct, straight carina ventrally. Metepisternum longitudinally costate and devoid of pubescence in upper part, conspicuously pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and almost straight; median propodeal area glabrate; median longitudinal carina percurrent, crossed by two transverse carinae. Rs+M of forewing arising from middle of basal vein. Marginal cell 3.4 times as long as wide, and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Abdominal petiole 0.33 times as long as wide in lateral view. Relative length of T3–8: 2.0:1.0:1.3:5.3:0.9:1.8; T3–4 glabrous; T5 glabrous anteriorly and densely finely punctate posteriorly; T6 glabrous anteriorly and

densely punctate posteriorly; T7 coarsely punctate anteriorly and finely punctate posteriorly, with a patch of sparse pubescence lateroventrally; and T8 coarsely punctate-foveate with pubescence. Legs sparsely pubescent except metatibia and metatarsomeres densely so. Apical teeth of metatibia short, stout, and blunt apically.  $1mt/2-5mt = 0.90$ .

MALE: Length 4.0 mm, otherwise similar to female.

The species is unique in all *Paramblynotus* species for the deductive nature of its sculptures, giving it the appearance of polished metal surface.

TYPE MATERIAL: HOLOTYPE: ♀, Laos: Ban Van Heue (20 km E Phou-kow-kuei), 1965-V-1–15, J. A. Rondon coll. (BPBM). PARATYPES: 2♀♀, Burma: Yanaungmyin, Res. pyinmana, 1932-V-13, R. Hia Ogh coll. (NHM).

BIOLOGICAL NOTES: The paratypes bear labels reading “ex *Dalbergia fusca*”.

DISTRIBUTION: Laos; Burma.

ETYMOLOGY: From Latin, *coruscus*, flashing, glimmering. The name refers to the polished sculpture of mesonotum of species.

#### *Paramblynotus carinivertex*, new species

FEMALE: Length 3.5 mm. Head and mesosoma black, metasoma, coxa and femur of fore- and middle legs, and hindlegs dark brown; antenna and tibia and tarsomeres of fore- and middle legs brown. Wings clear. Lateral surface of pronotum with very dense golden pubescence; mesopleural triangle and T6–8 of metasoma posteriorly with conspicuous patch of golden pubescence.

Antenna 13-segmented; flagellum filiform. Vertex mainly foveate-reticulate except a median triangular area finely longitudinally carinate. Eye prominent, distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate-foveate, and defined laterally by carina lined with a row of foveae on interior side. Median frontal carina percurrent to clypeus and distinctly raised into a ridge posterior to antennal sockets. Upper face foveate laterally; antennal scrobe glabrous with setigerous punctures anteriorly, defined by carina laterally. Lower face coarsely foveate-punctate; clypeus foveate-punctate posteriorly and

glabrous anteriorly; gena mostly glabrous and finely punctate, with a row of foveae along anterior side of lateral occipital carina. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Lateral occipital carina reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal pits distinctly separated medially. Anterior plate of pronotum densely punctate and pubescent with a row of foveae posteriorly. Pronotum dorsomedially distinctly raised, but lower than mesoscutum; pronotal crest medially raised medially into a small, distinct process. Lateral pronotal carina distinct and reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrous, reaching to one-fourth of posterior margin of pronotum. Mesoscutum slightly arched dorsally, transversely costate with foveae set in rows. Scutellar sulcus divided by median longitudinal carina and four submedian equally strong carinae; mesoscutellum foveate-reticulate, with posterior margin rounded in dorsal view. Mesopleural triangle well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, without transverse costae; upper mesopleuron glabrous; lower mesopleuron glabrous, and bordered by a distinct, straight carina ventrally. Metepisternum longitudinally costate and devoid of pubescence in upper part, conspicuously pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and distinctly diverging posteriorly; median propodeal area rugose; median longitudinal carina distinct only anteriorly, ending at anterior transverse carina. Rs+M of forewing arising from anterior third of basal vein. Marginal cell 3.4 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent. Marginal cell 2.7 times as long as wide and 1.2 times as long as submarginal cell.

Abdominal petiole as long as wide in lateral view; lateroposterior margin curved to form a wide angle. Relative length of T3–8: 2.0:1.0:1.1:4.2:0.9:1.6; T3–5 glabrous; T6 glabrous anteriorly, and densely punctate and pubescent dorsoposteriorly; T7 coarsely punctate with distinct pubescence anteriorly

and finely, densely punctate posteriorly; and T8 coarsely punctate/foveate with pubescence. Legs sparsely pubescent except metatibia and metatarsomeres densely so. Apical teeth of metatibia short, stout, and blunt apically.  $1mt/2-5mt = 0.90$ .

MALE: Unknown.

The new species is most easily distinguished from all other species of *Paramblynotus* by having a triangular area in the middle of the posterior part of vertex with fine, longitudinal carinae, and is further separated from all other species of the *ruficollis* group by having petiole as long as wide.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: N. Borneo, Tawau, Quoin Hill, Forest Camp (1.3–5 km WSW of Coca Research Station), 1962-VII-9–20, Y. Mirashima coll. (BPBM).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: From Latin, *carina*, keel, ridge, and *vertex*, top. The name refers to the longitudinally carinate triangular area in middle of posterior part of vertex

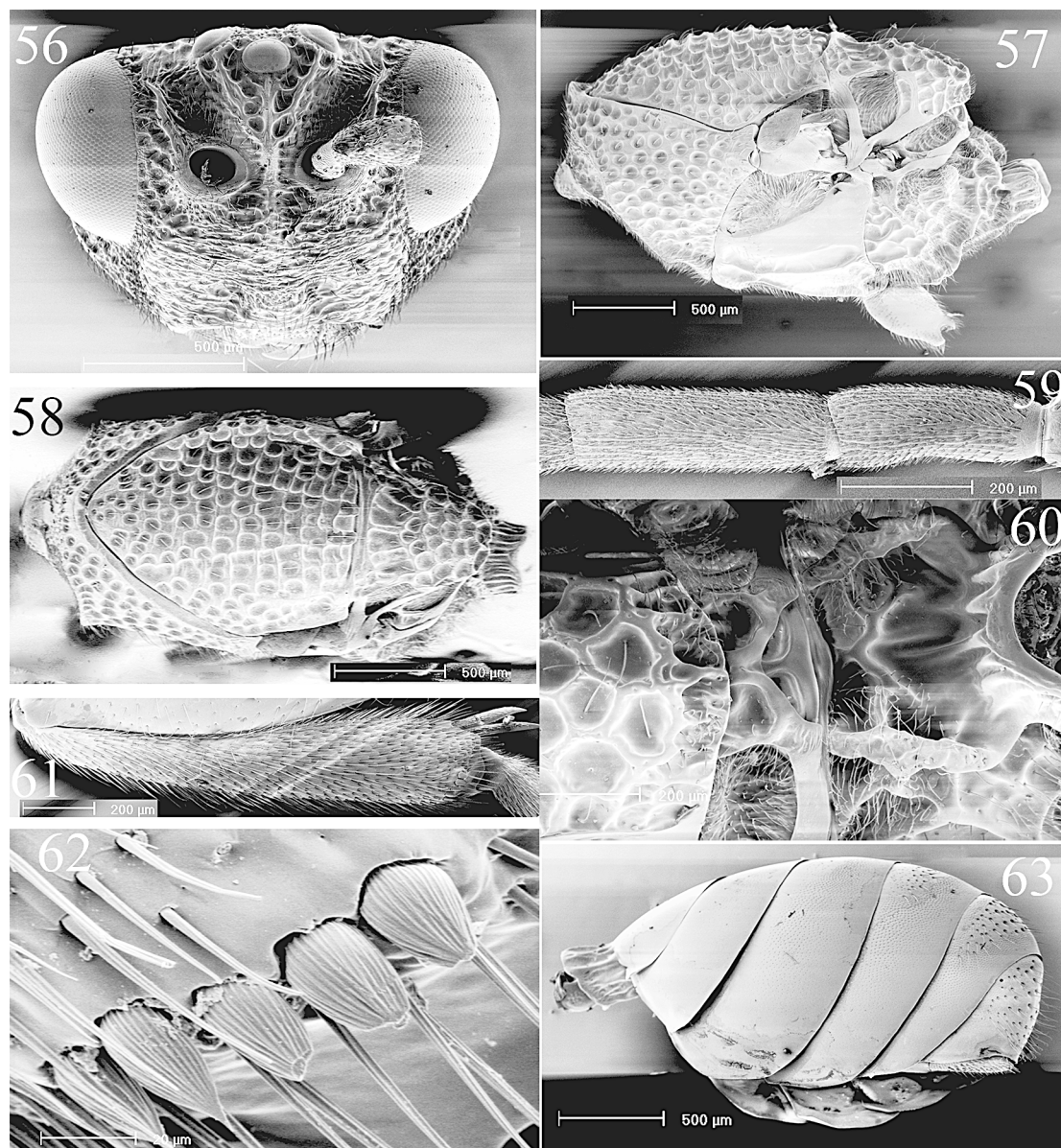
*Paramblynotus trisectus* Maa, 1962  
figures 56–63

*Paramblynotus trisectus* Maa, 1962: 126, ♀; Thailand; BPBM (HT♀).

FEMALE: Length 5.0–6.0 mm. Wings slightly ferruginous with marginal and submarginal cells of forewing darker. Body color is discussed in remarks below.

Vertex heavily foveate-reticulate; gena densely punctate and foveate (fig. 56). Ocellar plate well defined by lateral carina, along which lined large foveae (fig. 56). Antennal scrobe mainly densely punctate, posteriorly somewhat longitudinally rugose. Median frontal carina absent in lower face. Pronotal crest medially raised into a small, triangular process. Lateral surface of pronotum foveate-reticulate, with very sparse punctures (fig. 57). Mesoscutum transversely carinate with foveae set in between (fig. 58). Mesoscutellum sloped posteriorly (fig. 58). Lateral propodeal carina smoothly raised medially (fig. 60), arch-shaped in lateral view.  $1mt/2-5mt = 0.77$ .

MALE: Length about 4.5 mm, otherwise similar to female.



Figs. 56–63. *P. trisectus*. **56**, Head, front view, ♀; **57**, mesosoma, lateral view, ♀; **58**, mesosoma, dorsal view, ♀; **59**, antennal F1, dorsal view, ♂; **60**, propodeum, dorsal view, ♀; **61**, metatibia, lateral view, ♀; **62**, end of metatibia showing apical teeth, ♀; **63**, metasoma, lateral view, ♂.

*Paramblynotus trisectus* is distinguished from the other species of the group by its more or less red mesosoma and its highly raised, in lateral view, arch-shaped lateral propodeal carina.

**GEOGRAPHICAL VARIATION:** This species shows great variation in terms of body

color pattern. Specimens from localities in Thailand, including the type locality, northern Vietnam, and the southernmost province of China, Yunnan, have head and mesosoma orange, propodeum black, and metasoma brown. Specimens from Nepal and the southern province of China Guangxi are



darker, but the general color pattern differs only slightly and with mesoscutellum also black. The series of specimens from Hainan, China, are almost entirely dark, except small orange areas at the pronotum. The general trend of variation of color pattern appears to become increasingly darker from the south to the north. However, we otherwise have not found significant variation with respect to main structure and surface sculptures.

**MATERIAL EXAMINED:** BPBM: 2 (1HT); BAU: 1; CNCI: 1; ZICA: 11; ZMLU-MS: 6.

**DISTRIBUTION:** Thailand; China: Yunnan, Guangxi, and Hainan; Nepal.

*Paramblynotus braziliensis*, new species  
figures 45–55

**FEMALE:** Length 4.5–7.0 mm. Head, pronotum, antenna, and legs brown to dark brown; mesosoma except pronotum and metasoma, sometimes also pronotum, black. Forewing with a large macula covering marginal cell, distal third of first submarginal cell and basal third of second submarginal cell, a narrow band along interior side of basalis; both fore- and Hindwings have a lighter, wide band along outer margin.

Antenna 13-segmented; flagellum filiform. Vertex mainly foveate-reticulate posteriorly and glabrate anteriorly (fig. 46). Eye distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate-foveate, and defined laterally by carinae; a row of indistinct foveae lined between lateral carina of ocellar plate and a parallel, interior carina. Median frontal carina not extended to lower face and distinctly raised into a prominent, laminate, and apically flattened process. Upper face foveate laterally; antennal scrobe glabrous with setigerous punctures anteriorly; antennal scrobe deeply depressed and defined by carina laterally (figs. 45, 46). Gena foveate-punctate anteriorly and glabrous posteriorly, separated by a medial irregular vertical carina. Lower face foveate-reticulate and superficially transversely rugose. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Clypeus glabrous anteriorly, transversely carinate posteriorly, finely punctate both anteriorly and poster-

iorly, and anterior third separated by a transverse inflection (fig. 45). Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum indistinctly, finely longitudinally striate and punctate; submedian pronotal pits distinctly separated medially. Anterior plate of pronotum foveate and densely punctate with pubescence. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest medially broadly emarginate medially; two prominent submedian processes present immediately before crest, giving the impression that they are formed on the crest. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate (fig. 49). Dorsal pronotal area glabrous, present only along anterior part of posterior margin of pronotum. Mesoscutum slightly arched dorsally, transversely costate with foveae set in rows. Scutellar sulcus divided by median longitudinal carina and four submedian equally strong carinae; mesoscutellum foveate-reticulate and raised posteriorly; posterior margin truncate with a broad emargination in dorsal view and with conspicuous white pubescence. Axillar area with conspicuous white pubescence (figs. 49, 50). Mesopleural triangle well defined ventrally by a smoothly curved carina and with conspicuous white pubescence. Median mesopleural impression percurrent, without transverse costae; upper mesopleuron glabrous; lower mesopleuron glabrous and bordered by a distinct, straight carina ventrally. Metepisternum longitudinally irregularly costate, devoid of pubescence in upper part, and conspicuously pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and distinctly curved posteriorly; median propodeal area glabrous; median longitudinal carina distinct only anteriorly, ending at an anterior transverse carina; and posterior part of median propodeal area with two distinct submedian longitudinal carinae (fig. 50). Rs+M of forewing arising from anterior two-fifths of basal vein. Marginal cell 3.4 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent. Marginal cell 3.2 times as long as wide and 1.4 times as long as submarginal cell.



Abdominal petiole 0.92 times as long as wide in lateral view. Relative length of T3–8: 2.6:1.0:1.1:4.6:0.6:1.3; T3–5 glabrous; T3 with a small patch of sparse pubescence in punctures; T6 finely punctate anteriorly and posteriorly, more coarsely punctate with pubescence medially; T7 coarsely punctate with distinct pubescence anteriorly and very finely, densely punctate posteriorly; and T8 coarsely punctate/foveate with pubescence (fig. 53). Legs more or less densely pubescent. Apical teeth of metatibia short, stout, and blunt apically (fig. 52).  $1\text{mt}/2\text{--}5\text{mt} = 0.80$ .

**MALE:** Length about 4.0–6.0 mm. T3–6 subequal in length dorsally; T7 and T8 about 0.7 and 0.4 times the size of preceding tergites, respectively. Dorsal surface of T6–7 with setigerous punctures (fig. 55).

*Paramblynotus braziliensis* is very similar to the other two Neotropical *Paramblynotus* species (i.e., *P. zonatus* and *P. costaricanus*) and forms a distinct monophyletic clade defined by several characters, including (1) apical flagellomere apically compressed and broadly rounded, and almost as long as the subapical flagellomere (fig. 48); and (2) forewing with two dark brown maculae: a distal macula in marginal cell and basal part of Rs-cell and a proximal, transverse macula along outer side of vein basalis. It differs from the other two species of this clade in (1) vertex, especially medially, coarsely punctate; (2) two prominent, separate, triangular, submedian processes present immediately before pronotal crest; (3) lateral sides of posterior part of mesoscutellum abruptly narrowed behind dorsal lateral process (fig. 50); (4) forewing with a broad smoky band along outer margin; (5) petiole almost as long as wide; and (6) T6 of female metasoma with tip reaching as far as T7 posteriorly, dorsal margin evenly curved, and posterior margin distinctly concave (fig. 53).

**TYPE MATERIAL:** HOLOTYPE: ♀, Brazil, Nova Teutonia, F. Plauman leg. (AEI). PARATYPES: 236♂♂, Brazil: Nova Teutonia, 1944–1966, F. Plauman leg. (AEI: 116; NHM: 82, including 2 as SEM preparations; CMS: 16; CNCI: 8; NHRS: 5; ZML: 2; KJH: 5; UCDC: 1)

**ADDITIONAL MATERIAL:** CNCI: 1.

**DISTRIBUTION:** Brazil.

**ETYMOLOGY:** Named after type locality.

*Paramblynotus costaricanus*, new species

**FEMALE:** Length 4.5 mm. Head and pronotum yellow brown; mesonotum black; rest of the body, antenna, and legs brown to dark brown. Forewing with a large macula covering marginal cell, distal third of first submarginal cell and basal third of second submarginal cell, a narrow band along interior side of basal vein; both wings without a wide band along outer margin.

Antenna 13-segmented; flagellum filiform. Vertex glabrate except a posterior row of foveae along border between vertex and occiput. Eye prominent, distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate anterior to anterior ocellus and foveate-reticulate posteriorly, and defined laterally by distinct carina. Median frontal carina not extended to lower face and distinctly raised into a prominent, laminate, and apically flattened process. Upper face coriaceous laterally; antennal scrobe glabrous with setigerous punctures anteriorly; antennal scrobe deeply depressed and defined by carina laterally. Gena glabrous and sparsely foveate, without medial vertical carina. Lower face foveate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus transversely rugose and foveate posteriorly, and glabrous and finely punctate anteriorly, anterior third separated by a transverse inflection. Lateral occipital carina, reaching vertex. Occiput glabrous.

Anterior flange of pronotum longitudinally striate and punctate; submedian pronotal depressions distinctly separated medially. Anterior plate of pronotum foveate and densely punctate with pubescence medially, and glabrous laterally. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest broadly emarginate medially; two submedian processes present immediately before crest. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum transversely costate with superficial foveae set in rows between costae, and glabrate lateroposteriorly and lateroventrally. Dorsal pronotal area glabrous, present only along anterior

half of posterior margin of pronotum. Mesoscutum slightly arched dorsally, transversely costate with superficial foveae set in rows. Scutellar sulcus divided by four longitudinal, equally strong carinae; mesoscutellum foveate-reticulate and raised posteriorly; posterior margin with a deep, wide triangular emargination in dorsal view and with conspicuous white pubescence. Axillar area with conspicuous white pubescence. Mesopleural triangle well defined ventrally by a smoothly curved carina and with conspicuous white pubescence. Median mesopleural impression percurrent, without transverse costae; both upper and lower mesopleuron glabrous; lower mesopleuron bordered by a distinct, straight carina ventrally. Metepisternum longitudinally costate and devoid of pubescence in upper part, conspicuously pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent, distinctly curved posteriorly, and flattened inward dorsally to form a glabrous dorsal surface; median propodeal area glabrate with fine pubescence; median longitudinal carina distinct present anteriorly and absent posteriorly; two sinuated submedian longitudinal carinae present in posterior part of median propodeal area; transverse carina weak.  $Rs+M$  of forewing arising from anterior third of basal vein. Marginal cell 3.4 times as long as wide and 1.5 times as long as submarginal cell. Bulla on  $Sc+R_1$  absent.

Abdominal petiole 0.57 times as long as wide in lateral view. Relative length of T3–8: 2.4:1.0:1.3:5.3:0.6:1.6; T3 glabrous with a row of setigerous punctures; T4–5 finely punctate; T6 mostly more or less densely, finely punctate, except with a median patch of long pubescence in larger punctures dorsolaterally; T7 finely punctate with a row of pubescence in larger punctures anteriorly; and T8 coarsely punctate-foveate with pubescence. Legs more or less densely pubescent. Apical teeth of metatibia short, stout, and blunt apically.  $1mt/2-5mt = 0.68$ .

MALE: Unknown.

*Paramblynotus costaricanus* is most similar to *P. zonatus*. They can be separated from *P. braziliensis* by having (1) vertex glabrous with sparse punctures; (2) submedian processes before pronotal crest not as prominent; (3) lateral sides of posterior part of mesoscutel-

lum not abruptly narrowed behind dorsal lateral process; (4) forewing without a broad smoky band along outer margin; (5) T6 of female metasoma with tip distinctly not reaching as far as T7 posteriorly; dorsal margin abruptly curved posteriorly, and posterior margin slightly concave. *P. costaricanus* can be further separated from *P. zonatus* by having (1) lateral sides of pronotum largely glabrous and gena entirely glabrous, and (2) mesoscutellum posteriorly with a broad triangular emargination.

TYPE MATERIAL: HOLOTYPE: ♀, Costa Rica: Guanacaste: Santa Rosa National Park, 1985-IV-17-27, collected by D. Janzen and I. Gauld (with Malaise trap), deposited in the Natural History Museum, London (NHM). PARATYPES: 3♀♀, 2♀♀, locality and depository same as holotype, 1985-IV-17-27, collected by I. Gauld, and 1986-V-4-24, by D. Janzen and I. Gauld. 1♀, Guatemala: Zacapa (2 km from N. Santa Cruz), 1986-XI, collected by M. Sharkey (in dry river bed with Malaise trap), deposited in Canadian National Collection of Insects, Ottawa, Canada (CNCI).

DISTRIBUTION: Costa Rica; Guatemala.

ETYMOLOGY: Named after holotype locality.

#### *Paramblynotus zonatus* Weld, 1956

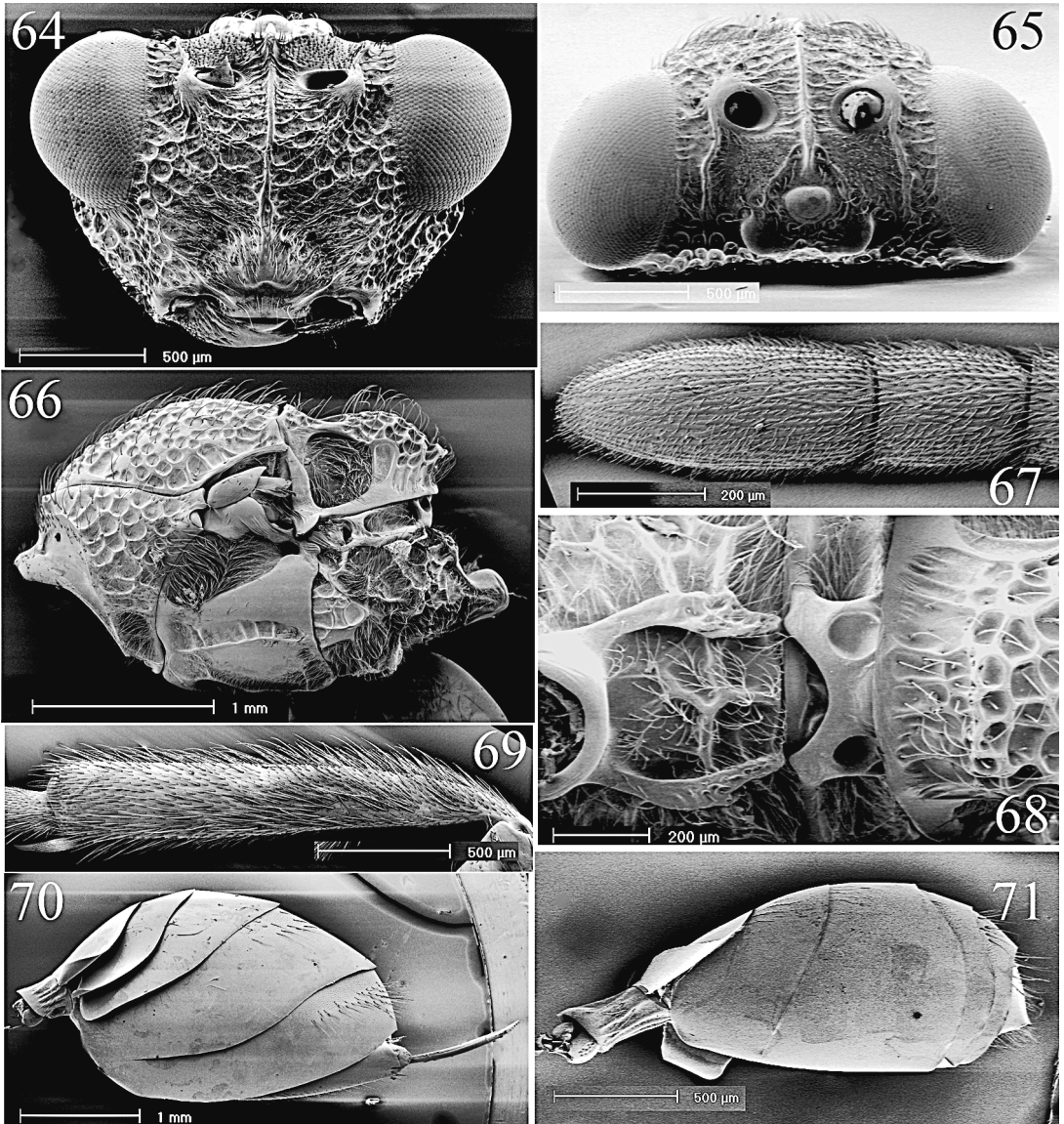
FEMALE: Length 5.2 mm. Head and pronotum yellow brown; mesonotum black; rest of the body, antenna, and legs brown to dark brown. Forewing with a large macula covering marginal cell, distal third of first submarginal cell and basal third of second submarginal cell a narrow band along interior side of the basal vein; both wings without a wide band along outer margin.  $1mt/2-5mt = 0.73$ .

MALE: Unknown.

*Paramblynotus zonatus* is most similar to *P. costaricanus*, but it is distinguished from the latter by having (1) lateral sides of pronotum foveate-reticulate and gena foveate- to alveolate-reticulate, and (2) mesoscutellum, as of *P. braziliensis*, posteriorly with a broad, evenly rounded emargination.

MATERIALS EXAMINED: USNM: 1 (T); CNCI: 1.

DISTRIBUTION: United States: Texas.



Figs. 64–71. *P. annulicornis*. 64, Head, front view, ♀; 65, head, dorsal view, ♀; 66, mesosoma, dorsal view, ♀; 67, antennal F10–11, lateral view, ♀; 68, propodeum, dorsal view, ♀; 69, metatibia, lateral view, ♀; 70, metasoma, lateral view, ♀; 71, metasoma, lateral view, ♂.

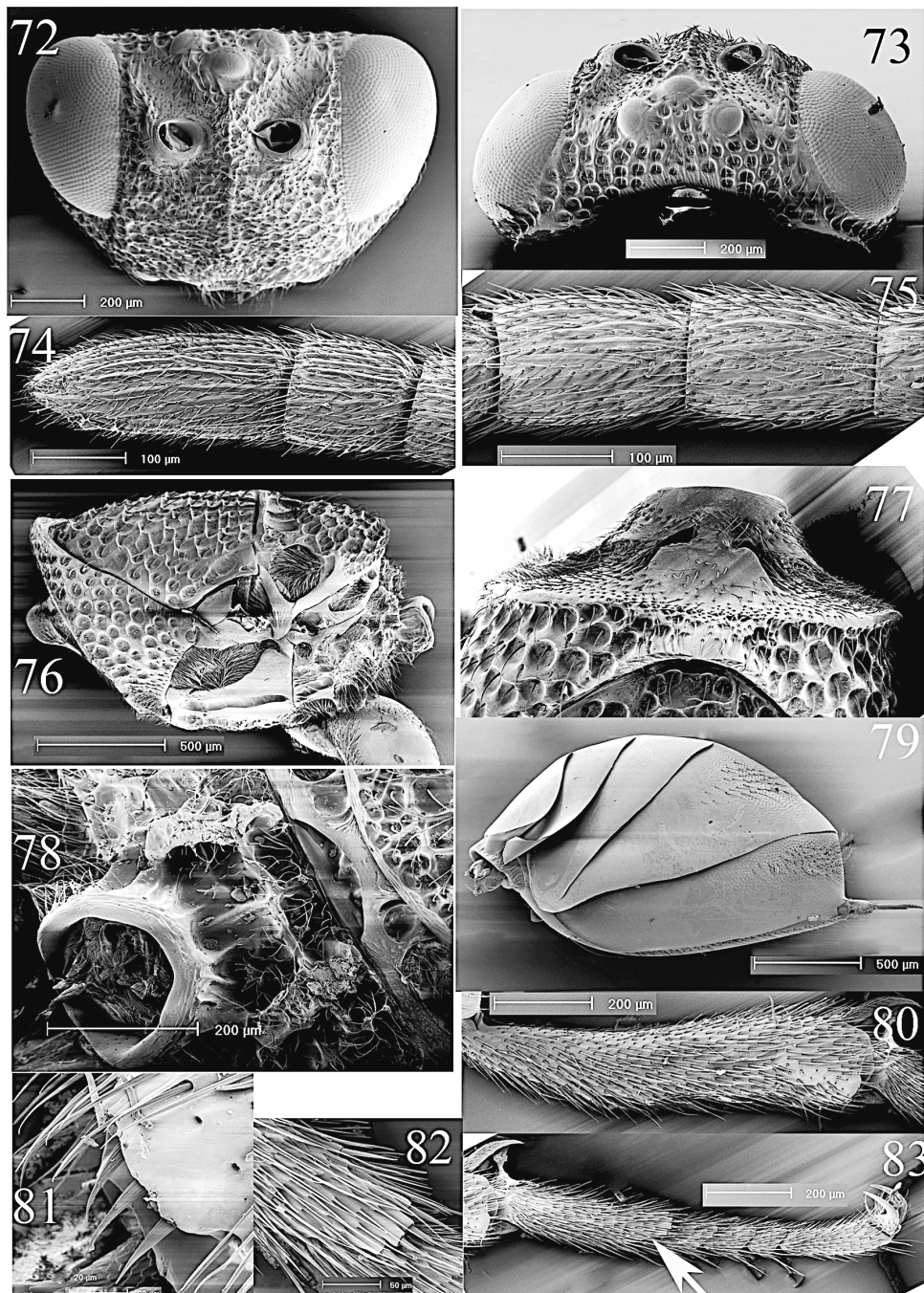
#### *PUNCTULATUS* GROUP

figures 64–83

The *punctulatus* species group is the most diverse among *Paramblynotus* groups, and almost all of its members are from the Oriental regions, with only a few exceptions from Papua New Guinea.

Ronquist (1995a) considered the species included in this group to form two possibly monophyletic species groups: the *borneanus* group and the *punctulatus* group. Our phylogenetic analysis suggests that they do not form two independent monophyletic groups, and several species cannot be readily placed into either of his groups on the basis of morphology.





Figs. 72–83. *P. dyak*. 72, Head, front view, ♀; 73, head, dorsal view, ♀; 74, antennal F10–11, lateral view, ♀; 75, antennal F6–7, lateral view, ♀; 76, mesosoma, lateral view, ♀; 77, anterior part of pronotum, ♀; 78, propodeum, dorsal view, ♀; 79, metasoma, lateral view, ♀; 80, metatibia, lateral view, ♀; 81, end of metatibia showing apical teeth, ♀; 82, apical protuberance of basal metatarsomere, ♀; 83, metatarsus, ♀.



**DIAGNOSTIC CHARACTERS:** Body size medium to relatively large. Antenna filiform, widened toward apex or not. Female antenna usually 13-segmented, occasionally 12-segmented, with F1 distinctly shorter than F2. All flagellomeres have placodes; placodes short, not as long as the segment, and usually densely distributed on each medial to distal segments (figs. 67, 74, 75, 86, 87, 95). Male antenna has 14 segments, F1 cylindrical. Median frontal carina absent or present in lower face, sometimes extended beyond the middle; dorsally sometimes raised between antennal sockets into a lamellate process, which sometimes has a flattened dorsal surface (fig. 64). Occiput glabrous or longitudinally carinate (fig. 73).

