Contribution to knowledge of the cockroach subfamilies Paranauphoetinae (stat. n.), Perisphaeriinae and Panesthiinae (Dictyoptera: Blaberidae)

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The systematic position and phylogeny of the subfamilies Perisphaeriinae and Panesthiinae, and the genus *Paranauphoeta* Brunn. are discussed. The tribe Paranauphoetini Rehn, 1951 is raised in rank to subfamily. The genera *Paranauphoeta*, *Trichoblatta* Sauss. & Zehn., *Glomerexis* B.-Bien. and *Perisphaerus* Serv. are rediagnosed. A new species, *T. beybienkoi* sp. n., and a new subspecies, *Paranauphoeta vicina vietnamensis* ssp. n., are described. For *T. valida* B.-Bien., *Perisphaerus semilunatus* Han. and *P. punctatus* B.-Bien., the male is described for the first time. For *Paranauphoeta nigra* B.-Bien., *P. vicina* Brunn., *P. visnica* B.-Bien., *P. lyrata* (Burm.), *P. rufipes* Brunn., *P. formosana* Mats., *T. magnifica* (Shelf.), *T. aerea* B.-Bien., *T. fallax* B.-Bien., *T. sculpta* (B.-Bien.), *T. tarsalis* (Walk.), *T. valida*, *T. v. moderata* B.-Bien.), *G. tibetana* B.-Bien., *Perisphaerus semilunatus*, data on the morphology and geographical distribution are given.

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Introduction

This paper is based on the material from the collection of the Zoological Institute, Russian Academy of Sciences. All the material examined, including the types of new taxa, is deposited in the Zoological Institute. For the male genitalia, the author follows the terminology of Grandcolas (1996), but the distal, cap-like part of sclerite L1 (L2d sensu McKittrick, 1964) is termed as apical sclerite L1, and proximal, rod-like part of sclerite L1 (L2vm sensu McKittrick, 1964) is termed as basal sclerite L1 (Fig. 101, *L1 ap, L1 bas*).

The subfamily Panesthiinae will be considered in detail in the next paper.

The methodology by the author is most similar to phylistic approach to taxonomy (Rasnitsyn, 2002).

Family **BLABERIDAE** Brunner von Wattenwyl, 1865

The systematic position and relationships of the subfamilies Perisphaeriinae and Panesthiinae were not investigated since publication of the famous monograph by F.A. McKittrick "Evolutionary Studies of Cockroaches" (1964). In this work, she placed Perisphaeriinae in the Epilamproid complex (along with Epilamprinae) and Panesthiinae, in the Blaberoid complex (along with Blaberinae and Zetoborinae).

The systematic position of the genus *Para-nauphoeta* Brunner von Wattenwyl is unclear. This genus was not mentioned in the study by McKittrick (1964). *Paranauphoeta* undoubtedly belongs to Blaberidae, but its position within the family is still questionable.

The genus Paranauphoeta was described in the family Panesthiidae (Brunner von Wattenwyl, 1865). Subsequently, it was transferred to the subfamily Perisphaeriinae of the family Blattidae (Saussure & Zehntner, 1895; Kirby, 1904; Hanitsch, 1915). These authors included all cockroaches in the family Blattidae. Later, Rehn (1951) described for this genus the monotypical tribe Paranauphoetini, which was placed by him in the subfamily Epilamprinae of Blattidae. Princis (1960, 1964) placed Paranauphoeta in the subfamily Gyninae of the family Perisphaeriidae and considered Paranauphoetini as a synonym of this subfamily. Grandcolas (1996) considered Paranauphoeta in Blaberidae but did not assign it to any tribe and subfamily. Roth (1999) provisionally attributed Paranauphoeta to Perisphaeriinae but did not assign it to any tribe either.



Figs 1-10. 1, cladogram of the subfamilies Perisphaeriinae, Panesthiinae and the genus *Paranauphoeta* (only synapomorphies are indicated); **2**, *Paranauphoeta indica* Sauss. & Zehn.; **3**, **5**, *Trichoblatta magnifica* (Shelf.); **4**, **9**, *Salganea* sp.; **6**, *Paranauphoeta vicina sinica* B.-Bien. (paratype); **7**, *Panesthia angustipennis* Illiger; **8**, *Perisphaerus* sp.; **10**, abdominal tergite of Perisphaeriinae and Panesthiinae from above, schematically. **3**, **8**, **9**, female; **2**, **4**, **5**, male. Lateral part of pronotum from below (2-5); proximal part of tegmen (6) and tegmen (7) from above; lateral part of abdominal tergite from above (8, 9).

Abbreviations: An.a., anal area of tegmina; i.v., incrassate veins of tegmina; l.c., lateral carina of pronotum; or., orifices on abdominal tergites; V, VI, VII, order numbers of abdominal tergites.

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Here, the hypothesis for the phylogeny of Perisphaeriinae, Panesthiinae and *Paranauphoeta* is presented (Fig. 1). I suggest that these taxa represent a monophyletic group. Since the genus *Paranauphoeta* is the sister group for the Perisphaeriinae + Panesthiinae, the rank of Paranauphoetini Rehn, 1951 is raised to subfamily.

There are four synapomorphies common to Paranauphoetinae, Perisphaeriinae and Panesthiinae (Fig. 1).

It is the author's opinion that characters of compound structures, for example, structure of the complex R+N of the male genitalia (Figs 72-77, 80-89), shape of tegmina (Figs 6, 7), structure of surfaces, each may be considered in a cladogram as a single feature, because separate structures of such a complex (for example, sclerites R3d, R2, R3v and N of the complex R+N; see Figs 72, 73, 80-82) are not independent and evidently function as a single whole.

1. The complex of sclerites R+N in the male genitalia is specifically shaped (Figs 72-77, 80-89): sclerite N large, well sclerotized and elongate, parallel to sclerite R2 and usually to R3v; sclerite R3v usually more or less elongate, parallel to R2.

This type of structure of the male genitalia is comparatively stable within the group, but sometimes sclerite R3v is somewhat shortened (Figs 76, 88). Weakening in sclerotization of the male genitalia as a whole is characteristic of many Panesthiinae (Roth, 1977, 1979a, 1979b, 1982). In that case, the complex R+N can be noticeably reduced. Such reduction is undoubtedly a secondary state.

To the author's knowledge, such a structure of R+N is unique within the family Blaberidae.

2. Lateral carinae of the pronotum are situated on lateral margins, which are curved ventrally, and thus, displaced medially [as described for Perisphaeriinae by Shelford (1908)] (Figs 2-5).

This feature is strongly pronounced in some representatives of Perisphaeriinae (Figs 3, 5) and expressed in many Panesthiinae (Fig. 4). Among species of *Paranauphoeta* examined by the author, displaced lateral carinae are visible only in *P. indica* Saussure & Zehntner (Fig. 2).

Displaced lateral carinae of the pronotum were not described for any other taxa of cockroaches.

3. The tegmina are distinctive in shape (Figs 6, 7): their anterior margin more or less projected proximally and narrowed distally, behind the distal end of the anal area (clavus). Several incrassate veins are situated immediately behind the prominent part of tegmina (Figs 6, 7, *i.v.*), constituting a kind of corrugate structure. Anal area of the tegmina is elongate (Figs 6, 7, *An.a.*), with distal angle more or less acute.

This feature was not observed in Perisphaeri-

inae (in the limits of the material examined by the author). In males of Perisphaeriinae, the tegmina have a plesiomorphic structure. The author considers this state a secondary return to the primitive type, probably due to the ephemerization of males. In females, such a state is unknown, because the females of Perisphaeriinae are completely apterous.

The above shape of the tegmina was not described at least in other blaberids.

4. The cerci are one-segmented (Figs 11, 12, 22, 42, 43, 46, 50, 54).

This feature is stable in both sexes of Panesthiinae and Paranauphoetinae; in Perisphaeriinae, it is expressed only in females. In males of Perisphaeriinae, the cerci are of plesiomorphic shape (Figs 45, 48, 49, 53). The author considers this state as a secondary return to the primitive type, probably due to the ephemerization of males.

In *Paranauphoeta*, the cerci retain elongate shape (Figs 11, 12). In several cases, they retain traces of segmentation. These traces are usually present in larvae and are rarely present in imagines. The cerci in both sexes of Panesthiinae and in females of Perisphaeriinae are noticeably shortened (Figs 22, 42, 43, 46, 50, 54). Such structure of the cerci is evidently a synapomorphy of these groups and is presumably correlated with progressive sclerotization of surfaces (see below).

The shortening of cerci is not uncommon for cockroaches, but, as a rule, shortened cerci retain the multisegmented structure. One-segmented cerci are known in several genera of Blattidae (*Archiblatta* Vollenhoven, *Protagonista* Shelford), but these cases result from evident convergence with groups considered in this paper.

According to the proposed cladogram (Fig. 1), the subfamilies Perisphaeriinae and Panesthiinae are sister groups. There are three synapomorphies of Perisphaeriinae and Panesthiinae (features 5-7 in Fig. 1).

5. The tergites, especially those of the abdomen, are strongly sclerotized, thickened and hardened. Abdominal sternites are sclerotized to a lesser extent. The cerci are distinctly shortened, pyramidal (Figs 22, 42, 43, 46, 50, 54).

In males of Perisphaeriinae, thickened surfaces are present only on the pronotum, and the cerci are of plesiomorphic shape (Figs 45, 48, 49, 53). As pointed out above, this state may be considered a secondary reversion to the primitive type, probably due to the ephemerization of males.

