New data on the family Blaberidae (Dictyoptera) from Southeast Asia: new species, morphological diversity and phylogeny on the base of ribosomal DNA sequences

Новые данные о семействе Blaberidae (Dictyoptera) из Юго-Восточной Азии: новые виды, морфологическое разнообразие и филогения на основании последовательностей рибосомальной ДНК

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New cockroaches of the family Blaberidae are described from Southern Sumatra: two new species of the genus *Cyrtonotula* Uvarov, 1939, *C. secunda* **sp. nov.** and *C. tertia* **sp. nov.** (Epilamprinae); and one new species of the genus *Paranauphoeta* J.W.H. Rehn, 1951, *P. pullata* **sp. nov.** (Paranauphoetinae). Detailed morphological descriptions of the new species are given. Structures of the male genitalia of the genus *Cyrtonotula* are described for the first time. Hypothesis on the relationships of these new taxa as well as *Morphna maculata* Brunner von Wattenwyl, 1865, *Rhabdoblatta* sp. and *Pseudophoraspis* sp. based on 28S ribosomal DNA sequences is discussed.

Из Южной Суматры описываются новые тараканы семейства Blaberidae: два новых вида рода *Cyrtonotula* Uvarov, 1939, *C. secunda* **sp. nov.** и *C. tertia* **sp. nov.** (Epilamprinae), и один новый вид из рода *Paranauphoeta* J.W.H. Rehn, 1951, *P. pullata* **sp. nov.** (Paranauphoetinae). Для новых видов дается детальное морфологическое описание. Строение гениталий самцов впервые описывается у представителей рода *Cyrtonotula*. Обсуждается выдвинутая на основании изучения 28S рибосомальной ДНК гипотеза о родственных отношениях новых таксонов, а также *Morphna maculata* Brunner von Wattenwyl, 1865, *Rhabdoblatta* sp. и *Pseudophoraspis* sp.

Key words: cockroaches, taxonomy, morphology, phylogeny, 28S ribosomal DNA, Southeast Asia, Dictyoptera, Blaberidae, Epilamprinae, Paranauphoetinae, *Cyrtonotula*, *Paranauphoeta*, new species

Ключевые слова: тараканы, таксономия, морфология, филогения, 28S рибосомальная ДНК, Юго-Восточная Азия, Dictyoptera, Blaberidae, Epilamprinae, Paranauphoetinae, *Cyrtonotula*, *Paranauphoeta*, новые виды

INTRODUCTION

In the present paper, new representatives of the family Blaberidae Brunner von Wattenwyl, 1865 are described from Southeast Asia. There are two new species of the genus *Cyrtonotula* Uvarov, 1939, belonging to the subfamily Epilamprinae Brunner von Wattenwyl, 1865, and one new species of *Paranauphoeta* Brunner von Wattenwyl, 1865, belonging to the subfamily Paranauphoetinae J.W.H. Rehn, 1951. Ribosomal DNA sequence data of the described taxa and males of the genus *Cyrtonotula* are considered for the first time. A provisional hypothesis regarding the relationships in the studied taxa is proposed on the base of the consensus cladogram that was inferred from the 28S ribosomal DNA fragment sequence data.

The subfamily Epilamprinae is one of the largest and most diverse subfamilies of Blaberidae. It is widely distributed in regions with wet tropical climate and is known since at least the Paleocene epoch (Vršansky et al., 2013). The subfamily Paranauphoetinae includes a single genus of uncertain systematical position, *Paranauphoeta*. It undoubtedly belongs to Blaberidae, but its relationships within the family are unclear (for details see: Anisyutkin, 2003a). There are no paleontological data on *Paranauphoeta* yet.

MATERIAL AND METHODS

The material studied was collected in tropical forests at light or during night work with the use of a flashlight on the leaves of trees and bushes. The material was preserved in 70% ethanol.

The male genitalia were processed with alkali by means of a standard procedure (Anisyutkin et al., 2013) for 12–24 hours for maceration of the soft tissues. The illustrations were sketched by means of a drawing tube on a Leica MZ 16 binocular microscope; further drawing and examination were made with an MBS–10 binocular microscope.

The ratio of "distance between eyes" to "length of eye" was measured as the interocular distance on the vertex (*i.o.* in Fig. 1A) to the dorsoventral length of eye (*d.e.* in Fig. 1A). Types of the anterior margin of fore femur armament are given according to Bey-Bienko (1950) and Roth (2003). The terminology of the male genital sclerites follows Klass (1997) but with some modifications (Anisyutkin, 2014; Anisyutkin et al., 2013). The terminology used by Grandcolas (1996) for genital structures is given in parentheses following the author's designations. The terms introduced by the author are given in quotation marks.

The material studied (including type specimens) is deposited at the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia.

Abbreviation used in figures

(see text for further details):

a.s., "additional spines", i.e. spines bordering euplantulae from inside and outside;

ap.scl., "apical sclerite" of sclerite L2D in the male genitalia;

b.hla., basal membranous part of sclerite L3;

b.L2D, basal part of sclerite L2D in the male genitalia;

b.L3, basal subsclerite of sclerite L3 in the male genitalia;

c.b.m.a., "chaetae-bearing membranous area" located between right phallomere and sclerite L2D;

c.b.m.l., "chaetae-bearing membranous lobe" located above basal part of sclerite L2D;

c.p.R1T, caudal part of the sclerite R1T in the male genitalia;

cr.p.R1T, cranial part of the sclerite R1T in the male genitalia;

d.e., dorsoventral length of the eye;

f.s., "folded structure" of the sclerite L3 in the male genitalia;

hge., groove of the sclerite L3 in the male genitalia (= hge);

hla, sclerotized apical part of the sclerite L3 in the male genitalia (sensu Klass, 1997);

hl., hollow on the sclerite R2 in the male genitalia;

i.o., interocular distance on the vertex;

L2D, L3, L4U, sclerites in the male genitalia;

Par., paraproct;

pr.s., preputial spines located at the "apical sclerite" of sclerite L2D of the male genitalia;

pv., sclerite at the base of the cerci (= pv-sclerite);

r.plm., right phallomere of the male genitalia;

R1T, *R2*, *R3*, *R4*, *R5*, sclerites in the male genitalia.