Lateral pronotal carinae reaching pronotal crest dorsomedially. Lateral surfaces of pronotum foveate to foveate-reticulate, with or without secondary transverse costae, and medially separated by an extended, less sculptured anterior surface of anterior plate. Pronotal crest not raised (fig. 66) or conspicuously raised dorsomedially into a peak (fig. 76). Mesoscutum predominantly transversely carinate with more or less obvious foveae in between (fig. 76) or entirely foveate-reticulate (fig. 66). Mesoscutellum flat to sloped posteriorly and foveate-reticulate. Scutellar sulcus mostly divided by a single median carina, occasionally divided into more than two foveae by several subequally strong longitudinal carinae (*P. chrysochaites* and *P. rufipes*). Axillar area usually without conspicuous hair tuft. Upper mesopleuron glabrous. Median mesopleural impression straight, with a few, sometimes reduced vertical carinae (e.g., fig. 66). Metepisternum irregularly alveolate. Dorsopical teeth of metatibia long and pointed (e.g., fig. 81); apical protuberance of first metatarsomere present (fig. 83) or absent.

Tergum7 of female metasoma with posterior margin usually not curved dorsolaterally, entirely covering T8, or occasionally curved dorsolaterally, distinctly exposing T8 (fig. 53). When T8 of female metasoma is exposed, the pronotum is always raised anterodorsally into a conspicuous peak (*P. chrysochaites* and *P. rufipes*). Terga 6–7/8 with more or less coarse punctures with hairs. Tergum5 of male metasoma expanded, par-

ticularly so ventrally, the largest postpetiolar tergum.

#### KEY TO SPECIES OF *PUNCTULATUS* GROUP

1. Occiput distinctly carinate vertically and first metatarsomere apically with a prolonged protuberance. Only one of the two features present in a few species . . . . . 2
  - Occiput glabrous, and first metatarsomere apically without a prolonged protuberance . . . . . 20
2. Pronotum not raised anterodorsally. T8 of female slightly exposed. Mesoscutum dorsally mainly transversely carinate . . . . .
  - . . . . . *P. conspiratus*, n.sp.
  - Pronotum conspicuously raised into a peak anterodorsally. T8 of female not exposed. Mesoscutum dorsally mainly foveate-reticulate (*borneanus* clade). . . . . 3
3. First metatarsomere without a distal protuberance . . . . . 4
  - First metatarsomere with a prominent distal protuberance. . . . . 6
4. Antennal flagellum distinctly widened apically, F11 almost twice as wide as the medial width of F1. Gena glabrate-punctate. Mesoscutellum not projected posteriorly. Body yellowish brown with head almost orange . . . . .
  - . . . . . *P. distinctus*, n.sp.
  - Antennal flagellum not distinctly widened apically, F11 subequal to the other flagellomeres in width. Gena coarsely foveate-punctate. Mesoscutellum distinctly projected posteriorly. Body black, except metasoma brown . . . . . 5
5. Mesoscutellum without an inflection prior to posterior projection; posterior margin rounded. Lateral propodeal carina strongly raised anterodorsally into a lobular process (best viewed laterally) . . . . .
  - . . . . . *P. fraxini* Yang and Liu, 1994
  - Mesoscutellum with an inflection prior to posterior projection; posterior margin truncate. Lateral propodeal carinae not raised anterodorsally. . . . .
    - . . . . . *P. kosugii* Watanabe and Sakagami, 1951
6. Occiput glabrous. . . . . *P. insolitus*, n.sp.
- Occiput carinate vertically . . . . . 7
7. Metatibia with three to four subtriangular dents dorsally . . . . . 8
  - Metatibia without dents dorsally . . . . . 9
8. Pronotum with dense hairs. Mesoscutellum flat; posterior margin truncate or slightly broadly emarginate. Body entirely black, legs dark brown, and forewing with a wide, gray band along outer margin . . . . .
  - . . . . . *P. nebulosus*, n.sp.

- Pronotum with only sparse hairs. Mesoscutellum sloped p[osteriorly]; posterior margin rounded posteriorly. Head and mesosoma black, metasoma brown, legs light brown, and forewing clear. . . . . *P. miniatus*, n.sp.
- 9. Gena strongly expanded laterally; margin much beyond outer margins of eyes. Forewing with a dark macula covering marginal cell, submarginal cell, and part of first radial cell behind marginal cell . . . *P. grossus*, n.sp.
- Gena not strongly expanded laterally; margin not to or slightly beyond the outer margins of eyes. Forewing evenly colored or, rarely, with a dark brown macula similar to above. . . . . 10
- 10. Dorsalmost part of anterior plate of pronotum strongly projected anteriorly and distinctly impressed medially in lateral view. Length of dorsal area of pronotum long along midline . . . . . 11
- Dorsalmost part of anterior plate of pronotum not strongly projected anteriorly, and not or slightly impressed medially in lateral view. Length of dorsal area of pronotum short along midline . . . . . 13
- 11. Forewing clear with a dark brown macula covering marginal cell, part of first radial cell behind marginal cell, and a small area at distal end of submarginal cell. . . . . *P. coracinus*, n.sp.
- Forewing tinted yellow and without macula. . . . . 12
- 12. Distal protuberance of first metatarsomere long, reaching almost to the end of second tarsomere. . . . . *P. lutepennis*, n.sp.
- Distal protuberance of first metatarsomere short, distinctly not reaching to end of second tarsomere. . . . . *P. obscurus*, n.sp.
- 13. Vertex, posterior of antennal scrobes, and lateral facial area longitudinally carinate. Lower face longitudinally to diagonally carinate-rugose. Gena, lower part of lateral sides of pronotum, and mesopleural triangle glabrous and finely punctate with hairs. Lateral sides of metapectal-propodeal complex covered entirely with long and dense white hairs so conspicuous that no sculpture in the area is observable . . . *P. fucosus*, n.sp.
- Vertex and facial areas not carinate as above. Lateral areas of the body, except gena, without glabrous areas. Lateral sides of metapectal-propodeal complex with more or less dense and long hairs, but never as conspicuous as above . . . . . 14
- 14. Pronotal crest expanded anteromedially, forming a relatively long dorsal pronotal area behind . . . . . *P. aptatus*, n.sp.
- Pronotal crest anteromedially bent posteriorly, forming a relatively short dorsal pronotal area behind . . . . . 15
- 15. Posterior margin of mesoscutellum truncate. . . . . *P. robustus*, n.sp.
- Posterior margin of mesoscutellum rounded . . . . . 16
- 16. Forewing with a dark macula covering marginal cell, submarginal cell, and part of first radial cell behind marginal cell. Gena with dense silvery hairs . . . . . *P. venoforticulus*, n.sp.
- Forewing without dark macula. Gena without dense hairs or with sparse hairs only. 17
- 17. Body not entirely dark; head orange. Tergum 7 of female has only a narrow band of sparse silvery hairs in anterior half. Tergum 8 of female slightly exposed . . . . . *P. kitrinocarus*, n.sp.
- Body dark entirely. Tergum 7 of female with a band of dense, silvery hairs in anterior half. Tergum 8 of female completely covered by T7. . . . . 18
- 18. Mesoscutellum very much narrowed posteriorly, appearing angular. Postpetiolar metasoma 1.5 times as long as the distance from anterior tip of pronotal crest to end of mesoscutellum; posterior margin of T5 of female dorsally almost vertical posteriorly. Metasoma brown . . . . . *P. borneanus* (Weld, 1922)
- Mesoscutellum broadly rounded. Postpetiolar metasoma 1.2 times as long as the distance from anterior tip of pronotal crest to end of mesoscutellum; posterior margin of T5 of female strongly oblique posteriorly. Metasoma black. . . . . 19
- 19. Eyes strongly protruding laterally. Mesoscutum slightly bent anteriorly. Antennae and all legs yellow brown . . . . . *P. beckeri*, n.sp.
- Eyes moderately protruding (figs. 72, 73). Mesoscutum flat and not bent anteriorly (fig. 76). Antennae and legs black, except pro- and mesotibia, and all tarsomeres red brown, and sometimes pro- and mesofemur dark brown . . . . . *P. dyak* (Weld)
- 20. Pronotum high in lateral view; pronotal crest anteromedially raised into a conspicuous peak. Mesoscutum distinctly transversely costate and relatively flat in lateral view. Scutellar furrow divided by at least three equally strong longitudinal carinae. Tergum 8 of female distinctly exposed. Posterior one-third of T6, posterior half of T7, and T8 very densely punctate and sparsely foveate . . . 21
- Pronotum low in lateral view; pronotal crest anteromedially not raised into a conspicuous peak. Mesoscutum usually foveate-reticulate

- and strongly convex in lateral view. Scutellar furrow divided by a single median longitudinal carina. Tergum 8 not exposed. Terga 6–7 more or less punctate and foveate with hairs, but always in band across the middle of the involved terga, and never so extensive and dense as above . . . . . 22
21. Pubescence on pronotum and T6–8 very dense and long so that sculptures of the terga barely visible. Pubescence of axillar area extended to cover lateral part of scutellar sulcus. The patch pubescence on T6–8 covers posterior one-third of postpetiolar metasoma. Tergum 6 distinctly longer than T3. . . . . *P. chrysochaïtes*, n.sp.
- Pubescence on pronotum and T6–8 less dense and shorter and sculptures easily observable. Pubescence of axillar area not extended to cover part of scutellar sulcus. The patch pubescence on T6–8 covers only posterior one-fifth of postpetiolar metasoma. Tergum 6 shorter than T3. . . . . *P. rufipes*, n.sp.
22. Ocellar plate strongly raised into a conspicuous hump. Lateral surface of pronotum foveate-reticulate above and punctate-reticulate below. . . . . *P. reticulatus* Kieffer, 1910
- Ocellar plate moderately raised, but never as strong as above. Lateral surface of pronotum not as above. . . . . (the *punctulatus* clade) 23
23. Wings clear or evenly smoky . . . . . 24
- Wings with colored bands or maculae in various shapes. . . . . 31
24. Antennae of female 12-segmented. . . . . *P. formosanus* Hedicke, 1922
- Antennae of female 13-segmented. . . . . 25
25. Mesoscutellum raised posteriorly; posterior margin emarginate or truncate. Body particolored; pronotum, mesoscutum, mesoscutellum, and anterior part of mesopleuron orange, legs brown, and the rest of the body black . . . . . *P. clarus* Weld, 1922
- Mesoscutellum sloped and rounded posteriorly. Body not particolored. . . . . 26
26. Head, pronotum, and hindlegs covered with very dense adpressed hairs. Metasomal T6–7 of female each with a conspicuous band of long hairs dorsolaterally. Hair tufts beneath lateral bar of mesoscutellum conspicuous. Lateral propodeal carina strongly and abruptly curved and strongly raised dorsolaterally into a triangular process. . . . . *P. pubifemoratus*, n.sp.
- Head, pronotum, and hindlegs covered with more or less adpressed hairs, but not dense (fig. 93, 94, 97). Metasomal T7 of female with sparse long hairs dorsolaterally (fig. 98). Hair tufts beneath lateral bar of mesoscutellum not conspicuous (fig. 97) . . . . . 27
27. Marginal cell short, about twice as long as width. Body entirely yellow to dark brown; rarely the mesosoma almost black . . . . . *P. ruficeps* Kieffer, 1914
- Marginal cell long, more than three times as long as width. Body mostly dark with metasoma dark brown. . . . . 28
28. Antennal scrobes indistinct, not distinctly depressed, and longitudinally rugose. Median frontal carina distinct and extended ventrally beyond the lower margin of eye. Tergum 6 of female strongly expanded lateroventrally, posterior margin parallel with that of T5. . . . . *P. cheni*, n.sp.
- Antennal scrobes distinctly depressed and glabrate to punctate. Median frontal carina absent in lower face (e.g., fig. 84). Tergum 6 of female not strongly expanded lateroventrally, posterior margin convergent with that of T5 toward ventral margin of metasoma (fig. 92) . . . . . 29
29. Lateral propodeal carina anteriorly raised conspicuously, forming a process almost right triangular in lateral view (figs. 88, 89) . . . . . *P. punctulatus* Cameron, 1908
- Lateral propodeal carina anteriorly not raised conspicuously, not forming a triangular process . . . . . 30
30. Antennal scrobes posteriorly longitudinally carinate. Scutellar foveae subdivided by one or two longitudinal submedian carinae . . . . . *P. nipponensis*, n.sp.
- Antennal scrobes entirely glabrous with fine punctures. Scutellar foveae not subdivided by extra longitudinal submedian carinae . . . . . *P. isolatus*, n.sp.
31. Both forewing and hindwing with wide, dark to smoky bands . . . . . 32
- Forewing with a dark brown macula covering marginal cell and part of Rs cell behind marginal cell, and hindwing clear . . . . . 33
32. Wings dark brown in basal half and clear in distal half. Head orange and the rest of body dark brown . . . . . *P. miltocephalus*, n.sp.
- Wings tinted yellow with a wide smoky band along outer margin or in distal half. Body yellow entirely or with metasoma dark brown . . . . . *P. ornatus*, n.sp.
33. Antennae dark brown entirely, without contrasting, white flagellomeres. Body black entirely. . . . . *P. hainanensis*, n.sp.
- Antennal flagellomeres 5–6/9 white, contrasting to the other, dark brown segments. Body mostly yellow and sometimes dark brown . . . . . 34
34. Mesoscutellum raised and projected posteriorly, and posterior margin truncate or emarginated . . . . . 35

- Mesoscutellum distinctly sloped posteriorly. . . . . 37
- 35. Antennal scrobes longitudinally carinate posteriorly. Gena with a median glabrate area. Posterior margin of mesoscutellum emarginate. Tergum 8 of female metasoma slightly exposed . . . . . *P. stigi*, n.sp.
- Antennal scrobes not longitudinally carinate posteriorly. Gena without a median glabrate area. Posterior margin of mesoscutellum emarginate or truncate. Tergum 8 of female metasoma covered by T7 entirely . . . . . 36
- 36. Antennal scrobes foveate. Posterior margin of mesoscutellum emarginate . . . . . *P. yuani*, n.sp.
- Antennal scrobes glabrate. Posterior margin of mesoscutellum truncate . . . . . *P. filippae*, n.sp.
- 37. Median frontal carinae not extended to lower face. Vertex foveate-reticulate entirely . . . . . *P. barbarae*, n.sp.
- Median frontal carina in lower face usually percurrent to clypeus, or at least extended to the middle . . . . . 38
- 38. Genae with a prominent vertical carina medially . . . . . *P. shimenensis*, n.sp.
- Genae without a distinct vertical carina. . . . . 39
- 39. Antennal scrobes and ocellar plate anterior to anterior ocellus glabrous. Genae mostly glabrous except being foveate along posterior margin of eye. Anterior plate of pronotum glabrous. Median propodeal area without distinct median carina . . . . . *P. glaberus*, n.sp.
- Antennal scrobes punctate and ocellar plate anterior to anterior ocellus more or less foveate. Genae mostly foveate-reticulate. Anterior plate of pronotum punctate. Median propodeal area always with a distinct median carina in anterior half . . . . . 40
- 40. Median frontal carinae present only in upper half of lower face. Mesoscutellum strongly sloped posteriorly; the height of the sloped part distinctly larger than that of the part beneath . . . . . *P. eriki*, n.sp.
- Median frontal carinae percurrent in lower face. Mesoscutellum moderately sloped posteriorly; the height of the sloped part at least approximately equal to that of the part beneath . . . . . 41
- 41. Ocellar plate lined with a row of distinct foveae along anterior sides. . . . . 42
- Ocellar plate with or without foveae along anterior sides, but not lined in a row . . . . . 43
- 42. Foveae along along anterior sides of ocellar plate not set between parallel carinae. Antennal scrobes glabrate with fine punctures. Median frontal carinae simple, not raised into a process between antennal sockets . . . . . *P. ebbae*, n.sp.

- Foveae along along anterior sides of ocellar plate not set between parallel carinae. Antennal scrobes coarsely punctate. Median frontal carinae raised into a distinct, dorsally flattened process between antennal sockets . . . . . *P. asae*, n.sp.
- 43. Median frontal carinae simple. Median propodeal carina rather weak, but percurrent . . . . . *P. weiae*, n.sp.
- Median frontal carinae raised into a distinct, dorsally flattened or lamellate process between antennal sockets (figs. 64, 65) . . . . . 44
- 44. Ocellar plate mostly glabrous and defined laterally by a distinct carina. Contrasting white ring of antenna mostly distinct. Median propodeal carina strong anterior to submedian transverse carina, and replaced by two submedian carinae posteriorly (fig. 68) . . . . . *P. annulicornis* Cameron, 1910
- Ocellar plate irregularly punctate and not defined by a distinct carina laterally. Ocellar plate mostly glabrous and defined laterally by a distinct carina. Contrasting white ring of antenna faint to indistinct. Median propodeal carina missing posterior to submedian transverse carina . . . . . *P. axeli*, n.sp.

#### *Paramblynotus conspiratus*, new species

FEMALE: Length 3.3 mm. Head and mesosoma black; metasoma dark brown. Antenna and legs yellow brown. Wings transparent.

Antenna 13-segmented; flagellum slightly widened apically. Vertex foveate-reticulate. Eye distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, foveate-reticulate, and defined laterally by carina lined by large foveae along interior side. Median frontal carina simple, not extended to lower face anteriorly, and bifurcated posteriorly to seclude a small, triangular glabrous area beneath anterior ocellus. Upper face longitudinally rugose with sparse foveae; antennal scrobe densely punctate, deeply depressed, and not well defined by a carina laterally. Gena foveate-rugose, with a medial vertical carina on upper half. Lower face foveate/punctate-reticulate, with distinct transverse rugosity in upper one-fifth. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Clypeus foveate-reticulate, anteriorly also pubescent. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate.



Anterior flange of pronotum glabrous; submedian pronotal pits separated far from each other medially. Anterior plate of pronotum densely punctate with pubescence, particularly laterally, and glabrous antero-medially. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carinae distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate and punctate, with superficial transverse carination. Dorsal pronotal area glabrous, present only along anterior half of posterior margin of pronotum. Mesoscutum almost flat dorsally; anteriorly and transversely costate with distinct foveae set in rows. Scutellar sulcus divided by a strong longitudinal carina into two large foveae, each being further divided by one or two weaker, oblique carinae. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Axillar area with long white pubescence. Mesopleural triangle well defined ventrally by smoothly curved carina and with white pubescence. Median mesopleural impression percurrent, with evenly spaced transverse costae; upper mesopleuron glabrous with sparse anterior setigerous punctures; lower mesopleuron glabrous and pubescent ventrally, bordered by a smoothly curved carina ventrally. Metepisternum areolate-reticulate, devoid of pubescence in upper part, and pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and slightly curved medially; median propodeal area glabrate with superficial rugosity; median longitudinal carina and a submedian transverse carina present. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.2 times as long as wide and 1.4 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent. Areolet small, but distinct.

Petiole 0.67 times as long as wide in lateral view. Relative length of T3–8: 3.1:1.0:1.2:2.6:1.4:0.45; T3 glabrous; T4–5 finely punctate dorsomedially and otherwise glabrous; T6–7 mostly more or less densely, finely punctate, except each with a median patch of sparse pubescence in larger punctures dorsolaterally; and T8 only slightly exposed, punctate with pubescence. Legs more or less densely pubescent. Apical teeth

of metatibia long, slender, and pointed apically.  $1\text{mt}/2\text{--}5\text{mt} = 0.65$ .

MALE: Unknown.

*Paramblynotus conspiratus* is unique among all species of the *punctulatus* group in having a mixture of characters that belong to the two major clades within this group that were previously recognized as two species groups, that is, the *punctulatus* group and the *borneanus* group (Ronquist, 1995b). Except for the few species that do not fall into either group, the groups sensu Ronquist (1995a) still hold as two distinct clades, which we hereby refer to as the *punctulatus* clade and the *borneanus* clade. The *punctulatus* clade is characterized by (1) occiput glabrous, (2) pronotum not raised, (3) mesoscutum foveate-reticulate, and (4) first metatarsomere without an apical protuberance. The *borneanus* clade is characterized by (1) occiput longitudinally carinate, (2) pronotum raised conspicuously into a peak, (3) mesoscutum distinctly transversely carinate with foveae set in between, and (4) first metatarsomere with an apical protuberance (with a few exceptions).

*Paramblynotus conspiratus* does not belong to either of the clades and is easily distinguished by (1) occiput longitudinally carinate, (2) pronotum not raised, (3) mesoscutum distinctly transversely carinate with foveae set in between, and (4) first metatarsomere without an apical protuberance.

TYPE MATERIAL: HOLOTYPE: ♀, China: Taiwan, Wushe (1,150 m), 1983-V-15, H. Townes coll. (AEI).

DISTRIBUTION: China: Taiwan.

ETYMOLOGY: Derived from Latin, *conspiro*, breathe together.

#### *Paramblynotus reticulatus* (Kieffer, 1910)

*Paraegilips reticulatus* Kieffer (1910b: 335, ♂); Indonesia: Bintan; ZMHB (HT♂).

*Paramblynotus reticulatus* Hedicke in Hedicke and Kerrich (1940: 179), by inference through generic synonymy.

FEMALE: Length 3.0 mm. Head and mesosoma black; metasoma and antenna dark brown; legs mostly dark brown except tibia and tarsus of fore- and middle legs, and tarsus of hindleg yellow brown.  $1\text{mt}/2\text{--}5\text{mt} = 0.57$ .

*Paramblynotus reticulatus* differs from all other *Paramblynotus* species in (1) ocellar plate raised strongly into a conspicuous hump and (2) lateral surface of pronotum foveate-reticulate above and punctate-reticulate below.

MALE: Similar to female.

MATERIAL EXAMINED: 7♀♀, 2♂♂. ZMHB: 1♀(HT); NHM: 5 (3♀♀, 2♂♂); BPBM: 3♀♀.

DISTRIBUTION: Indonesia: Bintang; Malaysia: Mardi; Laos: Vientiane Prov.

BIOLOGICAL NOTES: The specimens from Laos are collected between 750 and 800 m.

*Paramblynotus clarus* (Weld, 1922)

*Allocynips clarus* Weld (1922: 330, ♂); Mindanao; USNM (HT♂, no. 24 378).

*Paramblynotus clarus* Weld (1930: 137).

FEMALE: Length 4.8 mm. Pronotum, mesoscutum, and anterior part of mesoscutellum and mesopleuron brown; antenna and rest of body black to almost black; legs dark brown. Wings transparent. 1mt/2–5mt = 0.69.

*Paramblynotus clarus* differs from other species of the *punctulatus* clade in (1) its wings entirely transparent, (2) mesoscutellum raised and emarginate posteriorly, and (3) its unique body color pattern.

MALE: Similar.

MATERIAL EXAMINED: 2♀♀, 1♂. USNM: 2 (HT♂), CAS: 1♀.

DISTRIBUTION: Philippines: Mindanao; Ceylon: Kandy.

*Paramblynotus formosanus* (Hedicke, 1922)

*Mayrella formosana* Hedicke (1922: 190, ♀); Taiwan; DEIC (HT♀).

*Paramblynotus formosanus* Weld (1930: 137).

FEMALE: Length 6.5 mm. Antenna, mesosoma, and coxae of legs, tarsus of hindleg black; metasoma and rest of legs brown. Wings entirely transparent. 1mt/2–5mt = 0.80.

MALE: Unknown.

*Paramblynotus formosanus* is easily separated from all other species of the *punctulatus* clade in that the female antenna is 12-segmented. In addition, the lower face of *P.*

*formosanus* is densely punctate with sparse foveae, in contrast to the usual, mainly foveate-reticulate pattern of the *punctulatus* group.

MATERIAL EXAMINED: 1♀. DEIC: 1(HT).

DISTRIBUTION: China: Taiwan.

*Paramblynotus nipponensis*, new species

FEMALE: Length 3.3 mm. Antenna, head, and mesosoma deeply dark brown; metasoma and legs dark brown. Wings evenly, lightly ferruginous. 1mt/2–5mt = 0.68.

Antenna 13-segmented; flagellum slightly widened apically. Vertex foveate-reticulate with distinct longitudinally carinate component. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, foveate-reticulate, and defined laterally by carina lined by a row of large foveae along interior side of lateral carina. Median frontal carina simple, only present between antennal sockets, and bifurcated posteriorly to seclude a small, triangular glabrous area beneath anterior ocellus. Upper face longitudinally carinate and foveate laterally; antennal scrobe glabrate, densely punctate, longitudinally carinate posteriorly, deeply depressed, and well defined by carina laterally. Gena foveate-rugose anteriorly and horizontally costate posteriorly. Lower face foveate/punctate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a rectangle above the median transverse inflexion of clypeus. Clypeus punctate-reticulate. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal depressions slightly separated from each other medially. Anterior plate of pronotum mostly glabrous except punctate posteriorly. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate except transversely carinate lateroventrally. Dorsal pronotal area glabrate, present only along anterior half of posterior margin of pronotum. Mesoscutum

distinctly arched dorsally and transversely costate with distinct foveae set in rows. Scutellar sulcus divided by a median longitudinal carina and two equally strong submedian carinae. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Axillar area without distinct white pubescence. Mesopleural triangle well defined ventrally by a smoothly curved carina and with sparse white pubescence. Median mesopleural impression percurrent, not transversely costate medially; upper mesopleuron glabrous with sparse setigerous punctures anteriorly; lower mesopleuron glabrous, conspicuously depressed along ventral margin, and sparsely pubescent ventrally. Metepisternum longitudinally costate and devoid of pubescence in upper part, pubescent ventrally. Propodeum areolate-reticulate; lateral propodeal carina percurrent and curved medially; median propodeal area glabrate; median longitudinal carina present only anterior to the submedian transverse carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 3.5 times as long as wide and 1.6 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.55 times as long as wide in lateral view. Tergum 8 entirely covered by T7; relative length of T3–7: 2.6:1.0:1.6:4.3:2.1; T3–5 glabrous; T6 finely punctate dorsomedially and otherwise glabrous; T7 mostly densely, finely punctate, with larger setigerous punctures dorsolaterally. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.60.

MALE: Unknown.

*Paramblynotus nipponensis*, *P. punctulatus*, and *P. isolatus* form a species complex that is characterized by “lacking” distinguishing characters; for example, body mostly dark or brown; wings evenly, lightly ferruginous; female antenna 13-segmented. In a word, there is no special modification of any major structures in these species. *P. nipponensis* differs from *P. punctulatus* and *P. isolatus* in (1) lateral propodeal carina anteriorly not raised into an almost triangular process and (2) scutellar sulcus divided by several subequal, longitudinal carinae. It further differs from *P. isolatus* in (1) antennal scrobes longitudinally carinate posteriorly, (2) gena horizontally costate posteriorly, and (3)

mesoscutellum rounded posteriorly in dorsal view.

TYPE MATERIAL: HOLOTYPE: ♀, Japan: Ogasawara, Chichishima, Chuosan (300 m), 1980-VIII-15, J.L. Gressitt (BPBM).

DISTRIBUTION: Japan: Ogasawara.

ETYMOLOGY: This species is named after the type locality.

*Paramblynotus punctulatus* Cameron, 1908  
figures 84–92

*Paramblynotus punctulatus* Cameron (1908: 300, ♀); Borneo; BMNH (2T♀, in main coll.).

\**Allocynips borneensis* Weld (1922: 322, ♀); Borneo; USNM (HT♀, no. 24 380, 2 PT♀). Combination and synonymy by Weld (1930b: 137).

\**Paramblynotus rufiventris* Cameron (1910: 131, ♀; Borneo; BMNH (HT♀, no. 7.8). Synonymy by Ronquist (1995:37).

FEMALE: Length 2.5–4.5 mm. Antenna, head, and mesosoma deeply dark brown; metasoma and legs dark brown. Wings evenly, lightly ferruginous. 1mt/2–5mt = 0.70.

MALE: Unknown.

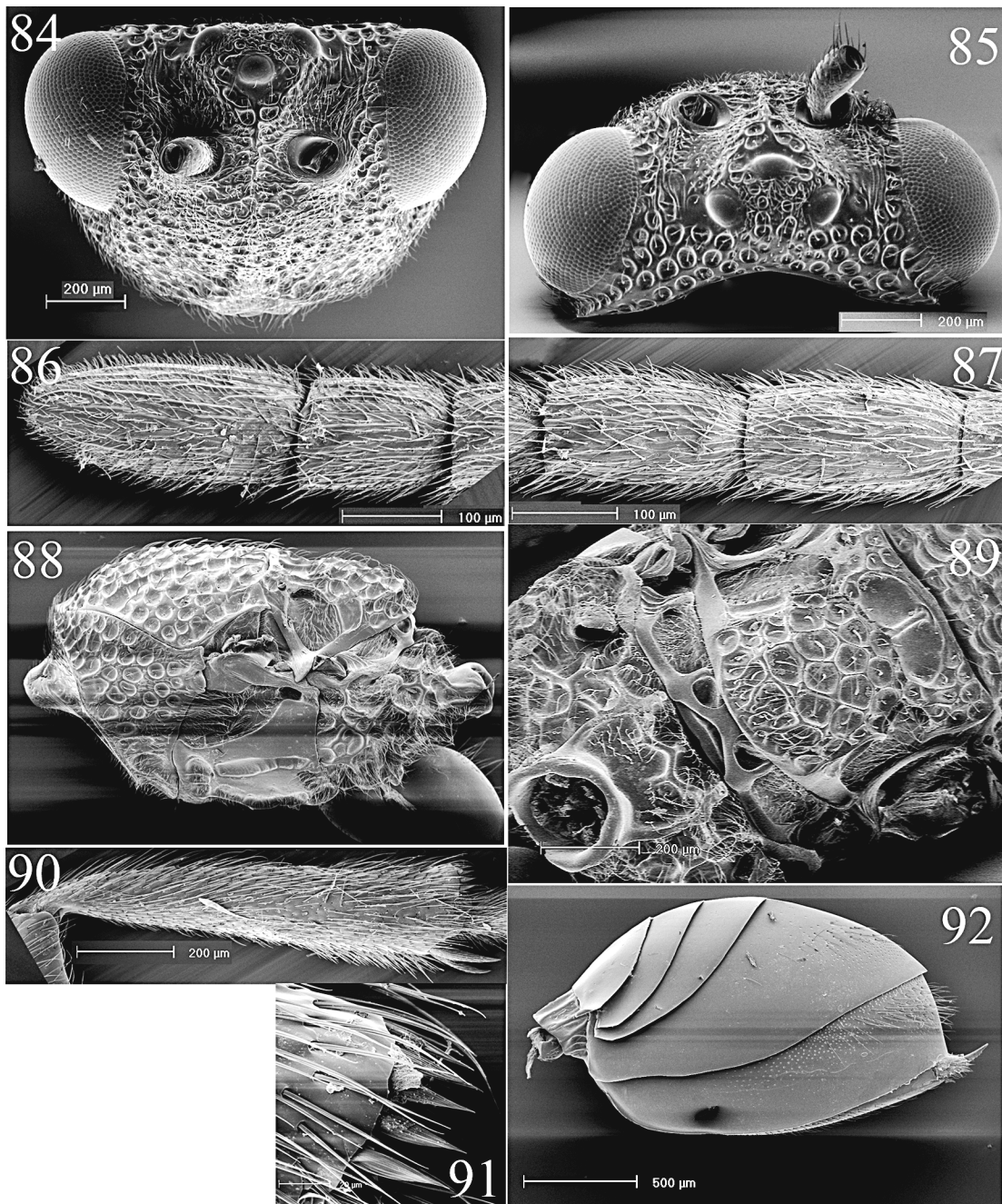
*Paramblynotus punctulatus* is similar to *P. nipponensis* and *P. isolatus*, but it differs from the latter in lateral propodeal carina anteriorly raised into a conspicuous, lamellate process (figs. 88, 89). In addition, lighter individuals of the species can be easily confused with darker individuals of the sympatric species *P. ruficeps* but can be distinguished from the latter with diagnostic characters listed under *P. ruficeps*.

MATERIAL EXAMINED: 87: AEI 63, BPBM 1, ZMLU-MS 1, CFR 2, NHM 13 (incl. 4T), NNMN 1, ROM 2, USNM 4 (incl. 3T).

DISTRIBUTION: Malaysia: Borneo; Malaya; Indonesia: Sulawesi.