Thickened and hardened surfaces are not uncommon in Blaberidae. Such groups as *Placoblatta* Bey-Bienko (Epilamprinae) and *Gromphadorhina* Brunner von Wattenwyl (Oxyhaloinae) are specialized and evidently convergent with Perisphaeriinae and Panesthiinae in structure of surfaces.



Figs 11-22. Genera Paranauphoeta, Trichoblatta, Glomerexis (12-15, 18, 19, female; 16, 17, 20, 21, male; 11, young larva). 11, 18, P. vicina sinica B.-Bien. (paratypes); 12, 17, 20, P. indica Sauss. & Zehn.; 13, T. sculpta (B.-Bien.) (holotype); 14, G. tibetana B.-Bien.; 15, 16, T. beybienkoi sp. n. (paratypes); 19, P. formosana Mats.; 21, P. vicina vietnamensis ssp. n. (paratype). Cercus from above (11, 12); hind metatarsus from side (13-19); head in frontal view (20); paraprocts from behind and somewhat from below (21); abdominal apex from above (22). Dotted area shows membranous parts (13-19, 21) and dark colour (20).

6. Abdominal tergites, usually the 3rd-7th ones, bear a furrow with a row of orifices (Figs 8-10, *or*), probably of glandular nature. This furrow usually runs along anterior and lateral margins of the tergite.

The above orifices are present in most of Perisphaeriinae (only in females; Fig. 8) and in many Panesthiinae (in both sexes; Fig. 9). The absence of these orifices within the two groups considered is evidently a secondary state, because the characteristic shape of tergite is usually retained in Panesthiinae, or represents a secondary reversion to the primitive type in males of Perisphaeriinae.

The considered tergal structure is unknown in any other taxa of cockroaches.

7. Sclerites N, R2 and R3d of the complex R+N of the male genitalia have similar shape and relative position (Figs 80-89).

This type of the complex R+N is comparatively stable in the Perisphaeriinae (Figs 81-89). In Panesthiinae, such structure can be modified due to not infrequent reduction of the male genitalia as a whole.

Such type of the complex R+N is unique for Perisphaeriinae and Panesthiinae.

Subfamily **PARANAUPHOETINAE** J.W.H. Rehn, 1951, stat. n.

Diagnosis. Sexual dimorphism not expressed, males and females with tegmina and wings fully developed. Cerci one-segmented, elongate (Figs 11-12). Male paraprocts typical for Blaberidae, asymmetrical; right paraproct with tooth-like projection (Fig. 21). Male genitalia with apical sclerite L1 cap-like with more or less expressed elongate projection (Figs 90-100); complex of sclerites R+N with a distinct hollow in point of junction of sclerites R2 and N (Figs 72-77).

As autapomorphies of Paranauphoetinae are considered here the following distinctive features of the male genitalia: presence of elongate processus on apical sclerite L1, hollow in point of junction of sclerites R2 and N of complex R+N.

Description. General colour, as a rule, with bright and contrasting pattern. Surfaces more or less smooth, not thickened or hardened by strong sclerotization. Head with comparatively wide interval between eyes (Fig. 20); facial part of head without any impression. Pronotum with truncate caudal margin (Figs 34, 35, 58, 59). Fore femur with one small apical spine or without such a spine; lower inner margin of fore femur, as a rule, unarmed or with small fringe of setae in proximal part. Hind metatarsus as long as or slightly longer than following segments combined. Metatarsal pulvilla of hind legs small subapical or larger (Fig. 19; estimation of precise size of pulvilla in dried specimens often difficult). Armament along lower margin of metatarsus varying from a single row of spines (Fig. 18) to a complete absence of these (Fig. 17); number of metatarsal spines relatively unstable within species. Arolium small. Anal plate more or less rounded, without caudal emargination; hypandrium asymmetrical, caudally prominent, styli present (Figs 66-69).

Male genitalia. Apical sclerite L1 without bristles but sometimes with spines (Figs 90, 91, 98); basal sclerite L1 simple, rod-like; sclerite L2d with median incision (Figs 126-132); sclerite L3d present (Fig. 126); complex of sclerites R+N (Figs 72-77): R3d comparatively elevated and rounded, R2 most sclerotized, R3v more or less elongate, rod-like or sometimes three-radial (*P. nigra*, Fig. 72), N usually well sclerotized.

Included genera. Only the type genus.

Genus **Paranauphoeta** Brunner von Wattenvyl, 1865

Type species: *Blatta/Nauphoeta circumdata* de Haan, 1842.

Diagnosis. Same as for subfamily.

Description. A detailed redescription of the genus was given by Roth (1989).

Included species. Those included by Princis (1964, 1971).

Paranauphoeta nigra Bey-Bienko, 1969 (Figs 34, 72, 90, 91, 130, 131)

Holotype. J, China, prov. Yunnan, env. of Yuili, 1300-1450 m, 8.VI.1956 (Chow Peng-show).

Paratype. 1 of, with same data as in holotype.

Description. Coloration uniform and dark, unusual for genus; colour blackish, with narrow yellow stripes on lateral sides of pronotum (Fig. 34) and small yellow spots at base of tegminal *R*. Fore femur with a small apical spine, without spines on lower inner margin; hind metatarsus with a few spines.

Male genitalia. Apical sclerite L1 strongly sclerotized, with several spines and comparatively weakly expressed projection (Figs 90, 91); L2d as in Figs 130, 131; complex of sclerites R+N as in Fig. 72, R3v three-radial in shape.

Length (mm): head 3.2-3.3 (3.2); pronotum 4-4.5 (4); tegmina 18-21 (21). Width (mm): head 3.2-3.3 (3.3); pronotum 5.6-6.1 (5.6). Measurements in parentheses are those of holotype.

Paranauphoeta indica Saussure & Zehntner, 1895 (Figs 2, 12, 17, 20, 68, 73, 92, 93, 132)

Material. India, Assam: 1 or, river Zizi, near Merigoon, 22.II.1902 (von Wick). China, prov. Yunnan: 1 9, Xiao Menle, 850 m, 7.V.1957 (Liang Tsiu-chen). Vietnam,



Figs 23-41. Genera Trichoblatta, Perisphaerus, Glomerexis and Paranauphoeta (25-28, 33, 37, 41, female; 23, 24, 29-32, 34, 35, 38-40, male). 23-26, 40, 41, T. magnifica (Shelf.); 27-30, 38, T. beybienkoi sp. n. (27, 28, holotype; 29, 30, 38, paratype); 31, 39, Perisphaerus semilunatus Han.; 32, T. valida B.-Bien.; 33, T. tarsalis (Walk.); 34, Paranauphoeta nigra B.-Bien. (paratype); 35, Paranauphoeta vicina vietnamensis subsp. n. (holotype); 36, Paranauphoeta vicina sinica B.-Bien. (paratype); 37, G. tibetana B.-Bien. Pronotum from above (23, 25, 27, 29, 31-35) and from side (24, 26, 28, 30); preanal part of wing (36); head in frontal view (38-41). Dotted area shows dark colour (34, 35, 36).

prov. Bac Hai: 1 ♀, NO of Thai Nguen, 19.III.1962 (O. Kabakov); 2 ♂, 2 ♀, same data, but 5-12.III.1963; *prov. Vinh Phu*: 1 ♀, Tamdao, VIII.1963 (O. Kabakov); *prov. Lang Son*: 1 ♀, Bac Son, 400-600 m, 19.I.1964 (O. Kabakov).

Description. Size large for genus. Colour lighter and more contrasting than in *P. nigra*; pronotum with yellow stripes; tegmina with yellow *C* and two large yellow spots in proximal part of anal area. Armament of fore femora similar to that in *P. nigra*; hind metatarsus without spines (Fig. 17).

Male genitalia. Apical sclerite L1 larger than in *P. nigra*, projection weakly expressed (Figs 92, 93); L2d with more angular apex (Fig. 132) as compared with *P. nigra*; complex of sclerites R+N as in Fig. 73, R3v comparatively elongate, subtriangular.

Length (mm): head of 4.4-4.5, $\[mathcal{Q} 4.5-5;\]$ pronotum of 6-6.3, $\[mathcal{Q} 6.3-6.9;\]$ tegmina of 22-23, $\[mathcal{Q} 25-27.\]$ Width (mm): head of 4.6-4.7, $\[mathcal{Q} 4.6;\]$ pronotum of 8.5-9.3, $\[mathcal{Q} 9-9.8.\]$

Note. P. indica was described from Assam, India (according to Kirby, 1904).

The shape of apical sclerite L1 in the male genitalia is somewhat distinctive in specimens from Assam (Fig. 92) and Vietnam (Fig. 93). The taxonomic value of these differences needs elucidation in further investigations.

Paranauphoeta vicina vicina Brunner

von Wattenwyl, 1893

Material. Bangladesh: 1 9, "Silhet Assam", "623 12 Indes or m' H. de Sauss.", "No 131-97.", "Paranauphoeta vicina Br. Saussure det.", "Paranauphoeta adjuncta Wl. Bey-Bienko det. 1968".

Description. Contrastingly- and bright-coloured species; pronotum with lateral yellow stripes similar to those in *P. nigra* and *P. indica*; tegmina with six yellow spots (three on each tegmen), yellow *C* and apex of tegmina. Hind metatarsus with a few spines.

Length (mm): head 3.9; pronotum 5.2; tegmina 22.5. Width (mm): head 4; pronotum 8.3.