DNA analysis

DNA extraction, PCR amplification and sequencing

Total genomic nucleic acids were extracted from ethanol-fixed insects using a standard DNA extraction buffer (Tris–HCl, proteinase K, SDS) according to the protocol described in Mukha et al. (1995). DAMS-18 (gtccctgccgtttgtacaca) and DAMS-28 (ctactagatggttcgattagtc) primers were used for DNA amplification and sequencing. The priming sites for DAMS-18 and DAMS-28 are highly conserved in eukaryotes; these primers are "universal" and may be used for the amplification of the corresponding ribosomal DNA fragments across a broad taxonomic range of organisms (Mukha & Sidorenko, 1995, 1996; Mukha et al., 2000; Mukha et al., 2002).

PCR amplification of the analyzed rDNA fragments was carried out using Master Mix (2X) (Fermentas, Vilnius, Lithuania) according to the manufacturer's recommendations and performed using a Primus 25 advanced Thermocycler (PEQLAB, Erlangen, Germany). The PCR regimen was as follows: initial template denaturation at 95°C for 5 min, followed by 30 cycles at 94°C for 1 min, 55°C for 2 min, and 72°C for 3 min, and a final 7 min elongation cycle at 72°C. PCR-amplified single bands were resolved on 1.0% agarose gels and were extracted with QIAquick Gel Extraction Kits (QIAGEN, Hilden, Germany). Cleaned products were cloned into pGEM-T Easy vectors (Promega), and transformed into *Escherichia coli* JM109 competent cells (Promega) following the manufacturer's protocol. Amplified DNA fragments and several clones were sequenced for each specimen.

Automated sequences were generated on an ABI PRISM® 310 Genetic Analyzer according to Sanger et al. (1977) with a BigDye Termination kit (Applied Biosystems). Opposite strands were confirmed for all templates. ABI trace files were edited and contigs were assembled using the program ChromasPro v. 1.7.6 (http://technelysium.com.au/?page_id=27).

Nucleotide alignment and phylogenetic analysis

Sequences from this study for *Paranauphoeta pullata* **sp. nov.**, *Cyrtonotula tertia* **sp. nov.**, *C. secunda* **sp. nov.**, *Pseudophoraspis* sp. and *Rhabdoblatta* sp. are under the accession numbers KJ194457, KJ184844, KJ194458, KJ194459 and KJ194460, respectively. Furthermore for the reconstruction of the phylogenetic tree, the following rDNA sequences were used: *Archimandrita tesselata* J.A.G. Rehn, 1903 (acc. # GU384924), *Blaberus atropos* (Stoll, 1813) (acc. # AF321252), *Morphna maculata* (acc. # KM659175), *Symploce pallens* (Stephens, 1835) (acc. # KF922887), *Parathemnopteryx couloniana* (Saussure, 1863) (acc. # KF922888), *Parcoblatta lata* (Brunner von Wattenwyl, 1865) (acc. # AF321247), *Blattella vaga* Hebard, 1935 (acc. # AF321246), *Blattella lituricollis* (Walker, 1868) (acc. # AF321245), *Blattella asahinai* Mizukubo, 1981 (acc. # AF321253), *Blattella germanica* (Linnaeus, 1767) (acc. # AF005243), *Archiblatta* sp. (acc. # KM659176), *Periplaneta americana* (Linnaeus, 1758) (acc. # AF321248), *Periplaneta brunnea* Burmeister, 1838 (acc. # AF321249), *Periplaneta fuliginosa* Serville, 1838 (acc. # AF321250), and *Mantis religiosa* (Linnaeus, 1758) (acc. # AY859585).

A fragment of the 28S gene from each of the analyzed species was used for analysis. Alignment was constructed using the MAFFT v.7 (Q-INS-I method) (http://mafft.cbrc.jp/alignment/server/) (Katoh & Standley, 2013) and Gblocks v.0.91b (http://www.phylogeny.fr/version2_cgi/one_task.cgi?task_type=gblocks) (Castresana, 2000; Dereeper et al., 2008) software programs. The combination of these two approaches allowed us to align the sequences and eliminate the poorly aligned and highly divergent regions. Default parameters were used for both of these methods.

rDNA-based phylogenetic trees were estimated using probabilistic (maximum likelihood [ML], Bayesian [MrBayes]) and parsimony (maximum parsimony [MP]) methods (Fitch, 1971; Felsenstein, 1981; Huelsenbeck et al., 2001; Huelsenbeck & Ronquist, 2001). MP and ML analyses were conducted using the program MEGA version 6.05 (Tamura et al., 2013). MrBayes analysis was conducted using the program MrBayes version 3.2.2 (Ronquist et al., 2012).

The MP tree was obtained using the Subtree-Pruning-Regrafting (SPR) algorithm (Nei & Kumar, 2000) with search level 1, in which the initial trees were obtained by the random addition of sequences (10 replicates).

For the ML analysis, the evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model (Nei & Kumar, 2000). The initial trees for the heuristic search were obtained automatically by applying the Neighbor-Joining and BioNJ algorithms to a matrix of pairwise distances, estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model the evolutionary rate differences among the sites (2 categories (+*G*, parameter = 0.2790)).

Branch support was assessed by the bootstrap method (Felsenstein, 1985) (1000 replicates) using the close-neighbor-interchange (CNI) algorithm with the heuristic search for the ML analysis, and by calculation of the percentage of replicate trees in which the associated taxa clustered together for the MP analysis.

Bayesian analysis was conducted using MrBayes version 3.2.2. We performed two replicate analyses of 1 million generations each for each data set, sampling every 100 generations. The hierarchical likelihood ratio test (hLRT) implemented in the MrModeltest version 2.3 (Nylander, 2004) was used to find the best fitting GTR+G model. Trees from the first 2500 generations were discarded as burn-in. The Bayesian tree was estimated from the majority-rule consensus of the post-burn-in trees.

SYSTEMATIC PART

Order **DICTYOPTERA** Clairville, 1798

Family **Blaberidae**
Brunner von Wattenwyl, 1865

Subfamily **Epilamprinae**
Brunner von Wattenwyl, 1865

Tribe **Morphnini** McKittrick, 1964

Genus ***Morphna*** Shelford, 1910

Type species *Epilampra maculata* Brunner von Wattenwyl, 1865, by subsequent designation.

Note. The genus includes 13 species from South and Southeast Asia (Beccaloni, 2015; Anisyutkin, 2014; Anisyutkin & Gorochov, 2001).