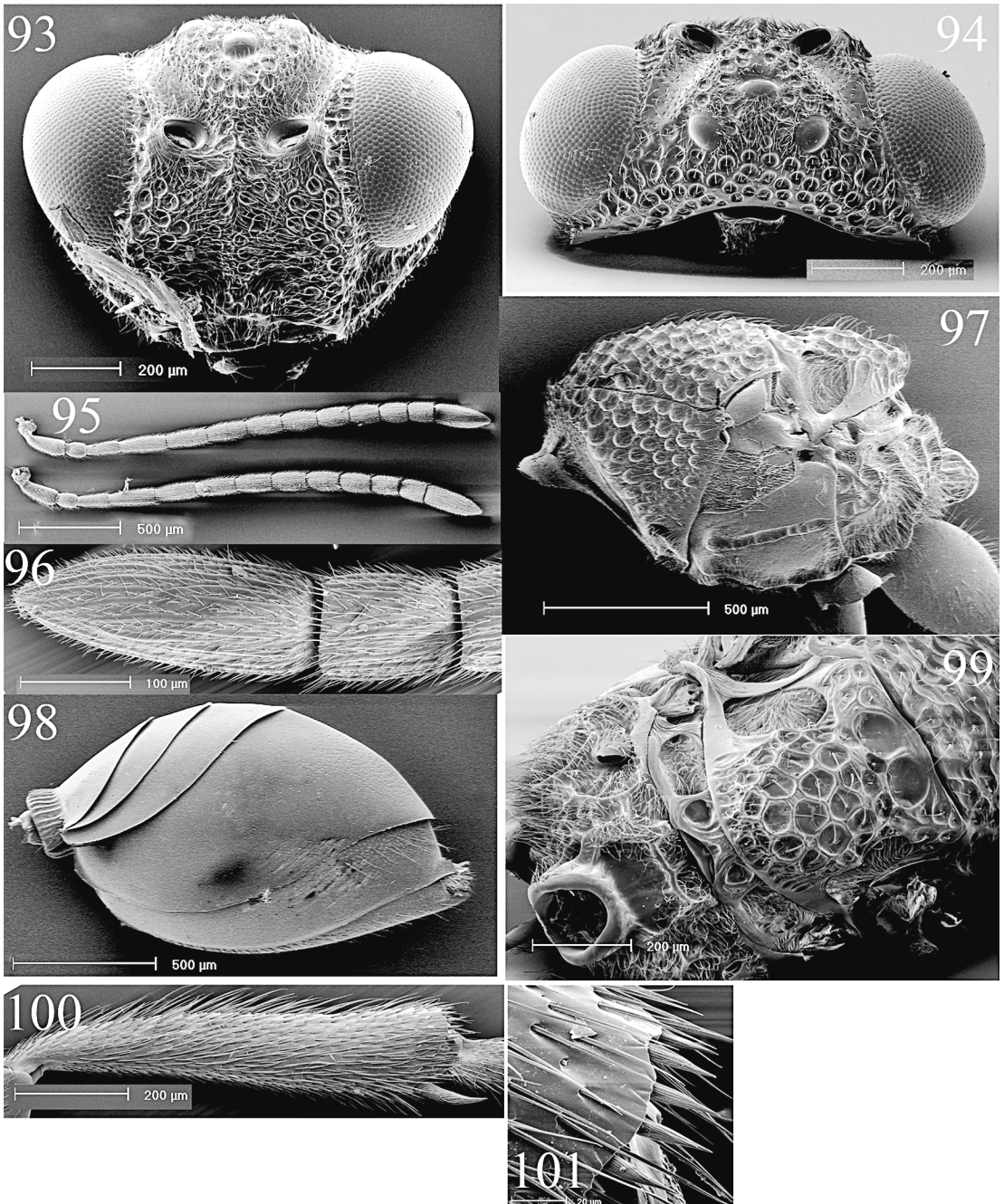
LECTOTYPE DESIGNATION: We hereby designate a female deposited in NHM as lectotype of *P. punctulatus*. Labels: “Cotype” (with yellow cycle), “Kuching, J.H.”, “*Paramblynotus punctulatus*, Cam. Type, Borneo”, “W 29”, “P. Cameron Coll. 1914-110”, and our lectotype and determination label. In addition to the two female types that Ronquist (1995a) examined from the NHM (in main collection), Z.L. found in the NHM one male in the Hymenoptera type collection





Figs. 84-92. *P. punctulatus*. **84**, Head, front view, ♀; **85**, head, dorsal view, ♀; **86**, antennal F6-7, lateral view, ♀; **87**, antennal F10-11, lateral view, ♀; **88**, mesosoma, lateral view, ♀; **89**, scutellum and propodeum, dorsoposterior view, ♀; **90**, metatibia, lateral view, ♀; **91**, end of metatibia showing apical teeth, ♀; **92**, metasoma, lateral view, ♀.





Figs. 93–101. *P. ruficeps*. 93, Head, front view, ♀; 94, head, dorsal view, ♀; 95, antennae, ♀; 96, antennal F10–11, lateral view, ♀; 97, mesosoma, lateral view, ♀; 98, metasoma, lateral view, ♀; 99, scutellum and propodeum, dorsoposterior view, ♀; 100, metatibia, lateral view, ♀; 101, end of metatibia showing apical teeth, ♀.

(B.M. TYPE 7.7.), which bears Cameron's designation label "*Paramblynotus punctulatus*, Cam. Type ♂". This male specimen also bears a round label reading "Type" with an orange cycle. However, the "Type" label is apparently a later addition. In addition, Cameron's original description was based on female specimen(s). Therefore, the male specimen is unlikely to be "the type" on which Cameron based his description of *P. punctulatus*. In addition, the male type specimen does not belong to the same species as the two female cotypes. Therefore, of the two female type specimens, the one that bears Cameron's type label is hereby selected among the three as the lectotype.

*Paramblynotus isolatus*, new species

FEMALE: Length 3.5 mm. Antenna, head, and mesosoma deeply dark brown; metasoma and legs dark brown. Wings evenly, lightly ferruginous.

Antenna 13-segmented; flagellum not widened apically. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate anteriorly, foveate-reticulate posteriorly, and defined laterally by carina lined by a row of large foveae along interior side. Median frontal carina simple, only present between antennal sockets, and bifurcated posteriorly to seclude a small, triangular glabrous area beneath anterior ocellus. Upper face foveate laterally; antennal scrobe glabrous and sparsely punctate; antennal scrobe deeply depressed and well defined by carina laterally. Gena foveate-reticulate anteriorly, glabrate with superficial foveae posteriorly, and with a weak vertical carina medially. Lower face and clypeus foveate/punctate-reticulate. Anterior tentorial pits distinct. Clypeo-pleurostomal sulcus and epistomal sulcus form a rectangle above transverse inflexion of clypeus. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous and finely punctate with pubescence. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest

not raised medially. Lateral pronotal carina distinct, not reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate mostly and transversely carinate lateroventrally. Dorsal pronotal area glabrate, present along anterior half of posterior margin of pronotum. Mesoscutum distinctly arched dorsally and foveate-reticulate with foveae set in rows between superficial transverse costae. Scutellar sulcus divided by a single median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin truncate in dorsal view. Axillar area without distinct white pubescence. Mesopleural triangle well defined ventrally by a smoothly curved carina and with white pubescence. Median mesopleural impression percurrent, not transversely costate; upper and lower mesopleuron glabrous, the latter also conspicuously depressed along ventral margin and sparsely pubescent ventrally. Metepisternum areolate-reticulate and devoid of pubescence in upper part, pubescent ventrally, and with a small elevated, glabrous area medially. Lateral propodeal carinae percurrent and subparallel to each other and not raised dorsally into a process; median propodeal area glabrate, median longitudinal carina percurrent crossed by submedian transverse carina. Rs+M of forewing arising from slightly behind middle of basal vein. Marginal cell 3.6 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.58 times as long as wide in lateral view. Tergum 8 almost entirely covered by T7 with tip slightly exposed; relative length of T3-7: 1.25:1.0:1.2:2.3:1.25; T3-5 glabrous; T6 finely punctate dorsomedially and otherwise glabrous; T7 mostly densely, finely punctate, with larger setigerous punctures dorsolaterally. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2-5mt = 0.70.

MALE: Unknown.

*Paramblynotus isolatus* is similar to *P. nipponensis* and *P. punctulatus*, but it differs from *P. punctulatus* in lateral propodeal carina not raised dorsally into an almost triangular process, and it differs from *P. nipponensis* in (1) antennal flagellum not widened apically, (2) scutellar sulcus divided by a single median longitudinal carina,

(3) antennal scrobes entirely glabrous with fine punctures, (4) gena glabrate posteriorly, and (5) mesoscutellum truncate posteriorly in dorsal view.

TYPE MATERIAL: HOLOTYPE: ♀, American Samoa: Tutuila, Mulinnuu, 1963-XII-8, T.C. Maa coll. (BPBM).

ETYMOLOGY: From Latin, *isolatus*, detached. The name refers to the relative geographic isolation of the type locality.

***Paramblynotus miltocephalus*, new species**

FEMALE: Length 9.0 mm. Head red orange. Antenna, meso- and metasoma, and legs dark brown. Wings bicolored, forewing dark ferruginous in basal half and clear in distal half; hindwing ferruginous in basal two-thirds and clear in distal one-third.

Antenna 13-segmented; flagellum filiform. Vertex foveate with black pubescence. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrous anteriorly and foveate posteriorly, and defined laterally by carina. Median frontal carina simple, extended to level of lower margin of antennal sockets anteriorly and bifurcated posteriorly to seclude a small, triangular glabrous area beneath anterior ocellus. Upper face foveate laterally; antennal scrobe glabrous, densely finely punctate, and longitudinally carinate posteriorly; and antennal scrobe deeply depressed and well defined by carina laterally. Gena glabrous and very sparsely punctate. Lower face and clypeus punctate-reticulate and sparsely foveate; clypeus punctate anterior to submedian transverse inflexion. Anterior tentorial pits distinct. Lateral occipital carina not reaching vertex. Occiput glabrous medially and densely punctate laterally.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous laterally and punctate with a few foveae medially. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate mostly and transversely carinate lateroventrally. Dorsal pronotal area glabrate, present along anterior

half of posterior margin of pronotum. Mesoscutum arched dorsally and foveate-reticulate, with foveae set in rows between superficial transverse costae posteriorly. Scutellar sulcus divided by a single median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Axillar area with distinct golden brown pubescence. Mesopleural triangle well defined ventrally by a smoothly curved carina and glabrate with sparse pubescence. Median mesopleural impression percurrent, not transversely costate; upper mesopleuron glabrous; lower mesopleuron glabrous, conspicuously depressed along ventral margin, and sparsely pubescent ventrally. Metepisternum glabrous and areolate-reticulate in upper part and pubescent ventrally. Lateral propodeal carinae percurrent and almost parallel to each other, and raised throughout into a conspicuous ridge; median propodeal area glabrate; median longitudinal carina only present before submedian transverse carina. Rs+M of forewing arising from anterior third of basal vein; basal vein nebulous. Marginal cell 3.5 times as long as wide and 1.8 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.64 times as long as wide in lateral view. Tergum 8 entirely covered by T7; relative length of T3–7: 20:1.0:1.1:3.9:1.65; T3–5 glabrous; T6 mostly glabrous and only very sparsely punctate; T7 punctate with pubescence dorsolaterally and otherwise glabrous. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.78$ .

MALE: Unknown.

*Paramblynotus miltocephalus* is easily recognized among all *Paramblynotus* species by color pattern of its body and wings.

TYPE MATERIAL: HOLOTYPE: ♀, Laos: Vientiane Prov., Phou-kow-kui (800 m), 1965-IV-12–13, G. Gressitt coll. (BPBM).

DISTRIBUTION: Laos: Vientiane Prov.

ETYMOLOGY: From Greek, *milto*, red, and *cephalo-*, head. The name describes the red orange color of the head in comparison to the dark brown color of its body.

***Paramblynotus ornatus*, new species**

FEMALE: Length 7.0 mm. Body entirely bright yellow, except antennal flagellum dark



brown. Forewing mostly smoky; marginal cell, first discoidal cell, and area interior to basal vein light yellow; hindwing smoky distally and light yellow proximally.

Antenna 13-segmented; flagellum filiform. Vertex glabrous and sparsely foveate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate not distinctly raised, glabrate and sparsely foveate-punctate, and defined laterally by weak carina. Median frontal carina very briefly present above antennal sockets. Upper face foveate laterally; antennal scrobe glabrous and finely punctate, deeply depressed, and well defined by carina laterally. Gena glabrous and very sparsely punctate. Lower face and clypeus punctate-reticulate and sparsely foveate; clypeus anterior to submedian transverse inflexion glabrate-punctate. Anterior tentorial pits small. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous, only punctate dorsomedially. Pronotum dorsomedially raised, slightly lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrate, present along anterior half of posterior margin of pronotum. Mesoscutum arched dorsally and foveate-reticulate, with foveae set in rows between transverse costae. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Axillar area without distinct pubescence. Mesopleural triangle well defined ventrally by a smoothly curved carina and glabrate with sparse pubescence. Median mesopleural impression percurrent, not transversely costate medially; upper and lower mesopleuron glabrous; lower mesopleuron conspicuously depressed along ventral margin and sparsely pubescent ventrally. Metepisternum glabrous, areolate-reticulate in upper part and pubescent ventrally. Lateral propodeal carina percurrent and distinctly directed toward outside posteriorly and raised throughout into a conspicuous ridge; median propodeal

area glabrate; median longitudinal carina present prior to submedian transverse carina. Rs+M of forewing arising from middle of basal vein; basal vein nebulous. Marginal cell 3.6 times as long as wide and 1.7 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.47 times as long as wide in lateral view. Tergum 8 slightly exposed; relative length of T3–8: 2.5:1.0:1.4:4.8:2.3:0.6; T3–5 glabrous; T6 mostly glabrous and punctate dorsomedially; T7 densely punctate and dorsolaterally coarsely punctate/foveate with pubescence. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.78.

MALE: Unknown.

*Paramblynotus ornatus* is similar to *P. miltocephalus*, but it differs from the latter readily by its entirely yellow color of body and the largely smoky wings.

TYPE MATERIAL: HOLOTYPE: ♀, Indonesia: Sumatra, Medan (NHRS). PARATYPES: 3♀♀, 1♂, Malaysia, Selangor (rubber plantation), probably collected in 1951-IV as indicated by the number “2.007-4-51” on the collection label (NHM); 1♂, Thailand: Tak Prov., Thung Thai (300 m), 1988-IV-27–V-6, M.J.D. Brendell coll. (NHM); 1♂, Vietnam: Tokin, Hoabinh, 1918-8, R.V. de Salvaza coll. (NHM).

DISTRIBUTION: Southeast Asia.

ETYMOLOGY: From Latin, *ornatus*, handsome.

*Paramblynotus cheni*, new species

FEMALE: Length 3.5 mm. Body entirely dark brown except metasoma ventrally and legs brown.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate, and defined laterally by weak carina. Median frontal carina simple, reaching to level of lower margin of eye. Upper face, including antennal scrobe, foveate to coarsely punctate; antennal scrobe slightly depressed, with longitudinal rugosity, and defined by carina laterally. Gena foveate-reticulate. Lower face and clypeus foveate-reticulate; anterior tentorial pits small. Lat-



eral occipital carina reaching posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous, finely punctate dorsomedially. Pronotum dorsomedially raised, slightly lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrate, present almost to end of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a single median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Axillar area without distinct pubescence. Mesopleural triangle pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and transversely costate; upper mesopleuron glabrous except finely punctate anteriorly; lower mesopleuron glabrous, conspicuously depressed along ventral margin, and sparsely pubescent ventrally. Metepisternum areolate-reticulate in upper part and pubescent ventrally. Lateral propodeal carina percurrent and raised throughout into a ridge; median propodeal area glabrate; median longitudinal carina present prior to submedian transverse carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.5 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.13 times as long as wide in lateral view. Tergum 8 not exposed; relative length of T3–7: 2.0:1.0:1.3:2.0:1.1; T3–4 glabrous; T5–6 densely punctate; T7 densely punctate and with row of sparse pubescence anteriorly. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.72.

*Paramblynotus cheni* is similar to *P. isolatus*, *P. nipponensis*, *P. punctulatus*, but it differs from the latter in the following characters: antennal scrobe slightly depressed and with longitudinal rugosity; median frontal carina distinct and extended in lower face beyond the lower margin of eye; longitudinal mesopleural impression distinctly transverse-

ly costate; petiole longer than width; and T6 of female strongly expanded lateroventrally with posterior margin parallel with the posterior margin of T5.

TYPE MATERIAL: HOLOTYPE: ♀, China: Zhejiang, Tianmu Mt., Zhutuoling, 1964-VI-11, L. Chen coll. (ZICA).

DISTRIBUTION: Eastern China.

ETYMOLOGY: This species is named after the collector Lutai Chen for his significant contribution to studies on Chinese Hymenoptera fauna.

### *Paramblynotus hainanensis*, new species

MALE: Length 5.0 mm. Head and metasoma deeply dark brown, metasoma black, and antenna, legs brown, and metasoma ventrally light brown to brown. Forewing with a deep ferruginous macula covering marginal cell and the part of third cubital cell behind marginal cell.

Antenna 14-segmented; flagellum filiform, F1 not sinuated. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate, and defined laterally by weak carina lined with a row of foveae along interior side. Median frontal carina raised into a laminate process, which is triangular in lateral view, above antennal sockets, bifurcated to seclude a small, glabrous triangular area beneath anterior ocellus, and reaching to level of lower margin of eye. Upper face foveate laterally; antennal scrobe deeply depressed, mostly densely punctate, foveate posteriorly, and distinctly defined by carina laterally. Gena foveate-reticulate and punctate. Lower face punctate/foveate-reticulate; clypeus densely punctate and longitudinally carinate; clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Anterior tentorial pits small. Lateral occipital carina not reaching posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum finely transversely striate; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous, densely punctate dorsomedially. Pronotum dorsomedially raised, but lower than mesoscutum; pronotal crest not raised medially. Lateral

pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and punctate. Dorsal pronotal area glabrate, present to middle of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin with a broad emargination in dorsal view; lateral dorsal process distinct. Axillar area without distinct pubescence. Mesopleural triangle pubescent, well defined ventrally by smoothly curved carina. Median mesopleural impression percurrent, transversely costate; upper mesopleuron glabrous except finely punctate anteriorly; lower mesopleuron glabrous, conspicuously depressed along ventral margin, and conspicuously pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina abruptly curved medially; median propodeal area areolate-reticulate; median longitudinal carina percurrent, crossed by submedian transverse carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.4 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.4 times as long as wide in lateral view. Relative length of T3–8: 1.7:1.0:1.1:1.0:0.8:1.1; T3–4 glabrous; T5–8 densely punctate; T6–8 also with sparse, larger puncture with pubescence. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.65.

FEMALE: Unknown.

*Paramblynotus hainanensis* is similar to *P. annulicornis* and the other species of the *annulicornis* species complex discussed below. It differs from the latter by its entirely brown to dark brown body, antenna with a submedial pale ring, and mesoscutellum with a broad posterior emargination.

TYPE MATERIAL: HOLOTYPE: ♂, China: Hainan, Tien Fong Mt. (as reads in the label, but most probably Tie Feng Mt.), 1983-V-16, Boucek coll. (USNM). PARATYPE: 1♂, same data (USNM).

DISTRIBUTION: Hainan, China.

ETYMOLOGY: This species is named after the type locality.

*Paramblynotus annulicornis* Cameron, 1910  
figures 64–71

*Paramblynotus annulicornis* Cameron (1910: 132, ♂; Borneo; BMNH HT♂, no. 7.11).

FEMALE: Length 4.0–8.0 mm. Body usually entirely light to dark brown; metasoma of some males nearly black. Antenna 13-segmented and parti-colored with a medial pale ring including distal half of F6, F7, usually F8, and occasionally F9; scape, pedicel, and F1–5 dark brown; flagellomeres beyond the pale ring black. Flowering with a deep ferruginous macula covering marginal cell and the basal part of submarginal cell.

MALE: Length 4.0–5.0 mm. Antenna 14-segmented. Pale ring of antenna usually less extensive than in female, only involves F6–7.

*Paramblynotus annulicornis*, *barbarae*, *stigi*, *shimenensis*, *glaberus*, *yuani*, *weiae*, *eriki*, *asae*, *filippae*, *ebbae*, and *axelli* form a monophyletic clade referred here as the *annulicornis* species complex. All of these species are distributed in the tropical southern Pacific islands, except *P. shimenensis* from the subtropical central south of China (also see earlier biogeographical discussion). The species complex is easily distinguished from other species of the genus in that the antenna has a submedial pale ring including F5/6–6/10, contrasting to the rest of flagellum; body mostly yellow and sometimes dark brown; and forewing with a deep ferruginous macula covering marginal cell and basal third of submarginal cell.

Considering the relatively small amount of effective distinguishing features among the species and variations across species of the species complex, it is likely that some of the species names described herein may eventually turn out to be synonymies of the others. Nonetheless, we think that it is advantageous to describe them as we perceive and provide a platform for future taxonomic revision when a greater number of specimens of the complex become available.

MATERIAL EXAMINED: NHM (1T), NNMN (5), ZMLU-MS (2); BPBM (1); AEI (10), ROM (7), USNM(1).

DISTRIBUTION: Indonesia: Kalimantan; Malaysia: Borneo.

*Paramblynotus barbarae*, new species

**FEMALE:** Length 3.5–4.0 mm. Body entirely brown. Antenna dark brown with submedial pale ring consisting of F6–7. Forewing with a deep ferruginous macula covering marginal cell and the part of third cubital cell behind the marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex heavily foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate, and defined laterally by weak, irregular carina. Median frontal carina simple, indistinct beyond lower margin of antennal sockets. Upper face foveate-reticulate; antennal scrobe distinctly depressed, glabrate with dense fine punctures, and defined by distinct carina laterally. Gena foveate-reticulate and densely pubescent. Lower face and clypeus foveate-rugose; clypeus with dense long pubescence. Anterior tentorial pits distinct. Lateral occipital carina not quite reaching posterior part of vertex. Occiput glabrous, anteriorly separated from vertex by an irregular transverse carina.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous, finely punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially, and distinctly separating lateral surface of pronotum in the middle. Lateral surface of pronotum foveate-reticulate with dense pubescence. Dorsal pronotal area glabrate, present to anterior two-thirds of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin rounded in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, not transversely costate; mesopleuron glabrous; lower mesopleuron distinctly depressed along ven-

tral margin, and sparsely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, slightly raised anterodorsally, and distinctly curved laterad submedially; median propodeal area glabrate; median longitudinal carina percurrent; submedian transverse carina distinct or not, always preceded by an additional transverse carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.2 times as long as wide and slightly shorter than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.6 times as long as wide in lateral view. Tergum 8 slightly exposed; relative length of T3–7: 1.6:1.0:0.9:1.6:0.9; T3–5 glabrous; T6 finely punctate with sparse pubescence; T7 finely punctate, with a band of sparse pubescence anteriorly. Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.63.

**MALE:** Unknown.

*Paramblynotus barbarae* differs from the other species of the *annulicornis* complex in having median frontal carina not extended beyond antennal sockets and vertex foveate-reticulate entirely.

**TYPE MATERIAL:** HOLOTYPE: ♀, Malaysia: Negri S., Posah Forest Reserve (primary forest), 1978-XII-5, P. and M. Becker coll. (AEI). PARATYPE: 1♀, 1979-VIII-14, other data as holotype (AEI).

**DISTRIBUTION:** Malaysia: Borneo.

**ETYMOLOGY:** This species is named after Dr. Barbara Ekbohm for her kind support and moral encouragement of the study.

*Paramblynotus stigi*, new species

**FEMALE:** Length 4.0 mm. Body entirely dark brown. Submedial pale ring of antenna consisting of F6–7; F8–11 almost black, all other segments dark brown. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with medially dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised,

foveate posterior to anterior ocellus, finely carinate anteriorly, and not defined laterally by carina. Median frontal carina raised into a simple lamellate process between antennal sockets and extended beyond lower margin of eyes. Upper face foveate to foveate-reticulate; antennal scrobe defined by distinct carina laterally, distinctly depressed, and glabrate with fine punctures and fine diagonal carination. Gena glabrate-foveate. Lower face and clypeus foveate-rugose with dense pubescence. Anterior tentorial pits indistinct. Lateral occipital carina not reaching posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum transversely striate; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous, finely punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest distinctly raised into a median lobular process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially, and distinctly separating lateral surface of pronotum in the middle. Lateral surface of pronotum foveate-reticulate with dense pubescence. Dorsal pronotal area glabrate, present to anterior third of posterior margin of pronotum. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum prominent; posterior margin projected into two submedial processes triangular in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with a few indistinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, dorsomedially strongly raised and distinctly curved laterad; median propodeal area punctate with sparse pubescence; median longitudinal carina only present anteriorly and submedian transverse carina prominent. Rs+M of forewing arising from

middle of basal vein. Marginal cell 2.5 times as long as wide and as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.1 times as long as wide in lateral view. Tergum 8 slightly exposed; relative length of T3-7: 1.6:1.0:1.0:1.3:1.0; T3-5 glabrous; T6 finely punctate with sparse pubescence; T7 finely punctate, with a band of sparse pubescence anteriorly. Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2-5mt = 0.80.

MALE: Unknown.

*Paramblynotus stigi* differs from all other species of *annulicornis* species complex in (1) mesoscutellum raised and projected posteriorly with a deep median triangular emargination, and (2) antennal scrobes and ocellar plate anterior to anterior ocellus finely longitudinally carinate.

TYPE MATERIAL: HOLOTYPE: ♀, Indonesia: W. Kalimantan, Gunung Palung National Park, 1991-VI-17-29, C. Darling and Rosichon coll. (Sutrisno. IIS 910136) (ROM).

DISTRIBUTION: Indonesia: Kalimantan.

ETYMOLOGY: This species is named after Dr. Stig Larsson for his support and encouragement of this study, and for his friendship.

*Paramblynotus yuani*, new species

FEMALE: Length 3.0 mm. Body light brown. Submedial pale ring of antenna consisting of F6-7. Flagellomeres beyond pale ring black, and all other segments brown. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate, defined laterally by carina, and with a row of large foveae along lateral carinae. Median frontal carina raised into a lamellate, apically slightly flattened process, and percurrent to clypeus. Upper face foveate to foveate-reticulate; antennal scrobe distinctly depressed, mostly foveate-reticulate



and somewhat longitudinally rugose in lower part, and defined by distinct carina laterally. Gena rough foveate-reticulate. Lower face foveate-rugose and irregularly punctate with sparse pubescence. Anterior tentorial pits distinct. Clypeus punctate with dense pubescence. Lateral occipital carina not reaching to posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous mostly and punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate with pubescence and distinctly separated in the middle. Dorsal pronotal area glabrate, narrow, but visible to end of posterior margin of pronotum. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum not prominent; posterior margin projected and medially emarginated in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent with a few indistinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, dorsomedially strongly raised into, in lateral view, an apically broadly rounded triangular process and distinctly curved laterad; median propodeal area glabrate with sparse pubescence; median longitudinal carina distinct prior to prominent submedian transverse carina and replaced by two distinct longitudinal submedian carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.1 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.8 times as long as wide in lateral view. Tergum 8 entirely covered by T7;

relative length of T3–7: 1.5:1.0:1.0:2.3:1.0; T3–5 glabrous; T6 finely punctate with sparse pubescence; T7 finely punctate, with row of sparse pubescence anteriorly. Tibiae and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.65$ .

MALE: Unknown.

*Paramblynotus yuani*, *P. stigi* and *P. filippae* are different from all other species of the *annulicornis* species complex with their mesoscutellum raised and projected posteriorly, and posterior margin truncate or emarginate. *P. yuani* differs from *P. stigi* in that antennal scrobes not longitudinally carinate posteriorly, gena without a median glabrate area, and tergum 8 of female metasoma completely covered by T7, and from *P. filippae* in that antennal scrobes foveate and posterior margin of mesoscutellum emarginate.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Pasoh Forest Reserve, Negri S., 1979-IV-2, P. & M. Becker coll. (AEI).

DISTRIBUTION: Malaysia: Negri S.

ETYMOLOGY: This species is named after Yuan Liu, son of Z.L.

#### *Paramblynotus filippae*, new species

FEMALE: Length 3.0–3.3 mm. Body brown to dark brown. Submedial pale ring of antenna consisting of F7–8 and sometimes also part of F6 and F9. Flagellomeres beyond pale ring black, and all other segments dark brown to black. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate, defined laterally by carina, and with a row of large foveae along lateral carinae. Median frontal carina raised into a lamellate process and percurrent to clypeus. Upper face foveate to foveate-reticulate; antennal scrobe distinctly depressed, glabrate with fine punctures, and defined by distinct carina laterally. Gena foveate-reticulate. Lower face foveate-rugose with dense pubes-

cence. Anterior tentorial pits distinct. Clypeus punctate. Lateral occipital carina not reaching to posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum transversely striate; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous mostly and punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate with pubescence and distinctly separated in the middle. Dorsal pronotal area glabrate, anteriorly with indistinct transverse striation, visible to end of posterior margin of pronotum. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum not prominent; posterior margin projected and truncate in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent with a few indistinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and sparsely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, dorsomedially strongly raised and distinctly curved laterad; median propodeal area glabrate with sparse pubescence; median longitudinal carina purcurrent and submedian transverse carina prominent. Rs+M of forewing arising from middle of basal vein. Marginal cell 3.1 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole as long as wide in lateral view. Tergum 8 entirely covered by T7; relative length of T3–7: 1.4:1.0:1.2:1.9:1.5; T3–5 glabrous; T6 finely punctate; T7 finely punctate, with row of sparse pubescence anteriorly. Tibiae and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.70.

MALE: Length 2.8 mm. Antenna 14-segmented. Pale ring of antenna absent.

*Paramblynotus filippae* is very similar to *P. yuani* and *P. stigi*, and can be distinguished from both by several characters as discussed under *P. yuani*.

TYPE MATERIAL: HOLOTYPE: ♀, Indonesia: Sumatra, Aceh Gunung Leuser National Park, Ketambe Research Station (3°41'N, 97°39'E, 300 m, Rain Forest, Young Forest Terrace 3, light gap), 1990-II-1–28, D.C. Darling coll. (ROM). PARATYPES: 3♀♀, 1♂: 1♀, data as holotype 1991-VI-17–29 (ROM); 2♀♀, data as holotype, 1991-VI-15–VIII-15 (ROM); 1♂, Malaysia: Sabah, near Danum Valley Field Center (ca. 140 m), 1987-II-24–III-24, C. v. Achterberg coll. (RMNH).

DISTRIBUTION: Indonesia: Sumatra.

ETYMOLOGY: This species is named after Filippa Ronquist, daughter of F.R.

*Paramblynotus shimenensis*, new species

FEMALE: Length 4.5 mm. Body entirely dark brown. Submedial pale ring of antenna consisting of F6–7, F8–11 almost black, and all other segments dark brown. Forewing with a deep ferruginous macula covering marginal cell and the part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, glabrate anteriorly, foveate posterior to anterior ocellus, and with a row of indistinctly defined foveae along interior side. Median frontal carina complete to clypeus and raised into a distinct lamellate process between antennal sockets. Upper face foveate-rugose; antennal scrobe defined by distinct carina laterally, distinctly depressed, and glabrate and finely punctate with apparent fine longitudinal striation. Gena areolate/foveate-reticulate with a median vertical carina. Lower face and clypeus foveate-rugose. Anterior tentorial pits indistinct. Lateral occipital carina reaching posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum transversely striate; submedian pronotal depressions sep-

arated medially. Anterior plate of pronotum glabrous, finely sparsely punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carinae distinct and reaching pronotal crest dorsomedially; lateral surface of pronotum distinctly separated in the middle. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area glabrate, present to anterior third of posterior margin of pronotum. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum smoothly curved lateroposteriorly to posterior margin of mesoscutellum; posterior margin broadly rounded in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with two more or less distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin, and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, distinctly raised dorsally throughout and slightly curved laterad in posterior half; median propodeal area glabrate with sparse pubescence; median longitudinal carina present anteriorly only, submedian transverse carina prominent, and two submedian longitudinal carinae present posteriorly. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.7 times as long as wide and slightly longer than submarginal cell. Bulla on Sc + R<sub>1</sub> absent.