Note. The single female in the collection of Zoological Institute, St.Petersburg, was labelled by Bey-Bienko as *P. adjuncta* Walker, 1868. *P. vicina* was described from Burma (Palon, Pegu), whereas *P. adjuncta* was described from Cambodia by Walker (1868).

The holotype of *P. adjuncta* is damaged (the abdomen is missing: see Princis, 1958) and, therefore, the status of this species is still questionable.

Paranauphoeta vicina sinica Bey-Bienko, 1957 (Figs 6, 11, 18, 36, 67, 77, 100)

Holotype. 9, China, prov. Yunnan, 50 km SW of Mokiang, 1200 m, 1.IV.1955 (O. Kryzhanovskij et al.).

Paratypes. China, prov. Yunnan: 6 9, 6 °, 14 larvae, with same data as in holotype; 1 °, env. of Kingtun, 29.V.1956 (O. Kryzhanovskij); 1 °, 2 9, same data, but 13.III.1957 (D. Panfilov); 1 larva, Santaishan Mt., 30 km SW of Luxi, 1200 m, 18.V.1955 (O. Kryzhanovskij); 1 larva, env. of Kingtun, Wuliangshan, 1700 m, 20.III.1957 (D. Panfilov); 1 larva, env. of Simao, 1500 m, 11.IV.1955 (O. Kryzhanovskij); 1 9, env. of Cheli, Shikuyao, 700 m, 26.IV.1957 (D. Panfilov); 1 °, Kinku, 1120-1200 m, 13.V.1957 (Hun Kuan-chi).

Description. Similar to nominotypical subspecies, differs from this in smaller size, shorter tegmina and some details of coloration (Bey-Bienko, 1958). Hind metatarsus with a single row of spines (Fig. 18).

Male genitalia. Apical sclerite L1 with wellexpressed processus (Fig. 100), without spines; L2d similar to that of *P. indica*; complex of sclerites R+N with R3v elongate (Fig. 77).

Length (mm): head σ 3.4-3.5, φ 3.2-3.7 (3.5); pronotum σ 4.1-4.5, φ 4.2-5 (4.6); tegmina σ 17-18, φ 17-20 (19). Width (mm): head σ 33-36, φ 3.3-3.6 (3.5); pronotum σ 6.3-6.7, φ 6.4-7.4 (6.9). Measurements in parentheses are those of holotype.

Note. Several specimens of *P. vicina sinica* in the collection of Zoological Institute, St.Petersburg, were redetermined by Bey-Bienko as *P. adjuncta*. The relationships of these species are unclear (see above).

Paranauphoeta vicina vietnamensis ssp. n. (Figs 21, 35, 78, 79, 94, 95, 126)

Holotype. o, Vietnam, prov. Gia Lai, 20 km N of Kannack, env. of Buon Luoi, 7.XI.1993 (A. Gorochov). Paratype. 1 o, Vietnam, prov. Dac Lac, Nature Re-

serve Yok Don, 23-28.XI.1993 (A. Gorochov). Description. Male (holotype). Similar to P. vicina sinica in appearance, but differs in structure of male genitalia: apical sclerite L1 large, elongate, strongly sclerotized, without bristles and additional sclerite (Figs 94, 95); sclerite L2d similar to that of P. indica, but its apex more rounded (Fig. 126); complex of sclerites R+N comparatively weakly sclerotized (damaged in holotype, Fig. 78): R3d widely rounded, R2 almost uncurved, R3v rod-like and weakly sclerotized (Fig. 79), N weakly sclerotized.

Variation. In paratype, genitalia less sclerotized.

Female unknown.

Length (mm): head 3.8-4 (3.8); pronotum 5 (5); tegmina 22 (22). Width (mm): head 3.9-4 (3.9); pronotum 7.9-8.3 (7.9). Measurements in parentheses are those of holotype.

Comparison. The new subspecies is the closest to *P. v. sinica*, differs from the latter in the much more elongate processus of apical sclerite L1 of the male genitalia (Figs 94, 95). The female of the nominotypical subspecies differs



Figs 42-57. Genera *Trichoblatta* and *Perisphaerus* (42, 43, 46, 50, 54, 55, 57, female; 44, 45, 47, 48, 49, 51-53, 56, male). **42-45**, *T. magnifica* (Shelf.); **46-48**, *T. beybienkoi* sp. n. (46, holotype; 47, 48, paratype); **49-51**, *T. aerea* (B. Bien.) (50, holotype; 49, 51, paratype); **52**, *T. semisulcata* (Han.); **53**, *T. fallax* B.-Bien. (paratype); **54**, *T. sculpta* (B. Bien.) (holotype); **55**, *T. tarsalis* (Walk.); **56**, *P. punctatus* B.-Bien.; **57**, *P. semilunatus* Han. Abdominal apex from below (42) and from above (43, 45, 46, 48-50, 53-55); hypandrium from below (44, 47, 51, 52, 56); anal plate from above (57). Dotted area shows dark colour.

from males of the new subspecies in the darker coloration and complete absence of lateral light spots on abdominal sternites. Unfortunately, structure of the male genitalia in the nominotypical subspecies is still undescribed.

Paranauphoeta lyrata (Burmeister, 1838) (Figs 59, 69, 75, 98, 127)

Material. Malaysia: 2 °, "Rolle 1904", "Kelanton [State Kelantan – L.A.]", "Paranauphoeta lyrata de Haan", "R. Shelford det."; 1 9, "Kina-Balu-Geb. 1500 m Coll. Waterstradt", "Paranauphoeta lyrata De H.", "R. Shelford det.". Indonesia, Java: 1 9, "No 131 – 97.", "Java", "Paranauphoeta lyrata Burm.", "Saussure det."; Sumatra: 1 9, "K. Baley Sumatra John", "Paranauphoeta lyrata Burm", "R. Shelford det.". Borneo: 1 9, "Paranauph. lyrata Bur. Borneo. Staudinger", "Paranauphoeta lyrata de Haan. R. Shelford det.".

Description. Similar to *P. vicina*, but readily differs in colour pattern of pronotum (Fig. 59). Coloration of nymphs strongly different from that of imago (Roth, 1999). Hind metatarsus usually with a single row of spines.

Male genitalia. Apical sclerite L1 comparatively weakly sclerotized, with several spines on adjacent membrane (Fig. 98); L2d as in Fig. 127; complex of sclerites R+N as in Fig. 75, R3v comparatively short and weakly sclerotized.

Length (mm): head of 3.1, φ 3.1-3.2; pronotum of 3.8-4, φ 3.8-4; tegmina of 15.8-16.5, φ 16-17.2. Width (mm): head of 3.1-3.2, φ 3.1-3.3; pronotum of 6-6.3, φ 6.1-6.3.

Paranauphoeta rufipes Brunner von Wattenwyl, 1865

(Figs 58, 76, 96, 97, 129)

Material. New Guinea: 1 of, "Rolle 1904", "Paranauphoeta rufipes Br. R. Shelford det.", "Paranauphoeta rufipes Br. !! New Guinea of"; 1 of, 1 of, "Paranauph, rufipes Br. N. Guinea, Staudinger.", "483.", "Paranauphoeta rufipes Br. R. Shelford det."; 1 of, "New-Guinea ex coll. Fruhstorfer", "70", "Paranauphoeta rufipes Br. var. R. Shelford det."; 1 of, "New-Guinea ex coll. Fruhstorfer", "70", "Paranauphoeta rufipes Br. var. R. Shelford det."; 1 of, "New-Guinea, Shelford det."; 1 of, "New-Guinea, [illegible inscription – L.A.], ex coll. Fruhstorfer", "No 130-97.", "Paranauphoeta rufipes Br. R. Shelford det."; 1 of, "Paranauphoeta rufipes Br. N-Guinea, of. G. Strobl, "purchase of H. Rolle"; 1 of, "New Guinea", "purchase of H. Rolle"; 2 of, "Rolle 1904", "Paranauphoeta rufipes Br. R. Shelford det."

This species was sumptuously illustrated by Hanitsch (1931: Pl. I, fig. 6) and redescribed by Roth (1989). The following data may be added to this latter.

Hind metatarsus usually with a single row of spines.

Male genitalia. Apical sclerite L1 elongate, spines absent (Figs 96, 97); L2d as in Fig. 129; complex of sclerites R+N as in Fig. 76, sclerite R3v comparatively short, similar to that of *P. lyrata*. Length (mm): head of 3-3.1, φ 3.1-3.7; pronotum of 3.9-4.2, φ 4-4.9; tegmina of 15.5-16.4, φ 13.5-20.7. Width (mm): head of 3.1-3.3, φ 3.3-3.7; pronotum of 5.8-6.5, φ 6.1-7.6.

Note. Yellowish marks on abdominal sternites are present only in females labelled as "*Para-nauphoeta rufipes* Br. var. R. Shelford det." These specimens also have uncharacteristic colour of the pronotum (Fig. 58) as compared with that described by Roth (1989).

Paranauphoeta formosana Matsumura, 1913 (Figs 19, 66, 74, 99, 128)

Material. **Taiwan**: 6 σ , 14 φ , "Taiuau, Formosa", "purchase of H. Rolle"; 1 σ , 3 φ , "Taiuau, Formosa"; 4 φ , "Taiuau IV, Formosa", "purchase of H. Rolle". 1 φ , without label.

Description. Comparatively large species. Pattern of coloration similar to that of *P. vicina sinica*, but only one pair of light spots present in proximal part of tegmina (Matsumura, 1913: pl. II, fig. 12). Hind metatarsus usually with incomplete single row of spines (Fig. 19).