Morphna maculata
Brunner von Wattenwyl, 1865

Material. Male (prep. 141012/03); **Malaysia**, Borneo I., Sarawak State, environs of Kuching City, Bako National Park, lowland forest and forest on hills, near sea bank, 18–22 March 2012, A. Gorochov, M. Berezin, E. Tkatsheva, I. Kamskov.

Note. Data on this specimen are here indicated, as it was used in the present molecular analysis.

Genus ***Cyrtonotula*** Uvarov, 1939

=*Cyrtonota* Hanitsch, 1929

Type species *Cyrtonota lata* Hanitsch, 1929, by monotypy.

Note. The genus *Cyrtonota* Hanitsch, 1929 was described from Sumatra as monotypical one from a single female (Hanitsch, 1929). Later, it was renamed by Uvarov (1939) due to the preoccupation of the name "*Cyrtonota*". Males of *C. lata* remain undescribed to the present.

Three complexes of diagnostic characters were indicated in the original description of the genus (Hanitsch, 1929): a comparatively large, semicircular, anteriorly and posteriorly produced pronotum; shortened tegmina and wings, not reaching the abdominal apex; and the following structure of the hind tarsi: "tarsi moderately long; posterior metatarsus barely as long as the succeeding joints, biseriately spined beneath, its pulvillus apical; remaining joints also biseriately spined beneath, with apical pulvilli; tarsal arolia present" (Hanitsch, 1929: 281, 282). The increasing size of the pronotum and the simultaneous shortening of the tegmina and wings are common in cases when there is a shift from a comparatively open mode of life to more hidden one. The type of hind tarsi described here is very common in epilamprines and is probably plesiomorphic. Thus, the present diagnosis of the genus is insufficient, and possibility of the independent appearance of these diagnostic characters in *C. lata* and in the species described below cannot be excluded. Thus, description of male and its genitalia in *C. lata* elucidates the taxonomic position of the genus *Cyrtonotula*.

Females of both new species of the genus *Cyrtonotula* described below are unknown, but we can deduce that they have an expressed reduction of the tegmina and wings, which is the general rule for the cockroaches: shortening of the tegmina and wings due to sexual dimorphism is always more expressed in females. Since the males have somewhat reduced organs of flight, it can be concluded that their females are also brachypterous (possibly apterous).

Composition. The type species; *C. secunda* **sp. nov.**; *C. tertia* **sp. nov.**

***Cyrtonotula secunda* sp. nov.**
(Figs 1A–N, 4A, B)

Holotype. Male (prep.: Epil. ex 1908/01), **Indonesia**, Sumatra I., Bengkulu Prov., 25 km S of Bintuan Town, environs of Tanjung Baru Maje vill., 04°50.279′S 103°28.071′E, ~100 m, 2–3 May 2009, A. Gorochov, M. Berezin, E. Tkatsheva.

Description. Male. General colour yellowish brown with scattered brown spots (Figs 1A, 4A, B); facial part of head and eyes black; vertex speckled with black; upper and lateral parts of head yellowish; ocellar spots, clypeus and labrum whitish; pronotum with central part darker; tegmina yellowish brown, lighter in apical parts, with pale spots; legs reddish brown, but with coxae and femora darker (partly blackish) and tarsi yellowish; abdomen brownish, but its sternites darker and with dark (nearly black) dots; anal plate in caudal part pale; cerci light yellow with ultimate segment darkened. Surfaces smooth and lustrous. Head in front with rounded vertex (Figs 1A, 4B); ocellar spots distinct; facial part without impressions or wrinkles; distance between eyes about equal to length of eye; distance between antennal sockets approximately 1.7 times the length of the scape (1.0 mm); approximate length ratio of 3rd–5th segments of maxillary palps 1.1 : 1.0 : 1.6. Pronotum as in Figs 1B, 4A. Tegmina and wings weakly abbreviated, not reaching abdominal apex. Venation of tegmina distinct; *Sc* thickened (easily visible on ventral side of tegmen); branches of *R*, *M* and *CuA* numerous and parallel; *CuP* distinct; apices of tegmina rounded. Anterior margin of fore femur armed according to type B (*sensu* Bey-Bi-