Petiole 1.1 times as long as wide in lateral view. Tergum 8 completely hidden beneath T7; relative length of T3–7: 2.0:1.0:1.2:2.5:1.2; T3–5 glabrous; T6 finely punctate with single row of pubescence; T7 finely punctate, with a band of sparse pubescence anteriorly. Tibiae and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.56.

MALE: Unknown.

*Paramblynotus shimenensis* differs from all other species of *annulicornis* species complex by combination of the following characters: (1) median frontal carina raised into a distinct lamillate process between antennal sockets and complete to clypeus, (2) gena areolate/foveate-reticulate with a median vertical carina, and (3) T6 longer than T3.

TYPE MATERIAL: HOLOTYPE: ♀, China: Hunan, Shimen, Jiangping, Xiaoxi (1,470 m, mixed evergreen and deciduous broad-leaved forest), 1992-VIII-16–IX-15, F. Du and Z. Liu coll. (ZICA).

DISTRIBUTION: China: Hunan.

ETYMOLOGY: The species is named after the type locality.

#### *Paramblynotus glaberus*, new species

FEMALE: Length 3.5 mm. Body entirely yellow brown. Submedial pale ring of antenna consisting of F6–8, F9–11 dark brown, and all other segments brown. Forewing with a deep ferruginous macula covering marginal cell and the part of third cubital cell behind marginal cell. Body parts, except as specified below, with medially dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, defined by distinct carinae laterally, foveate posterior to anterior ocellus, and glabrate anteriorly. Median frontal carina complete to clypeus and raised between antennal sockets to form a distinct lamillate process. Upper face glabrate-foveate; antennal scrobe distinctly depressed, glabrous, and defined by a distinct carina laterally. Gena areolate-rugulose with a median vertical carina. Lower face and clypeus foveate-rugose. Anterior tentorial pits indistinct. Lateral occipital carina reaching posterior part of vertex. Occiput glabrous, anteriorly separated by a transverse carina from vertex.

Anterior flange of pronotum transversely striate; submedian pronotal pits separated from each other medially. Anterior plate of pronotum glabrous. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina

distinct, reaching pronotal crest dorsomedially; lateral surface of pronotum distinctly separated in the middle. Lateral surface of pronotum foveate-reticulate. Dorsal pronotal area punctate with pubescence, complete to end of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum distinctly projected laterad; posterior margin rounded in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with two more or less distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin, and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and distinctly pubescent ventrally. Lateral propodeal carina percurrent, distinctly raised dorsomedially into lobular process and slightly curved laterad medially; median propodeal area glabrous; median longitudinal carina weakly percurrent; and median transverse carina distinct. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.6 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole as long as wide in lateral view. Tergum 8 completely hidden beneath T7; relative length of T3-7: 1.9:1.0:1.1:2.8:2.1; T3-5 glabrous; T6 finely punctate with a few scattered pubescence; T7 finely punctate, with a narrow band of sparse pubescence anteriorly. Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.60$ .

MALE: Unknown.

*Paramblynotus glaberus* is similar to *P. shimenensis* in that both species have (1) median frontal carina raised into a distinct lamellate process between antennal sockets and complete to clypeus, (2) gena areolate/foveate-reticulate with a median vertical carina, and (3) T6 longer than T3. The species is further separated from *P. shimenensis* by its (1) mainly glabrous upper face, (2) presence of a dorsal occipital carina,

(3) distinctly projected dorsolateral process of mesoscutellum, and (4) T7 only slightly shorter than T6.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Posah Forest Reserve, 1978-VIII-22, P. and M. Becker coll. (AEI).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: This species is derived from *glaber* (Latin), meaning smooth without hair, referring to its glabrous upper face.

### *Paramblynotus weiae*, new species

FEMALE: Length 2.8 mm. Body entirely dark brown. Submedial pale ring of antenna consisting of F6-7, and the other segments brown. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, defined by weak carina laterally, foveate posterior to anterior ocellus, and glabrate anteriorly. Median frontal carina raised into a low, dorsally flattened ridge between antennal sockets, and distinctly extending to clypeus. Upper face glabrate-foveate; antennal scrobe defined by distinct carina laterally, distinctly depressed, and glabrous with faint diagonal carination and punctate with distinct pubescence. Gena areolate-rugulose anteriorly and glabrate posteriorly. Lower face and clypeus foveate-rugose with apparent radiating carination in lower part of lower face and clypeus. Anterior tentorial pits small. Lateral occipital carina reaching posterior part of vertex. Occiput glabrous, anteriorly not separated by a transverse carina from vertex.

Anterior plate of pronotum glabrous. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially; lateral surface of pronotum foveate-reticulate and distinctly separated in the middle. Dorsal pronotal area glabrous, present to long posterior margin of pronotum to middle part. Mesoscutum strongly arched



dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum moderately projected laterad and low triangular in dorsal view; posterior margin rounded. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with four more or less distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin. Metepisternum areolate-reticulate without distinct pubescence ventrally. Lateral propodeal carina percurrent, raised dorsomedially, subsemicircular in lateral view, and slightly curved laterad medially; median propodeal area glabrate with long, sparse pubescence; median longitudinal carina and median transverse carina distinct. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.3 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.2 times as long as wide in lateral view. Tergum 8 completely hidden beneath T7; relative length of T3–7: 2.7:1.0:2.0:2.3:1.5; T3–5 glabrous; T6–7 finely punctate, without pubescence (which could have been removed artificially). Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.67.

MALE: Unknown.

*Paramblynotus weiae* is similar to *P. annulicornis*, but it differs in (1) antennal F1/F2 = 0.6 (usually F1/F2 = 0.8–0.9 in *P. annulicornis* species complex), (2) median frontal carina not raised into a laminate process, and (3) median propodeal carina percurrent, not bifurcated posteriorly.

TYPE MATERIAL: HOLOTYPE: ♀, Vietnam: Fyan (900–1,000 m), 1961–VII–11–VIII–9, N.R. Spencer coll. (BPBM).

DISTRIBUTION: Vietnam.

ETYMOLOGY: This species is named after Wei Liu (Vivian), daughter of Z.L.

*Paramblynotus eriki*, new species

FEMALE: Length 4.0 mm. Body entirely yellow brown. Submedial pale ring of anten-

na consisting of F5–8, F9–11 nearly black, and all other segments dark brown. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, defined by distinct carina laterally, foveate posterior to anterior ocellus, and glabrate anteriorly with indistinct foveae along sides. Median frontal carina complete to clypeus and raised into a prominent laminate, triangular (in lateral view) process between antennal sockets. Upper face foveate; antennal scrobe distinctly depressed, defined by distinct carina laterally, and densely punctate with pubescence. Gena shallowly foveate-reticulate. Lower face and clypeus foveate-rugose. Anterior tentorial pits indistinct. Lateral occipital carina not reaching posterior part of vertex. Occiput glabrous, anteriorly not separated by a transverse carina from vertex.

Anterior flange of pronotum transversely striate; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest slightly raised medially but not into a distinct process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and distinctly separated in the middle. Dorsal pronotal area glabrate, only present along median part of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum distinctly projected laterad and lobular; posterior margin rounded in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with five distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and

conspicuously pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, distinctly raised dorsomedially into lobular process (triangular in lateral view) and strongly curved laterad medially; median propodeal area glabrate with sparse pubescence; median longitudinal carina percurrent and median transverse carina distinct. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.0 times as long as wide and slightly shorter than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.75 times as long as wide in lateral view. Tergum 8 completely hidden beneath T7; relative length of T3-7: 1.6:1.0:1.1:1.3:0.8; T3-5 glabrous; T6 finely punctate with scattered pubescence; T7 finely punctate, with a narrow band of sparse pubescence anteriorly. Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.64$ .

MALE: Unknown.

*Paramblynotus eriki* differs from all other species of the *annulicornis* complex by a combination of (1) median frontal carina raised into a prominent laminate process between antennal sockets and complete to clypeus, (2) pronotal crest slightly raised medially, (3) petiole 1.75 times as long as wide, and (4) T5-6 not particularly larger compared to the other tergites.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Pasoh Forest Reserve (secondary forest), 1979-I-25, coll. P. and M. Becker (AEI).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: This species is named after Erik Nordlander, son of G.N.

*Paramblynotus asae*, new species

FEMALE: Length 2.5-3.0 mm. Body entirely dark brown. Submedial pale ring of antenna consisting of F6-7, and all other segments dark brown. Forewing with a deep ferruginous macula covering marginal cell and the part of third cubital cell behind marginal cell. Body parts, except as specified below, with medially dense long golden pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, foveate-reticulate entirely, and not defined by distinct carina laterally. Median frontal carina extended to the level of lower margin of eyes and raised into a laminate, dorsally flattened process between antennal sockets. Upper face foveate; antennal scrobe distinctly depressed, punctate to punctate-reticulate, and defined by distinct carina laterally. Gena foveate-rugose. Lower face and clypeus foveate-rugose, clypeus also with apparent longitudinal striation. Anterior tentorial pits indistinct. Lateral occipital carina barely reaching posterior part of vertex. Occiput glabrous, anteriorly not separated by a transverse carina from vertex.

Anterior flange of pronotum transversely striate; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous and finely punctate with pubescence dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised medially. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and distinctly separated in the middle. Dorsal pronotal area glabrate, present to middle of posterior margin of pronotum. Mesoscutum strongly arched dorsally and foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum indistinct; lateral sides convergent posteriorly, and posterior margin rounded in dorsal view. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with many more or less distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and conspicuously pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, distinctly raised throughout into a high ridge and strongly curved laterad medially; median propodeal area foveate with sparse pubescence; median

longitudinal carina percurrent and median transverse carina distinct. Rs+M of forewing arising from middle of basal vein. Marginal cell 2.0 times as long as wide and slightly longer than submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 1.1 times as long as wide in lateral view. Tergum 8 completely hidden beneath T7; relative length of T3–7: 1.75:1.0:1.2:1.6:0.9; T3–5 glabrous; T6–7 finely punctate, each with a single row of long pubescence/setae. Tibia and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.85$ .

MALE: Unknown.

*Paramblynotus asae* is close to *P. ebbae* but differs in (1) median frontal carina raised into a distinct, dorsally flattened process between antennal sockets, and (2) antennal scrobes densely and coarsely punctate.

TYPE MATERIAL: HOLOTYPE: ♀, Indonesia: Sulawesi, Dumoga-Bone N.P., Toraut (680 m), 1985-V, J.S. Noyes coll. (NHM, B.M. 1985-10). PARATYPES: 4♀♀, 2♀♀, same data (except at 600 m) as holotype (NHM); 1♀, Indonesia: Sulawesi, Dumoga-Bone N.P. (Platc. F.I.T.2), 1985-II-6–13 (NHM); 1♀, Indonesia: N. Sulawesi (7 km from N. Malibagu, 0°27'N, 123°58'E, 125 m), C. v. Achterberg (NNMN).

DISTRIBUTION: Indonesia: Sulawesi.

ETYMOLOGY: This species is named after Asa Nordlander, daughter of G.N.

### *Paramblynotus ebbae*, new species

FEMALE: Length 2.8 mm. Body dark brown. Submedial pale ring of antenna consisting of F6–7. Flagellomeres other than F6–7 black. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, not defined laterally by distinct carina, surface foveate, and with a row of large foveae lining each side. Median frontal carina raised into a low lamellate process and percurrent to clypeus. Upper face foveate to

foveate-reticulate; antennal scrobe distinctly depressed, with dense and fine punctures, and defined by distinct carina laterally. Gena foveate-reticulate. Lower face foveate-reticulate with dense pubescence. Anterior tentorial pits distinct. Clypeus punctate/foveate-reticulate. Lateral occipital carina not reaching posterior part of vertex. Occiput glabrous.

Anterior flange of pronotum glabrate with trace of fine, transverse striation; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous and punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate with pubescence and distinctly separated in the middle. Dorsal pronotal area glabrous, only visible as a crescent area anteriorly. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum not prominent; posterior margin not projected. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, with a few indistinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, dorsomedially strongly raised and distinctly curved laterad; median propodeal area glabrate with sparse pubescence; median longitudinal carina percurrent (less distinct posteriorly) and submedian transverse carina prominent. Rs+M of forewing arising from posterior third of basal vein. Marginal cell 2.5 times as long as wide and almost as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.7 times as long as wide in lateral view. Tergum 8 entirely covered by T7; relative length of T3–7: 1.1:1.0:1.5:1.9:0.9; T3–5 glabrous; T6 finely punctate with sparse

pubescence; T7 densely and finely punctate, with row of sparse pubescence anteriorly. Tibiae and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1mt/2-5mt = 0.65$ .

MALE: Unknown.

*Paramblynotus ebbae* is unique among species of the *annulicornis* complex by having Rs+M of forewing arising from posterior third of basal vein. It is more similar to *P. asae* than to the other species of the complex, but it can be distinguished from *P. asae* by the following additional characters: antennal scrobes densely, but finely punctate, triangular ocellar plate not defined by lateral carinae, and median frontal carina not forming a dorsally flattened process between antennal sockets.

TYPE MATERIAL: HOLOTYPE: ♀, Indonesia: W. Kalimantan, Gunung Palung National Park, Kabang Panti Research Station (1°15'S, 110°5'E, 100 m, Rain Forest, Closed canopy), 1991-VI-17-29, D.C. Darling coll. (ROM).

DISTRIBUTION: Indonesia: Kalimantan.

ETYMOLOGY: This species is named after Ebba Ronquist, daughter of F.R.

*Paramblynotus axeli*, new species

FEMALE: Length 3.1 mm. Body dark brown. Submedial pale ring of antenna consists of F7-8. Flagellomeres basal to F6-7 brown and distal to F6-7 black to dark brown. Forewing with a deep ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell. Body parts, except as specified below, with moderately dense silvery pubescence.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate slightly raised, not defined laterally by distinct carina, surface obliquely striate prior to anterior ocellus and foveate posteriorly. Median frontal carina raised into a lamellate process, and percurrent to clypeus. Upper face foveate to foveate-reticulate; antennal scrobe distinctly depressed, glabrate with moderately dense and fine punctures, and defined by distinct carina laterally. Gena strongly foveate-reticulate with sparse long pubescence.

Lower face foveate-reticulate and irregularly punctuate with pubescence. Anterior tentorial pits distinct. Clypeus punctate/foveate-reticulate. Lateral occipital carina not reaching posterior part of vertex. Occiput mostly foveate-reticulate with very lower part glabrate.

Anterior flange of pronotum glabrate with superficial punctures; submedian pronotal depressions separated medially. Anterior plate of pronotum glabrous and punctate dorsomedially. Pronotum dorsomedially not raised, distinctly lower than mesoscutum; pronotal crest not raised into a median process. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate with pubescence and distinctly separated in the middle. Dorsal pronotal area glabrate, only visible as a crescent area anteriorly. Mesoscutum strongly arched dorsally and heavily foveate-reticulate. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; laterodorsal process of mesoscutellum not prominent; posterior margin not projected. Pubescence in axillar area distinct but not conspicuous. Mesopleural triangle densely pubescent, well defined ventrally by a smoothly curved carina. Median mesopleural impression straight and percurrent, with a many distinct transverse costae; mesopleuron glabrous; lower mesopleuron strongly depressed along ventral margin and densely pubescent ventrally. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, dorsomedially strongly raised and distinctly curved laterad; median propodeal area glabrate with sparse pubescence; median longitudinal carina purcurrent, but weak, especially posteriorly, and submedian transverse carina prominent. Rs+M of forewing arising from posterior third of basal vein. Marginal cell 2.0 times as long as wide and almost as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole distinctly longitudinally carinate and 1.5 times as long as wide in dorsal view. Tergum 8 entirely covered by T7; relative length of T3-7: 1.9:1.0:1.3:1.8:1.3; T3-5 glabrous; T6 finely punctate with scattered long pubescence; T7 densely and finely



punctate, with row of sparse pubescence anteriorly. Tibiae and tarsi conspicuously pubescent. Apical teeth of metatibia long, slender, and pointed apically.  $1\text{mt}/2-5\text{mt} = 0.67$ .

**MALE:** Body length 3.5 mm. Antenna 14-segmented. T3 and T5 distinctly larger than the other terga.

*Paramblynotus axeli* is unique among species of the *annulicornis* complex by having Rs+M of forewing arising from posterior third of basal vein. It is more similar to *P. asae* than to the other species of the complex, but it can be distinguished from *P. asae* by the following additional characters: antennal scrobes densely, but finely punctate, triangular ocellar plate not defined by lateral carinae, median frontal carina not forming a dorsally flattened process between antennal sockets, and occiput mostly foveate-reticulate.

**TYPE MATERIAL:** HOLOTYPE: ♀, Indonesia: Sumatra, Aceh Gunung Leuser National Park, Ketambe Research Station (3°41'N, 97°39'E, 400 m, 1° Rain Forest, Mature Forest, Terrace 4, Closed canopy), Malaise Trap with pan, 1989-XI-1–30, D.C. Darling coll., IIS 890012 (ROM). PARATYPE: 1♂, 1990-III-1–31, 900022, other data as Holotype.

**DISTRIBUTION:** Indonesia: Sumatra.

**ETYMOLOGY:** This species is named after Axel Ronquist, son of F.R.

*Paramblynotus ruficeps* Cameron, 1910

*Paramblynotus ruficeps* Cameron, 1908: 300, ♂; Borneo; BMNH (HT♂, main coll.).

\**Allocynips isosceles* Weld (1922: 331, ♂♀; Singapore; USNM (HT♀, no. 24 379, 3 PT♂), combination by Weld (1930:137), and synonymy by Ronquist (1995a: 37).

**FEMALE:** Length 2.6–3.8 mm.  $1\text{mt}/2-5\text{mt} = 0.55$ . Body usually yellowish brown to dark brown, mesosoma and/or head sometimes black. Antenna 13-segmented and dark brown. Wings clear, except marginal cell of forewing deep ferruginous.

**MALE:** Length 1.8–2.5 mm. Antenna 14-segmented.

The generally yellowish to brown body of *P. ruficeps* color resembles species of the *annulicornis* species complex, but *P. ruficeps*

lacks a pale ring on the antenna, the median frontal carina is only weakly present between antennal sockets, and the macula of the forewing is only limited to a marginal cell. Darker individuals of the species can be more easily confused with lighter individuals of its sympatric species *P. punctulatus*. Nonetheless, the two species can be distinguished relatively easily. *P. ruficeps* has clear wings with a ferruginous marginal cell, the angle between Rs and 2r is less than 90°, and the marginal cell is about 2.5 times as long as wide. *P. punctulatus* has relatively evenly smoke-tinted wings, the angle between Rs and 2r is distinctly larger than 90°, and the marginal cell is about 3.3 times as long as wide.

**MATERIALS EXAMINED:** 37. NHM: 1(T), AEI: 25, USNM: 6 (5T), ROM: 4, ZMLU-MS: 1.

**DISTRIBUTION:** Malaysia: Borneo; Singapore.

*Paramblynotus pubifemoratus*, new species

**FEMALE:** Length 4.0 mm. Body entirely black, and antenna and legs yellow to yellow brown. Wings completely transparent. The species is unusually hairy, particularly on head and lateral surface of pronotum.

Antenna 13-segmented; flagellum filiform, not widened apically. Vertex foveate-reticulate and punctate with distinct pubescence. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate raised, foveate/punctate-reticulate, and defined laterally by weak carina. Median frontal carina simple, reaching to lower margin of antennal sockets. Upper face foveate laterally; antennal scrobe distinctly depressed, glabrous, densely punctate anteriorly, and defined by weak carina laterally. Gena glabrate and densely and finely punctate with pubescence. Lower face and clypeus foveate/punctate-reticulate with dense pubescence; anterior tentorial pits small. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum glabrate to finely transversely striate, submedian pronotal depressions separated from each other medially. Anterior plate of pronotum densely finely punctate and pubescent. Pronotum

dorsomedially raised, slightly lower than mesoscutum; pronotal crest gradually raised medially into a small peak. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum mostly foveate-reticulate and longitudinally costate lateroventrally. Dorsal pronotal area granulate, present only along anterior part of posterior margin of pronotum. Mesoscutum arched dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina. Mesoscutellum foveate-reticulate; posterior margin narrowly truncate in dorsal view. Axillar area with conspicuous pubescence. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, sparsely transversely costate; upper and lower mesopleuron glabrous; lower mesopleuron sparsely pubescent ventrally. Metepisternum irregularly areolate-reticulate in upper part, conspicuously pubescent ventrally, and with a small elevated glabrous area medially. Lateral propodeal carina percurrent, strongly and abruptly curved, and strongly raised dorsolaterally into a triangular process with distinct pubescence; median propodeal area glabrate with two submedian longitudinal carina crossed by submedian transverse carina. Rs+M of forewing arising from middle of basal vein. Marginal cell 3.2 times as long as wide and 1.6 as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.44 times as long as wide in lateral view. Tergum 8 very slightly exposed; relative length of T3–7: 2.2:1.0:1.5:3.6:1.6; T3–5 glabrous; T6 mostly glabrous and densely punctate posterodorsally with a conspicuous band of pubescence; T7 with a conspicuous band of pubescence dorsomedially and almost entirely densely punctate with a narrow glabrous area along posterior margin. Apical teeth of metatibia long, slender, and pointed apically. 1mt/2–5mt = 0.61.

MALE: Unknown.

*Paramblynotus pubifemoratus* is similar to *P. ruficeps*, but it differs from the latter in (1) head, pronotum, and hindlegs covered with very dense adpressed hairs; (2) metasomal T6–7 of female each with a conspicuous band of long hairs dorsolaterally; (3) hair

tufts beneath lateral bar of mesoscutellum conspicuous; and (4) lateral propodeal carina strongly and abruptly curved and strongly raised dorsolaterally into a triangular process.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Posah Forest Reserve (forest), 1978-IV-23, P. and M. Becker coll. (AEI). PARATYPES: 3♀♀, 2♂, 1978-V-6, and 1978-V-9, other data as holotype (except from forest gap) (AEI), Sabah, Sipitang, Mendolong, 1988-V-13, S.A. Adebratt coll. (ZULU).

DISTRIBUTION: Malaysia.

ETYMOLOGY: From Latin, *pubi*, hairy, and *femor*, femur, suggesting its hairy legs.

*Paramblynotus chrysochaetes*, new species

FEMALE: Length 4.5–5.0 mm. Body entirely black. Antenna red brown. Legs red brown except coxae and metatarsus black. Wings transparent and slightly tinted. Body pubescence conspicuous and golden-tinted.

Antenna 13-segmented; flagellum filiform, not widened apically. Vertex foveate-reticulate with dense golden pubescence. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate raised, foveate-reticulate and finely carinate laterally, and defined laterally by distinct carina lined by a row of large foveae along interior side; a small triangular area present beneath anterior ocellus glabrous. Median frontal carina present only as a raised laminate process above antennal sockets, semicircular in lateral view. Upper face conspicuously pubescent entirely and foveate laterally; antennal scrobe distinctly depressed, glabrous, densely punctate anteriorly, and defined by carina laterally. Gena densely punctate and sparsely foveate, and densely pubescent. Lower face and clypeus densely punctate and foveate with conspicuous pubescence; anterior tentorial pits small; clypeopleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum finely longitudinally striate, submedian pronotal depressions separated far from each other medially. Anterior plate of pronotum densely finely punctate and pubescent. Pronotum dorsome-

dially raised, slightly higher than mesoscutum; pronotal crest gradually raised medially into a small peak. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate with fine oblique striate component and conspicuously pubescent. Dorsal pronotal area superficially transversely striate, present only along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina and four submedian longitudinal carinae. Axillar area with conspicuous pubescence extended to cover lateral part of scutellar sulcus. Mesoscutellum foveate-reticulate; posterior margin raised and projected posteriorly into two apically rounded processes. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrate; upper mesopleuron glabrous; speculum sparsely punctate; and lower mesopleuron glabrous and pubescent. Metepisternum longitudinally carinate-rugose in upper part, conspicuously pubescent ventrally. Lateral propodeal carina percurrent, strongly raised dorsolaterally into a large, laterally inclined lobular process with very dense pubescence; median propodeal area finely pubescent with a complete median longitudinal carina crossed by submedian transverse carina. Rs+M of forewing arising from anterior third of basal vein. Marginal cell 4.0 times as long as wide and 1.8 as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.56 times as long as wide in lateral view. Tergum 8 distinctly exposed; relative length of T3–8: 1.5:1.0:1.1:1.9:1.0:1.1; T3–4 glabrous with a few setigerous punctures; T5 punctate dorsolaterally, punctures coarse and sparse anteriorly; T6 with a large patch of conspicuous pubescence and finely punctate lateroventrally; T7 with a band of conspicuous pubescence dorsolaterally and finely punctate lateroventrally; and T8 pubescent. Apical teeth of metatibia short and blunt apically. 1mt/2–5mt = 1.2.

MALE: Unknown.

*Paramblynotus chrysochaites* and *P. rufipes* are unique in the *punctulatus* group in (1) scutellar sulcus divided by several more

or less equal longitudinal carinae into several foveae, (2) T8 of female metasoma distinctly exposed, (3) axillar area with conspicuous hair tuft, (4) T6–8 with conspicuous patch of long, golden hairs, and (5) apical teeth of metatibia short and blunt apically. In fact, they are more like the species of the *ruficollis* group in terms of these characters. However, they differ from the *ruficollis* group by the following characters: pronotal crest raised into a conspicuous peak anteromedially and mesoscutum flat dorsally. The species is further distinguished from *P. rufipes* in having pubescence of axillar area extended to cover lateral part of scutellar sulcus; mesoscutellum with a distinct emargination posteriorly and that posterior projection separated into two lobular processes; pubescence on pronotum and T6–8 very dense and long so that sculpture of the body parts is barely visible; the patch of pubescence on T6–8 covers posterior third of postpetiolar metasoma; and T6 distinctly longer than T3.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Pasoh Forest Reserve (Forest gap), 1978-IV-8, P. and M. Becker coll. (AEI). PARATYPES: 3♀♀, 1978-V-28-X-14, other data as holotype (AEI).

DISTRIBUTION: Malaysia, Borneo.

ETYMOLOGY: From Greek, *chryso*, gold, and *chaites*, long hairs, referring to the conspicuous and golden-tinted body pubescence of the species.

### *Paramblynotus rufipes*, new species

FEMALE: Length 6.0 mm. Body almost entirely black except metasoma anteroventrally red brown. Antenna red brown. Legs red brown except metatarsi black. Wings transparent and slightly tinted. Body pubescence conspicuous and golden-tinted.

Antenna 13-segmented; flagellum filiform, not widened apically. Vertex foveate-reticulate with dense pubescence. Eye prominent and distinctly extended laterally beyond outer margin of gena. Ocellar plate raised, foveate-reticulate, and defined laterally by distinct carina lined by a row of large foveae; a small glabrous triangular area present beneath anterior ocellus. Median frontal carina only present as a raised lamellate process, semicircular in lateral view and

distinctly flattened dorsally, above antennal sockets. Upper face conspicuously pubescent entirely and punctate and foveate laterally; antennal scrobe distinctly depressed and densely punctate and defined by carina laterally. Gena, lower face, and clypeus densely punctate and sparsely foveate with very dense pubescence; anterior tentorial pits small; clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput glabrous.

Anterior flange of pronotum finely longitudinally striate, submedian pronotal depressions separated far from each other medially. Anterior plate of pronotum densely finely punctate and pubescent. Pronotum dorsomedially raised, slightly higher than mesoscutum; pronotal crest gradually raised medially into a small peak. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and conspicuously pubescent. Dorsal pronotal area superficially transversely striate, present only along anterior fourth of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina and four strong submedian longitudinal carinae. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; posterior margin raised and projected with small median emargination posteriorly. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrate with three transverse carinae in anterior half; upper mesopleuron glabrous except sparsely punctate anteriorly; speculum sparsely punctate; and lower mesopleuron glabrous and pubescent. Metepisternum longitudinally carinate-rugose in upper part, pubescent ventrally. Lateral propodeal carina percurrent, strongly raised dorsolaterally into a large, lobular process with very dense pubescence; median propodeal area glabrous; median longitudinal carina present anterior to submedian transverse carina; two curved longitudinal carinae present posteriorly, each with a lateral transverse costa at middle point connecting to lateral propodeal carina. Rs+M of fore-

wing arising from anterior third of basal vein. Marginal cell 3.75 times as long as wide and 1.7 as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.50 times as long as wide in lateral view. Tergum 8 distinctly exposed; relative length of T3-8: 1.8:1.0:1.0:1.5:0.8:1.3; T3-4 glabrous with a few setigerous punctures; T5 punctate dorsolaterally, punctures coarse and sparse dorsoanteriorly; T6 with a large patch of conspicuous pubescence and finely punctate lateroventrally; T7 with a patch of conspicuous pubescence dorsolaterally and finely punctate lateroventrally; and T8 pubescent. Apical teeth of metatibia short and blunt apically. 1mt/2-5mt = 1.1.

MALE: Unknown.

*Paramblynotus rufipes* is most similar to *P. chrysochaïtes*, differing from the latter in (1) process of median frontal carina distinctly flattened dorsally; pubescence of axillar area not extended to cover part of scutellar sulcus; mesoscutellum with only a small emargination posteriorly; pubescence on pronotum and T6-8 less dense and shorter; the patch of pubescence on T6-8 covers only posterior one-fifth of postpetiolar metasoma; and T6 shorter than T3.

TYPE MATERIAL: HOLOTYPE: ♀, Laos: Wapikhamthong Prov., Wapi, 1967-V-31, Native Collector (BPBM).

DISTRIBUTION: Laos.

ETYMOLOGY: The species name is derived from Latin, *rufus*, red, reddish, and *pes*, foot, referring to the species' reddish legs.

#### *Paramblynotus lutepennis*, new species

FEMALE: Length 6.5 mm. Body almost entirely black except postpetiolar metasoma red brown basally. Antenna and legs black, tarsi of legs brown. Wings transparent and slightly yellow-tinted. Body pubescence golden-tinted.

Antenna 13-segmented; flagellum filiform, not distinctly expanded toward apex. Vertex foveate-reticulate with pubescence. Eye slightly extended laterally beyond outer margin of gena. Ocellar plate raised, foveate-reticulate, with a row of large foveae, and not defined laterally by carina. Median frontal carina present only between antennal sockets. Upper face foveate-reticulate to



foveate-rugose and pubescent entirely; antennal scrobe distinctly depressed and defined by a carina laterally. Gena glabrous and coarsely punctate. Lower face foveate-reticulate with dense appressed pubescence, clypeus densely punctate and pubescent; anterior tentorial pits small and close to each other; clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Lateral occipital carina not reaching posterior part of vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrate with apparent, fine striation; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous and densely finely punctate with conspicuous pubescence. Pronotum dorsomedially raised, slightly higher than mesoscutum; pronotal crest gradually raised medially into a distinct peak. Lateral pronotal carina distinct, reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and pubescent. Dorsal pronotal area long, superficially transversely striate, present only along anterior one-fifth of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; lateral dorsal process prominent and lobular; posterior margin of mesoscutellum rounded in dorsal view. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrate; upper and lower mesopleuron glabrous; lower mesopleuron densely pubescent in ventral depression. Metepisternum areolate-reticulate in upper part, pubescent ventrally, and with a small elevated glabrous area posteromedially. Lateral propodeal carina percurrent, strongly raised dorsomedially into broad triangle in lateral view and densely pubescent; median propodeal area pubescent; and median longitudinal carina percurrent, crossed by a submedial transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 2.5 times as long as wide and almost as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.60 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative length of T3–7: 2.0:1.0:1.2:2.6:1.1; T3–5 glabrous; T6–7 densely punctate; T6 with a small patch of sparse pubescence dorsolaterally; and T7 with a band of sparse pubescence dorsolaterally. Apical teeth of metatibia long, slender, and pointed apically. first metatarsomeres with an apical protuberance extending to five-sixths of second metatarsomeres. 1mt (excluding apical process)/2–5mt = 0.6.

MALE: Unknown.

*Paramblynotus luteipennis* is most similar to *P. obscurus*, but it differs from the latter in having distal protuberance of first metatarsomere long, reaching almost to the end of second tarsomere.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Sabah, Sipitang, Mendolong, 1987-XII-12, S. Adebratt coll. (ZMLU).

DISTRIBUTION: Malaysia: Sabah.