Male genitalia. Apical sclerite L1 similar to that of *P. vicina sinica*, spines absent (Fig. 99); L2d as in Fig. 128; complex of sclerites R+N as in Fig. 74, sclerite R3v comparatively short, similar to that of *P. lyrata* and *P. rufipes*.

Length (mm): head of 3.6-4, 9 4-4.3; pronotum of 4.8-5.3, 9 4-4.3; tegmina of 18-20.3, 9 20.8-22. Width (mm): head of 3.5-3.9, 9 4-4.3; pronotum of 7-8.1, 9 7.9-8.4.

Note. This series was determined by G.Ya. Bey-Bienko.

P. formosana was described as a variety of *P. circumdata* de Haan, 1842 from Taiwan (Formosa, Suishako, see Matsumura, 1913).

Subfamily **PERISPHAERIINAE** Brunner von Wattenvyl, 1865

The monophyly of Perisphaeriinae was analyzed by Grandcolas (1997). Five synapomorphies for genera of this subfamily were suggested by this author.

It must be noted that two synapomorphies (numbers 1 and 2 in the list by Grandcolas) cannot be considered synapomorphies of Perisphaeriinae.

The first synapomorphy was defined as follows: "...the sclerite R3v is most often absent, or if not absent, extremely reduced in the genus *Bantua* and in some species of the genus *Laxta*" (Grandcolas, 1997: p. 124). However, sclerite R3v in all representatives of the genera *Trichoblatta* Saussure & Zehntner and *Perisphaerus* Serville (Figs 81-89) which were investigated by the author of the present work is always present



Figs 58-71. Genera Paranauphoeta, Trichoblatta and Perisphaerus (58, 61, female; 59, 60, 62-71, male). 58, Paranauphoeta rufipes Brunn. (atypical coloration in female); 59, 69, Paranauphoeta lyrata (Burm.); 60, 61, T. humbertiana (Sauss.); 62-64, T. pilosa B.-Bien. (holotype); 65, 70, Perisphaerus semilunatus Han.; 66, Paranauphoeta formosana Mats.; 67, Paranauphoeta vicina sinica B.-Bien. (paratype); 68, Paranauphoeta indica Sauss. & Zehn.; 71, Perisphaerus punctatus B.-Bien. Pronotum from above (58-62); abdominal apex from above (63); hypandrium from below (64-69); outlines of anal plate (70, 71). Dotted area shows dark colour.

and not smaller than in representatives of many other blaberid subfamilies [for example, in most representatives of subfamilies Paranauphoetinae (Figs 72-77, 79), Panesthiinae (Fig. 80), Epilamprinae (Anisyutkin, 1999), Pycnoscelinae and Diplopterinae (Anisyutkin, 2002)].

The second synapomorphy was defined as "...the sclerite N is caudally protruding and grooved to receive the tip of the cleft R2" (Grandcolas, 1997: p. 124). The shape of sclerite N in Perisphaeriinae (Figs 81-89) and some Panesthiinae (Fig. 80) is similar. In both the cases, sclerite N forms a large grooved plate occupying lateral part of the complex R+N. Apparently, such structure is a synapomorphy of the subfamilies Perisphaeriinae and Panesthiinae (see above).

Deviation from this shape of sclerite N in Panesthiinae is mainly related to weakening in sclerotization of the male genitalia as a whole.

Genus Trichoblatta Saussure & Zehntner, 1895

= Glomeriblatta Bey-Bienko, 1950.

Type species: Perisphaeria sericea Saussure, 1863.

Diagnosis. Sexual dimorphism strongly expressed: male with tegmina and wings fully developed, female completely wingless. Body of female distinctly depressed dorsoventrally. The female of *Trichoblatta* cannot roll itself into a ball. Orifices, probably those of glandular nature, comparatively numerous on the abdominal tergites of female (Fig. 10), with number noticeably varying within species.

Notes. By now, no autapomorphies of *Trichoblatta* are discovered. It is not improbable that the genus is paraphyletic with respect to some more specialized genera of the subfamily (e. g., *Glomerexis* Bey-Bienko or *Perisphaerus* Serville).

Description. General colour usually without contrasting elements. In females, surfaces thickened and hardened (as a result of strong sclerotization); in males, such type of surfaces present only on pronotum; sometimes, surfaces with metallic lustre. Head often with comparatively small interval between eyes (Figs 37-41). In males, caudal margin of pronotum truncate (Figs 23, 29, 31, 32, 60, 62); that in females, more or less crescent-like (Figs 25, 27, 33, 61). Hind metatarsus shorter than or rarely (mainly in males) subequal to following segments combined, usually more robust in females (Fig. 15) and slenderer in males (Fig. 16); metatarsal pulvilla large, longer than half of metatarsus; armament along lower margin of metatarsus and following tarsomeres absent; arolium large. Anal plate subrectangular, more or less rounded caudally (Figs 43, 46, 50, 54, 55, 57); cerci one-segmented, short and pyramidal in female (Figs 43, 46, 50,

54, 55), multisegmented in male (Figs 45, 48, 49, 53, 63, 124); hypandrium asymmetrical, its caudal margin prominent (Figs 44, 47, 51, 52, 56, 64); styli present (Figs 47, 52), reduced (Fig. 51), or absent (Figs 44, 56).

Male genitalia. Apical sclerite L1 in shape of a large plate, without bristles (Figs 102-106, 112, 115, 116, 120), often with small additional sclerite or more or less expressed projection at articulation with basal sclerite L1 (Figs 104-106); basal sclerite L1 simple, rod-like (Figs 101, 123, 125); sclerite L2d usually with a median incision (Figs 107-111, 113, 118, 119); L3d present (Figs 107, 114); complex of sclerites R+N (Figs 81-89): R3d more or less elongate and parallel to R2, R2 well sclerotized and sometimes curved, R3v large and often partially membranous, N large and well sclerotized.

Included species. Those included by Princis (1964, 1971) and *T. beybienkoi* sp. n.

Trichoblatta beybienkoi sp. n.

(Figs 15, 16, 27-30, 38, 46-48, 82, 104-107)

Holotype. 9, China, prov. Yunnan, env. of Kingtun, Wuliangshan, 1800-2430 m, 21.III.1957 (Hun Kuan-chi).

Paratypes. China, prov. Yunnan: 1 σ , 2 φ , 3 larvae, with same data as in holotype; 9 larvae, same data, but 1900 m (D. Panfilov); 3 φ , 2 larvae, same data, but 2300 m, 22.III.1957; 2 φ , 1 larva, Mts. E of Tenchung, 10.V.1955 (Xue Yui-fyn).

Description. Female (holotype). Upper side of body and lower side of abdomen greenish bronze; cerci yellow; legs, most of head and lower parts of thorax more or less reddish brown; facial part of head and eves dark brown, almost black; antennae lighter; labrum, maxillary and labial palpi and tarsi yellowish. Upper side of body strongly punctate; lower side of abdomen and facial part of head less punctate; all surfaces shining. Facial part of head flat, with characteristic semilunar hollow; interval between eyes about 0.25 times the length of eye; interval between antennal sockets about 2.5 times the length of scapus. Pronotum widely rounded anteriorly, slightly convex posteriorly (Figs 27, 28). Each side of 3rd-7th abdominal tergites with 1, 1, 1, 1-2, 1-2 orifices (in holotype, 1, 1, 1, 1, 1), respectively. Anal plate rounded posteriorly (Fig. 46).

Male (paratype). Colour similar to that of female, but lower parts of thorax and legs somewhat lighter; anal plate yellowish; tegmina and wings yellowish brown, except almost transparent anal area; anal plate yellow; hypandrium brownish, with a pale spot. Head with interval between eyes about 0.2 times the length of eye (Fig. 38); pronotum subpentagonal (Figs 29, 30). Anal plate caudally rounded (Fig. 48); hypandrium asymmetrical, styli present (Fig. 47).

Male genitalia. Apical sclerite L1 well sclerot-



Figs 72-79. Genus Paranauphoeta, male genitalia. 72, P. nigra B.-Bien. (holotype); 73, P. indica Sauss. & Zehn.; 74, P. formosana Mats.; 75, P. lyrata (Burm.); 76, P. rufipes Brunn.; 77, P. vicina sinica B.-Bien. (paratype); 78, 79, P. vicina vietnamensis ssp. n. (holotype). Complex R+N from above (72-77); sclerites R3d and R2 from below (78); sclerite R3v (79). Dotted area shows sclerotized parts.

Abbreviations: R3d, R2, R3v, N, sclerites of male genitalia (see text).

ized, broad, semicircular, with lateral part somewhat elevated (Figs 104-106); L2d comparatively robust (Fig. 107); complex of sclerites R+N well sclerotized (Fig. 82): R3d comparatively weakly sclerotized, R2 almost straight, R3v and N comparatively large.

Larva. Similar to female, but smaller. Lateral parts of tergites with orifices. Last instars of male larvae with lateral parts of meso- and metathorax distinctly enlarged.

Length (mm): head \circ 2.4-2.8 (2.7), σ 2.6; pronotum \circ 4.1-4.4 (4.4), σ 4.2; tegmina σ 22. Width (mm): head \circ 2.2-2.6 (2.6), σ 2.2; pronotum \circ 7.2-7.9 (7.9), σ 6.3. Measurements in parentheses are those of holotype.