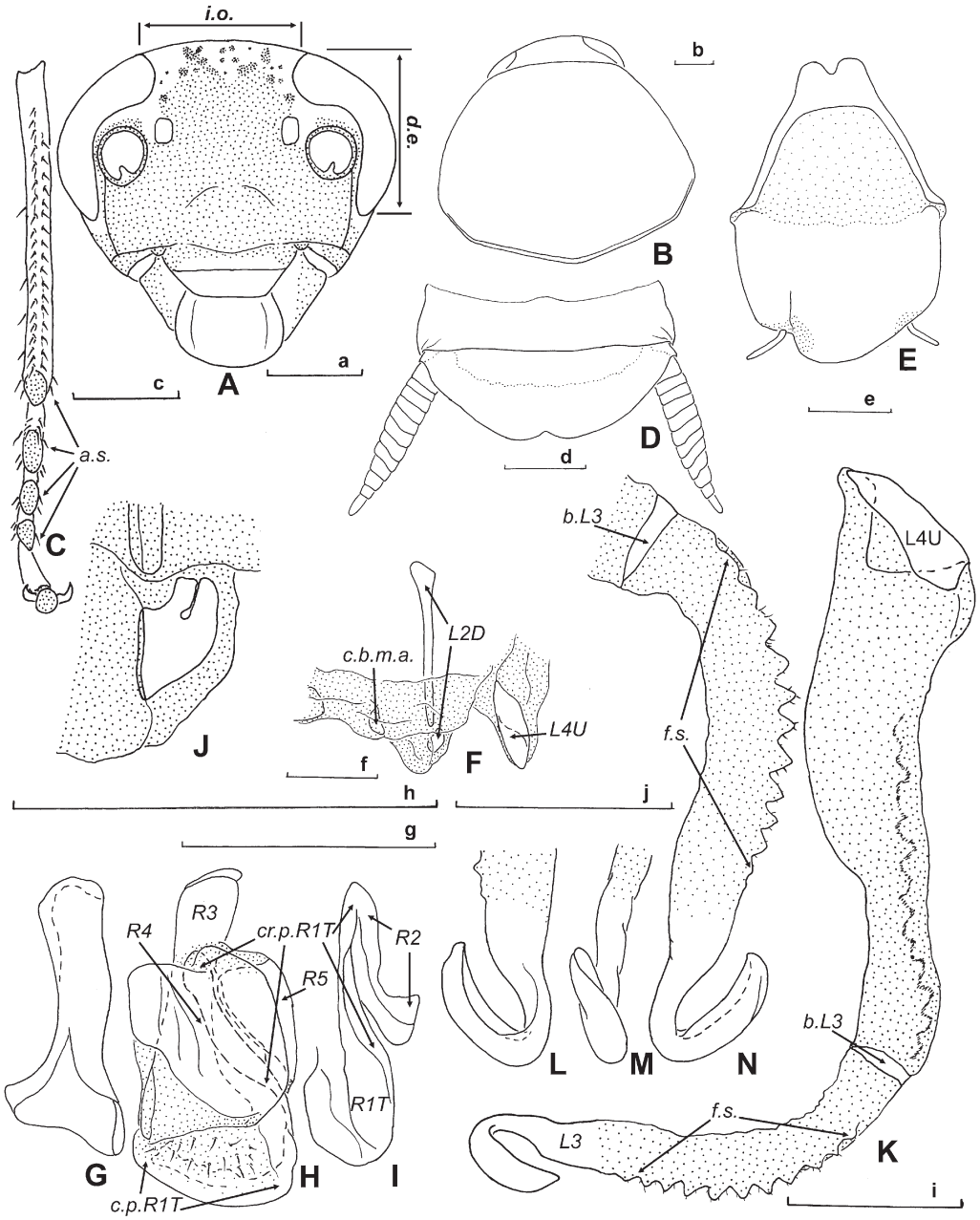

Fig. 1. *Cyrtonotula secunda* **sp. nov.**, holotype. A – facial part of head; B – pronotum and head from above; C – right hind tarsus from below; D – abdominal apex from above; E – hypandrium from below; F – sclerites L2D, L4U and adjacent structures of the male genitalia from above; G – sclerite R3 from below; H – right phallomere from above; I – sclerites R1T and R2 of the right phallomere from side; J – caudal part of sclerite L2D from above; K – left hook (*hla*) in everted station and sclerite L4U; L–N – apical part of hook *hla*. Dotted area shows dark colour (A) or membranous parts (C, E, F, H, J–N). Abbreviations: *a.s.*; *b.L3*; *c.b.m.a.*; *c.p.R1T*; *cr.p.R1T*; *d.e.*; *f.s.*; *i.o.*; *L2D*; *L3*; *L4U*; *R1T*; *R2*; *R3*; *R4*; *R5* – see text. Scale bars 1 mm (**a** for A; **b** for B; **c** for C; **d** for D; **e** for E; **f** for F; **g** for G–I; **h** for J; **i** for K; **j** for L–N).

enko, 1950; Roth, 2003): with 6–7 spines including two apical ones. Fore tibiae not thickened distally. Structure of hind tarsus (Fig. 1C): metatarsus distinctly longer than other segments combined; metatarsus and 2nd segment with two relatively equal rows of spines along lower margin; 1st–4th segments with "additional spines" bordering euplantulae from inside and outside (Fig. 1C: *a.s.*); euplantula small and apical; claws symmetrical and simple; arolium well developed, slightly shorter than claw. Abdomen without visible specializations. Anal plate (tergite X) wide and rounded, with weak caudal incision (Fig. 1D). Cerci slightly flattened dorsoventrally, with segments distinctly separated (Fig. 1D). Paraprocts of blaberid type; pv–sclerites indistinct. Hypandrium asymmetrical (as in Fig. 1E); styli slender, more or less equal in size, cylindrical (Fig. 1E).

Male genitalia (Fig. 1F–N). Right phallomere (R+N) with caudal part of sclerite R1T subrectangular in shape (Fig. 1H: *c.p.R1T*), covered with few bristles; cranial part of R1T nearly straight (Fig. 1H: *cr.p.R1T*); R2 distinctly curved (Fig. 1I); R3 elongated (Fig. 1G, H); R4 and R5 large (Fig. 1H); R5 fused with sclerite R3 in caudal part (Fig. 1H). Small "chaetae-bearing membranous area" located between right phallomere and sclerite L2D (Fig. 1F: *c.b.m.a.*). Sclerite L2D (L1) divided into basal and apical parts (Fig. 1F, J); basal part rod-like, moderately widened cranially (Fig. 1F); apical part in shape of curved sclerotized plate (Fig. 1F, J); very weak bristles present (visible at high magnification) on membranous lobe located in posterior part of sclerotized plate (not shown in Fig. 1F, J). Sclerite L3 (L2d) with distinct basal subsclerite (Fig. 1K, N: *b.L3*); "folded structure" distinct, with bristles (Fig. 1K, N: *f.s.*); hge absent. Sclerite L4U (L3d) large (Fig. 1F, K).

Female unknown.

Measurements (mm). Head length 3.4; head width 3.5; pronotum length 5.1; pronotum width 6.4; tegmen length 15.5; tegmen width (in place where *CuP* running into anal margin of tegmen) 5.5.

Comparison. The new species readily differs from *C. lata* (the single previously known species of the genus *Cyrtonotula*) in the colour of the head (partly black in *C. secunda* **sp. nov.** but testaceous in *C. lata*) and in a comparatively longer hind metatarsus [distinctly longer than the other tarsal segments combined in *C. secunda* **sp. nov.**; in *C. lata*, this metatarsus is "as long as the remaining joints" (Hanitsch, 1929: 283)].

Cyrtonotula tertia sp. nov.
(Figs 2A–O, 4C, D)

Holotype. Male (prep.: Epi1 1908/02); **Indonesia**, Sumatra I., Bengkulu Prov., environs of Curup Town (not far from Bengkulu City), 03°28–29'S, 102°31–38'E, 1000–1500 m, 24 April – 2 May 2009, A. Gorochov, M. Berezin, E. Tkatsheva.

Paratypes. Three males; same data as for holotype.