ETYMOLOGY: The species name is derived from Latin *luteus*, yellow, and *penna*, wing, describing the species' yellowish tint of the wings.

#### *Paramblynotus nebulosus*, new species

FEMALE: Length 5.0–8.0 mm. Body entirely black. Antenna brown and darker toward apex. Legs black, except fore- and middle tibiae and tarsi brown. Wings slightly tinted yellow and with a broad dark gray band along outer margin of forewing. Body pubescence golden-tinted, except pubescence on mesopleural triangle white.

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye extended laterally, distinctly beyond outer margin of gena. Ocellar plate slightly raised and foveate-rugose and defined laterally by superficial carina lined by irregular large foveae along interior side. Median frontal carina briefly present above antennal sockets, raised into a low, rounded process in lateral view. Upper face rugose-foveate/punctate laterally; antennal scrobe distinctly depressed, defined by a thin carina laterally, and coarsely punctate anteriorly and glabrate with longitudinal carination posteriorly. Gena coarsely foveate-reticulate with dense,

appressed pubescence; lower face and clypeus coarsely foveate and punctate with dense appressed pubescence; anterior tentorial pits small and distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum finely coriaceous; submedian pronotal depressions separated from each other medially; anterior pronotal plate glabrous and finely, densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak higher than mesoscutum. Lateral pronotal carina distinct, present only along lower half of posterior margin of anterior pronotal plate. Lateral surface of pronotum foveate-reticulate and densely punctate with conspicuous appressed pubescence. Dorsal pronotal area finely transversely striate, present along anterior fourth of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows and evenly distributed appressed pubescence. Scutellar sulcus divided only by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum broadly trapezoid posteriorly in dorsal view, with posterior margin distinctly emarginate; lateral dorsal process distinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrous. Upper mesopleuron glabrous and with short pubescence anteriorly; lower mesopleuron glabrous and densely pubescent in ventral impression. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carina percurrent, strongly curved laterally, and distinctly raised dorsally to form in the middle a strong, broadly rounded process with sparse dorsal pubescence; median propodeal area glabrate, with median longitudinal carina anterior to median transverse carina and two submedian carinae posteriorly. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.5 times as long as wide and 1.6 times as

long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.60 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3–7: 1.6:1.0:1.0:2.1:0.9; T3 glabrous; T4 glabrous with a narrow band of fine punctures across anterior second fifth; T5 glabrous and finely punctate; T6 finely and densely punctate dorsolaterally, with an extensive patch of dense pubescence covering posterior two-thirds of upper half of the tergite; and T7 densely punctate, with a broad band of conspicuous pubescence dorsolaterally in the middle and posteriorly glabrous. Apical teeth of metatibia slender and pointed apically. Metatibia with two to three dorsal dents. Apical protuberance of first metatarsomeres reaching slightly beyond middle of second metatarsomere.  $1mt \text{ (excluding apical protuberance)} / 2-5mt = 0.66$ .

MALE: Unknown.

*Paramblynotus nebulosus* differs from all other species of the genus except *P. miniatus* in having its metatibia dorsally with dents. It differs from the latter in (1) forewing with a broad dark gray band along outer margin; (2) upper metepisternum without a large, glabrous elevated median area; (3) head, pronotum, and metasomal T6–7 covered with conspicuous pubescence; and (4) distinctly larger.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: NW Sabah, near Long Pa Sia (west), ca. 1,200 m, 1987-IV-2–14, C.v. Arhterberg coll. (NNMN). PARATYPES: 8♀♀. 1♀, data as holotype (NNMN); 1♀, Indonesia: Sulawesi, near Sangona, Base Camp, Gn. Watuwila, ca. 200 m, 1989-X-10–15, C. v. Achterberg coll. (NNMN); 1♀, Indonesia: Sulawesi, near Mamasa, Penannang, 1,700 m, 1991-IV-10–22, C. v. Achterberg coll. (NNMN); 3♀♀, Malaysia, Negri S., Pasoh Research Station, coll. By P. and M. Becker in 1978-VII-14, 1978-XII-5, and 1979-II-20, respectively (AEI); 1♀, Malaysia: Sabah, Sipitang, Mendolong, T3/W5, 1989-III-8, S. Adebratt coll. (ZML); 1♀, Indonesia: Sulawesi, Dumoga-BoneTaraut “Edwards”, 680 m, 1985-IV-26, J. Martin coll. (NHM).

DISTRIBUTION: Malaysia, Borneo; Indonesia, Sulawesi.

ETYMOLOGY: From Latin, *nebulosus*, meaning misty, foggy, cloudy, or dark, referring to the broad gray band along the outer margin of forewing.

*Paramblynotus dyak* (Weld, 1922)

*Allocynips ruficeps* Weld, 1922: 329, ♀; Borneo; USNM (HT♀, no. 24 376, PT♀).

*Paramblynotus ruficeps* Weld, 1930: 137, combination.

FEMALE: Length 3.0–5.5 mm. Body entirely black. Antenna 13-segmented and dark brown. Wings evenly, lightly tinted ferruginous. Head and pronotum and fore- and middle legs with dense, long pubescence. Pubescence in metapleural triangle, axillar area, propodeum, and hindlegs long and conspicuous. Pronotum gradually, strongly raised into a keel anteriorly with peak distinctly higher than mesoscutum. Mesonotum flat. Metasoma glabrous on T3–5 and densely punctate on T6–7; T6–7 also with a conspicuous dorsomedial hair band. Tergum 8 completely covered by T7. All legs, except tibia and tarsi of fore- and middle legs, dark brown to black.  $1\text{mt}/2\text{--}5\text{mt} = 0.60$ .

MALE: Length 3.2 mm. Antenna 14-segmented.

MATERIAL EXAMINED: 41: BPBM (5), AEI (12), NHM (8), USNM (2T), ROM (9), NNMN (5).

DISTRIBUTION: Borneo, Sulawesi, Sumatra, Sarawak.

*Paramblynotus beckeri*, new species

FEMALE: Length 3.0–4.0 mm. Body entirely black. Antenna, legs, and metasoma ventrally red brown. Wings transparent. Body pubescence white.

Antenna 13-segmented; flagellum filiform, not widened toward apex. Vertex foveate-reticulate. Eye prominent, extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, defined laterally by a carina lined with a row of large foveae along interior side, and mostly punctate-reticulate laterally; a small glabrous triangular area present beneath anterior ocellus. Median frontal carina simple, present only above antennal sockets. Upper face foveate laterally; antennal scrobe distinctly depressed, defined by distinct carina laterally, and glabrous and

finely punctate with sparse pubescence. Gena densely punctate and sparsely foveate with dense pubescence; lower face and clypeus foveate-reticulate; anterior tentorial pits distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous, submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrate and densely finely punctate with pubescence. Pronotum dorsomedially raised, slightly higher than mesoscutum; pronotal crest gradually raised medially into a low peak. Lateral pronotal carina distinct, almost reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and densely pubescent. Dorsal pronotal area granulate with indistinct punctures and sparse pubescence, present only along anterior one-fifth of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum projected posteriorly and rounded in dorsal view. Axillar area with conspicuous pubescence. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrous; upper and lower mesopleuron glabrous; lower mesopleuron pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, conspicuously pubescent ventrally, and with a small elevated glabrous strip medially. Lateral propodeal carina percurrent, curved laterally at middle, and strongly raised dorsomedially into a large, lobular process with sparse dorsal pubescence; median propodeal area glabrate; median longitudinal carina percurrent crossed by submedial transverse carina.  $\text{Rs}+\text{M}$  of forewing nebulous, arising from middle of basal vein. Marginal cell 3.4 times as long as wide and 1.4 times as long as submarginal cell. Bulla on  $\text{Sc}+\text{R}_1$  absent.

Petiole 0.60 times as long as wide in lateral view. Tergum 8 not exposed; relative length

of T3–7: 1.6:1.0:1.2:1.9:1.0; T3–4 glabrous; T5 finely densely punctate; T6 densely punctate with a narrow band of sparse pubescence dorsolaterally; T7 entirely punctate, with a band of conspicuous pubescence dorsolaterally. Metatibia with two strong denticles dorsally. Apical teeth of metatibia long, slender, and pointed apically. Apical protuberance of first metatarsomeres extending to middle of second metatarsomeres.  $1\text{mt} (\text{excluding apical process})/2-5\text{mt} = 0.54$ .

MALE: Unknown.

The species is similar to *P. dyak*, but it can be distinguished from the latter by (1) eyes more strongly protruding laterally, (2) pronotal crest lower than mesoscutum, (3) mesoscutum slightly bent anteriorly, and (4) antennae and legs red brown.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Posah Forest Reserve (secondary forest), 1979-III-29, P. and M. Becker coll. (AEI). PARATYPES: 7♀♀, 1978-XI-8–1980-IV-30, other data as holotype (except one from forest gap) (AEI, 6; CRF, 1).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: This species is named after the collector.

*Paramblynotus venoforticulus*, new species

FEMALE: Length 5.0 mm. Body and antenna entirely black. Fore- and middle legs red brown with coxae black; hindleg with coxa dark brown, femur red brown, and tibia and tarsus black. Wings transparent; forewing with a rectangular macula along the middle of anterior margin, covering marginal cell, distal one-third of first submarginal cell, and basal part of second submarginal cell anteriorly.

Antenna 13-segmented; flagellum filiform. Vertex foveate-reticulate. Eye prominent, extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, mostly foveate-reticulate, and defined laterally by carina lined along interior side with a row of large foveae, and with a small glabrous triangular area beneath anterior ocellus. Median frontal carina simple and present only between antennal sockets. Upper face longitudinally carinate laterally; antennal scrobe distinctly depressed, punctate-reticulate, longitudinally carinate posteriorly, and

defined by distinct carina laterally. Gena punctate-reticulate and sparsely foveate with dense pubescence; lower face foveate-reticulate, and clypeus foveate/punctate-reticulate; anterior tentorial pits distinct; and clypeo-pleurostomal sulcus and epistomal sulcus indistinct. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous, submedian pronotal depressions separated from each other medially. Anterior plate of pronotum densely finely punctate and laterally also with dense pubescence. Pronotum dorsomedially raised, distinctly higher than mesoscutum; pronotal crest raised medially into a distinct process-like peak. Lateral pronotal carina distinct, almost reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and densely pubescent. Dorsal pronotal area present only along anterior third of posterior margin of pronotum and superficially transversely carinate anteriorly. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided only by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum truncate posteriorly in dorsal view. Axillar area with conspicuous pubescence. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrous with several superficial transverse costae. Upper mesopleuron glabrous; lower mesopleuron glabrous and pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, with a small elevated glabrous area medially, and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, almost parallel to each other, and strongly raised anterodorsally into a conspicuous, dorsally rounded triangular process with dense dorsal pubescence; median propodeal area glabrate; median longitudinal carina percurrent, crossed by a submedian transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide and 1.4 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.



Petiole 0.70 times as long as wide in lateral view. Tergum 8 not exposed; relative length of T3–7: 1.7:1.0:1.3:2.4:1.3; T3 glabrous; T4–5 finely densely punctate; T6 coarsely densely punctate; and T7 densely punctate except glabrous posteriorly, with a band of conspicuous pubescence dorsolaterally. Apical teeth of metatibia long, slender, and pointed apically. First metatarsomeres with apical protuberance extending to one-third of second metatarsomeres. 1mt (excluding apical process)/2–5mt = 0.78.

MALE: Unknown.

*Paramblynotus venoforticulus* is separated from all other *Paramblynotus* species except *P. grossus* by the combination of having (1) occiput longitudinally carinate, (2) pronotum raised into a peak, and (3) forewing with a rectangular macula along middle of anterior margin. It differs from *P. grossus* in that its gena is not expanded behind eyes and its legs are mostly red brown.

TYPE MATERIAL: HOLOTYPE: ♀, Vietnam: Fyan (900–1,000 m), 1961-VII-11–VIII-9, N.R. Spencer (BPBM).

DISTRIBUTION: Vietnam.

ETYMOLOGY: From Latin, *veno*, vein, and *forticulus*, strong. The name refers to the heavy veins of the species.

*Paramblynotus distinctus*, new species

FEMALE: Length 3.5 mm. Head yellow brown; rest of body, antenna, and legs dark brown. Wings transparent.

Antenna 13-segmented; flagellum distinctly widened apically. Vertex foveate-reticulate. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, mostly glabrate-foveate, and defined laterally by carina lined along interior side with a row of large, superficial foveae, and with a small glabrous area beneath anterior ocellus. Median frontal carina present only between antennal sockets, raised dorsally into a ridge. Upper face superficially foveate laterally; antennal scrobe distinctly depressed, glabrous, and defined by weak carina laterally. Gena with a row of large foveae along eye margin, otherwise glabrous with sparse punctures and pubescence; lower face and clypeus foveate/punctate-reticulate; anterior tentorial pits distinct; clypeo-pleurostomal

sulcus and epistomal sulcus form a smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally. Anterior flange of pronotum glabrous, submedian pronotal depressions separated medially.

Anterior plate of pronotum densely punctate medially and glabrous laterally. Pronotum dorsomedially raised, distinctly higher than mesoscutum; pronotal crest gradually raised medially into a peak. Lateral pronotal carina weak, almost reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and pubescent. Dorsal pronotal area glabrate, present only along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum broadly rounded posteriorly in dorsal view. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, glabrous, and transversely costate. Upper mesopleuron glabrous; lower mesopleuron glabrous and pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, with a small elevated glabrous area medially, and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, strongly curved laterally at middle, and strongly raised anterodorsally into a conspicuous, lobular process with dorsal pubescence; median propodeal area glabrate; median longitudinal carina present anteriorly, and two submedian longitudinal carinae present behind submedian transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 2.7 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.33 times as long as wide in lateral view. Tergum 8 slightly exposed; relative length of T3–7: 2.2:1.0:1.2:2.8:1.4; T3–4 glabrous; T5 finely densely punctate; T6 densely punctate with a band of sparse pubescence dorsolaterally; and T7 densely punctate with anterior band of of conspicuous pubescence dorsolaterally. Apical teeth of metatibia long, slender, and pointed

apically. Apical process of first metatarsomeres very reduced.  $1mt/2-5mt = 0.5$ .

MALE: Unknown.

*Paramblynotus distinctus* is very similar to *P. fraxini* and *P. kosugii*. It can be easily separated from all other *Paramblynotus* species by having a longitudinally carinate occiput and pronotum raised anteriorly into a peak, yet lacking apical protuberance of first metatarsomere. It differs from *P. fraxini* and *P. kosugii* in (1) antennal flagellum distinctly widened apically, apical flagellomere two times as wide as medial width of F1; (2) gena glabrate punctate; (3) mesoscutellum not projected posteriorly; and (4) body orange brown entirely.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S., Pasoh Forest Reserve (forest gap), 1979-II-10, coll. P. and M. Becker (AEI).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: From Latin, *distinctus*, distinct.

*Paramblynotus fraxinii* Yang, 1994

*Paramblynotus fraxinii* Yang, 1994: 157–164, ♀; China: Helongjiang; NWCF (HT♀, paratype 2♀♀).

FEMALE: Length 4.5 mm. Head, mesosoma, and antenna black. Legs brown except coxae black. Metasoma brown. Wings transparent. Relative size of abdominal T3–T7: 1.9:1.0:1.1:2.4:0.9. Metatarsomere  $1mt/2-5mt = 0.95$ .

MALE: Unknown.

*Paramblynotus fraxinii* is most similar to *P. kosugii*, but it differs from the latter in (1) mesoscutellum without transverse inflection before the posterior projection, and rounded posteriorly in dorsal view; (2) lateral propodeal carina strongly raised anterodorsally into a lobular process; and (3) size smaller. An additional character to separate *P. fraxinii* from most other species of *Paramblynotus* is that the female antenna is 12-segmented.

MATERIAL EXAMINED: 1♀ (paratype), China: Helongjiang, 1989-VI-30, Z. Yang and X. Xu coll. (NWCF).

DISTRIBUTION: China: Helongjiang.

BIOLOGICAL NOTES: Collected on dead trunk of *Fraxinus mandruschica* (Oleaceae)

infested with *Mesosamyops* (Cerambycidae) and *Tremex simulacrum* (Siricidae). (Ronquist, 1995a; Yang and Cui, 1994).

*Paramblynotus kosugii* Watanabe and Sakagami, 1951

*Paramblynotus kosugii* Watanabe and Sakagami, 1951: 129, ♂; Japan: Honshu; EIHU (HT♂, paratypes 4♂♂).

MALE: Length 6.0 mm. Head, mesosoma, and antenna black. Legs brown except coxae black. Metasoma brown. Wings transparent.  $1mt/2-5mt = 0.84$ .

FEMALE: Unknown.

*Paramblynotus kosugii* is most similar to *P. fraxinii*, but it differs from the latter in (1) mesoscutellum with an inflection prior to the posterior projection, and truncate posteriorly in dorsal view; (2) lateral propodeal carina not raised anterodorsally into a lobular process; and (3) size distinctly larger.

MATERIAL EXAMINED: 5♂♂ (holotype and 4 paratypes), Japan: Sapporo, 1949-VII-23, K. Kosugi coll. (EIHU).

DISTRIBUTION: Japan: Sapporo.

*Paramblynotus borneanus* (Weld, 1922)

*Paribalia borneana* Weld, 1922: 326, ♂♀; Borneo; USNM (HT♀, paratype ♂).

*Paramblynotus borneanus* (Weld) Ronquist, 1994, combination.

FEMALE: Length 4.8 mm. Head and thorax black to dark brown; antennae, legs, and metasoma reddish brown. Head, mesosoma, and legs densely pubescent; mesopleural triangle and axillar area with conspicuous pubescence. Wings entirely transparent.

Vertex foveate-reticulate. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, mostly foveate-reticulate, and defined laterally by carina lined along interior side with a row of large foveae. Median frontal carina present between antennal sockets and simple. Upper face foveate-rugose laterally; antennal scrobe distinctly depressed, glabrate with sparse punctures and pubescence, and defined by carina laterally. Gena glabrate with dense punctures and pubescence; lower face and clypeus foveate/punctate-reticulate with

dense pubescence. Lateral occipital carina not reaching vertex.

Anterior plate of pronotum glabrate anteromedially and otherwise densely punctate with appressed pubescence. Pronotum with dorsomedial peak distinctly higher than mesoscutum and slightly bent backward apically. Lateral pronotal carina distinct, present only in lower two-thirds. Dorsal pronotal area glabrate, present along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Mesoscutellum inclined laterally and narrowly rounded posteriorly; lateral dorsal process not raised. Mesopleural triangle conspicuously pubescent. Metepisternum areolate-reticulate in upper part, with a small elevated glabrous area medially, and conspicuously pubescent ventrally. Lateral propodeal carinae strongly curved laterally at middle, and strongly raised anterodorsally into a lobular process with dorsal pubescence; median propodeal area glabrate; median longitudinal carina present anteriorly and two weaker submedian longitudinal carinae present behind median transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.5 times as long as wide in lateral view. Tergum 8 entirely hidden by T7; relative size of abdominal T3–7: 1.8:1.0:1.0:3.9:1.9; T3–5 glabrous; T6 mostly glabrous and punctate with a middle transverse band of sparse pubescence dorsolaterally; and T7 densely punctate with anterior band of of conspicuous pubescence dorsolaterally. Apical teeth of metatibia reduced, but distinctly slender and pointed apically.

MALE: Length 3.8 mm.

MATERIAL EXAMINED: 2: ♀ (type) and ♂ (paratype), USNM.

DISTRIBUTION: Borneo.

*Paramblynotus aptatus*, new species

FEMALE: Length 3.0 mm. Body entirely black except antenna, base and ventral side of postpetiolar metasoma, fore- and middle leg, and metatarsus brown to dark brown.

Wings transparent. Metatarsomere 1mt/2–5mt = 0.60.

Antenna filiform; flagellum not widened apically. Vertex foveate-reticulate with longitudinal components laterally and longitudinally carinate medially. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrate-foveate, and not defined laterally by carina; a small glabrous area present beneath anterior ocellus. Median frontal carina weakly present between antennal sockets. Upper face superficially foveate laterally; antennal scrobe distinctly depressed, glabrous, and defined by weak carina laterally. Gena glabrate and densely punctate with pubescence; lower face and clypeus foveate/punctate and longitudinally rugose; anterior tentorial pits distinct; clypeo-pleurostomal sulcus and epistomal sulcus form an indistinct, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous, submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrate anteromedially and otherwise densely punctate. Pronotum dorsomedially raised; pronotal crest gradually raised medially into a peak distinctly higher than mesoscutum. Lateral pronotal carina distinct and almost reaching pronotal crest dorsomedially. Lateral surface of pronotum foveate-reticulate and densely pubescent. Dorsal pronotal area glabrate, present only along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate and rounded posteriorly in dorsal view. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrous with several unevenly spaced, superficial transverse costae. Upper mesopleuron glabrous; lower mesopleuron glabrous, and pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, with a very small elevated glabrous area medially, and conspicuously pubescent ventrally. Lat-

eral propodeal carinae percurrent, strongly curved laterally at middle, and strongly raised anterodorsally; median propodeal area superficially areolate; median longitudinal carina distinct anterior to submedian transverse carina and reduced posteriorly. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide and 1.6 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.65 times as long as wide in lateral view. Tergum 5 the largest tergite, comprising more than half of postpetiolar metasoma in lateral view. Apical teeth of metatibia long, slender, and pointed apically. Apical protuberance of first metatarsomere absent.  $1mt/2-5mt = 0.5$ .

MALE: Unknown.

*Paramblynotus aptatus* is unique among all *Paramblynotus* species in having a combination of characters: (1) medial occiput longitudinal carination extends to vertex longitudinally carinate, (2) pronotum strongly raised anteromedially, (3) lateral surfaces of pronotum discontinuous dorsomedially, (4) apical protuberance of first metatarsomeres absent, and (5) T6 four times as large as T5.

TYPE MATERIAL: HOLOTYPE: ♀, Laos: Vientiane Province: Ban Van Eue, 1965-XII-31, Native Collector coll. (BPBM).

DISTRIBUTION: Laos.

ETYMOLOGY: From Latin, *aptatus*, meaning appropriate, fit, and suitable.

*Paramblynotus kitrinocarus*, new species

FEMALE: Length 4.8 mm. Head orange. Antenna black with scape orange; meso- and metasoma black. Legs black except tibiae and tarsi of fore- and middle legs yellow brown. Wings transparent.  $1mt/2-5mt = 0.5$

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, foveate to foveate-reticulate, and not defined laterally by carina. Median frontal carina weakly present from between antennal sockets to clypeus. Upper face foveate-punctate laterally; antennal scrobe distinctly depressed, densely punctate, and not defined by carina laterally. Gena glabrate and foveate with pubescence; lower face and clypeus

foveate and densely punctate-reticulate; anterior tentorial pits small, but distinct; clypeo-pleurostomal sulcus and epistomal sulcus form smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous, submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrous anteromedially and otherwise densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak as high as mesoscutum. Lateral pronotal carina distinct, present only in lower two-thirds. Lateral surface of pronotum foveate-reticulate and pubescent. Dorsal pronotal area glabrate, present along anterior third of posterior margin of pronotum. Mesoscutum mostly flat dorsally and slightly inclined anteriorly, and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate, broadly rounded posteriorly in dorsal view; lateral dorsal process distinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent, glabrous, and with a few unevenly spaced, superficial transverse costae. Upper mesopleuron glabrous; lower mesopleuron glabrous and densely pubescent in ventral impression. Metepisternum areolate-reticulate in upper part and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, strongly curved laterally at middle, strongly raised anterodorsally, and flattened dorsally with coarse punctures; median propodeal area glabrate; median longitudinal carina present anteriorly and absent behind submedian transverse carina. Rs+M of forewing arising from middle of basal vein, weak and nebulous toward base. Marginal cell 2.5 times as long as wide and 1.2 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.6 times as long as wide in lateral view. Tergum 8 slightly exposed; relative size of abdominal T3-8: 2.1:1.0:1.4:2.9:1.0:0.3; T3-5 glabrous; T6 densely punctate with a middle transverse band of sparse pubes-



cence dorsolaterally; T7 densely punctate with anterior band of dense pubescence dorsolaterally; exposed part of T8 coarsely punctate with pubescence. Apical teeth of metatibia reduced, but distinctly slender and pointed apically. Apical protuberance of first metatarsomere reaching to middle of second metatarsomere.

MALE: Unknown.

*Paramblynotus kitrinocarus* is unique among all species of the *punctulatus* group by its color pattern, and it can be further distinguished from those species of the group that have a longitudinally carinate occiput by having (1) a simple, but percurrent median frontal carina, and (2) an exposed T8.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Sabah, Sipitang: Mendolong, 1988-V-11, S. Adebratt (ZMLU, 1996-089).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: From Greek, *kitrino*, red, and *carus*, head. The name refers to the orange color of the head in contrast to the black color of the rest of the body.

#### *Paramblynotus insolitus*, new species

FEMALE: Length 5.1 mm. Head, metasoma, coxa and femur of front and middle leg, and hindleg dark brown to black, mesosoma and antenna black. Wings entirely transparent.  $1\text{mt}/2-5\text{mt} = 0.48$ .

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex glabrous and finely punctate with pubescence. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised, glabrous and finely punctate with pubescence, and not defined laterally by carinae. Median frontal carina weakly present between antennal sockets. Upper face punctate laterally; antennal scrobe distinctly depressed and densely punctate and not defined by a lateral carina. Gena glabrous and finely punctate with pubescence; lower face and clypeus foveate and densely punctate with dense, appressed pubescence; anterior tentorial pits small but distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput entirely glabrous, without medial longitudinal carination.

Anterior flange of pronotum coarsely punctate, submedian pronotal depressions almost fused with each other medially. Anterior plate of pronotum glabrate and densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak as high as mesoscutum. Lateral pronotal carina distinct, present only in lower two-thirds. Lateral surface of pronotum very densely pubescent entirely, foveate-reticulate in upper part and glabrous with dense, fine punctures in lower part. Dorsal pronotal area glabrate, present along anterior third of posterior margin of pronotum. Mesoscutum mostly flat dorsally and slightly inclined anteriorly, and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum trapezoidal posteriorly in dorsal view; lateral dorsal process distinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression reduced and glabrous. Upper mesopleuron glabrous and with short pubescence anteriorly; lower mesopleuron glabrous and densely pubescent in ventral impression. Metepisternum superficially areolate in upper part and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, strongly and abruptly curved laterally and strongly raised dorsally to form in the middle a large triangular process, which is bent laterad dorsally and coarsely punctate with sparse pubescence on upper surface; median propodeal area glabrate with sparse pubescence; median longitudinal carina present anteriorly and two short submedian longitudinal carinae present behind median transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 3.0 times as long as wide and 1.4 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.5 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3–7:1.8:1.0:1.1:2.6:1.3; T3–5 sparsely punctate with fine pubescence; T6 densely punctate with a broad middle transverse band of dense pubescence dorsolaterally; T7 very densely punctate with

conspicuous pubescence anteriorly and glabrous posteriorly. Apical teeth of metatibia reduced but distinctly slender and pointed apically. Apical process of first metatarsomere reaching to middle of second metatarsomere.

MALE: Unknown.

*Paramblynotus insolitus* differs from all other *Paramblynotus* species in possession of the combination of several characters: (1) pronotum anterodorsally raised conspicuously into a peak, (2) first metatarsomere with apical protuberance, and (3) occiput glabrous. In addition, this species is also unique in having upper face, vertex, and gena entirely glabrous with fine punctures, lower part of lateral surface of pronotum glabrous with dense, fine punctures, and mesopleural impression only superficially present, especially posteriorly.

TYPE MATERIAL: HOLOTYPE: ♀, Philippines: Mindoro: S. Luis Calapan, 1954-IV-14, H.M. and D. Townes coll. (AEI).

DISTRIBUTION: Philippines: Mindoro.

ETYMOLOGY: From Latin, *distinctus*, meaning different.

#### *Paramblynotus robustus*, new species

FEMALE: Length 6.0 mm. Body, antenna, and legs entirely black except eyes orange. Wings transparent.  $1\text{mt}/2-5\text{mt} = 0$ .

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate with pubescence. Eye extended laterally beyond outer margin of gena. Ocellar plate distinctly raised and foveate, with a row of large foveae along sides, and laterally not defined by carina. Median frontal carina weakly and very briefly present above antennal sockets. Upper face foveate-reticulate laterally; antennal scrobe distinctly depressed and densely punctate with pubescence, and not defined by carina laterally. Gena foveate-reticulate with dense, appressed pubescence; lower face and clypeus foveate and densely punctate with dense, appressed pubescence; anterior tentorial pits small and distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum finely transversely striate; submedian pronotal depressions separated from each other medially. Anterior plate of pronotum glabrate and densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak slightly higher than mesoscutum. Lateral pronotal carinae distinct, not reaching pronotal crest dorsally. Lateral surface of pronotum very densely pubescent, foveate-reticulate and densely punctate. Dorsal pronotal area glabrate, present along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum broadly rounded posteriorly and slightly truncate apically in dorsal view; lateral dorsal process distinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by a smoothly curved carina. Median mesopleural impression percurrent and glabrous with a few unevenly spaced transvers costae. Upper mesopleuron glabrous and with short pubescence anteriorly; lower mesopleuron glabrous and densely pubescent above and in ventral impression. Metepisternum areolate in upper part and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, strongly and abruptly curved laterally and strongly raised dorsally to form in the middle a triangular process with top bent laterad; upper side of the process coarsely punctate with sparse pubescence; median propodeal area glabrate with sparse pubescence; median longitudinal carina present anteriorly and two submedian longitudinal carinae present behind median transverse carina.  $\text{Rs}+\text{M}$  of forewing nebulous and brownish, arising from middle of basal vein. Marginal cell 2.9 times as long as wide and 1.4 times as long as submarginal cell. Bulla on  $\text{Sc}+\text{R}_1$  absent.

Petiole 0.35 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3-7: 2.1:1.0:1.2: 2.1:1.0; T3 glabrous, T4-5 densely punctate without pubescence; T6 densely and coarsely punctate with a broad median transverse

band of sparse pubescence dorsolaterally; T7 very densely and coarsely punctate with conspicuous pubescence anteriorly and glabrous posteriorly. Apical teeth of metatibia distinctly slender and pointed apically. Apical protuberance of first metatarsomere reaching to middle of second metatarsomere.

MALE: Unknown.

This species is very similar to *P. grossus*, but it differs from the latter in (1) forewing without macula and (2) gena not expanded behind eye.

TYPE MATERIAL: HOLOTYPE: ♀, Laos: Ban Van Heue (20 km east of Phou-kow-kuei), 1965-IV-15-31, Native Collector coll. (BPBM).

DISTRIBUTION: Laos.

ETYMOLOGY: From Latin, *robustus*, strong.

*Paramblynotus miniatus*, new species

FEMALE: Length 2.5 mm. Head and mesosoma black. Antenna, metasoma, and legs brown to dark brown. Wings transparent.  $1\text{mt}/2-5\text{mt} = 0.53$ .

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye extended laterally beyond outer margin of gena. Ocellar plate only slightly raised and glabrate with sparse punctures and superficial foveae, and not defined laterally by carina. Median frontal carina weakly and very briefly present above antennal sockets. Upper face rugose-foveate/punctate laterally; antennal scrobe distinctly depressed and glabrous with sparse punctures, and defined by very weak carina laterally. Gena glabrous and superficially foveate with sparse, appressed pubescence; lower face and clypeus glabrate and densely punctate/foveate with appressed pubescence; anterior tentorial pits small and distinct; clypeopleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior plate of pronotum glabrate and densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak distinctly higher than mesoscutum. Lateral

pronotal carinae distinct, not reaching pronotal crest dorsally. Lateral surface of pronotum foveate-reticulate with sparse pubescence. Dorsal pronotal area glabrate, present along anterior one-fifth of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows. Scutellar sulcus divided only by a median longitudinal carina. Axillar area with distinct pubescence. Mesoscutellum foveate-reticulate; mesoscutellum broadly rounded posteriorly in dorsal view; lateral dorsal process indistinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by smoothly curved carina. Median mesopleural impression percurrent and glabrous. Upper mesopleuron glabrous with short pubescence anteriorly; lower mesopleuron glabrous with dense pubescence in ventral impression. Metepisternum areolate in upper part, with a large central elevated glabrous area, and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, strongly curved laterally and distinctly raised dorsally to form in the middle a broadly rounded process with sparse pubescence dorsally; median propodeal area glabrate; median longitudinal carina present anterior to median transverse carina and absent posteriorly. Rs+M of forewing pale, arising from middle of basal vein. Marginal cell 2.4 times as long as wide and 1.3 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.40 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3-7: 2.3:1.0:1.4: 2.9:1.7; T3-5 glabrous; T6 and T7 densely and finely punctate, each with a single row of pubescence dorsolaterally in the middle. Apical teeth of metatibia slender and pointed apically. Metatibia with two dorsal (posterior) dents. Apical protuberance of first metatarsomere reaching to middle of second metatarsomere.