Comparison. The new species is closely related to *T. magnifica* Shelford. The female of *T. beybienkoi* readily differs from that of *T. magnifica* in the smaller size, duller colour and rounded anal plate. The male of *T. beybienkoi* differs from that of *T. magnifica* in the shape of pronotum, presence of styli and some structures of the genitalia: shape of sclerites L1, L2d and complex R+N.

Note. The type series of this species was prepared for description by G.Ya. Bey-Bienko, who tentatively identified some specimens of the type series as "*Glomeriblatta magnifica* Sh." and "*Trichoblatta dubia* Han.". However, later he marked the series as belonging to a new species and labelled it as "Comp.[ared – L.A.] with holotype *Pseudogl. dubia* Han. – quite differ.[ent – L.A.] species! London, VII 1970 G. Bey-Bienko".

Trichoblatta magnifica (Shelford, 1907) (Figs 3, 5, 23-26, 40, 41, 42-45, 81, 101-103, 109, 110)

= Pseudoglomeris dubia Hanitsch, 1924.

Material. Vietnam, prov. Ha Son Binh: 1 or, 1 larva, distr. Hoa Binh, "Mai Chau", 250 m, 30.X.-4.II.1990 (A. Gorochov); prov. Vinh Phu: 1 Q, Tam Dao, 800-900 m, 9-18.II.1990 (A. Gorochov); 2 φ , same data, but 1-10.VI.1995; 1 larva, My Duc, SW Dong Hoi, 28.XI.-2.XII.1961 (O. Kabakov); 1 larva, same data, but 28.X.-2.XII.1961 (O. Kabakov); 1 9, same data, but "near Dao Tru", 16-18.XI.1961 (O. Kabakov); 2 9, Qui Chau, near Vihn, 17-20.III.1962 (O. Kabakov); 2 larvae, same data, but 1.I.1963 (O. Kabakov); 1 Q, Cua Rao, near Vihn, 26.IV.1962 (O. Kabakov); prov. Thanh Hoa: 1 9, SW of Bai Thuong, 8-9.VII.1962 (O. Kabakov); 1 9, same data, but 11.VII.1962; 1 9, same data, but 30 km SW of Bai Thuong, 5-8.I.1963; 1 9, Hanoi, 31.VIII.1962 (O. Kabakov); 1 9, N of Cua Rao, 600 m, 25.IX.1962 (O. Kabakov); 1 larva, Ban-Yang, Con River, near Vihn, 14.IV.1963 (O. Kabakov); 1 9, Mts. N of Ha Giang, 4. VII. 1963 (O. Kabakov); prov. Bac Hai: 1 9, Thai Nguen, 28.VII.1963 (Ο. Kabakov); 1 φ, NO of Thai Nguen, 29.X.1963 (Ο. Kabakov); 1 σ, Sam Mok, NO of Thai Nguen, 12.I.1964 (O. Kabakov); 3 9, 4 larvae, Con River, near Vinh, 10-15.II.1964 (O. Kabakov); 4 larvae, 20 km E of Ba Thuoc, 28.I.1989 (B. Korotyaev).

Description. Female. Upper side of body emerald-green; cerci yellow; lower side of abdomen and facial part of head slightly darker, with bronze shade; eyes, lower parts of thorax and, mostly, coxae and femora blackish; labrum, maxillary and labial palpi, trochanters, distal and proximal parts of femora, tibiae, tarsi and proximal parts of antennae yellowish; distal part of antennae greyish brown. Upper side of body strongly and densely punctate, shining. Head and pronotum as in Figs 23, 24, 41. Each side of 3rd-7th abdominal tergites with 1-3, 2-4, 4-5, 4-6, 4-5 orifices, respectively. Anal plate trapezoidal (Fig. 42, 43).

Male. Colour similar to that of female, but abdomen brown, darker from below; tegmina dark brown, with emerald shade proximally; wings yellowish-brown, except almost transparent anal area; anal plate yellowish; hypandrium brownish, with a pale spot. Head and pronotum as in Figs 23, 24, 40. Anal plate rounded (Fig. 45); hypandrium asymmetrical, styli absent (Fig. 44).

Male genitalia (Fig. 101). Apical sclerite L1 large (Figs 102, 103); L2d without median incision, only with a small emargination at apex (Figs 109, 110); complex of sclerites R+N (Fig. 81) similar to that of *T. beybienkoi*, differing from it in more curved R2 and in shape of N.

Larva. Very similar to female, but smaller. In young larvae, colour somewhat bronze.

Length (mm): head φ 3.8-4.7, σ 3-3.2; pronotum φ 5.9-8, σ 5.2-5.4; tegmina σ 20. Width (mm): head φ 3.2-3.8, σ 2.5-2.6; pronotum φ 11.3-14.8, σ 8.8-9.

Note. T. magnifica is rather widely distributed; it is one of the most common species of the genus in North Vietnam.

Trichoblatta aerea (Bey-Bienko, 1957) (Figs 49-51, 83, 111, 112)

Holotype. 9, China, prov. Yunnan, Longling-Baoshan, 21.V.1955 (V. Popov).

Paratypes. China, prov. Yunnan: 1 9, with same data as in holotype; 1 larva, Baoshan, 1600 m, 13.V.1955 (O. Kryzhanovskij); 1 9, 1 larva, Baoshan-Yonping, 28.V. 1955 (V. Popov, U Lo); 1 o', env. of Longling, 1600 m, 12.V.1955 (Ou Peng-yun); 1 larva, Mekong valley, env. of Baoshan, 1200 m, 28.V.1955 (O. Kryzhanovskij).

Other material examined. China, prov. Yunnan: 1 larva, with same data as in holotype; 2 \overline\$, Longling, 1450 m, 21.VI.1956 (Chow Peng-show); 1 \overline\$, env. of Longling, 1050 m, 25.VI.1956 (Chow Peng-show); 1 \overline\$, 1 larva, same data, but 800 m, 26.VI.1956.

The original description by Bey-Bienko (1957) may be supplemented with the following data.

Female. Each side of 3rd-7th abdominal tergites with 3, 3, 3, 3 and 1-3 orifices (in holotype, 3, 3, 3, 3, 3), respectively.

Male. Anal plate caudally protruding (Fig. 49); cerci abbreviated and incrassate; hypandrium asymmetrical, styli clearly reduced (Fig. 51).



Figs 80-89. Genera Panesthia, Perisphaerus and Trichoblatta, complex R+N of male genitalia (from above). 80, P. cognata B.-Bien. (holotype); 81, T. magnifica (Shelf.); 82, T. beybienkoi sp. n. (paratype); 83, T. aerea (B.-Bien.) (paratype); 84, T. fallax B.-Bien. (paratype); 85, T. montshadskii B.-Bien. (paratype); 86, T. semisulcata (Han.); 87, T. valida B.-Bien.; 88, P. semilunatus Han.; 89, P. punctatus B.-Bien. Dotted area shows sclerotized parts. Abbreviations: R3d, R2, R3v, N, sclerites of male genitalia (see text).

Male genitalia. Apical sclerite L1 similar to that of *T. beybienkoi*, but somewhat different in shape (Fig. 112); sclerite L2d comparatively robust (Fig. 111); complex of sclerites R+N as in Fig. 83.

Length (mm): head φ 2.7-3 (2.9), σ 2.7; pronotum φ 4-4.6 (4.3), σ 4; tegmina σ 20. Width (mm): head φ 2.2-2.5 (2.5), σ 2.3; pronotum φ 7.3-8.5 (8), σ 6.4. Measurements in parentheses are those of holotype.

Note. This species was described in the genus *Glomeriblatta* Bey-Bienko. The additional material was determined by Bey-Bienko after the description of the new species, in 1968, judging from labels.

Trichoblatta fallax Bey-Bienko, 1969 (Figs 53, 84, 108)

= Pseudoglomeris flavicornis: Bey-Bienko, 1950, 1954, non Burmeister, 1838.

Holotype. 9, China, prov. Fujian, Shaowu, 1500 m, 8.VII.-30.VIII.1937 (J. Klapperich).

Paratypes. China, prov. Fujian: 2 9, 2 larvae, with same data as in holotype; 1 9, Kwangtseh, 30.VIII.1937 (J. Klapperich); 2 °, Kuatun, "27,40 n. Br. 117,40 ö. L.", 2-31.V.1938 (J. Klapperich); prov. Yunnan: 1 9, Wuliangshan, env. of Kingtun, 2300 m, 22.III.1957 (D. Panfilov).

The original description by Bey-Bienko (1969) may be supplemented with the following data.

Female. In specimens from Fukien and Kuatun (including holotype), each side of 3rd-7th abdominal tergites with 1, 1, 1, 1, 1 orifices, respectively, but specimen from Yunnan with 1, 2, 2, 2, 2 orifices; medial pair of orifices on 4th tergite very indistinct.

Male. Anal plate similar to that of *T. aerea*, but differs from it in more expressed posterolateral angles and more elongate cerci (Fig. 53); hypandrium similar to that of *T. aeria*, but slightly more projected medially.

Male genitalia. Apical sclerite L1 similar to that of *T. beybienkoi*, but slightly more robust; L2d comparatively short, similar to that of *T. aerea* (Fig. 108); complex of sclerites R+N similar to that of *T. beybienkoi*, but N more elongate (Fig. 84).