Description. Male (holotype). General colour yellowish brown, with scattered brown spots (Figs 2A, 4C, D); facial part of head and eyes black; vertex and occiput with yellowish striation; ocellar spots, anteclypeus and labrum pale yellowish; pronotum bordered with yellow, with scattered black dots; tegmina yellowish brown, with dark spots along costal margins; coxae partly blackish; tarsi yellowish; abdomen brownish; anal plate pale, speckled with small brownish dots; cerci yellowish, with proximal (partly) and ultimate segments darkened. Surfaces smooth and lustrous, only costal area of tegmina moderately punctured. Head in front with rounded vertex, about as long as wide (Figs 2A, 4C); ocellar spots distinct; facial part without impressions or wrinkles; distance between eyes approximately 0.9 of eye length; distance between antennal sockets approximately 1.8 times as great as scape length (0.8 mm); approximate length ratio of 3rd–5th segments of maxillary palps 1.0 : 1.0 : 1.1. Pronotum as in Figs 2B, 4C. Tegmina distinctly shortened (Figs 2B, 4C); wings vestigial, completely covered with tegmina.

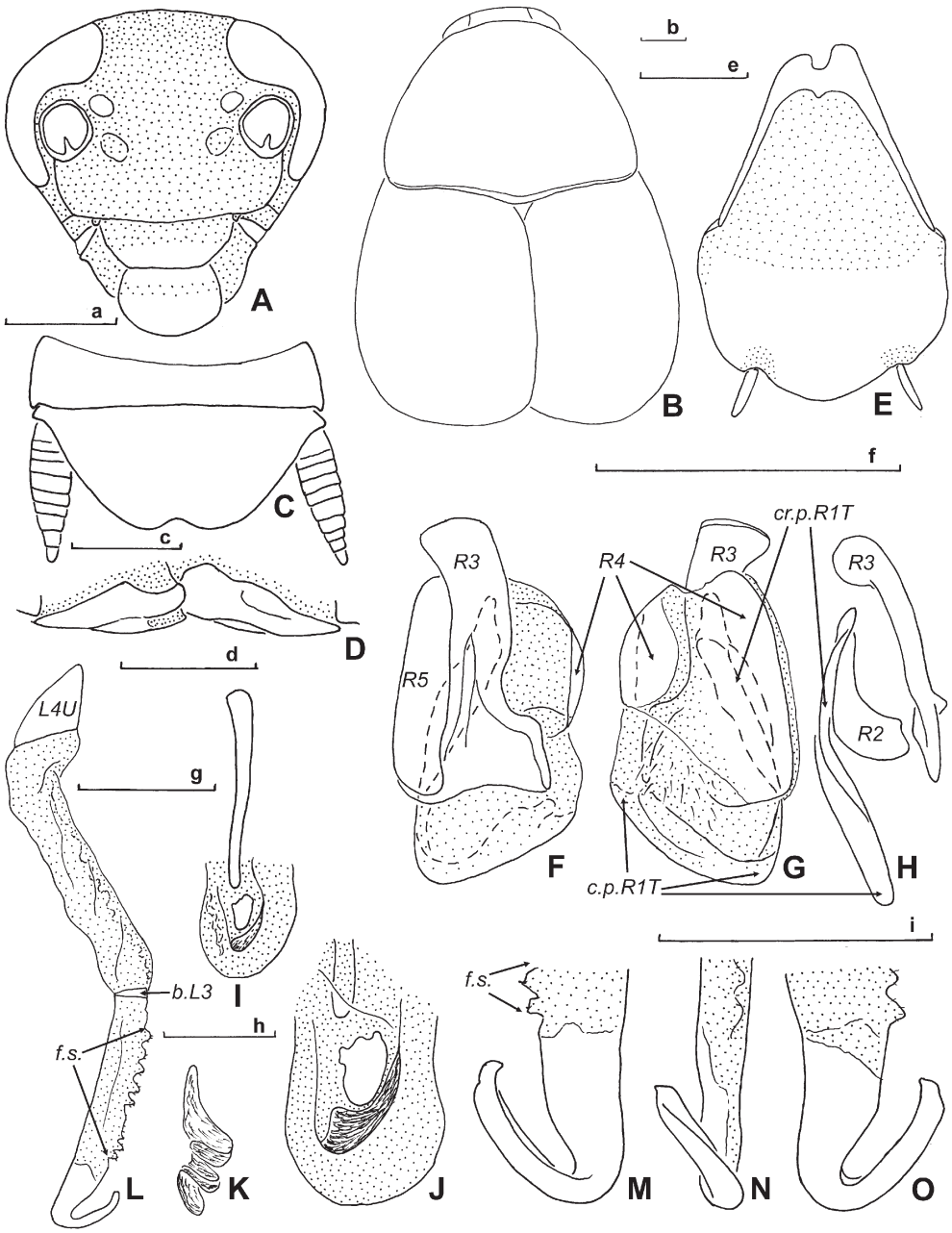

Fig. 2. *Cyrtonotula tertia* **sp. nov.,** (A–K, M–O – holotype; L – paratype). A – facial part of head; B – anterior part of body from above; C – abdominal apex from above; D – paraprocts from below; E – hypandrium from below; F, G – right phallomere of the male genitalia from below (F) and above (G); H – sclerites R1T, R2 and R3 from side; I – sclerite L2D from above; J – caudal part of sclerite L2D from above; K – "chaetae-bearing membranous area" from above; L – left hook (*hla*) in everted station and sclerite L4U; M–O – apical part of hook *hla*. Dotted area shows dark colour (A) or membranous parts (D–G, I, J, L–O). Abbreviations: *b.L3*; *c.p.R1T*; *cr.p.R1T*; *f.s.*; *L4U*; *R2*; *R3*; *R4*; *R5* – see text. Scale bars 1 mm (**a** for A; **b** for B; **c** for C; **d** for D; **e** for E; **f** for F–H, J, K; **g** for I; **h** for L; **i** for M–O).

Venation of tegmina simplified, but main veins (*Sc*, *R* and *CuP*) distinct, *Sc* thickened (clearly visible on ventral side of tegmen). Anterior margin of fore femur armed according to type B (sensu Bey-Bienko, 1950; Roth, 2003): with 5–6 spines, including two apical ones. Fore tibiae distally not thickened. Structure of hind tarsi similar to that of *C. secunda* **sp. nov.** Abdomen without visible specializations. Anal plate (tergite X) triangular in shape, with weak caudal incision (Fig. 2C). Cerci slightly flattened dorsoventrally, with segments distinctly separated (Fig. 2C). Paraprocts of blaberid type (Fig. 2D); pv–sclerites distinct. Hypandrium weakly asymmetrical (as in Fig. 2E); styli slender, approximately equal in size, cylindrical (Fig. 2E).