MALE: Unknown.

*Paramblynotus miniatus* differs from all other species of the genus except *P. nebulosus* in having metatibia dorsally with dents. It differs from the latter in (1) forewing without a broad dark gray band along outer margin; (2) upper metepisternum with a large, gla-

brous elevated median area; and (3) body size much smaller.

**TYPE MATERIAL:** HOLOTYPE: ♀, Borneo: Sarawak (4<sup>th</sup> div., Gn. Mulu, RGS. Exp.), 1977-IX-17-X-23, D. Hollis coll. (BMNH, BM77-543).

**DISTRIBUTION:** Indonesia: Borneo.

**ETYMOLOGY:** From Latin, *miniatus*, red. The name refers to its brown metasoma.

*Paramblynotus obscurus*, new species

**FEMALE:** Length 3.5–4.5 mm. Body and antenna entirely black. Legs black except tibiae and tarsi of fore- and middle legs yellow brown. Wings transparent. 1mt/2–5mt = 0.60.

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye extended laterally to as wide as outer margin of gena. Ocellar plate raised and foveate-reticulate and defined laterally by carina lined along interior side with a row of uniform large foveae; a glabrous triangular area present beneath anterior ocellus. Median frontal carina briefly present between antennal sockets. Upper face rugose-foveate/punctate laterally; antennal scrobe distinctly depressed, glabrate and punctate with long, appressed pubescence, and defined by a carina laterally. Gena glabrate and foveate-punctate with dense, appressed pubescence; lower face and clypeus foveate-reticulate and densely punctate with dense appressed pubescence; anterior tentorial pits small and distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum finely coriaceous; submedian pronotal depressions separated from each other medially; anterior pronotal plate glabrate and finely densely punctate with appressed pubescence. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak higher than mesoscutum. Lateral pronotal carina distinct, present only along lower third of posterior margin of anterior pronotal plate. Lateral surface of pronotum foveate-reticulate and densely punctate with transverse carinate component and conspicuous ap-

pressed pubescence. Dorsal pronotal area finely transversely striate, present along anterior fourth of posterior margin of pronotum. Mesoscutum flat dorsally and strongly transversely costate with superficial foveae set in rows and evenly distributed appressed pubescence. Scutellar sulcus divided by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate; mesoscutellum broadly rounded posteriorly in dorsal view; lateral dorsal process visible, but indistinct in dorsal view. Mesopleural triangle conspicuously pubescent and well defined ventrally by smoothly curved carina. Median mesopleural impression percurrent and glabrous. Upper mesopleuron glabrous and with sparse, short pubescence anteriorly; lower mesopleuron glabrous and densely pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, conspicuously pubescent ventrally, and with a large central elevated glabrous area. Lateral propodeal carinae percurrent, distinctly curved laterad and distinctly raised dorsally to form a broadly rounded lobe; median propodeal area glabrate; median longitudinal carina percurrent crossed by median transverse carina. Rs+M of forewing nebulous, arising from middle of basal vein. Marginal cell 2.2 times as long as wide and 1.5 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.50 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3–7: 1.9:1.0:1.2:2.7:0.8; T3–4 glabrous; T5 densely finely punctate; T6 finely and densely punctate with a narrow band of sparse pubescence across anterior two-fifths of the tergite; and T7 densely punctate, with a band of relatively dense pubescence dorsolaterally in anterior half and glabrous posteriorly. Apical teeth of metatibia slender and pointed apically. Apical protuberance of first metatarsomere reaching slightly beyond middle of second metatarsomere.

**MALE:** Body length 3.6 mm. Antenna 14-segmented. Terga 3–8 subequal with T3 and T5 larger than the others.

*Paramblynotus obscurus* differs from all other species of the genus except *P. miniatus* in having metatibia dorsally with dents. It differs from the latter in (1) forewing with



a broad dark gray band along outer margin; (2) upper metepisternum without a large, glabrous elevated median area; (3) head, pronotum, and metasomal T6–7 covered with conspicuous pubescence; and (4) body size much larger.

**TYPE MATERIAL:** HOLOTYPE: ♀, Borneo: North Borneo (Forest Camp, 19 km north of Kalabakan), 1962-XI-12, Y. Hiroshima coll. (BPBM). PARATYPES: 2♀♀, 1♂. 1♂, Philippines: Palawan, Brooke's Pt., Macagua (75 m), 1962-IV-1–4, M. Thompson coll. (BPBM); 1♀, Malaysia: Sabah, Danum Valley (forest), 1986-X-23–XI-10, P. Eggleton coll. (BMNH); 1♀, Sarawak, Gunung Buda, 64 km S Limbang (4°13'N, 114°56'E), 1996-XI-22–28, S.L. Heydon and S. Fung coll. (UCDC).

**ADDITIONAL MATERIAL EXAMINED:** 1♂, Philippines: Mindanao (paratype of *P. borneanus*) (USNM).

**DISTRIBUTION:** Malaysia: Borneo; Indonesia: Sarawak; Philippines: Palawan.

**ETYMOLOGY:** From Latin, *obscurus*, meaning dark. The name describes the entirely dark color of its body.

***Paramblynotus coracinus*, new species**

**FEMALE:** Length 3.5–4.5 mm. Body and antenna entirely black. Legs black except tibiae and tarsi of fore- and middle legs yellow brown. Wings transparent, with a ferruginous macula covering marginal cell and part of third cubital cell behind marginal cell.  $1\text{mt}/2-5\text{mt} = 0.54$ .

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye extended laterally, slightly not as wide as to outer margin of gena. Ocellar plate distinctly raised and foveate and not defined laterally by carina. Median frontal carina weakly present between antennal sockets and slightly beyond ventrally. Upper face rugose-foveate/punctate laterally; antennal scrobe distinctly depressed and coarsely punctate with distinct pubescence, longitudinally carinate posteriorly, and distinctly defined by carina laterally. Gena glabrate and superficially foveate and punctate with sparse pubescence; lower face and clypeus foveate and densely punctate with dense appressed pubescence; anterior tentorial pits small and

distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial, smoothly curved arch. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated from each other medially; anterior pronotal plate glabrous medially and finely densely punctate with appressed pubescence, especially laterally. Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak higher than mesoscutum. Lateral pronotal carina distinct, present in lower half of posterior margin of anterior pronotal plate. Lateral surface of pronotum foveate-reticulate with transverse costate components, and distinctly pubescent. Dorsal pronotal area finely transversely striate, present along anterior third of posterior margin of pronotum. Mesoscutum flat dorsally and transversely costate with superficial foveae set in rows and evenly distributed appressed pubescence. Scutellar sulcus divided by a single median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate, broadly rounded posteriorly in dorsal view; lateral dorsal process indistinct. Mesopleural triangle conspicuously pubescent and well defined ventrally by smoothly curved carina. Median mesopleural impression percurrent and glabrous. Upper mesopleuron glabrous; lower mesopleuron glabrous and densely pubescent in ventral impression. Metepisternum areolate-reticulate in upper part, with a large elevated, glabrous median area medially, and conspicuously pubescent ventrally. Lateral propodeal carinae percurrent, distinctly curved laterally and strongly raised dorsally to form in the middle a low triangular process; median propodeal area glabrate; median longitudinal carina weak and percurrent.  $Rs+M$  of forewing arising from middle of basal vein and nebulous in basal half. Marginal cell 2.5 times as long as wide and nearly as long as submarginal cell. Bulla on  $Sc+R_1$  absent.

Petiole 0.50 times as long as wide in lateral view. Tergum 8 slightly exposed; relative size of abdominal T3–7: 2.0:1.0:1.1:2.5:1.4; T3 glabrous; T4 glabrous with a narrow band of fine punctures across anterior the second

fifth; T5 glabrous and finely punctate; T6 finely and densely punctate dorsolaterally, and with a narrow band of sparse pubescence in the middle; and T7 densely punctate entirely, with a band of dense pubescence dorsolaterally in the middle. Apical teeth of metatibia slender and pointed apically. Metatibia with two to three dorsal (posterior) denticles. Apical protuberance of first metatarsomere reaching to distal two-thirds of second metatarsomere.

MALE: Unknown.

*Paramblynotus coracinus* is most similar to *P. luteipennis* and *P. obscurus*, but it can be easily distinguished from the latter two by the ferruginous mark on forewing.

TYPE MATERIAL: HOLOTYPE: ♀, Malaysia: Negri S.: Posah Forest Reserve (Forest gap), 1979-II-28, P. and M. Becker coll. (AEI). PARATYPES: 3♀♀, locality and collectors as holotype, 1978-XII-3–1979-II-18 (AEI: 2; CFR: 1).

DISTRIBUTION: Malaysia: Borneo.

ETYMOLOGY: From New Latin, *coracinus*, meaning crowlike. The name refers to the entirely dark body color of the species.

*Paramblynotus grossus*, new species

FEMALE: Length 6.0–8.0 mm. Body, antenna, and legs entirely black. Wings transparent; forewing with a rectangular macula along the middle of anterior margin, covering marginal cell, distal third of first submarginal cell, and basal part of second submarginal cell anteriorly.  $1mt/2-5mt = 0$ .

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate. Eye not extended laterally, outer margin of gena expanded much beyond outer margin of eyes. Ocellar plate distinctly raised and foveate and not defined laterally by carina. Median frontal carina briefly but strongly present between antennal sockets. Upper face rugose-foveate/punctate laterally; antennal scrobe distinctly depressed and coarsely punctate with distinct pubescence, longitudinally carinate posteriorly, and distinctly defined by carina laterally. Gena glabrate, and foveate and punctate with sparse pubescence; lower face and clypeus foveate and densely punctate with apparent transverse costate component and appressed pubescence; ante-

rior tentorial pits distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial trapezoid. Lateral occipital carina reaching to middle height of gena. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated medially; anterior pronotal plate glabrous medially and otherwise finely densely punctate with appressed pubescence (especially so laterally). Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak higher than mesoscutum. Lateral pronotal carinae distinct, present in lower two-thirds of posterior margin of anterior pronotal plate. Lateral surface of pronotum foveate-reticulate with transversely costate components, and distinctly pubescent. Dorsal pronotal area glabrate, present along anterior third of posterior margin of pronotum. Mesoscutum almost flat dorsally and transversely costate with superficial foveae set in rows and with sparse, evenly distributed appressed pubescence. Scutellar sulcus divided only by a median longitudinal carina. Pubescence of axillar area distinct but not conspicuous. Mesoscutellum foveate-reticulate; mesoscutellum broadly rounded posteriorly in dorsal view; lateral dorsal process not apparent in dorsal view. Mesopleural triangle conspicuously pubescent and well defined ventrally by smoothly curved carina. Median mesopleural impression percurrent and glabrous. Upper mesopleuron glabrous; lower mesopleuron also with dense pubescence in ventral impression. Metepisternum areolate-reticulate to rugose in upper part, conspicuously pubescent ventrally, and with an elevated, glabrous median area. Lateral propodeal carinae percurrent, nearly parallel to each other, and strongly raised dorsally to form in middle a distinct triangular process; median propodeal area areolate with sparse pubescence; median longitudinal and transverse carinae hardly distinguishable from ridges of areolate structure.  $Rs+M$  of forewing nebulous in basal third, arising from middle of basal vein. Marginal cell 3.1 times as long as wide and 1.1 times as long as submarginal cell. Bulla on  $Sc+R_1$  absent.

Petiole 0.45 times as long as wide in lateral view. Tergum 8 completely covered by T7;

relative size of abdominal T3–7: 2.0:1.0:2.0.:2.4:1.5; T3–4 glabrous; T5 glabrous and finely punctate; T6 finely and densely punctate dorsolaterally and with a narrow band of sparse pubescence in the middle; T7 punctate with pubescence dorsolaterally in anterior third. Apical teeth of metatibia slender and pointed apically. Metatibia with two to three dorsal (posterior) dents. Apical process of first metatarsomeres reaching to middle of second metatarsomere.

MALE: Unknown.

*Paramblynotus grossus* differs from all other species of the *punctulatus* group except *P. venoforticulus*, n.sp. by the presence of a rectangular macula along the middle of anterior margin of forewing. It differs from *P. venoforticulus* by its conspicuously expanded gena behind eye. The combination of robust shape, big size, and entirely black body color also make the identification of the species easy.

TYPE MATERIAL: HOLOTYPE: ♀, Papua New Guinea: Bulolo, Mankila, 1981-XII-24, H. Roberts coll. (NHM). PARATYPES: 15♀♀, 5♀♀, data as holotype (NHM); 1♀, New Guinea, Wau (1,200 m), 1955-XII-22, I. and M. Sedlacek coll. (NHM); 1♀, Laos: Vientiane Prov., Ban Van Eue, 1965-VII-31, Native Collector coll. (BPBM); 2♀♀, Malaysia: Sabah, Sipitang: Mendolong, 1989-III-8–14, S. Adebratt, (ZMLU); 6♀♀, Indonesia: Sulawesi: Kunogon-Bone, 1984-IV–V, Martin coll. (NHM), 1985-XI-27–XII-4 (NHM), Dumoga-Bone (200 m), 1985-XI-16–23, C. v. Achterberg coll. (NNMN); Sumatra, Aceh, G. Leuser National Park, Ketambe Research Station, 1989-XI–1990-II, C.D. Darling coll. (ROM).

DISTRIBUTION: Indonesia: Sulawesi, Sumatra; Malaysia: Borneo; Laos: Vientiane; Papua New Guinea.

ETYMOLOGY: From Latin, *grossus*, big, coarse, referring to the big size and robust shape of the species.

BIOLOGY: Specimens from Papua New Guinea, including the holotype, were collected on *Syzgium* sp. log.

#### *Paramblynotus fuscus*, new species

FEMALE: Length 4.2 mm. Body, antenna, and legs entirely black. Wings trans-

parent, without any marking. 1mt/2–5mt = 0.

Antenna 13-segmented, flagellum filiform, not widened apically. Vertex foveate-reticulate with distinct longitudinally carinate component. Eye expanded laterally, slightly beyond outer margin of gena. Ocellar plate distinctly raised, glabrate and longitudinally carinate, and defined laterally by carina. Median frontal carina distinct between antennal sockets. Upper face longitudinally carinate laterally; antennal scrobe distinctly depressed and distinctly defined by carina laterally, longitudinally carinate lateroposteriorly, and glabrous anteriorly. Gena glabrous and finely punctate, and with dense pubescence in posterior upper part; lower face and clypeus glabrate with fine longitudinal carination and finely punctate with dense appressed pubescence; anterior tentorial pits small and distinct; clypeo-pleurostomal sulcus and epistomal sulcus form a superficial trapezoid. Lateral occipital carina not reaching vertex. Occiput longitudinally carinate medially and glabrous laterally.

Anterior flange of pronotum glabrous; submedian pronotal depressions separated medially; anterior pronotal plate glabrous medially and finely densely punctate with appressed pubescence (more so laterally). Pronotum raised dorsomedially; pronotal crest gradually raised medially into a peak, slightly not as high as mesoscutum. Lateral pronotal carina indistinct, present in lower two-thirds along posterior margin of anterior pronotal plate. Lateral surface of pronotum foveate-reticulate with weak transverse costae, and distinctly pubescent in upper half, and glabrous and finely punctate ventrally. Dorsal pronotal area glabrate, present along anterior two-thirds of posterior margin of pronotum. Mesoscutum almost flat dorsally, except slightly inclined anteriorly, and transversely costate with superficial foveae set in rows and with sparse, evenly distributed appressed pubescence. Scutellar sulcus divided by a median longitudinal carina. Axillar area with conspicuous pubescence. Mesoscutellum foveate-reticulate and broadly rounded posteriorly in dorsal view; lateral dorsal process indistinct in dorsal view. Mesopleural triangle conspicuously pubescent with a narrow, hairless strip above the

smoothly curved carina delimiting the triangle. Median mesopleural impression percurrent and glabrate with apparent transverse carinae. Upper and lower mesopleuron glabrous; lower mesopleuron also pubescent in ventral impression. Metepisternum conspicuously pubescent entirely. Lateral propodeal carinae percurrent, distinctly divergent posteriorly, and strongly raised dorsally to form in the middle a distinct triangular process; median propodeal area conspicuously pubescent anteriorly and glabrous posteriorly; median longitudinal carina anterior to the median transverse carina barely visible due to conspicuous pubescence. Rs+M of forewing distinct except slightly nebulous in basal third, arising from middle of basal vein. Marginal cell 3.5 times as long as wide and 1.7 times as long as submarginal cell. Bulla on Sc+R<sub>1</sub> absent.

Petiole 0.40 times as long as wide in lateral view. Tergum 8 completely covered by T7; relative size of abdominal T3–7: 2.3:1.0:1.2.:3.8:1.4; T3 glabrous; T4–5 glabrous and finely punctate dorsally; T6 finely and densely punctate dorsolaterally, with a single row of pubescence in the middle; T7 punctate with pubescence dorsolaterally in anterior third and glabrous posteriorly. Apical teeth of metatibia slender and pointed apically. Apical process of first metatarsomeres reaching to two-thirds of second metatarsomere.

MALE: Unknown.

*Paramblynotus fucus* is unique among all *Paramblynotus* species for its very conspicuous patch of silvery hairs covering the metepisternum and propodeum, its evenly ferruginous wings, and its relatively long apical process of first metatarsomeres.

TYPE MATERIAL: HOLOTYPE: ♀, Papua New Guinea: Bulolo Dist., 1982, H. Roberts coll. (NHM).

DISTRIBUTION: Papua New Guinea

ETYMOLOGY: From Latin, *fucus*, colored, painted. The name refers to the ferruginous wings of the species.

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# APPENDIX 1

## LIST OF MATERIAL STUDIED, SORTED TO SPECIES, WITH DEPOSITORIES

Acronyms for insect collections are explained under Materials. Distribution records in the southeastern Pacific and Australian regions refer to islands rather than countries. Asterisks (\*) indicate new species described elsewhere (Liu, in prep.). CL = clades of the strict consensus tree of the shortest trees (fig. 12–14). T = type specimens.

| Genus, species                    | CL  | No. | Sex | Distribution                   | Depositories                        |
|-----------------------------------|-----|-----|-----|--------------------------------|-------------------------------------|
| <b><i>Kiefferiella</i></b>        |     |     |     |                                |                                     |
| n.sp. 1                           |     | 23  | m f | Texas, USA                     | USNM                                |
| n.sp. 2                           |     | 9   | m f | California, USA                | CAS                                 |
| <b><i>Paramblynotus</i></b>       |     |     |     |                                |                                     |
| <b><i>virginianus</i> group</b>   |     |     |     |                                |                                     |
| <i>virginianus</i> *              | vir | 19  | f   | USA: Virginia; Canada: Ontario | USNM (18), CNCI (1)                 |
| <b><i>scaber</i> group</b>        |     |     |     |                                |                                     |
| <i>scaber</i>                     | A   | 9   | m f | Far east Russia                | ZISP (7T+2)                         |
| <i>belizini</i> *                 | A   | 1   | f   | Russia: Vladivostok            | NHRM                                |
| <i>atratus</i> *                  | atr | 9   | m f | Russia: Primorskij             | ZISP                                |
| <i>irkutskensis</i> *             | irk | 1   | f   | Russia: Irkutsk                | ZISP                                |
| <i>marginatus</i> *               | B   | 1   | f   | Russia: Primorje               | ZISP                                |
| <i>pausatus</i> *                 | B   | 1   | f   | Russia: Primorje               | ZISP                                |
| <i>pronus</i> *                   | B   | 1   | f   | Russia: Primorje               | ZISP                                |
| <i>liaoi</i> *                    | B   | 1   | f   | China: Yunan                   | ZICA                                |
| <b><i>yangambicolus</i> group</b> |     |     |     |                                |                                     |
| <i>mixtus</i> *                   | D   | 1   | f   | Kenya                          | USNM                                |
| <i>yangambicolus</i>              | D   | 6   | f   | Zaire, Uganda                  | MRAC (1T), NHM (5)                  |
| <i>alveolatus</i> *               | D   | 1   | f   | Cameroon                       | MNCN                                |
| <b><i>trisetosus</i> group</b>    |     |     |     |                                |                                     |
| <i>prinsloo</i> *                 | pri | 1   | f   | South Africa                   | PPRI                                |
| <i>nigricornis</i>                | C   | 1   | f   | Zaire                          | MRAC (T)                            |
| <i>samiatus</i> *                 | C   | 1   | f   | South Africa                   | MRAC (T)                            |
| <i>claripennis</i> *              | C   | 1   | f   | Uganda                         | NHM                                 |
| <i>maculipennis</i> *             | C   | 1   | f   | Zaire                          | IRCT                                |
| <i>townesorum</i> *               | C   | 1   | f   | South Africa                   | AEI                                 |
| <i>femoratus</i> *                | C   | 1   | f   | South Africa                   | CNCI                                |
| <i>fuscipiculus</i> *             | C   | 13  | f   | South Africa, Zimbabwe         | AEI (4), CMS (2), NHM (2), PPRI (5) |
| <i>rwandensis</i> *               | C   | 1   | f   | Rwanda                         | CNCI                                |
| <i>trisetosus</i>                 | C   | 1   | f   | Zaire                          | MRAC (T)                            |
| <i>zairensis</i> *                | C   | 2   | f   | Zaire                          | NHM                                 |
| <i>cameroonensis</i> *            | C   | 1   | f   | Cameroon                       | NHM                                 |
| <i>kekenboschi</i> *              | C   | 2   | f   | Zaire                          | NHM                                 |
| <i>jackson</i> *                  | C   | 7   | m f | Cameroon                       | NHM                                 |
| <i>carinatus</i> *                | C   | 1   | f   | Zaire                          | NHM                                 |
| <i>immaculatus</i> *              | C   | 1   | f   | Namibia                        | NHM                                 |
| <i>antistatus</i> *               | C   | 1   | f   | Zaire                          | NHM                                 |
| <i>scalptus</i> *                 | C   | 4   | m f | South Africa                   | CNCI (2), PPRI (2)                  |
| <i>vannoorti</i> *                | C   | 1   | f   | South Africa                   | SAM                                 |
| <i>diminutus</i> *                | C   | 1   | m   | Zimbabwe                       | NHM                                 |
| <i>angolensis</i> *               | C   | 1   | f   | Angola                         | NHM                                 |
| <i>minutus</i> *                  | C   | 1   | f   | South Africa                   | NHM                                 |
| <b><i>apeosus</i> group</b>       |     |     |     |                                |                                     |
| <i>apeosus</i> *                  | E   | 1   | f   | Russia: Primorskij             | ZISP                                |
| <i>friatus</i> *                  | E   | 1   | f   | Russia: Primorje               | ZISP                                |

APPENDIX 1  
(Continued)

| Genus, species                  | CL | No. | Sex | Distribution                           | Depositories  |
|---------------------------------|----|-----|-----|--|---|
| <b><i>ruficollis</i> group</b>  |    |     |     |  |   |
| <i>malayensis</i>               | L  | 1   | f   | Borneo                                 | USNM (1T)   |
| <i>badius</i> *                 | L  | 1   | f   | Borneo                                 | NHM   |
| <i>coruscus</i> *               | L  | 3   | m f | Burma, Laos                            | BPBM (1), NHM (2)   |
| <i>carinivertex</i> *           | L  | 1   | f   | Borneo                                 | BPBM  |
| <i>trisectus</i>                | L  | 8   | m f | China: Guangxi, Yunan; Nepal, Thailand | CAU (1), CMS (3), CNC (1), CZL (1), NHM (1)                                     |
| <i>ruficollis</i>               | L  | 15  | m f | Laos, Malaya, Borneo, Luzon            | NHM (2+4T), AEI (1), BPBM (3), NNMN (2), USNM (3)                               |
| <i>braziliensis</i> *           | M  | 236 | m f | Brazil                                 | AEI (117), NHM (82), CMS (16), CNCI (8), NHRS (5), ZML (2) KJH (5), UCDC (1)    |
| <i>costaricanus</i> *           | M  | 4   | f   | Costa Rica, Guatemala                  | CNC (1), NHM (3)  |
| <i>zonatus</i>                  | M  | 2   | f   | USA: Texas                             | USNM (1T), CNC (1)  |
| <b><i>punctulatus</i> group</b> |    |     |     |  |   |
| <i>conspiratus</i> *            | K  | 1   | f   | Taiwan                                 | AEI   |
| <i>reticulatus</i>              | K  | 8   | m f | Bitan, Laos, Malaya                    | ZMHB (1T), NHM (5), BPBM (2)  |
| <i>clarus</i>                   | K  | 3   | f   | Mindanao, Ceylon                       | USNM (1T+1), CASC (1)   |
| <i>formosanus</i>               | K  | 1   | f   | Taiwan                                 | DEIC (T)  |
| <i>nipponensis</i> *            | K  | 1   | f   | Japan                                  | BPBM  |
| <i>punctulatus</i>              | K  | 87  |     | Borneo, Malaya, Sulawesi               | AEI (63), BPBM (1), CMS(1), CFR (2), NHM (4T+9), NNMN (1), ROM (2), USNM (3T+1) |
| <i>isolatus</i> *               | K  | 1   | f   | American Samoa                         | BPBM  |
| <i>miliocephalus</i> *          | H  | 1   | f   | Laos                                   | BPBM  |
| <i>ornatus</i> *                | H  | 4   | f   | Thailand, Vietnam, Sumatra, Malaya     | NHM (3), NHRS (1)   |
| <i>cheni</i> *                  | K  | 1   | f   | China: Zhejiang                        | ZICA  |
| <i>hainanensis</i> *            | K  | 2   | m   | China: Hainan                          | USNM  |
| <i>annulicornis</i>             | F  | 37  | m f | Borneo, Malaya, Sumatra                | NHM (1T), AEI (11), NNMN (7), ROM (7), USNM (1)                                 |
| <i>barbarae</i> *               | F  | 2   | m f | Borneo                                 | AEI (1), NNMN (1)   |
| <i>stigi</i> *                  | F  | 1   | f   | Borneo                                 | ROM   |
| <i>shimenensis</i> *            | F  | 1   | f   | China: Hunan                           | CZL   |
| <i>glaberus</i>                 | F  | 1   | f   | Borneo                                 | AEI   |
| <i>yuani</i> *                  | F  | 1   | f   | Borneo                                 | AEI   |
| <i>weiae</i> *                  | F  | 1   | f   | Vietnam                                | BPBM  |
| <i>eriki</i> *                  | F  | 1   | f   | Borneo                                 | AEI   |
| <i>asae</i> *                   | F  | 5   | m f | Sulawesi                               | NHM (4), NNMN (1)   |
| <i>filippae</i> *               | F  | 5   | f   | Borneo                                 | ROM   |
| <i>ebbae</i> *                  | F  | 1   | f   | Borneo                                 | ROM   |
| <i>axeli</i> *                  | F  | 1   | f   | Sumatra                                | ROM   |
| <i>ruficeps</i>                 | K  | 37  | m f | Borneo, Singapore                      | NHM (1T), AEI (25), USNM (5T+1), ROM (4), CMS (1), AEI (3), ZML (1)             |
| <i>pubifemoratus</i> *          | K  | 4   | f   | Borneo                                 | AEI (3), ZML (1)  |
| <i>chrysochaetes</i> *          | G  | 4   | f   | Malaya                                 | AEI   |
| <i>rufipes</i> *                | G  | 1   | f   | Laos                                   | BPBM  |
| <i>lutepennis</i> *             | K  | 1   | f   | Borneo                                 | ZMLU  |
| <i>nebulosus</i> *              | K  | 9   | f   | Borneo, Sulawesi                       | AEI (3), NHM (1), NNMN (4), ZMLU (1)  |

APPENDIX 1  
(Continued)

| Genus, species         | CL | No. | Sex |   | Distribution                       | Depositories  |
|------------------------|----|-----|-----|---|------------------------------------|---|
| <i>dyak</i>            | I  | 41  | m   | f | Borneo, Sulawesi, Sumatra, Sarawak | BPBM (5), AEI (12), NHM (8), USNM (2T), ROM (9), NNMN (5) |
| <i>beckeri</i> *       | I  | 8   |     | f | Borneo                             | AEI (7), CRF (1)  |
| <i>venforticulus</i> * | K  | 1   |     | f | Vietnam                            | BPBM  |
| <i>distinctus</i> *    | K  | 1   |     | f | Borneo                             | AEI   |
| <i>fraxinii</i>        | J  | 1   |     | f | Chian: Helongjiang                 | NWCF (T)  |
| <i>kosugii</i>         | J  | 5   | m   |   | Japan                              | EIHU  |
| <i>borneanus</i>       | K  | 2   | m   | f | Borneo                             | USNM (2T)   |
| <i>aptatus</i> *       | K  | 1   |     | f | Laos                               | BPBM  |
| <i>kitrinocarus</i> *  | K  | 1   |     | f | Borneo                             | ZMLU  |
| <i>insolitus</i> *     | K  | 1   |     | f | Mindoro                            | AEI   |
| <i>robustus</i> *      | K  | 1   |     | f | Laos                               | BPBM  |
| <i>miniatus</i> *      | K  | 1   |     | f | Sarawak                            | AEI   |
| <i>obscurus</i> *      | K  | 3   | m   | f | Borneo, Palawan                    | BPBM  |
| <i>coracinus</i> *     | K  | 4   |     | f | Borneo                             | AEI (3), CFR (1)  |
| <i>grossus</i> *       | K  | 16  |     | f | Sulawesi, Laos, Borneo, Papua N.G. | BPBM (1), NHM (12), NNMN (1), ZMLU (2), ROM (1)           |
| <i>fucosus</i> *       | K  | 1   |     | f | Papua N. G.                        | NHM   |

## APPENDIX 2

## LIST OF CHARACTERS ANALYZED USING THE FMCK METHOD

Asterisks (\*) indicate characters that are phylogenetically informative using FMCK. The numbers of such characters in the character list (appendix 3) are given in parentheses.

1. Length of eye/length of malar space
2. Length of eye/width of eye
3. Maximum distance between outer margin of eyes/distance between the midpoints of genae from dorsal view
- 4.\* Distance between posterior ocelli/distance between posterior ocellus and eye (125)
5. Distance between posterior ocellus and eye/distance between anterior and posterior ocelli
6. Maximum distance between outer margin of eyes/minimum distance between inner margin of eyes
- 7.\* Length of first flagellomere/length of pedicel (126)
- 8.\* Length of first flagellomere/length of second flagellomere (127)
9. Width of first flagellomere/width of apical flagellomere
10. Length of apical flagellomere/length of subapical flagellomere
11. Width of second flagellomere/width of first flagellomere
12. Width of second flagellomere/distance between the anterior end of pronotal carina and the mesoscutal sulcus
13. Height of pronotum/length of posterolateral margin of pronotum
14. Width/height of pronotum
15. Distance between the anterior point of the pronotal carina and the mesoscutal sulcus/height of pronotum
- 16.\* Length of R1/length of 2r of forewing (128)
17. Length/width of submarginal cell of forewing
18. Length/width of metacoxa
- 19.\* Length of first/second metatarsomeres (129)
20. Length of metasoma/distance between the anterior point of pronotal carina and the mesoscutal sulcus
- 21.\* Combined length of abdominal third through fifth tergum/length of postpetiolar metasoma (130)
- 22.\* Length of fifth tergum/length of postpetiolar metasoma (131)
- 23.\* Length of sixth tergum/length of postpetiolar metasoma (132)

## APPENDIX 3

## CHARACTERS USED FOR PHYLOGENETIC ANALYSIS

Several of the character states are subdivided; that is, one character state of a main character is more finely divided in a subsidiary character. For example, state 1 of character 4 is further subdivided in character 5, indicated by [4:1→] preceding the description. When multistate characters were treated as ordered in the analysis, it is so stated. The consistency index (CI) and retention index (RI) on the most parsimonious tree are given after each listed character, except for the three autapomorphies.