Length (mm): head $\[mathcal{2}.9-3\] (2.9), \[mathcal{o}'\] 2.6-2.7; pronotum <math>\[mathcal{2}.4.5-4.7\] (4.7), \[mathcal{o}'\] 4.1-4.3; tegmina \[mathcal{o}'\] 19-21. Width (mm): head \[mathcal{o}\] 2.4-2.7\] (2.7), \[mathcal{o}'\] 2.2-2.3; pronotum \[mathcal{o}\] 7.7-8.3\] (8.2), \[mathcal{o}'\] 6.5-6.9. Measurements in parentheses are those of holotype. \]$

Trichoblatta montshadskii Bey-Bienko, 1969 (Figs 85, 113)

Holotype. 9, China, prov. Yunnan, env. of Kingtun, 2000 m, 11.IV.1957 (A. Montschadsky).

Paratypes. 5 \circ , 1 σ , 3 larvae, with same data as in holotype.

The original description by Bey-Bienko (1969) may be supplemented with the following data.

Female. Each side of 3rd-7th abdominal tergites with 1, 1, 2, 2, 1-3 orifices (in holotype, 1, 1, 2, 2, 2-3), respectively; all orifices very indistinct.

Male. Anal plate, cerci and hypandrium similar to those of *T. fallax*.

Male genitalia. Apical sclerite L1 similar to that of *T. beybienkoi* and *T. fallax*; L2d comparatively robust, with a small hook (Fig. 113); complex of sclerites R+N similar to that of *T. beybienkoi* (Fig. 85).

Length (mm): head \circ 2.2-2.4 (2.4), σ 2.4; pronotum \circ 3.3-3.4 (3.4), σ 3.1; tegmina σ 16. Width (mm): head \circ 2-2.2 (2.2), σ 2; pronotum \circ 5.9-6.3 (6.2), σ 5. Measurements in parentheses are those of holotype.

Note. T. montshadskii is a very distinctive species, because of characteristic coloration: the first abdominal and all thoracal tergites are distinctly reddish brown, while all other abdominal tergites are almost black (sometimes, the second abdominal tergite is partially reddish).

Trichoblatta semisulcata (Hanitsch, 1924) (Figs 52, 86, 114, 115, 118)

Material. China, prov. Yunnan: 1 9, 1 o', env. of Yuili (near Burmese frontier), 1300-1400 m, 10-11.VI.1956 (Chow Peng-show); 1 o', 3 larvae, Santaishan Mt., 30 km SW of Luxi, 1200 m, 18.V.1955 (Chao J.); 1 larva, Luxi, 900 m, 8.V.1955 (Xue Yui-fyn); 1 larva, env. of Simao, 1300 m, 5.IV.1957 (D. Panfilov); 1 o', Cheli, 500 m, 10.IV. 1955 (O. Kryzhanovskij); 1 larva, same data, but 600 m, 22.IV.1957 (Hun Kuan-chi).

Description. Female. Upper side of body, lower sides of abdomen and thorax and, mostly, coxae and facial part of head black; posterior margins of pro-, meso-, metanotum, anal plate and, less distinctly, posterior margins of 1st and 2nd abdominal tergites reddish; eyes, antennae, labrum, maxillary and labial palpi and tarsi yellowish; legs, cerci and lateral parts of head reddish. Upper side of body punctate, shining; size of punctures and density of punctation increasing caudally. Head with eyes noticeably approached but not contiguous: pronotum similar to that of T. magnifica, but posterior margin slightly more prominent. Each side of 3rd-7th abdominal tergites with 0, 0, 1, 1-2, 1-2 orifices, respectively, with all orifices very indistinct; anal plate similar to that of T. bevbienkoi.

Male. Colour similar to that of female, but lighter, brownish black; anal plate yellowish, hypandrium partly yellowish. Pronotum similar to that of *T. beybienkoi*. Anal plate similar to that of *T. fallax*; hypandrium asymmetrical, styli present, asymmetrical (Fig. 52).

Male genitalia. Apical sclerite L1 large, somewhat similar to that of *T. beybienkoi* (Fig. 115); L2d comparatively short (Figs 114, 118); complex of sclerites R+N as in Fig. 86.

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Figs 90-100. Genus *Paranauphoeta*, apical sclerite L1 of male genitalia. **90**, **91**, *P. nigra* B.-Bien. (holotype); **92**, **93**, *P. indica* Sauss. & Zehn. [specimens from Bangladesh (92) and from Vietnam (93)]; **94**, **95**, *P. vicina vietnamensis* ssp. n. (holotype); **96**, **97**, *P. rufipes* Brunn.; **98**, *P. lyrata* (Burm.); **99**, *P. formosana* Mats.; **100**, *P. vicina sinica* B.-Bien. (paratype). Apical sclerite L1 from above (90, 92, 93, 95, 96), from side (91), and from below (94, 97-100). Dotted area shows sclerotized parts.

Larva. Very similar to female in appearance, but colour lighter, reddish.

Length (mm): head $\[mathbf{2}3.3, \[mathbf{s}'2.7-3];\]$ pronotum $\[mathbf{s}'2.7, \[mathbf{s}'4.4.5];\]$ tegmina $\[mathbf{s}' 19-21]$. Width (mm): head $\[mathbf{s} 2.7, \[mathbf{s}' 2.1-2.3];\]$ pronotum $\[mathbf{s} 10, \[mathbf{s}' 6.4-7.8].$

Note. This species was described in the genus *Pseudoglomeris* Brunner von Wattenwyl. All the material cited was determined by Bey-Bienko.

This species demonstrates a bicolorous pattern of coloration, similar to that of *T. montshadskii* but less contrasting.

Trichoblatta valida valida Bey-Bienko, 1969 (Figs 32, 87, 116, 119)

Holotype. 9, Vietnam, 50 km N of Thai Nguen, 300-400 m, 19.XII.1962 (O. Kabakov).

Paratypes. 1 \circ , with same data as in holotype; 2 \circ , same data, but 8.II.1963.

Other material examined. Vietnam, 1 9, NO of Thai Nguen, 19.XII.1962 (O. Kabakov); 2 9, 1 °, same data, but 5-12.III.1963; 1 larva, Qui Chau, near Vinh, 400-700 m, 26-27.VIII.1962 (O. Kabakov); 1 larva, between Fu Qui and Qui Chau, 11.I.1963 (O. Kabakov); 1 larva, Naghen, SE of Qui Chau, 3.X.1963 (O. Kabakov); 1 larva, Con River, near Vihn, 10-15.II.1964 (O. Kabakov).

The original description by Bey-Bienko (1969) may be supplemented with the following data.

Female. Each side of 3rd-7th abdominal tergites with 1-2, 2-3, 3, 3, 3 orifices (in holotype, 2, 3, 3, 3, 3), respectively; each side of abdominal tergites, as a rule, with three hollows, but only some of them bear orifices.

Male (nov.). General colour reddish brown; antennae, maxillary and labial palpi, tarsi and cerci yellowish. Head somewhat similar to that of *T. beybienkoi*; pronotum subtriangular anteriorly (Fig. 32). Anal plate somewhat similar to that of *T. magnifica*; hypandrium similar to that of *T. beybienkoi*, but styli asymmetrical, similar to those in *T. semisulcata*.

Male genitalia. Apical sclerite L1 comparatively broad (Fig. 116); L2d with strongly curved hook (Fig. 119); in the only known male specimen, complex of sclerites R+N damaged; R2 strongly curved, N as in Fig. 87.

Length (mm): head \circ 4.4-5 (4.6), σ 3.3; pronotum \circ 7.6-8.9 (7.6), σ 5.5; tegmina σ 22. Width (mm): head \circ 3.4-4 (3.5), σ 2.2; pronotum \circ 13.7-15.4 (13.9), σ 8.3. Measurements in parentheses are those of holotype.

Note. T. valida is one of the largest species of the genus.

Trichoblatta valida moderata Bey-Bienko, 1969

Holotype. 9, China, prov. Yunnan, Damonlung, 50 km SW of Cheli, 700 m, 10-12.IV.1957 (D. Panfilov et al.).

Paratypes. **China**, *prov. Yunnan*: 2 9, 8 larvae, with same data as in holotype; 3 9, Ganlanba, 560-650 m, 17-19.IV.1957 (Wang Shu-yun); 2 larvae, Xiao Menle, 25

km NO of Cheli, 800 m, 6.IV.1955 (V. Popov); 1 9, 1 larva, gorge Liusahe, env. of Cheli, 31.III.1957 (A. Montschadsky); 1 larva, Shikuyao, env. of Cheli, 750 m, 27.IV. 1957 (D. Panfilov); 2 larvae, 40 km SE of Kinku, 1000 m, 13.V.1957 (D. Panfilov).

The original description by Bey-Bienko (1969) may be supplemented with the following data.

Female. Each side of 3rd-7th abdominal tergites with 1-3, 1-3, 3, 3, 3 orifices (in holotype, 1, 1, 3, 3, 3), respectively; as a rule, each tergite with three hollows on sides.

From the brood sac of the specimen collected from the Liusahe Gorge, env. of Cheli, the ootheca was extracted. Ootheca typical for Blaberidae (Roth, 1968), containing about 28 eggs (extremities of ootheca strongly shrunken, making difficulties for accurate observation).

Male unknown.

Length (mm): head 3.6-4.2 (3.9); pronotum 5.7-6.2 (5.9). Width (mm): head 3-3.4 (3.2); pronotum 9.8-11.4 (11.2). Measurements in parentheses are those of holotype.

Note. According to Bey-Bienko (1969: p. 836), *T. valida moderata* differs from the nominotypical subspecies in the smaller size, less expressed concavity on the frons and the distance between the eyes across the vertex equal to or exceeding the width of the 3rd antennal segment (in nominotypical subspecies, the distance between the eyes is shorter than the width of the 3rd antennal segment).