Male genitalia (Fig. 2F–O). Right phallomere (R+N) with caudal part of sclerite R1T subrectangular in shape (Fig. 2F, G: *c.p.R1T*), covered with few bristles, cranial part of R1T nearly straight (Fig. 2F–H: *cr.p.R1T*); R2 short and curved (Fig. 2G, H); R3 long (Fig. 2F–H); R4 large, divided into two parts by medial membranous strip; R5 weakly sclerotized, covered with sclerite R4 (Fig. 2G) and fused with sclerite R3 (Fig. 2F). Small folded "chaetae-bearing membranous area" located between right phallomere and sclerite L2D (Fig. 2K). Sclerite L2D (L1) divided into basal and apical parts (Fig. 2I); basal part rod-like; apical part in shape of sclerotized plate (Fig. 2I, J), with weak bristles (visible at high magnification) on membranous lobe located in posterior part of sclerotized plate. Sclerite L3 (L2d) with distinct basal subsclerite (Fig. 2L: *b.L3*); "folded structure" distinct, with short bristles (Fig. 2L–O: *f.s.*); hge absent. Sclerite L4U (L3d) large (Fig. 2L).

Variations. Distance between antennal sockets approximately 1.6–1.8 times as great as length of scape (0.8 mm); approximate length ratio of 3rd–5th segments of maxillary palps 1.0–1.3 : 1.0 : 1.1–1.3. Anterior margin of fore femur with 5–7 spines including 1–2 apical ones. The male genitalia: sclerite R4 of the right phallomere in one paratype whole (without membranous strip).

Female unknown.

Measurements (mm). Head length 2.9–3.1 (3.0); head width 2.9–3.0 (2.9); pronotum length 4.1–4.5 (4.5); pronotum width 5.2–5.7 (5.2); tegmen length 5.4–5.5 (5.5); tegmen width (in place where *CuP* running into anal margin of tegmen) 3.8–4.0 (4.0). Holotype measurements in parentheses.

Comparison. C. tertia **sp. nov.** is most closely related to *C. secunda* **sp. nov.** The new species readily differs from the latter species and *C. lata* in strongly abbreviated tegmina.

Genus ***Pseudophoraspis*** Kirby, 1903

Type species *Epilampra nebulosa* Burmeister, 1838, by original designation.

Note. The genus includes 18 species from South China and Southeast Asia (Beccaloni, 2015), and several new species await description (Anisyutkin, unpublished data). This genus needs revision, that is why we prefer to postpone a precise determination of the specimen listed below.

***Pseudophoraspis* sp.**

Material. 1 male (prep.: Pseudo ex 2408/3); **Indonesia**, Sumatra I., Sumatera Selatan Prov., environs of Banding Agung Vill. on Ranau Danau Lake, 04°48.695′S, 103°55.289′E, 600–700 m, 19–22 April 2009, A. Gorochov, M. Berezin, E. Tkatsheva.

Note. Data on this specimen are here indicated, as it was used in the present molecular analysis.

Genus ***Rhabdoblatta*** Kirby, 1903

Type species *Epilampra praecipua* Walker, 1868, by monotypy.

Note. The genus *Rhabdoblatta* is one of the largest in the subfamily Epilamprinae and includes over 100 species (Beccaloni, 2015). It is distributed from Japan and South China to South Asia and Australia

(Beccaloni, 2015). Greater Sunda Islands are characterized by a diverse and insufficiently studied fauna of *Rhabdoblatta*, and it is evident that many species remain to be discovered. Taking that into consideration, we postpone a precise determination of single species.

Also, it is reasonable to mention that the authors treated *Rh. praecipua* as a valid species, but not as a synonym of *Polyzosteria terranea* Walker, 1868 (Anisyutkin, 2014).

Rhabdoblatta sp.

Material. 1 male (prep.: Rh. ex 2408/05); **Indonesia**, Sumatra I., Bengkulu Prov., environs of Curup Town (not far from Bengkulu city), 03°28–29´S, 102°31–38´E, 1000–1500 m, 24 April – 2 May 2009, A. Gorochov, M. Berezin, E. Tkatsheva.

Note. Data on this specimen are here indicated, as it was used in the present molecular analysis.

Subfamily **Paranauphoetinae** J.W.H. Rehn, 1951

Genus *Paranauphoeta* Brunner von Wattenwyl, 1865

Type species *Blatta circumdata* (de Haan, 1842), by subsequent designation.

The genus includes 16 species from Indian subcontinent, Southeast Asia, South China and New Guinea (Beccaloni, 2015).

Paranauphoeta pullata sp. nov.
(Fig. 3A–Q, 4E, F)

Holotype. Male (prep.: ex. 2108/03, prep. 18); **Indonesia**, Sumatra I., Sumatera Selatan Prov., environs of Banding Agung Vill. on Ranau Danau Lake, 04°48.695´S, 103°55.289´E, 600–700 m, 19–22 April 2009, A. Gorochov, M. Berezin, E. Tkatsheva.

Paratypes. One male (prep.: ex. 2108/01, prep. 8), 1 female (prep.: ex. 2108/02); same data as for holotype.

Description. Male (holotype). General colour blackish brown, partly yellowish (Figs 3A, 4E, F); head and eyes black; ocellar spots and adjacent areas, areas near eyes, and clypeus whitish; labrum yellowish; antennae dark brown with apical segments (starting from 44th–46th segments) whitish; pronotum black, laterally bordered with yellow; tegmina blackish, slightly lighter toward apex; each tegmen with small indistinct yellow spot at base of *CuP*; legs with coxae, trochanters and partly femora yellowish brown, with distal parts of femora, tibiae and tarsi dark brown, and with tibiae darker than tarsi (nearly black); abdominal tergites and sternites dark brown, with lateral yellow spots; anal plate finely bordered with pale colour; cerci black, with pale apices. Surfaces smooth and lustrous; antennae with lustrous proximal 10–11 segments and rest part mat; facial part of head, pronotum and costal area of tegmina moderately punctured. Head in front with rounded vertex, slightly longer than wide (Figs 3A, 4E); ocellar spots small; facial part with very weak impression between antennal sockets (visible at high magnification); distance between eyes about equal to length of eye; distance between antennal sockets approximately 1.4 times as great as length of scape (1.3 mm); approximate length ratio of 3rd–5th segments of maxillary palps 1.1 : 1.0 : 1.3. Pronotum as in Figs 3B and 4F, caudally truncated, with lateral carinae (*sensu* Shelford, 1908; Anisyutkin, 2003a) very weak. Tegmina and wings fully developed, projected behind abdominal apex, rounded apically. Venation of tegmina partly obliterated (obliteration more expressed in proximal half of tegmina), with *Sc*, *R* and *CuP* distinct; *Sc* thickened (easily visible on ventral side of tegmen); anterior branches of R incrassate and constituting corrugated structure. Anterior margin of fore femur unarmed. Fore tibiae not thickened distally; all tibiae with spines weak and not numerous. Fore left tarsus abnormal: 2nd and 3rd segments fused. Structure of hind tarsus (Fig. 3C): metatarsus shorter than other segments combined, with several spines along lower margin arranged in single incomplete row;