## MAIN STRUCTURES

1. Ocellar plate: (0) not distinctly raised; (1) distinctly raised. (CI = 0.25, RI = 0.93).
2. Glabrous triangular area immediately beneath anterior ocellus: (0) absent; (1) present. (CI = 0.23, RI = 0.68).
3. Lateral limit of ocellar plate: (0) indistinct, not marked by a carina; (1) marked by a carina from posterior ocellus to the middle of upper face below anterior ocellus. (CI = 0.17, RI = 0.67).
4. Median frontal carina: (0) absent; (1) present. (CI = 0.25, RI = 0.80).
5. [4:1→]. Dorsal extent of median frontal carina: (0) not reaching ocellar plate; (1) reaching or nearly reaching anterior ocellus. (CI = 0.13, RI = 0.77).
6. [4:1→]. Ventral extent of median frontal carina at lower face: (0) not reaching below antennal sockets; (1) reaching to about middle of lower face; (2) reaching almost to clypeus. Ordered. (CI = 0.15, RI = 0.67).
7. [4:1→]. Shape of median frontal carina: (0) not raised; (1) raised into a process above antennal sockets. (CI = 0.20, RI = 0.75).
8. [7:1→]. Shape of process of median frontal carina: (0) thin and laterally compressed; (1) pyramidal and blunt at top; (2) with an oval flat surface on top. Ordered. (CI = 0.33, RI = 0.64).
9. Lateral limit of antennal scrobe: (0) not marked by a distinct carina; (1) marked by a distinct carina. (CI = 0.33, RI = 0).
10. Antennal scrobes: (0) not or slightly impressed; (1) distinctly impressed. (CI = 0.20, RI = 0.43).
11. Shape of lower face in lateral view: (0) flat; (1) slightly convex; (2) distinctly convex and protruding. Ordered. (CI = 0.29, RI = 0.85).



12. Anterior tentorial pits: (0) indistinct to almost invisible; (1) distinct; (2) conspicuously large. Ordered. (CI = 0.17, RI = 0.70).
13. Distinct carina on dorsal part of occiput: (0) absent; (1) present. (Autapomorphy).
14. Shape of upper part of gena in dorsal view: (0) distinctly expanded lateroposteriorly, much wider than outer margins of eyes; (1) laterally extended to or almost to outer margin of eye, but always smoothly rounded anteriorly with outer margin of eye; (2) distinctly narrower than eyes, anteriorly forming an angle with outer margin of eye. Ordered. (CI = 0.29, RI = 0.90).
15. Shape of eye in dorsal view: (0) low and not protruding laterally; (1) high and protruding laterally. (CI = 0.25, RI = 0.93).
16. Ridge running vertically on gena: (0) absent; (1) present. (CI = 1.00, RI = 1.00).
17. Number of flagellomeres (female): (0) 11; (1) 10. (CI = 0.50, RI = 0.75).
18. Number of flagellomeres (male): (0) 13; (1) 12; (2) 11. Ordered. (CI = 1.00, RI = 0.00).
19. Shape of flagellum (female): (0) cylindrical, not or slightly widened apically; (1) cylindrical, distinctly widened toward apex; (2) widened and slightly compressed toward apex. (CI = 0.50, RI = 0.92).
20. Distribution of placodes on flagellomeres (female): (0) on all; (1) on all except F1; (2) on all except F1 and F2. Ordered. (CI = 0.22, RI = 0.59).
21. Shape of F1 (male): (0) excavated laterally; (1) not excavated laterally. (CI = 0.50, RI = 0.67).
22. Shape of F3–11 (male): (0) almost cylindrical; (1) distinctly narrowed both proximally and distally. (CI = 0.50, RI = 0.67).
23. Number, length, and spacing of placodes of F6 (female): (0) many, mostly much shorter than length of the flagellomere, and irregularly spaced; (1) a few, much shorter than length of the flagellomere; (2) a few, as long as the flagellomere, evenly spaced, and nearly parallel to each other. (CI = 0.29, RI = 0.88).
24. Shape of F7–9 (female): (0) cylindrical; (1) distinctly narrowed proximally; (2) distinctly narrowed both proximally and distally. Ordered. (CI = 0.40, RI = 0.82).
25. Density of placodes on apical flagellomere (female): (0) dense; (1) sparse. (CI = 0.09, RI = 0.55).
26. Shape of apical flagellomere (female): (0) not compressed and apically conical; (1) compressed and apically broadly rounded. (CI = 0.33, RI = 0.50).
27. Submedian depression of pronotum: (0) laterally open, (1) laterally closed. (CI = 0.20, RI = 0.60).
28. Prominence of lateral carina of pronotum: (0) weakly raised; (1) distinctly raised; (2) strongly raised, crestlike. Ordered. (CI = 0.22, RI = 0.89).
29. Dorsal extent of lateral carina of pronotum: (0) not reaching pronotal crest dorsally; (1) distinctly reaching pronotal crest dorsally. (CI = 1.00, RI = 1.00).
30. Delimitation and extent of dorsal area of pronotum: (0) not delimited by the pronotal crest, posteriorly continuous with lateral surface of pronotum; (1) delimited by the complete pronotal crest throughout, posteriorly extended to tegula or almost so; (2) delimited by the pronotal crest, posteriorly ending far before reaching tegula. Ordered. (CI = 0.18, RI = 0.81).
31. Shape of pronotal crest medially: (0) not or indistinctly raised; (1) distinctly and evenly raised, anteriorly forming a conspicuous peak in lateral view; (2) abruptly raised into a small but distinct median triangular process; (3) abruptly raised into two small but distinct submedian processes. (CI = 0.50, RI = 0.90).
32. [31:1→]. Shape of the highly raised pronotal crest: (0) without emargination; (1) with a shallow median emargination; (2) with a deep median emargination. Ordered. (CI = 0.40, RI = 0.40).
33. Surface of dorsal pronotal area: (0) flat; (1) with a wide median depression. (CI = 1.00, RI = 1.00).
34. Glabrous to glabrate area anteroventrally on lateral surface of pronotum: (0) absent; (1) present. (CI = 0.40, RI = 0.25).
35. Lateroventral margin of pronotum: (0) evenly curved; (1) angled where it meets lateral pronotal carina. (CI = 0.20, RI = 0.89).
36. Height of pronotum in lateral view: (0) low; (1) high. (CI = 0.33, RI = 0.91).
37. Shape of surface of mesoscutum in lateral view: (0) flat; (1) convex only anteriorly, posteriorly flat; (2) evenly convex; (3) strongly evenly convex. Ordered. (CI = 0.33, RI = 0.94).
38. Posterior part of parascutal carinae: (0) not distinctly raised, rounded posteriorly; (1) distinctly raised, posteriorly broadly rounded; (2) conspicuously raised, posteriorly angular. (cf. Ronquist 1995a: char 11). Ordered. (CI = 0.29, RI = 0.77).
39. Large depression at anterior end of notaulus: (0) absent; (1) present. (CI = 0.67, RI = 0.95).

40. Subdivision of scutellar foveae: (0) not subdivided by carinae as strong as median ridge; (1) subdivided by a few additional strong parallel ridges into several smaller foveae. (CI = 0.29, RI = 0.72).
41. Shape of the of laterodorsal process of scutellum posterolaterally: (0) broadly rounded; (1) angled. (CI = 0.50, RI = 0.50).
42. Shape of dorsal surface of scutellum: (0) dorsally convex, gradually sloping posteriorly; (1) dorsally convex, laterally sloping gradually but steeply, posteriorly sloping more or less abruptly; (2) dorsally slightly convex, abruptly sloping posteriorly, forming a distinct vertical surface; (3) dorsally flat, posteriorly produced, posteriorly and laterally abruptly sloping. (CI = 0.33, RI = 0.88).
43. [42:2]. Posterior margin of scutellum: (0) rounded; (1) truncate; (2) emarginate. Ordered. (CI = 0.20, RI = 0.68).
44. Vertical surface of scutellum posterior to auricula: (0) foveate-reticulate; (1) vertically costate or irregularly carinate; (2) rugose. (CI = 0.33, RI = 0.50).
45. Shape of scutellum behind lateral bar in dorsal view: (0) not or slightly expanded; (1) distinctly expanded. (CI = 0.11, RI = 0.74).
46. Longitudinal carinae on speculum: (0) absent; (1) present. (CI = 0.33, RI = 0.80).
47. Ventral margin of mesopleural triangle: (0) not well defined; (1) well defined. (CI = 0.33, RI = 0.50).
48. Mesopleural impression: (0) distinct and complete; (1) indistinct and incomplete. (Autapomorphy).
49. Width and sculpture of mesopleural impression: (0) broad, without distinct vertical costa; (1) narrow with one or two distinct vertical costae; (2) narrow with several distinct vertical costae. Ordered. (CI = 0.29, RI = 0.92).
50. Presence of a posterior vertical impression on the lower mesopleuron and its connection with the posterior end of mesopleural impression: (0) absent; (1) present, but not continuous with mesopleural impression; (2) present, continuous with mesopleural impression. (CI = 0.17, RI = 0.79).
51. Strength of intermesocoxal processes: (0) weak, indistinct in lateral view; (1) strong, distinct in lateral view. (CI = 0.11, RI = 0.11). (Ronquist, 1995a: char. 22).
52. Lateroventral carina of mesospectus: (0) anteriorly absent; (1) complete. (CI = 1.00, RI = 1.00).
53. Shape of ventral margin of mesopleuron: (0) ventrally not protruding; (1) ventrally protruding. (CI = 1.00, RI = 1.00).
54. Nude and glabrous elevated area of metepisternum: (0) absent; (1) present. (CI = 0.20, RI = 0.85).
55. Structure and extent of lateral propodeal carinae: (0) distinctly percurrent; (1) anteriorly distinct, posteriorly disappearing in areolate sculpture; (2) anteriorly raised to a robust process, absent posteriorly. (CI = 0.33, RI = 0.56).
56. [55:1]. Direction of the percurrent lateral propodeal carina: (0) almost parallel; (1) medially distinctly curved laterad. (CI = 0.14, RI = 0.68).
57. [55:1]. Shape of lateral propodeal carina: (0) not raised; (1) medially moderately raised, in lateral view posteriorly forming an obtuse angle with dorsal surface of nucha; (2) conspicuously raised, in lateral view posteriorly forming almost a right angle with dorsal surface of nucha. Ordered. (CI = 0.33, RI = 0.95).
58. Dorsal edge of lateral propodeal carina: (0) narrow; (1) flat and broad. (CI = 0.25, RI = 0.93).
59. Posterolateral propodeal process: (0) absent; (1) low; (2) high. Ordered. (CI = 0.20, RI = 0.82).
60. Shape of metapectal-propodeal complex in lateral view: (0) posteriorly not or slightly protruding, nucha low with postsubpleuron nearly horizontal; (1) posteriorly distinctly protruding, and nucha high, postsubpleuron slightly oblique; (2) posteriorly slightly protruding, nucha high, postsubpleuron distinctly oblique. (CI = 0.25, RI = 0.82). (cf. Ronquist, 1995a: char. 27).
61. Longitudinal costae on dorsal surface of annulus: (0) distinct; (1) indistinct or absent. (CI = 0.25, RI = 0.25).
62. Anterior glabrous strip along anterior dorsal margin of annulus: (0) absent; (1) present. (CI = 0.25, RI = 0.86).
63. Lateral compression of metasoma: (0) strongly compressed, knife-shaped; (1) distinctly compressed, but not knife-shaped. (CI = 1.00, RI = 1.00).
64. Direction of lateral part of posterior margin of the third tergum (female): (0) more or less vertical; (1) oblique. (CI = 1.00, RI = 1.00). (cf. Ronquist, 1995a: char 43).
65. Abdominal fourth through sixth sternum (female): (0) at least partly exposed; (1) entirely covered by abdominal third sternum. (CI = 0.50, RI = 0.67). (cf. Ronquist, 1995a: char 44).
66. Size of the fifth tergum (male): (0) medially subequal in length to other postpetiolar terga; (1) medially distinctly longer

than other post-petiolar terga. (CI = 0.50, RI = 0.86).

67. Relative position of sixth and seventh terga (female): (0) sixth tergum not entirely covering the seventh; (1) sixth tergum entirely or almost entirely covering the seventh. (CI = 0.33, RI = 0.71).
68. Shape of posterior margin of seventh tergum (female): (0) slightly or not emarginate dorsoposteriorly; (1) distinctly, broadly emarginate. (CI = 0.17, RI = 0.85).
69. Relation between seventh and eighth tergum (female): (0) seventh tergum entirely covering the eighth; (1) seventh tergum not entirely covering the eighth, leaving the eighth tergum partly distinctly exposed. (CI = 0.25, RI = 0.93).
70. Rs+M arising from basalis: (0) at upper third; (1) about at middle; (2) at lower third; (3) Rs+M indistinct or absent; (4) at the cross of basalis and M-Cu1. (CI = 0.33, RI = 0.64).
71. Lobelike process ventroanteriorly on metacoxa: (0) absent; (1) present. (Autapomorphy).
72. Shape of metatibial apical teeth: (0) short and blunt; (1) long and pointed; (2) short and pointed. (CI = 0.50, RI = 0.80).
73. Apical protuberance of first metatarsomere: (0) absent; (1) present. (CI = 1.00, RI = 1.00).
74. Teeth on posterior surface of metatibia: (0) absent; (1) with two to four robust, triangular teeth. (CI = 1.00, RI = 1.00).
75. Dorsal impression of metacoxa: (0) absent; (1) superficial; (2) distinct. Ordered. (CI = 0.20, RI = 0.76).

#### SURFACE SCULPTURE AND PUBESCENCE

76. Major longitudinal sculpture on vertex: (0) absent; (1) limited to lateral parts; (2) covering most of vertex. Ordered. (CI = 0.17, RI = 0.47).
77. Subordinate nonlongitudinal sculpture of vertex: (0) glabrate; (1) foveate-reticulate; (2) foveate; (3) foveate and punctulate; (4) punctate. (CI = 0.36, RI = 0.42).
78. Sculpture on central part of ocellar plate: (0) glabrate to glabrous; (1) longitudinally carinate with punctures; (2) punctate; (3) foveate to foveate-reticulate; (4) foveate and punctate. (CI = 0.50, RI = 0.69).
79. Sculpture along anterior lateral sides of ocellar plate: (0) glabrous to glabrate; (1) longitudinally carinate; (2) more or less foveate, foveae not set in a row; (3) with distinct foveae set in a row. (CI = 0.15, RI = 0.68).
80. Secondary longitudinal sculpture of antennal scrobes: (0) absent; (1) partly carinate posteriorly; (2) carinate almost throughout. (CI = 0.25, RI = 0.78).
81. Primary sculpture of antennal scrobes: (0) sparsely punctate; (1) densely punctate; (2) weakly areolate; (3) coriaceous. (CI = 0.28, RI = 0.62).
82. Sculpture of lower face: (0) glabrate; (1) densely punctate; (2) foveate; (3) foveate-reticulate; (4) foveate-reticulate and punctate; (5) areolate; (6) irregularly carinate; (7) rugose to rugulose; (8) coriaceous. (CI = 0.43, RI = 0.81).
83. Sculpture of gena (0) glabrous to glabrate; (1) coriaceous; (2) punctate to foveate; (3) sparsely and weakly foveate; (4) foveate-reticulate; (5) foveate and punctate; (6) areolate; (7) rugose to rugulose; (8) foveate-reticulate and punctate. (CI = 0.35, RI = 0.73).
84. Sculpture on occiput: (0) glabrous; (1) coriaceous; (2) dorsally vertically carinate and ventrally glabrous; (3) entirely vertically carinate. (CI = 0.75, RI = 0.94).
85. Surface sculpture and pubescence on apex of apical flagellomere (female): (0) with distinct placodes and more or less pubescent; (1) glabrous and nude. (CI = 1.00, RI = 1.00).
86. Sculpture on anterior flange of pronotum: (0) glabrous; (1) coriaceous; (2) longitudinally striate; (3) diagonally to transversely striate; (4) punctate. (CI = 0.24, RI = 0.71).
87. Sculpture of anterior part of anterior plate of pronotum: (0) glabrous; (1) coriaceous; (2) coarsely punctate to rugulose. (CI = 0.29, RI = 0.72).
88. Sculpture on main part of anterior plate of pronotum: (0) finely punctate; (1) coarsely punctate, sometimes with punctures set in rows; (2) glabrous or coriaceous with more or less fine punctures. (CI = 0.33, RI = 0.75).
89. Extent of sculpture dorsally on anterior surface of pronotum: (0) as coarsely sculptured as the lateral surfaces, forming a coarsely sculptured bridging strip; (1) less sculptured than the lateral surfaces, separating the latter. (CI = 0.20, RI = 0.73).
90. Sculpture of submedian depression of pronotum: (0) glabrous to glabrate; (1) punctate; (2) carinate. (CI = 0.25, RI = 0.67).
91. Main sculpture component on central part of lateral surface of pronotum: (0) glabrate; (1) foveate-reticulate; (2) foveate-reticulate and punctulate. (CI = 0.33, RI = 0.94).

92. Minor sculpture component on lateral surface of pronotum: (0) absent; (1) posteriorly broadly costate; (2) posteriorly glabrate; (3) posteriorly finely and densely carinate. (CI = 0.63, RI = 0.63).
93. Dominant sculpture on mesoscutum: (0) strongly transversely costate with superficial foveae; (1) transversely costate with distinct foveae set in rows; (2) foveate-reticulate without costae; (3) foveate without costae. (CI = 0.23, RI = 0.76).
94. Sculpture on dorsal surface of scutellum: (0) foveate; (1) foveate-reticulate; (2) transversely costate with foveae set in rows anteriorly and foveate-reticulate posteriorly; (3) transversely costate with foveae set in rows. (CI = 0.75, RI = 0.00).
95. Sculpture of anterior part of upper pleuron: (0) glabrate; (1) punctate; (2) foveate-reticulate; (3) with a large impression and punctate with hairs; (4) longitudinally carinate. (CI = 0.33, RI = 0.67).
96. Sculpture of posterior part of upper pleuron: (0) glabrous; (1) sparsely punctulate; (2) foveate; (3) foveate-reticulate; (4) longitudinally carinate. (CI = 0.43, RI = 0.43).
97. Sculpture of median part of lower pleuron: (0) glabrous to glabrate and nude; (1) densely punctulate and pubescent. (CI = 0.20, RI = 0.43).
98. Sculpture on upper half of metepisternum: (0) horizontally costate; (1) areolate; (2) rugose; (3) indistinct from the extension of the elevated glabrous nude area. (CI = 0.33, RI = 0.79).
99. Sculpture of lateral propodeal carinae dorsally: (0) glabrous to glabrate; (1) sculptured. (CI = 0.14, RI = 0.85).
100. Sculpture on dorsal surface of nucha: (0) glabrous to glabrate; (1) punctulate; (2) superficially longitudinally sculptured; (3) distinctly longitudinally costulate; (4) rugose. (CI = 0.33, RI = 0.79).
101. Strong median longitudinal carina of median propodeal area: (0) with no distinct longitudinal carina; (1) distinctly present anteriorly, posteriorly absent; (2) percurrent. (CI = 0.20, RI = 0.53).
102. Strong median transverse carina of median propodeal area: (0) absent; (1) present. (CI = 0.14, RI = 0.50).
103. Pubescence of pronotum, especially dorsomedially: (0) sparse; (1) dense. (CI = 0.33, RI = 0.89).
104. Long hairs of axilla: (0) absent or inconspicuous; (1) conspicuous. (CI = 0.25, RI = 0.88).
105. Patch of long hairs posteriorly on scutellum: (0) absent; (1) present. (CI = 1.00, RI = 1.00).
106. Conspicuous hairs of mesopectal triangle: (0) more or less densely pubescent, but not conspicuous; (1) conspicuous. (CI = 0.50, RI = 0.97).
107. Pubescence on lower half of metepisternum: (0) sparse; (1) dense. (CI = 0.13, RI = 0.68).
108. Pubescence of lateral propodeal carina: (0) absent to sparse; (1) dense. (CI = 0.50, RI = 0.83).
109. Coarse punctures with hairs on dorsal surface of sixth through eighth terga (male): (0) absent; (1) present. (CI = 1.00, RI = 1.00).
110. Patch/patches of hairs on sixth through eighth terga (female): (0) absent; (1) not conspicuous; (2) conspicuous. Ordered. (CI = 0.29, RI = 0.83).
111. [110:2]. Shape and extent of the conspicuous patch of hairs on sixth tergum (female): (0) a narrow strip, posteriorly distinctly separated from the hair patch on seventh through eighth terga; (1) a rectangular strip, covering posterior half of sixth tergum, posteriorly close to the hair patch on seventh through eighth terga; (2) a triangular patch, covering posterior one-third to half of sixth tergum, posteriorly continuous with hair patches on seventh through eighth terga. (CI = 1.00, RI = 1.00).

#### COLORATION

112. Color of head: (0) black; (1) yellow to reddish brown. (CI = 0.33, RI = 0.90).
113. Color of antennal flagellum: (0) entirely black to dark gray; (1) almost entirely yellow to reddish brown, apical second to third flagellomeres contrastingly black; (2) entirely yellow to reddish brown; (3) yellowish with a pale-colored ring comprising two to three flagellomeres in the middle (flagella 6–7, sometimes extended to 8 or 9). (CI = 0.33, RI = 0.67).
114. Pronotum: (0) black; (1) yellow to reddish brown. (CI = 0.33, RI = 0.81).
115. Mesoscutum: (0) black; (1) yellow to reddish brown. (CI = 0.20, RI = 0.78).
116. Mesoscutellum: (0) black; (1) yellow to reddish brown. (CI = 0.50, RI = 0.87).
117. Background color of wings: (0) evenly transparent; (1) transparent with wide smoky band along outer margins of wings; (2) entirely evenly smoky; (3) yellowish. (CI = 1.00, RI = 1.00).



118. Contrasting large continuous ferruginous area of forewings: (0) absent; (1) entirely brownish ferruginous in basal two-thirds and transparent distally; (2) entirely brownish ferruginous in distal half and transparent basally; (3) medially widely ferruginous, basally and distally transparent. (CI = 0.80, RI = 0.83).
119. [118:0]. Anterior ferruginous marking at marginal cell and adjacent areas of forewing: (0) absent; (1) only limited to marginal cell; (2) extending to include distal two-thirds of first submarginal cell and anterior half of basal part of third submarginal cell behind marginal cell; (3) extending to include the entire basal part of third submarginal cell behind marginal cell; (4) extending to include the entire basal part of third submarginal cell behind marginal cell and a short band along the distal third of Rs+M. (CI = 0.50, RI = 0.83).
120. [118:0]. Distinct transverse ferruginous band along interior side of basalis of forewing starting from anterior margin of the wing and ending at Cu-a: (0) absent; (1) present. (CI = 0.33, RI = 0.82).
121. Metapectal-propodeal complex: (0) black; (1) yellow to reddish brown. (CI = 0.25, RI = 0.82).
122. Metasoma posterior to petiole: (0) black to dark brown; (1) reddish to yellowish. (CI = 0.25, RI = 0.75).
123. Color of body pubescence and hairs: (0) white; (1) brownish yellow. (CI = 1.00, RI = 1.00).
124. Color of legs: (0) entirely black to dark brown; (1) entirely reddish brown; (2) coxa, sometimes also femur, black, other parts yellow to reddish brown; (3) entirely yellow to yellowish brown; (4) all yellowish except the dark metatibia and metatarsomeres. (CI = 0.33, RI = 0.79).
- (0)  $X = 1.14 \pm 0.29$  ( $X_{\min} = 0.5$ ,  $X_{\max} = 1.9$ ); (1)  $X = 4.4 \pm 0.88$  ( $X_{\min} = 3.1$ ,  $X_{\max} = 5.8$ ). Ordered. (CI = 1.00, RI = 1.00).
126. Ratio of length of first flagellomere to length of pedicel: (0)  $X = 1.86 \pm 0.25$  ( $X_{\min} = 1.2$ ,  $X_{\max} = 2.3$ ); (1)  $X = 2.92 \pm 0.56$  ( $X_{\min} = 2.3$ ,  $X_{\max} = 4.4$ ). Ordered. (CI = 0.13, RI = 0.59).
127. Ratio of length of first flagellomere to length of second flagellomere (female): (0)  $X = 0.8 \pm 0.09$  ( $X_{\min} = 0.6$ ,  $X_{\max} = 0.95$ ); (1)  $X = 1.16 \pm 0.14$  ( $X_{\min} = 1.0$ ,  $X_{\max} = 1.5$ ). Ordered. (CI = 0.25, RI = 0.87).
128. Ratio of length of R1 and 2r of forewing: (0)  $X = 2.60 \pm 0.36$  ( $X_{\min} = 1.57$ ,  $X_{\max} = 3.0$ ); (1)  $X = 3.64 \pm 0.39$  ( $X_{\min} = 3.05$ ,  $X_{\max} = 5.3$ ). Ordered. (CI = 0.11, RI = 0.47).
129. Ratio of length of first metatarsomere to length of second (female): (0)  $X = 2.27 \pm 0.25$  ( $X_{\min} = 1.6$ ,  $X_{\max} = 2.88$ ); (1)  $X = 3.15 \pm 0.37$  ( $X_{\min} = 3.00$ ,  $X_{\max} = 4.86$ ); (2)  $X = 6.61 \pm 1.59$  ( $X_{\min} = 5.67$ ,  $X_{\max} = 9.0$ ). Ordered. (CI = 0.25, RI = 0.80).
130. Ratio of combined length of third through fifth terga to distance from anterior margin of third tergum to distal end of eighth tergum (female): (0)  $X = 0.22 \pm 0.02$  ( $X_{\min} = 0.20$ ,  $X_{\max} = 0.24$ ); (1)  $X = 0.31 \pm 0.03$  ( $X_{\min} = 0.25$ ,  $X_{\max} = 0.36$ ); (2)  $X = 0.43 \pm 0.05$  ( $X_{\min} = 0.36$ ,  $X_{\max} = 0.54$ ); (3)  $X = 0.72 \pm 0.11$  ( $X_{\min} = 0.62$ ,  $X_{\max} = 0.94$ ). Ordered. (CI = 0.14, RI = 0.72).
131. Ratio of length of the dorsal margin of fifth tergum to length of metasoma measured from middle of anterior margin of third tergum to distal end of last visible tergum (female): (0)  $X = 2.68 \pm 0.37$  ( $X_{\min} = 2.4$ ,  $X_{\max} = 3.5$ ); (1)  $X = 4.70 \pm 0.44$  ( $X_{\min} = 3.8$ ,  $X_{\max} = 5.9$ ); (2)  $X = 6.4 \pm 0.55$  ( $X_{\min} = 6.2$ ,  $X_{\max} = 8.3$ ). Ordered. (CI = 0.13, RI = 0.74).
132. Ratio of length of the dorsal margin of sixth tergum to length of metasoma measured from middle of anterior margin of third tergum to distal end of last visible tergum (female): (0)  $X = 2.29 \pm 0.35$  ( $X_{\min} = 1.5$ ,  $X_{\max} = 3.0$ ); (1)  $X = 4.36 \pm 1.00$  ( $X_{\min} = 3.2$ ,  $X_{\max} = 6.4$ ). Ordered. (CI = 0.25, RI = 0.73).