Trichoblatta sculpta (Bey-Bienko, 1957) (Figs 13, 54)

Holotype. 9, China, prov. Yunnan, Salwen valley W of Baoshan, 800 m, 4.V.1955 (O. Kryzhanovskij).

Paratypes. 4 9, 1 larva, with same data as in holotype. Other material examined. China, prov. Yunnan: 1 9, 2 larvae, Nannoshan Mts. near Fohay, 1100-1250 m, 24.IV. 1957 (Hun Kuan-chi, D. Panfilov); 1 larva, Yonping, 28.V. 1955 (Yang Sin-chi). Vietnam, 1 9, Sapa, SW of Lao Cai, 12.VIII.1962 (O. Kabakov).

The original description by Bey-Bienko (1957) may be supplemented with the following data.

Female. Surfaces, especially those of upper side of body, strongly sculptured, dull, not shining, covered with short and dense bristles. Hind metatarsus comparatively long and slender (Fig. 13).

Each side of 3rd-7th abdominal tergites with 4-6, 4-6, 4-7, 5-7, 4-6 orifices (in holotype, 4-6, 4-6, 4-5, 6-7, 4-5), respectively; medial orifices smaller and very poorly visible. Anal plate rounded, with two lateral swellings over cerci; a third, smaller swelling located in the middle of anal plate (Fig. 54).

Male unknown.

Length (mm): head 2.8-3.3 (3.3); pronotum 4.3-4.8 (4.6). Width (mm): head 2.4-2.8 (2.7); pronotum 8.2-9.2 (8.7). Measurements in parentheses are those of holotype.



Figs 101-122. Genera Trichoblatta and Perisphaerus, male genitalia. 101-103, 109, 110, T. magnifica (Shelf.); 104-107, T. beybienkoi sp. n. (paratype); 108, T. fallax B.-Bien. (paratype); 111, 112, T. aerea (B.-Bien.) (paratype); 113, T. montshadskii B.-Bien. (paratype); 114, 115, 118, T. semisulcata (Han.); 116, 119, T. valida B.-Bien.; 117, 120, P. semilunatus Han.; 121, 122, P. punctatus B.-Bien. General view from above (101); apical sclerite L1 from above (102, 104, 112, 115, 116, 120, 122), from side (103, 106), from above and from side (105); sclerites L2d and L3d from above (107, 114); sclerite L2d from above (108, 109, 111, 113, 117-119, 121) and from side (110). Dotted area shows membranous (101) and sclerotized parts (102-106, 112, 114-116, 120, 122).

Notes. This species was described in the genus *Glomeriblatta* Bey-Bienko.

Female of *T. sculpta* readily differs from those of other representatives of the genus *Trichoblatta* in the structure of surfaces and hind metatarsus, which is more similar to the metatarsus in males. Orifices on lateral parts of tergites in female are comparatively numerous and, probably, somewhat unstable in number.

Trichoblatta tarsalis (Walker, 1868) (Figs 33, 55)

= Pseudoglomeris planiuscula Brunner von Wattenwyl, 1893.

Material. China, prov. Yunnan: 8 9, 2 larvae, 50 km SW of Mokiang, 1200-1300 m, 31.III-1.IV.1955 (O. Kryzhanovskij et al.); 2 9, 2 larvae, Cheli, 500-580 m, 8.IV.1955 (O. Kryzhanovskij et al.); 3 larvae, same data, but 14.IV.1957 (Hun Kuan-chi); 1 larva, Cheli, Montze, 620 m. 22.IV.1957 (Tsang Lin-chao); 1 9, 1 larva, Puerh, 1400 m, 21.IV.1955 (O. Kryzhanovskij et al.); 2 9, 1 larva, Salwen valley, W of Baoshan, 800 m, 4.V.1955 (O. Kryzhanovskij); 1 9, Mindin, 600 m, 6.V.1955 (Hwang Tien-yun); 2 9, 1 larva, Luxi, 900 m, 17.V.1955 (O. Kryzhanovskij); 2 9, 4 larvae, 30 km SW of Jinping, 370-400 m, 16-27.IV.1956 (Hwang Ke-yen et al.); 11 9, 2 lar-vae, env. of Kingtun, 22.V-26.VI.1956 (O. Kryzhanovskij et al.); 1 larva, env. of Yuili (near Burmese frontier), 1300 m, 10.VI.1956 (Chow Peng-show); 2 9, 1 larva, env. of Kingtun, Jingdong, 1200 m, 28.V.1956 (O. Kryzhanovskij); 14 9, 11 larvae, Ganlanba, 540-650 m, 16.III-17.IV.1957 (Tsang Lin-chao et al.); 19 Q, 1 larva, env. of Kingtun, 1200 m, 21.III-15.V.1957 (A. Montschadsky et al.); 3 9, 1 larva, env. of Simao, 1200 m, 26.III-10.V.1957 (A. Montschadsky); 1 9, 2 larva, env. of Puven, 27.III-11.V.1957 (A. Montschadsky et al.); 2 9, 2 larvae, Damonlung, 50 km SW of Cheli, 700 m, 11-12.IV.1957 (Hun Kuan-chi et al.); 1 9, 2 larvae, Xiao Menle, 850 m, 4.V.1957 (Liang Tsiu-chen).

Description. Female. General colour black, shining; antennae, maxillary palpi, mouthparts, tarsi and cerci yellowish; trochanters sometimes reddish brown. Upper side of body comparatively finely and densely punctate. Head subtriangular, distance between eyes across vertex about 0.33 times the length of scapus. Pronotum as in Fig. 33.

Each side of 3rd-7th abdominal tergites with 0-1, 0-2, 2-3, 1-3, 2-3 orifices, respectively. Anal plate subrectangular (Fig. 55).

Male. Typical of genus (Brunner von Wattenwyl, 1893). Author had no possibility to examine male specimens undoubtedly belonging to *T. tarsalis*.

Length (mm): head 3.2-3.7; pronotum 4.7-5.2. Width (mm): head 2.5-3.2; pronotum 8.8-9.6.

Note. T. tarsalis was described by F. Walker in the genus *Perisphaeria* from females collected in Cambodia and Burma (Tenasserim) (Walker, 1868: p. 171). Later, *Pseudoglomeris planiuscula* Brunner von Wattenwyl, 1893 was synonymized with *T. tarsalis* (Princis, 1957). *P. planiuscula* was described from female and male collected in different localities of Burma. In South China, *T. tarsalis* was discovered by Bey-Bienko (1957) and cited under the name *Glomeriblatta planiuscula* Brunner von Wattenwyl. According to the catalogue by Princis (1964), *T. tarsalis* has a very wide range, which includes "Malakka, Birma, Tonkin, Siam, China". Nevertheless, taking into account difficulties in determination of this species and lack of adequate descriptions, whether the species described belongs to *T. tarsalis* needs confirmation in further investigations.

Trichoblatta humbertiana (Saussure, 1863) (Figs 60, 61, 124, 125)

Material. India (south), 1 of, 2 o, 7 larvae, Nilgiri Hills, 13 km W of Coimbatore, 6.I.1964 (K. Breev); 1 of, Makdapan, at light, 18.I.1964 (K. Breev). Sri Lanka: 1 of, "Ceylan [sic! – L.A.] W. Morton", "purchase of H. Rolle".

Description. Female. Upper side of thorax and that of abdomen almost black, slightly reddish; cerci yellow; facial part of head, legs and ventral parts of thorax reddish; eyes black; antennae, maxillary and labial palpi, tarsi yellowish. Thorax from above and abdomen densely but not deeply punctate, facial part of head less punctate; all surfaces shining. Head typical of genus; interval between eyes about 0.3 times the length of eye; interval between antennal sockets about twice as long as scapus. Pronotum widely rounded anteriorly, angularly prominent posteriorly (Fig. 61). Each side of 3rd-7th abdominal tergites with 1, 1-2, 2, 3, 2-3 orifices, respectively. Anal plate subrectangular, similar to that in *T. tarsalis*.

Male. Colour similar to that of female, but lighter and reddish; tegmina reddish brown. Pronotum and proximal part of tegmina densely but not deeply punctate, shining. Eyes large, subcontiguous on vertex. Pronotum as in Fig. 60. Anal plate rounded caudally, somewhat similar to that of *T. magnifica*; hypandrium asymmetrical, styli present (Fig. 124).

Male genitalia (Fig. 125). Apical sclerite L1 comparatively broad, similar to that of *T. magnifica*; L2d compatively short, indistinctly serrate on inner side, without median incision; complex of sclerites R+N somewhat similar to that of *T. montshadskii*, differing from it in shape of sclerite R3v.

Length (mm): head of 2.4-2.6, 9 2.9-3.1; pronotum of 2.6-3.3, 9 3.7-3.8; tegmina of 12.3-15.7. Width (mm): head of 1.8-2.1, 9 2.3-2.4; pronotum of 4.4-5.5, 9 7.4-7.5.

Note. This series was determined by G.Ya. Bey-Bienko.



Figs 123-132. Genera *Trichoblatta* and *Paranauphoeta*, males. 123, *T. pilosa* B.-Bien. (holotype); 124, 125, *T. humbertiana* (Sauss.); 126, *P. vicina vietnamensis* ssp. n. (holotype); 127, *P. lyrata* (Burm.); 128, *P. formosana* Mats.; 129, *P. rufipes* Brunn.; 130, 131, *P. nigra* B.-Bien. (holotype); 132, *P. indica* Sauss. & Zehn. (specimen from Assam). Male genitalia, general view from above (123, 125); abdominal apex from below (124); sclerites L2d and L3d from above (126); L2d from above (127-129, 131, 132) and from side (130). Dotted area shows membranous (123, 125) and sclerotized parts (124).