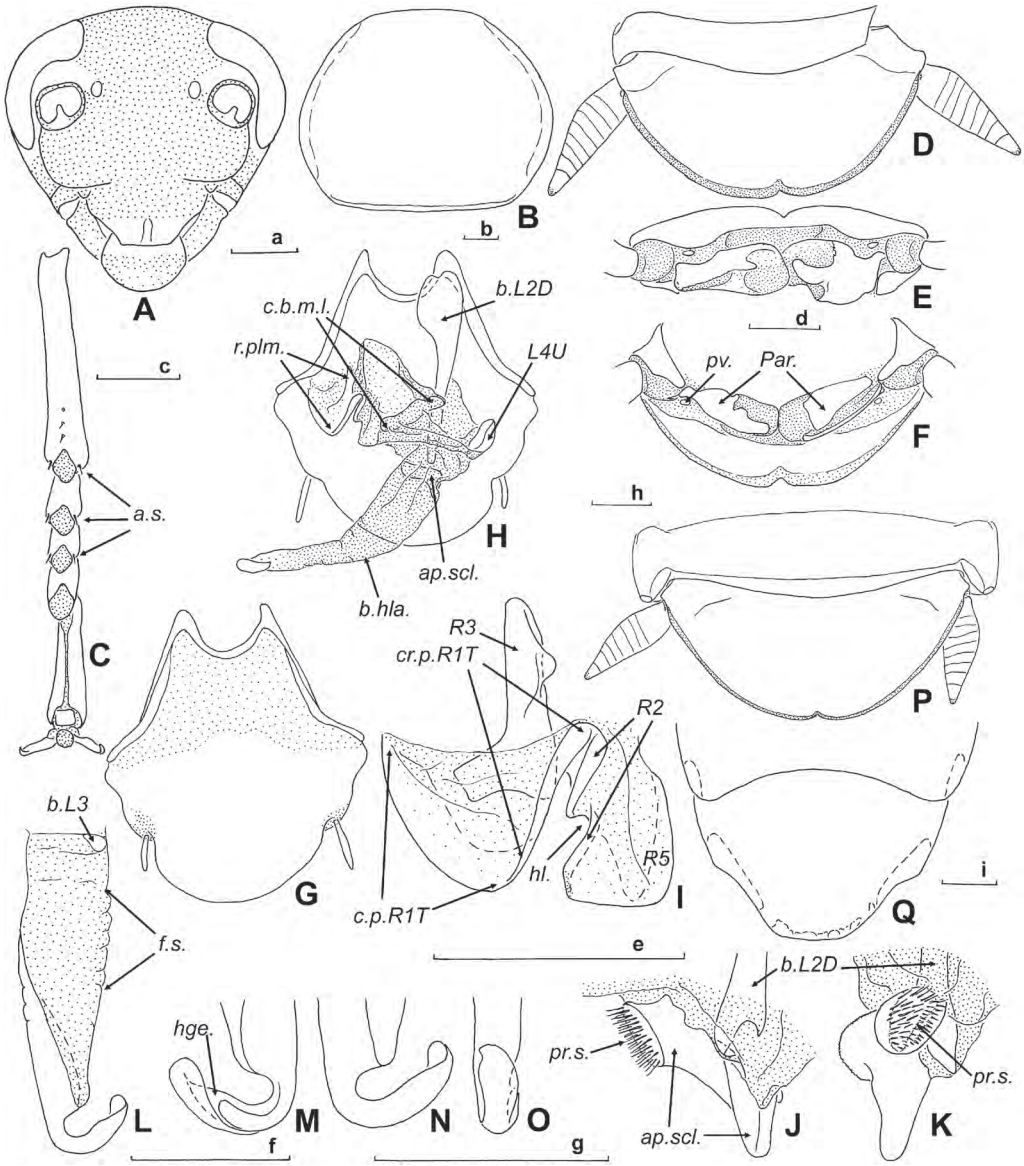

Fig. 3. *Paranauphoeta pullata* **sp. nov.** (A–O – holotype, male; P, Q – paratype, female). A – facial part of head; B – pronotum from above; C – left hind tarsus from below; D–F, P – abdominal apex from above (D, P), caudal (E) and below, hypandrium and genitalia removed (F); G – hypandrium from below; H – hypandrium and genitalia from above; I – right phallomere of the male genitalia from above; J, K – caudal part of sclerite L2D from above (J) and side (K); L – left hook (*hla*); M–O – apical part of hook *hla*; Q – genital plate from below. Dotted area shows dark colour (A) or membranous parts (C–L, P). Punctured lines (B, Q) show yellow spots. Abbreviations: *a.s.*; *ap.scl.*; *b.hla.*; *b.L2D*; *b.L3*; *c.b.m.l.*; *c.p.R1T*; *cr.p.R1T*; *f.s.*; *hge.*; *hl.*; *L4U*; *Par.*; *pr.s.*; *pv.*; *r.plm.*; *R2*; *R3*; *R5* – see text. Scale bars 1 mm (**a** for A; **b** for B; **c** for C; **d** for D–H; **e** for I–K; **f** for L; **g** for M–O; **h** for P; **i** for Q).