#### QUANTITATIVE CHARACTERS

125. Ratio of distance between posterior ocelli to distance between posterior ocellus and eye:

APPENDIX 4  
OBSERVED CHARACTER STATES  
(? = uncertainty, p = 0/1, q = 0/1/2).

|                            | Character  |             |             |            |             |
|----------------------------|------------|-------------|-------------|------------|-------------|
|                            | 1          | 11          | 21          | 31         | 41          |
| <i>Kiefferiella</i>        |            |             |             |            |             |
| n.sp. 1                    | 1111100?11 | 2101000101  | 1010001000  | 0?00003000 | 00???100022 |
| n.sp. 2                    | 1111000?11 | 2101000001  | 1010111000  | 0?00003000 | 02?1100022  |
| <i>Paramblynotus</i>       |            |             |             |            |             |
| <i>virginianus</i> group   |            |             |             |            |             |
| <i>virginianus</i>         | 1101010?11 | 1102100?01  | ??10000001  | 0?00002100 | 00???101000 |
| <i>scaber</i> group        |            |             |             |            |             |
| <i>scaber</i>              | 1p01000?11 | 1001000101  | 1010100001  | 0?00002100 | 01???001022 |
| <i>belizini</i>            | 1101000?11 | 1101000?01  | ??10100001  | 0?00002100 | 01???001022 |
| <i>atratus</i>             | 1101000?11 | 1101000101  | 1010100001  | 0?00002100 | 01???001022 |
| <i>irkutskensis</i>        | 1111010?11 | 1001000?01  | ??10100001  | 0?00002100 | 01???001022 |
| <i>marginatus</i>          | 1101010?11 | 1101000?00  | ??00000001  | 0?00000100 | 01???001022 |
| <i>pausatus</i>            | 1111000?11 | 1101000?00  | ??10100001  | 1200000100 | 01???001020 |
| <i>pronus</i>              | 1101000?11 | 1101000?00  | ??10100001  | 1200010200 | 0210001020  |
| <i>liaoi</i>               | 1101001?01 | 010100????0 | ???0?1001   | 1100010201 | 0201001022  |
| <i>yangambiculus</i> group |            |             |             |            |             |
| <i>mixtus</i>              | 0001120?10 | 2002000?10  | ??1000?200  | 1000000101 | 00???011020 |
| <i>yangambiculus</i>       | 0001000?10 | 2000000?20  | ??00010101  | 1000010100 | 03100101?2  |
| <i>alveolatus</i>          | 0001100?10 | 200000????0 | ??????0101  | 1000010100 | 0310110022  |
| <i>trisetosus</i> group    |            |             |             |            |             |
| <i>prinslooii</i>          | 1101100?11 | 0001000?00  | ??11000001  | 0?01003101 | 00???000021 |
| <i>nigricornis</i>         | 1100????11 | 0101000?10  | ??21100201  | 0?00003200 | 00???10102? |
| <i>samiatus</i>            | 1000????11 | 010100????0 | ??????0200  | 2?00003201 | 00???001021 |
| <i>claripennis</i>         | 1010????11 | 0101001?10  | ??21000200  | 2?00003201 | 00???101021 |
| <i>maculipennis</i>        | 1010????11 | 0101001?10  | ??2110?000  | 2?00003200 | 00???001021 |
| <i>townesorum</i>          | 1010????11 | 0101001?10  | ??21001001  | 0?00003201 | 00???001021 |
| <i>femoratus</i>           | 0011100?11 | 0101000?10  | ??21100102  | 0?00003200 | 00???101021 |
| <i>fuscapiculus</i>        | 0111100?11 | 0101000?11  | ??21100100  | 0?00003101 | 00???001020 |
| <i>rwandensis</i>          | 1111110?11 | 0101000?11  | ??21000100  | 0?00003200 | 00???101020 |
| <i>trisetosus</i>          | 0001000?11 | 1001000?11  | ??21100101  | 0?00103200 | 00???101020 |
| <i>zairensis</i>           | 0111000?11 | 0102100?11  | ??22100101  | 0?00003200 | 00???101020 |
| <i>cameroonensis</i>       | 0011110?11 | 0102100?10  | ??21100101  | 0?00003200 | 00???101020 |
| <i>kekenboschi</i>         | 0111100?11 | 0002100?11  | ??2110?101  | 0?00003200 | 00???101020 |
| <i>jacksoni</i>            | 0110????11 | 0002100100  | 0122000101  | 0?00003200 | 00???101020 |
| <i>carinatus</i>           | 0110120?11 | 0002100?00  | ??22000000  | 0?00003200 | 00???101020 |
| <i>immaculatus</i>         | 0101100?11 | 0201000?10  | ??20100001  | 0?00003100 | 002?011021  |
| <i>antistatus</i>          | 0001100?10 | 0101000?11  | ??20100001  | 0?00003100 | ?1???011021 |
| <i>scalptus</i>            | 0001100?11 | 0101000?11  | ??20000001  | 0?00003100 | 00???111020 |
| <i>vannoorti</i>           | 0011100?11 | 0101000?10  | ??20100001  | 0?00003100 | 00???111020 |
| <i>diminutus</i>           | 0101100?10 | 020100?1??  | 01????0001  | 0?00003100 | 00???111022 |
| <i>angolensis</i>          | 0011100?11 | 0201000112  | 0120100001  | 0?00003100 | 00???111020 |
| <i>minutus</i>             | 0101100?11 | 0201000?11  | ??20100001  | 0?00003100 | 000?111020  |
| <i>apeosus</i> group       |            |             |             |            |             |
| <i>apeosus</i>             | 1101000?11 | 1001000?00  | ??00000001  | 0?00101200 | 00???101022 |
| <i>friatus</i>             | 1101000?11 | 1101000?00  | ??00000001  | 0?00101200 | 00???101022 |
| <i>ruficollis</i> group    |            |             |             |            |             |
| <i>malayensis</i>          | 0101020?10 | 010210????0 | ???????1202 | 0?0p102101 | 0201001021  |
| <i>badius</i>              | 0001100?10 | 0102100?00  | ??00001202  | 2?00102201 | 0201001021  |
| <i>coruscus</i>            | 0000000?11 | 1102100100  | 1000000200  | 0?00002201 | 0201001001  |

APPENDIX 4  
(Continued)

|                          | Character  |            |               |            |            |
|--------------------------|------------|------------|---------------|------------|------------|
|                          | 1          | 11         | 21            | 31         | 41         |
| <i>carinivertex</i>      | 0011000?11 | 1112100?00 | ??00000200    | 2?00102201 | 0201001001 |
| <i>trisectus</i>         | 0011100?11 | 1102100?00 | ??00000201    | 2?00102201 | 0201001001 |
| <i>ruficollis</i>        | 0011100?11 | 0102100100 | 1000001200    | 2?0110220p | 0201001001 |
| <i>braziliensis</i>      | 0011101211 | 1101000100 | 0010111200    | 3210102211 | 0321101001 |
| <i>costaricanus</i>      | 0011101211 | 1101000?00 | ??10011200    | 0?10102211 | 1321101001 |
| <i>zonatus</i>           | 0011101011 | 1101000?00 | ??10111200    | 0?10102211 | 0321101001 |
| <b>punctulatus group</b> |            |            |               |            |            |
| <i>conspiratus</i>       | 1101000?11 | 1002100?00 | ??01000211    | 0?00103201 | 00??101021 |
| <i>reticulatus</i>       | 1101000?11 | 1002100100 | 1111000102    | 0?00103200 | 02?1111021 |
| <i>clarus</i>            | 0111110?11 | 1102100?00 | ??00001211    | 0?00103200 | 1320101011 |
| <i>fainosanus</i>        | 0111100?11 | 0002101?00 | ??0000?211    | 0?00003200 | 02?1001011 |
| <i>nipponensis</i>       | 0111000?11 | 1102100?00 | ??10000212    | 0?00103201 | 00??001011 |
| <i>punctulatus</i>       | 0111000?11 | 1102100?00 | ??00000212    | 0?00103200 | 00??001011 |
| <i>isolatus</i>          | 0111000?11 | 1102100?00 | ??00100212    | 0?00103200 | 00??001011 |
| <i>mitocephalus</i>      | 0111100?11 | 0102100?00 | ??00000211    | 0?00103200 | 00??001011 |
| <i>ornatus</i>           | 0111100?11 | 0102100?00 | ??00000211    | 0?001032p0 | 00??001011 |
| <i>cheni</i>             | 0011110?10 | 1002100?00 | ??00000202    | 0?00003200 | 00??001021 |
| <i>hainanensis</i>       | 0111111211 | 000210?1?? | 1? ??? ?0212  | 0?00103210 | 0321101011 |
| <i>annulicornis</i>      | 0111121011 | 0102100100 | 1000000212    | 0?00103210 | 02?1101010 |
| <i>barbarae</i>          | 0101111011 | 0102100?10 | ??00000211    | 0?00103210 | 0321101010 |
| <i>stigi</i>             | 0111100?11 | 0102100?00 | ??00000212    | 0?00103210 | 02?1101010 |
| <i>shimenensis</i>       | 0111121011 | 0102110?00 | ??10000212    | 0?00103210 | 02?1101011 |
| <i>glaberus</i>          | 0111121011 | 0102100?10 | ??10000212    | 0?00103210 | 02?1101020 |
| <i>yuani</i>             | 0011111011 | 0102100?10 | ??10000211    | 0?00103210 | 0201101011 |
| <i>weiae</i>             | 0111121011 | 0102100?10 | ??1000?212    | 0?00003210 | 02?1101011 |
| <i>eriki</i>             | 0111121011 | 0102100?10 | ??00000211    | 0?00103210 | 02?1101021 |
| <i>asae</i>              | 0111121211 | 0002100?10 | ??10000211    | 0?00103210 | 02?1101021 |
| <i>filippae</i>          | 0011121211 | 0202100?10 | ??00000211    | 0?00103210 | 0211101020 |
| <i>ebbae</i>             | 0111010?11 | 0202110?11 | ??10000211    | 0?01103210 | 0201101020 |
| <i>axeli</i>             | 0111121211 | 020210?1?? | 10? ??? ?0211 | 0?00103210 | 0301101010 |
| <i>ruficeps</i>          | 1111010?11 | 0102100100 | 1000000201    | 0?00103200 | 02?1101021 |
| <i>pubifemoratus</i>     | 11p1000?11 | 1002100?00 | ??00000212    | 0?00103200 | 02?1101021 |
| <i>chrysochaïtes</i>     | 1011100?11 | 0102100?00 | ??00000200    | 1000110201 | 0321101000 |
| <i>rufipes</i>           | 1101101101 | 0002100?00 | ??00000200    | 1000110201 | 0321101001 |
| <i>lutepennis</i>        | 1011000?11 | 1002100?00 | ??00000112    | 1000110210 | 02?1101002 |
| <i>nebulosus</i>         | 1111100?11 | 0002100?00 | ??00000102    | 1000110200 | 0321101010 |
| <i>dyak</i>              | 1p11000?11 | 0002100100 | 1000000102    | 1000110200 | 0201101000 |
| <i>beckeri</i>           | 1111000?11 | 0002100?00 | ??00000102    | 1000110200 | 0201101000 |
| <i>venoforticulus</i>    | 1110????11 | 0002100?00 | ??00000102    | 1000110200 | 0201101010 |
| <i>distinctus</i>        | 1011000?01 | 0102100?00 | ??10000102    | 1000110210 | 0211101010 |
| <i>fraxinii</i>          | 1111100?11 | 0101001?00 | ??00000112    | 1000110210 | 0201001011 |
| <i>kosugii</i>           | 1111100?11 | 010100?1?? | 10? ??? ?0112 | 1000110210 | 0211001011 |
| <i>borneanus</i>         | 1110????11 | 010100???? | ????? ?0102   | 1000110200 | 02??101000 |
| <i>aptatus</i>           | 1000????11 | 010210???? | 10? ??? ?0102 | 1000110200 | 00??101010 |
| <i>kitrinocarus</i>      | 1011011011 | 0100000?00 | ??00?00102    | 1000110200 | 02?1101001 |
| <i>insolitus</i>         | 1000????11 | 0101000?00 | ??00000102    | 1001110200 | 0201101000 |
| <i>robustus</i>          | 1010????11 | 0001000?00 | ??00000102    | 1000110200 | 1211101001 |
| <i>miniatus</i>          | 1110????11 | 0001000?01 | ??10000102    | 1000110200 | 02?1101000 |
| <i>obscurus</i>          | 1110????11 | 0100000?00 | ??00000102    | 1000110200 | 0201101010 |
| <i>grossus</i>           | 1111000?11 | 0000000?00 | ??00000102    | 1000110200 | 00??101000 |
| <i>coracinus</i>         | 1100????11 | 0001000?00 | ??10000102    | 1000110200 | 0200101000 |
| <i>fucosus</i>           | 1111100?11 | 0101000?00 | ??10000102    | 1001?10200 | 00??10102? |

## APPENDIX 4

(Continued)

|                                   | Character   |             |            |            |            |
|-----------------------------------|-------------|-------------|------------|------------|------------|
|                                   | 51          | 61          | 71         | 81         | 91         |
| <b><i>Kiefferiella</i></b>        |             |             |            |            |            |
| n.sp. 1                           | 11110000000 | 11110000110 | 0200001320 | 1320042100 | 1103100000 |
| n.sp. 2                           | 011010?000  | 11110000110 | 0200p01331 | 5340042100 | 1101100100 |
| <b><i>Paramblynotus</i></b>       |             |             |            |            |            |
| <b><i>virginianus</i> group</b>   |             |             |            |            |            |
| <i>virginianus</i>                | 11110000001 | 01111?0112  | 0100211321 | 1340032101 | 1001100100 |
| <b><i>scaber</i> group</b>        |             |             |            |            |            |
| <i>scaber</i>                     | 11111000000 | 01111100111 | 0100221111 | 0670032101 | 1101100203 |
| <i>belizini</i>                   | ?1100?0000  | 01111?0113  | 0100221321 | 0340032101 | 10010002?3 |
| <i>atratus</i>                    | 01110000000 | 01111?0111  | 0100211321 | 1340030100 | 1001100203 |
| <i>irkutskensis</i>               | 01110000000 | 01111?0111  | 0100211320 | 0320002000 | 1001100204 |
| <i>marginatus</i>                 | 01111000000 | 0111?0111   | 0100221321 | 0340032000 | 1001100210 |
| <i>pausatus</i>                   | 11110000000 | 011???0011  | 0100221321 | 0340022000 | 1001110113 |
| <i>promus</i>                     | 11110000000 | 01111?0111  | 0100201321 | 0340022100 | 1001100110 |
| <i>liaoi</i>                      | 11110000010 | 01111?0111  | 0100201331 | 0440?22100 | 10012002?3 |
| <b><i>yangambicolus</i> group</b> |             |             |            |            |            |
| <i>mixtus</i>                     | 111101?0000 | 00111?0111  | 0?00101320 | 43400??10? | 1001431103 |
| <i>yangambicolus</i>              | 00102??012  | 00010?0111  | 0200002312 | 5330020311 | 1021440203 |
| <i>alveolatus</i>                 | 10102??022  | 00010?0111  | 0200001302 | 5330?20311 | 1001441203 |
| <b><i>trisetosus</i> group</b>    |             |             |            |            |            |
| <i>prinsloo</i>                   | 11110010010 | 01111?0112  | 0100204300 | 11200?0100 | 1031100101 |
| <i>nigricornis</i>                | ?110010001  | 01111?0111  | 0100101321 | 0370032100 | 1011100103 |
| <i>samiatus</i>                   | 11110000002 | 01111?0113  | 0100121321 | 0370?32102 | 1011000003 |
| <i>claripennis</i>                | 01110000012 | 00111?0113  | 0???221321 | 0370002100 | 1113100103 |
| <i>maculipennis</i>               | 11110000002 | 01111?0111  | 0100201311 | 03700???0? | 10?2201103 |
| <i>townesorum</i>                 | 11110000112 | 00111?0113  | 0100101311 | 2370002112 | 1011101203 |
| <i>femoratus</i>                  | 11111010000 | 01111?0001  | 1100201320 | 1340030110 | 1021000103 |
| <i>fuscicapillus</i>              | 11111010000 | 01111?0001  | 0100201331 | 1340000110 | 1011000103 |
| <i>rwandensis</i>                 | 11111010000 | 11111?0001  | 0100101331 | 1340030110 | 1001000103 |
| <i>trisetosus</i>                 | 11111010000 | 00111?0001  | 0100101320 | 0340000100 | 1021000103 |
| <i>zairensis</i>                  | 11111000000 | 00111?0001  | 0100101320 | 0340000110 | 1021000103 |
| <i>cameroonensis</i>              | 11111010002 | 00111?0001  | 0100101300 | 0340030110 | 1021000103 |
| <i>kekenboschi</i>                | 11111010001 | 00111?0001  | 0100201331 | 03400????? | 1021000103 |
| <i>jacksoni</i>                   | ?111010000  | 1011110001  | 0100101330 | 03400321p0 | 102100010? |
| <i>carinatus</i>                  | 11111010100 | ??111?0001  | 0100101330 | 13400?0110 | 1021000113 |
| <i>immaculatus</i>                | 01111?0000  | 0111??1114  | 0100101320 | 0370030110 | 1021200302 |
| <i>antistatus</i>                 | 01111?0000  | 01111?0113  | 0100100000 | 3210000110 | 1021000302 |
| <i>scalptus</i>                   | 11111?0000  | 01111?1114  | 0100102200 | 3340002110 | 1011000303 |
| <i>vannoorti</i>                  | ?1111?0000  | 01111?1114  | 0100120000 | 3810000110 | 1021040303 |
| <i>diminutus</i>                  | 11111000000 | ?????11??4  | 0100000000 | 3810??011? | 1001000300 |
| <i>angolensis</i>                 | 11111?0000  | 01111?1114  | 01??100000 | 381000?100 | 1001000300 |
| <i>minutus</i>                    | ?1111?0000  | 01111?111?  | 0100112030 | 2810002100 | 1001240300 |
| <b><i>apeosus</i> group</b>       |             |             |            |            |            |
| <i>apeosus</i>                    | 111100?0000 | 0?111?1001  | 0100201320 | 142300?002 | 2001300103 |
| <i>friatus</i>                    | 11110010000 | 00111?1001  | 0100201320 | 0443000002 | 2011300113 |
| <b><i>ruficollis</i> group</b>    |             |             |            |            |            |
| <i>malayensis</i>                 | 010?011012  | 00111??011  | 0100101220 | 0420?30110 | 2001100013 |
| <i>badius</i>                     | 11110000012 | 00111?0111  | 0100201320 | 1730030110 | 2011111003 |
| <i>coruscus</i>                   | 11000?1012  | 0011100111  | 0000203200 | 1451p31110 | 10301100?3 |
| <i>carinivertex</i>               | 11000000011 | 00111?0113  | 0000101230 | 0752000000 | 2001000003 |
| <i>trisectus</i>                  | 1100012112  | 0011100111  | 0100101321 | 0750030100 | 1011000013 |



APPENDIX 4  
(Continued)

|                                 | Character  |             |            |            |            |
|---------------------------------|------------|-------------|------------|------------|------------|
|                                 | 51         | 61          | 71         | 81         | 91         |
| <i>ruficollis</i>               | 1100012022 | 00111100011 | 0000004000 | 0100021110 | 1001001013 |
| <i>braziliensis</i>             | 1100011121 | 01111100110 | 0000201300 | 0330120100 | 1001000003 |
| <i>costaricanus</i>             | 1100011121 | 01111?0110  | 0000202300 | 0330120110 | 1201000003 |
| <i>zonatus</i>                  | 1100011121 | 0p111?0110  | 0000202300 | 0330120110 | 1001000003 |
| <b><i>punctulatus</i> group</b> |            |             |            |            |            |
| <i>conspiratus</i>              | 1111011112 | 00111?0011  | 0100201331 | 1343000012 | 2301000113 |
| <i>reticulatus</i>              | 1110012112 | 0011110001  | 0100201320 | 0440030110 | 2011000113 |
| <i>clarus</i>                   | 1110012110 | 00111?0001  | 0100201431 | 2440031210 | 1011000113 |
| <i>formosanus</i>               | 1110012122 | 00111?0001  | 0100201321 | 24700?001? | 2011000010 |
| <i>nipponensis</i>              | 1110012012 | 00111?0001  | 0100101332 | 0420030110 | 2011000100 |
| <i>punctulatus</i>              | 1110012112 | 00111?0001  | 0100101331 | 1440030110 | 2021000110 |
| <i>isolatus</i>                 | 1111011112 | 00111?0001  | 0100101300 | 0440030110 | 2011000110 |
| <i>mitocephalus</i>             | 1110012122 | 00111?0000  | 0100101301 | 0440010110 | 1011000110 |
| <i>ornatus</i>                  | 1110012122 | 00111?0000  | 010010230p | 0440030010 | 1011000110 |
| <i>cheni</i>                    | 1110011112 | 01111?0001  | 0100201330 | 1340010110 | 1021200110 |
| <i>hainanensis</i>              | 1110011112 | 01???10??1  | 0100101330 | 1440?30110 | 2021000110 |
| <i>amulicornis</i>              | 1110012112 | 0111110011  | 0100101320 | 0320030110 | 1021000110 |
| <i>barbari</i>                  | 1110012102 | 01111?0111  | 0100201321 | 1330030110 | 1021000110 |
| <i>stigi</i>                    | 1110011112 | 0111110011  | 0100101330 | 1420030110 | 1021000110 |
| <i>shimenensis</i>              | 1110012112 | 01111?0001  | 0100001301 | 0320030110 | 1021000110 |
| <i>glaberus</i>                 | 1110012112 | 01111?0001  | 0100001300 | 0320030110 | 1021000110 |
| <i>yuani</i>                    | 1110012112 | 01111?0001  | 0100001300 | 2340030110 | 1021000110 |
| <i>weiae</i>                    | 1110012112 | 01111?0001  | 0100101331 | 03200?01?  | 1021000110 |
| <i>eriki</i>                    | 1110012112 | 11111?0001  | 0100101330 | 1420030110 | 1021000110 |
| <i>asae</i>                     | 1111011112 | 01111?0001  | 0100001330 | 1440010110 | 1021000110 |
| <i>filippae</i>                 | ?110012112 | 01111?0001  | 0100101320 | 0340030110 | 1021000100 |
| <i>ebbae</i>                    | ?110012122 | 00111?0001  | 0100101330 | 0440030110 | 1021000100 |
| <i>axeli</i>                    | 1110012112 | 01???1???1  | 0100101300 | 0430?30110 | 1021000110 |
| <i>ruficeps</i>                 | 1110012112 | 0011110001  | 0100201020 | 0420000011 | 2011000113 |
| <i>pubifemoratus</i>            | 1111012112 | 00111?0001  | 0100201230 | 0420010010 | 2001000113 |
| <i>chrysochaites</i>            | 1110002122 | 00111?0110  | 0000203320 | 0420020010 | 2001111013 |
| <i>rufipes</i>                  | 1110011122 | 00111?0110  | 0000203330 | 1220020010 | 2001111003 |
| <i>lutepennis</i>               | 1111112122 | 0011?00000  | 0111201331 | 1453000011 | 2001000113 |
| <i>nebulosus</i>                | 1110012102 | 01111?0001  | 0111201331 | 0453000012 | 2q01000113 |
| <i>dyak</i>                     | 1110012112 | 00111?0001  | 0110201331 | 0453000101 | 2301000113 |
| <i>beckeri</i>                  | 1110012112 | 00111?0001  | 0110201331 | 0353000110 | 2301000112 |
| <i>venoforticulus</i>           | ?1100?2??2 | 00111?0001  | 0110201331 | 1483000102 | 20010001?0 |
| <i>distinctus</i>               | 1110012112 | 00111?0011  | 0?10201430 | 0453000110 | 2001000110 |
| <i>fraxinii</i>                 | 1110012112 | 00111?0000  | 0100201330 | 0443000112 | 2001000010 |
| <i>kosugii</i>                  | 1110012112 | 00111?0001  | 0100211331 | 0443?00110 | 2001000012 |
| <i>borneanus</i>                | 11100120?2 | 00111?0001  | 0110201331 | 0453?00112 | 2301000113 |
| <i>aptatus</i>                  | ?110012112 | 00???1???1  | 0110201320 | 0443?00000 | 2001000113 |
| <i>kitrinocarus</i>             | 1110012112 | 00111?0010  | 0110201330 | 1450000101 | 2001000113 |
| <i>insolitus</i>                | 1110012112 | 01111?0003  | 0?10204000 | 0400000000 | 2001000113 |
| <i>robustus</i>                 | 1110012112 | 00111?0001  | 0?10201331 | 1453030010 | 2001000110 |
| <i>miniatus</i>                 | 0111012112 | 00111?0001  | 0110201321 | 04530?0000 | 2001000110 |
| <i>obscurus</i>                 | 1111012112 | 0011100001  | 0110201331 | 0453000010 | 2001000112 |
| <i>grossus</i>                  | 1111002112 | 01111?0001  | 0?10201332 | 1353000012 | 1101000110 |
| <i>coracinus</i>                | 1111012112 | 01111?0011  | 0110201331 | 0353000012 | 2301000110 |
| <i>focosus</i>                  | 111?012112 | 01111?0001  | 0110221211 | 0603000010 | 2001000??0 |

APPENDIX 4  
(Continued)

|                            | Character  |             |            |     |
|----------------------------|------------|-------------|------------|-----|
|                            | 101        | 111         | 121        | 131 |
| <i>Kiefferiella</i>        |            |             |            |     |
| n.sp. 1                    | 1100000000 | ?000000000  | 0000100011 | 01  |
| n.sp. 2                    | 1000000000 | ?000000000  | 0000110110 | 01  |
| <i>Paramblynotus</i>       |            |             |            |     |
| <i>virginianus</i> group   |            |             |            |     |
| <i>virginianus</i>         | 11000000?0 | ?000000000  | 0000100010 | 20  |
| <i>scaber</i> group        |            |             |            |     |
| <i>scaber</i>              | 2000000000 | ?000000000  | 0000101110 | 20  |
| <i>belizini</i>            | ??000000?0 | ?000000000  | 0000100110 | 20  |
| <i>atratus</i>             | 10000000?0 | ?000000000  | 0000100110 | 00  |
| <i>irkutskensis</i>        | 10000000?0 | ?000000000  | 0000100110 | 00  |
| <i>marginatus</i>          | 11000000?0 | ?000000000  | 0000100100 | 00  |
| <i>pausatus</i>            | 11000000?0 | ?000000000  | 0000100110 | 00  |
| <i>pronus</i>              | 11000000?0 | ?000000000  | 0000100100 | 00  |
| <i>liaoi</i>               | 11000010?0 | ?000000000  | 0000100100 | 20  |
| <i>yangambicolus</i> group |            |             |            |     |
| <i>mixtus</i>              | 10000010?0 | ?000000000  | 0000111121 | 11  |
| <i>yangambicolus</i>       | 11000000?0 | ?000002010  | 0100111120 | 00  |
| <i>alveolatus</i>          | 11000000?1 | ?000002010  | 010011?120 | 00  |
| <i>trisetosus</i> group    |            |             |            |     |
| <i>prinslooii</i>          | 21010000?0 | ?000000000  | 0102101010 | 00  |
| <i>nigricornis</i>         | 20000010?0 | ?000000000  | 0000101110 | 20  |
| <i>samiatus</i>            | ??000000?0 | ?000000010  | 0000111012 | 00  |
| <i>claripennis</i>         | 20000010?0 | ?000000000  | 01001011?0 | 20  |
| <i>maculipennis</i>        | 20000010?0 | ?000000010  | 0100101000 | 00  |
| <i>townesorum</i>          | 20000010?0 | ?000000010  | 0100101110 | 00  |
| <i>femoratus</i>           | 21000010?0 | ?010000000  | 0002101112 | 00  |
| <i>fuscapiculus</i>        | 11000010?0 | ?010000000  | 0002101100 | 00  |
| <i>rwandensis</i>          | 20100010?0 | ?101100000  | 0002100112 | 00  |
| <i>trisetosus</i>          | 11000010?1 | ?0?0000000  | 0003101112 | 00  |
| <i>zairensis</i>           | 11000010?0 | ?0111110000 | 1103101112 | 20  |
| <i>cameroonensis</i>       | 11000010?0 | ?020000000  | 0003101112 | 20  |
| <i>kekenboschi</i>         | 21000010?0 | ?000000000  | 0003101112 | 00  |
| <i>jacksoni</i>            | 2100001000 | ?000000000  | 0003101112 | 20  |
| <i>carinatus</i>           | 21000010?0 | ?000000000  | 0003101110 | 00  |
| <i>immaculatus</i>         | 11000010?0 | ?000000000  | 0000011111 | 11  |
| <i>antistatus</i>          | 11000010?0 | ?0000003?0  | 0000001011 | 11  |
| <i>scalptus</i>            | 11000010?0 | ?0000003?0  | 0000001011 | 11  |
| <i>vannoorti</i>           | 11000010?0 | ?0100003?0  | 0000001011 | 11  |
| <i>diminutus</i>           | 110000100? | ?0000001?0  | 00000??01? | ??  |
| <i>angolensis</i>          | 11000010?0 | ?0100003?0  | 00000110?1 | 11  |
| <i>minutus</i>             | 21000000?0 | ?0100003?0  | 0000011011 | 11  |
| <i>apeosus</i> group       |            |             |            |     |
| <i>apeosus</i>             | 21000000?0 | ?000000000  | 0000100102 | 00  |
| <i>friatus</i>             | 21000000?0 | ?000000000  | 0000100102 | 00  |
| <i>ruficollis</i> group    |            |             |            |     |
| <i>malayensis</i>          | 11000011?1 | ?000000000  | 0002100100 | 20  |
| <i>badius</i>              | 11100110?1 | ?000000020  | 0000110102 | 20  |
| <i>coruscus</i>            | 1110011010 | ?000000000  | 0001110100 | 20  |
| <i>carinivertex</i>        | 00100110?1 | ?000000010  | 0000100002 | 20  |
| <i>trisectus</i>           | 1100011011 | ?0011p0000  | 0000100102 | 20  |

APPENDIX 4  
(Continued)

|                          | Character  |            |            |     |
|--------------------------|------------|------------|------------|-----|
|                          | 101        | 111        | 121        | 131 |
| <i>ruficollis</i>        | 1100011112 | 1101000000 | 0000110102 | 20  |
| <i>braziliensis</i>      | 1101111011 | ?12p000041 | 0003110102 | 20  |
| <i>costaricanus</i>      | 10011110?1 | ?121000041 | 1003110103 | 20  |
| <i>zonatus</i>           | 10011110?1 | ?121000041 | 1003110002 | 20  |
| <b>punctulatus group</b> |            |            |            |     |
| <i>conspiratus</i>       | 11000010?0 | ?000000000 | 0000100002 | 00  |
| <i>reticulatus</i>       | 1100001000 | ?0000004?0 | 0000100113 | 00  |
| <i>clarus</i>            | 11010110?0 | ?001100000 | 0003100112 | 00  |
| <i>formosanus</i>        | 11010011?0 | ?000000020 | 0103100100 | 00  |
| <i>nipponensis</i>       | 11000010?0 | ?000000000 | 0000100113 | 00  |
| <i>punctulatus</i>       | 11000010?0 | ?000000000 | 0p00100102 | 20  |
| <i>isolatus</i>          | 11000010?0 | ?000000000 | 0000100102 | 20  |
| <i>mitocephalus</i>      | 11000000?0 | ?10000?1?? | 0000110102 | 20  |
| <i>ornatus</i>           | 11000000?0 | ?1011132?0 | 11031101?2 | 20  |
| <i>cheni</i>             | 11000000?0 | ?000000000 | 0000100112 | 00  |
| <i>hainanensis</i>       | 110101100? | ?000000031 | 00001??10? | ??  |
| <i>annulicornis</i>      | 1101001000 | ?101110030 | 1103100012 | 00  |
| <i>barbarae</i>          | 21000010?0 | ?131110030 | 1103100112 | 01  |
| <i>stigi</i>             | 2100001000 | ?131110031 | 1103100112 | 00  |
| <i>shimenensis</i>       | 11000010?0 | ?101110031 | 1103100112 | 00  |
| <i>glaberus</i>          | 11000010?0 | ?131110031 | 1103100112 | 01  |
| <i>yuani</i>             | 11000010?0 | ?131110030 | 1103100112 | 00  |
| <i>weiae</i>             | 11000000?0 | ?131110031 | 1103100100 | 00  |
| <i>eriki</i>             | 11000010?0 | ?131110031 | 1103100112 | 01  |
| <i>asae</i>              | 11000010?0 | ?131110031 | 1103100112 | 00  |
| <i>filippae</i>          | 11000010?0 | ?131110031 | 1103100102 | 00  |
| <i>ebbae</i>             | 11000010?0 | ?131110031 | 1103100112 | 00  |
| <i>axeli</i>             | 110000100? | ?131110030 | 10031??11? | ??  |
| <i>ruficeps</i>          | 1100001000 | ?101110010 | 1103100112 | 00  |
| <i>pubifemoratus</i>     | 11110111?0 | ?000000000 | 0014100112 | 20  |
| <i>chrysochaites</i>     | 11110111?2 | 2000000000 | 0011100120 | 00  |
| <i>rufipes</i>           | 11110111?2 | 2000000000 | 0011110120 | 00  |
| <i>lutepennis</i>        | 11110110?2 | ?000003000 | 0010110112 | 00  |
| <i>nebulosus</i>         | 11110110?1 | ?0000032?0 | 0000100112 | 00  |
| <i>dyak</i>              | 11110110?2 | 0000000000 | 0002100112 | 00  |
| <i>beckeri</i>           | 11110110?2 | 0000000000 | 0001100113 | 00  |
| <i>venoforticulus</i>    | ??110110?1 | ?000000020 | 0002100102 | 00  |
| <i>distinctus</i>        | 11110110?1 | ?101110000 | 1101100112 | 00  |
| <i>fraxinii</i>          | 11000110?0 | ?000000000 | 0102100100 | 00  |
| <i>kosugii</i>           | 11000100?1 | ?000000000 | 010210010? | ??  |
| <i>borneanus</i>         | 11110100?1 | ?000000000 | 0102100112 | 20  |
| <i>aptatus</i>           | 110101101? | ?000000000 | 000010?11? | ??  |
| <i>kitrinocarus</i>      | ??010110?1 | ?100003000 | 0000100112 | 00  |
| <i>insolitus</i>         | 11110110?1 | ?000000000 | 0010100112 | 00  |
| <i>robustus</i>          | 11110110?1 | ?000000000 | 0000100110 | 00  |
| <i>miniatus</i>          | 21010110?0 | ?020000000 | 0001100112 | 00  |
| <i>obscurus</i>          | 2111011010 | ?000000000 | 0010100110 | 00  |
| <i>grossus</i>           | 11010110?0 | ?000000020 | 0000101112 | 00  |
| <i>coracinus</i>         | 11110110?1 | ?000000000 | 0000100012 | 00  |
| <i>fucosus</i>           | 11110111?1 | ?000000000 | 0000100112 | 00  |

## APPENDIX 5

## LIST OF ABBREVIATIONS USED IN FIGURES 5-8

|     |                                    |     |                                    |
|-----|------------------------------------|-----|------------------------------------|
| aas | anteroadmedian signum              | mes | metepisternum                      |
| afo | antennal foramen                   | mfc | median frontal carina              |
| ap  | anterior plate of pronotum         | mi  | mesopleural impression             |
| as  | antennal scrobe                    | mmi | median mesoscutal impression       |
| au  | auricula                           | mpc | metapleural carina                 |
| ax  | axilla                             | mps | metapleural sulcus                 |
| cl  | clypeus                            | mpt | mesopleural triangle               |
| d   | depression beneath eye             | ms  | malar space                        |
| do  | dorsellum                          | msc | mesoscutum                         |
| em  | metepimeron                        | not | notaulus                           |
| g   | gena                               | op  | ocellar plate                      |
| Ib  | lateral bar                        | p   | process from median frontal carina |
| Ic  | lateroventral carina of mesopectus | pa  | prespiracular area                 |
| Id  | lateral depression of dorsellum    | pc  | pronotal crest                     |
| Idp | laterodorsal process of scutellum  | pi  | parascutal impression              |
| If  | lower face                         | ppp | posteroateral propodeal process    |
| Ifc | lateral frontal carina             | ps  | parapsidal signum                  |
| Inc | lateral pronotal carina            | psc | parascutal carina                  |
| Ip  | lower pleuron                      | psp | postsubpleuron                     |
| Ipa | lateral propodeal area             | sc  | scutellum                          |
| Ipc | lateral propodeal carina           | scf | scutellar fovea                    |
| Is  | lateral surface of pronotum        | sd  | submedian depression of pronotum   |
| md  | mandible                           | sp  | speculum                           |
|     |                                    | teg | tegula                             |
|     |                                    | up  | upper pleuron                      |
|     |                                    | vx  | vertex                             |



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