Trichoblatta? **pilosa** (Bey-Bienko, 1965) (Figs 62-64, 123)

Holotype. J, Indonesia, Komodo Is., 5.VIII.1962 (I.S. Darevsky).

The original description by Bey-Bienko (1965) may be supplemented with the following data.

Male (holotype). General colour yellowish brown; vertex, antennae, maxillary and labial palpi, lower parts of thorax and abdomen lighter; eyes black. Head comparatively wide (Bey-Bienko, 1965: Fig. 1); pronotum as in Fig. 62. Anal plate weakly prominent caudally, its posterolateral angles distinct (Fig. 63); hypandrium asymmetrical, styli absent (Fig. 64).

Male genitalia (Fig. 123). Apical sclerite L1 weakly sclerotized, its lateral parts membranous; sclerite L2d without median incision, with a small tooth near apex; complex of sclerites R+N weakly sclerotized, R2 almost straight.

Female unknown.

Length (mm): head 1.8; pronotum 3.1; tegmina 10.2. Width (mm): head 1.5; pronotum 4.4.

Note. This species was described in the genus *Glomeriblatta* Bey-Bienko, which is a synonym of *Trichoblatta*. However, the generic position of *T. pilosa* cannot be precisely determined without examining the female.

Genus Glomerexis Bey-Bienko, 1938

Type species: *Glomerexis tibetana* Bey-Bienko, 1938. *Diagnosis*. Sexual dimorphism weakly expressed; males and females completely wingless.

The feminization of males may be considered an autapomorphy of this genus.

Both sexes similar to females of *Trichoblatta*. *Included species*. Only the type species.

Note. It is possible that *Glomerexis* is nothing more than a subgenus of *Trichoblatta*. However, more accurate assessment of the systematic position of this genus is impossible without examination of the male genitalia.

Glomerexis tibetana Bey-Bienko, 1938 (Figs 14, 37)

Paratype. 1 9, "East Tibet: Poshö. 9-12000 ft. 12-28.VIII.1936", "R.J.H. Kaulback. B.M. 1937-547".

Other material examined. 3 9, "A-tun-tse (Nord Yunnan), Taleohle (ca. 3500 m), 20-26.VI.1936, H. Höne".

The original description by Bey-Bienko (1938) may be supplemented with the following data.

Female. Head elongate, eyes not contiguous at vertex (Fig. 37).

Each side of 3rd-7th abdominal tergites with 2, 2-3, 2-3, 3-4, 3-4 orifices (in paratype, 3, 3, 3, 3), respectively; some of orifices very poorly visible and probably rudemintary.

Male. Similar to female, not examined in scope of this work.

Length (mm): head 2.9-3.2 (3.2); pronotum 4.5-5 (5). Width (mm): head 2.3-2.6 (2.5); pronotum 7.8-8.6 (8.4). Measurements in parentheses are those of paratype.

Note. This species was described from Tibet (Bey-Bienko, 1938) and later was found in Yunnan, South China (Bey-Bienko, 1954).

Genus Perisphaerus Serville, 1831

Type species: Perisphaera armadillo Serville, 1831.

Diagnosis. Sexual dimorphism strongly expressed: males with tegmina and wings fully developed, females completely wingless. Body of female distinctly arcuate in section. Female can roll itself into a ball. In female, abdominal tergites with few orifices, probably of glandular nature (Fig. 8); number of orifices more or less stable within species.

The capability of females of *Perisphaerus* to roll itself into a ball probably may be considered an autapomorphy of this genus.

Female of *Perisphaerus* is similar to that of *Trichoblatta*, except for diagnostic features. Males of these genera are practically indistinguishable.

Included species. Those included by Princis (1964, 1971).

Perisphaerus semilunatus Hanitsch, 1927 (Figs 31, 39, 57, 65, 70, 88, 117, 120)

Material. China, prov. Yunnan: 2 larvae, 30 km SW of Jinping, 400 m, 25.IV.1956 (Hwang Ke-yen et al.); 1 9, env. of Pingbian, 1500 m, 17.VI.1956 (Hwang Ke-yen et al.). Vietnam, prov. Vinh Phu: 3 larvae, Tam Dao, 800-900 m, primary forest, 9-18.II.1990 (A. Gorochov); 1 o', same data, but 8.V.1994 (collector unknown); 2 9, 1 or, 5 larvae, same data, but 17.V-10.VI.1995 (A. Gorochov); prov. Bacthai: 2 9, distr. Phu Luong, Quang Chu, 300 m, 15-23.IV.1986 (A. Gorochov); prov. Son La: 1 9, 1 larva, env. of Song Ma, 400-600 m, 3-14.V.1986 (A. Gorochov); prov. Gia Lai: 2 larvae, 20 km N of Kannack, Buon Luoi, 21-30.XI.1988 (A. Gorochov); 1 9, 1 larva, same data, but 1-10.V.1995; 1 9, NO of Thai Nguyen, 5-12.III.1963 (O. Kabakov); 1 larva, Cat-ba I., 31.X.1979 (V. Januschev); 1 larva, 50 km N of An Khe, 31.X.1979 (V. Januschev); 1 9, 3 larvae, Tham I., near Da Nang, 4-29.III.1987 (V. Januschev).

The original description by Hanitsch (1927) may be supplemented with the following data.

Female. Frons with a black macula considerably varying in shape and intensity of coloration; antennae of specimens examined, except yellowish scapus, from light to dark brown, not black as indicated by Hanitsch. Each side of 3rd-7th abdominal tergites with 0, 1, 1, 1, 1 orifices, respectively; two specimens from "Phu Luong" and one specimen from Pingbian with 0, 1, 1, 2, 2 orifices. Anal plate trapezoidal (Fig. 57).

Description of male (nov.). General colour brownish; pronotum, proximal half of tegmina, head and eyes dark brown; thorax except pronotum, distal half of tegmina, abdomen dorsally and ventrally, scapus and, mostly, legs yellowish brown, partially yellow; ocelli, labrum and mouthparts, maxillary palpi, tarsi, anal plate and hypandrium yellow; hind wing translucent, except part anterior to R, slightly darkened (brownish) only along anterior margin of wing. Head as in Fig. 39; facial part of head somewhat rugose, sculptured between antennal pits. Pronotum subpentagonal, sculptured (Fig. 31). Anal plate trapezoidal, its posterior margin slightly projected (Fig. 70); hypandrium asymmetrical, styli present but strongly abbreviated (Fig. 65).

Male genitalia. Apical sclerite L1 wide, with membranous lateral parts (Fig. 120); L2d short, without median incision (Fig. 117); complex of sclerites R+N (Fig. 88): R3d comparatively slightly sclerotized, R2 strongly curved, R3v short, N large.

Length (mm): head φ 4.5-4.8, σ 3.1-3.2; pronotum φ 7.7-9.9, σ 5.5; tegmina σ 19-20. Width (mm): head φ 3.3-3.9, σ 2.4-2.6; pronotum φ 10.8-13, σ 8.5-8.7.

Notes. This species was described from "Langbian Peaks, S. Annam, 5.500-7.500 feet" from two females (Hanitsch, 1927: p. 28).

The identification of male of this species is based on two specimens only and, consequently, needs confirmation in future.

Perisphaerus punctatus Bey-Bienko, 1969 (Figs 56, 71, 89, 121, 122)

Holotype. 9, Vietnam, prov. Vihn Phu, Tam Dao, near "Dao Tru", 16-18.XI.1961 (O. Kabakov).

Paratype. 1 larva, **China**, *prov. Yunnan*: mouth of river Nandinhe, 200 m, no. 1026 A, 7.VI.1956 (V. Popov).

Other material examined. Vietnam, prov. Ha Son Binh: 1 o, distr. Hoa Binh, Ky Son, vill. Cao Phong, 250 m, 24-29.X.1990 (A. Gorochov); prov. Quang Nam Da Nang: 1 o, near Da Nang, 3-4.XII.1993 (A. Gorochov); prov. Gia Lai: 1 larva, 20 km N of Kannack, Buon Luoi, 24-27.III.1995 (A. Gorochov); 1 o, Tham I., near Da Nang, 4.III.1987 (V. Januschev); 2 larvae, Baitylong Is., Dongkho I., 22.III.1987 (V. Januschev); 1 larva, Siam Bay, Thotu I., 8-10.IV.1987 (V. Januschev).

The original description by Bey-Bienko (1969) may be supplemented with the following data.

Female. Each side of 3rd-7th abdominal tergites with 0, 2, 2, 2, 2 orifices (in holotype, 0, 2, 2, 2, 2), respectively.

Description of male (nov.). Similar to that of *P. semilunatus*, differing from it in smaller size, more rounded and caudally prominent anal plate (Fig. 71), absence of styli (Fig. 56), shape of sclerite L1 (Fig. 122) and complex of sclerites R+N (Fig. 89).

Length (mm): head 9 2.6-2.9 (2.6), of 2; pro-

notum 9 4.1-5.2 (5), σ 3.1; tegmina σ 12.5. Width (mm): head 9 2-2.6 (2.3), σ 1.7; pronotum 9 6.2-7.3 (6.8), σ 4.8. Measurements in parentheses are those of holotype.

Note. The identification of male of this species is based on a single specimen only and, consequently, needs confirmation in future.

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