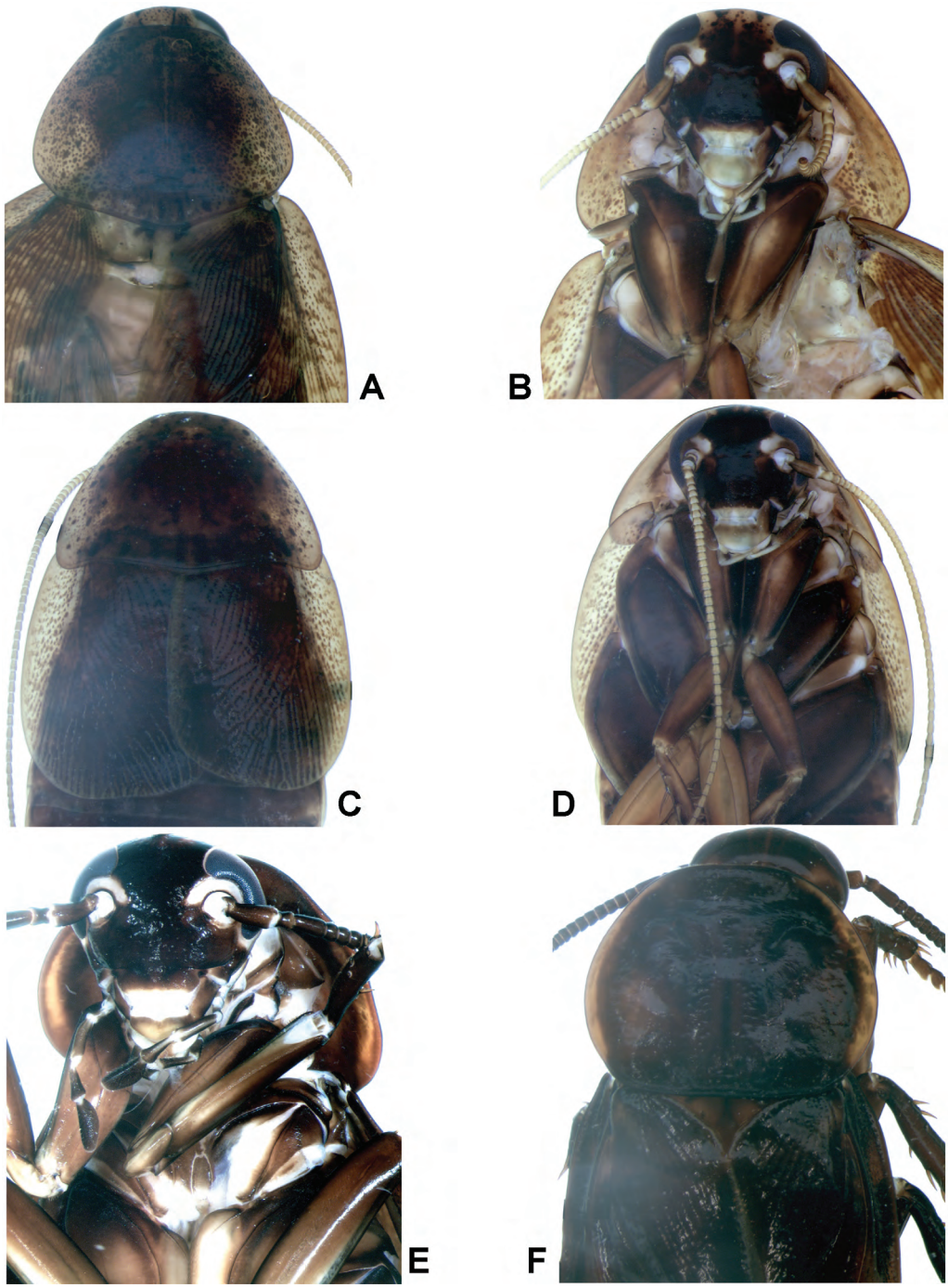

Fig. 4. Anterior part of body from above (A, C, F) and below (B, D, E). A, B – *Cyrtonotula secunda* **sp. nov.** (male, holotype); C, D – *C. tertia* **sp. nov.** (male, paratype); E, F – *Paranauphoeta pullata* **sp. nov.** (male, holotype). All specimens are kept in alcohol.

1st–3rd segments with "additional spines" bordering euplantulae from inside and outside (Fig. 3C: *a.s.*); euplantula small and apical; claws symmetrical and simple; arolium small. Abdomen without visible specializations. Anal plate (tergite X) widely rounded caudally, with weak caudal incision (Fig. 3D, F). Cerci slightly flattened dorsoventrally, densely covered by hairs on ventral side; segments pressed to each other (Fig. 3D, F). Paraprocts of blaberid type; pv-sclerites distinct (Fig. 3E, F: *pv.*). Hypandrium asymmetrical, with posteromedian part rounded and protruded (lobe-like); styli cylindrical and asymmetrical (left stylus distinctly longer than right one; Fig. 3G, H).

Male genitalia (Fig. 3H–O). Right phallomere (R+N) as in Fig. 3I; caudal part of sclerite R1T widely rounded (Fig. 3I: *c.p.R1T*), with bristles absent and cranial part of R1T nearly straight (Fig. 3I: *cr.p.R1T*); R2 nearly straight, with distinct hollow (Fig. 3I: *hl.*); R3 well sclerotized, subtriangular in shape; R4 absent; R5 tray-like and angular. Sclerite L2D (L1) divided into two sclerites, basal and apical (Fig. 3H, J, K); basal sclerite strongly widened cranially (Fig. 3H: *b.L2D*); apical sclerite of complicated shape (Fig. 3H, J, K: *ap. scl.*), with bundle of preputial spines located on rounded area (Fig. 3J, K: *pr.s.*). Elongate "chaetae-bearing membranous lobe" located above L2D (Fig. 3H: *c.b.m.l.*). Sclerite L3 (L2d) with small basal subsclerite (Fig. 3L: *b.L3*); "folded structure" weak, without bristles (Fig. 3L: *f.s.*); hge present (Fig. 3M: *hge.*). Sclerite L4U (L3d) rounded (Fig. 3H).

Variations. Paratype (male) with yellow spots in cubital field of tegmina larger than in holotype and with hind right leg abnormal: tibia distinctly curved, and tarsus consisting of four segments.

Female. Similar to male but more robust. Fore right tarsus abnormal: tarsus consisting of 4 segments. Anal plate slightly more elongate, and cerci comparatively shorter (Fig. 3P) than in male; genital plate as in Fig. 3Q.

Measurements (mm). Head length: male 4.4–4.5 (4.4), female 4.7; head width: male 4.1–4.2 (4.2), female 4.5; pronotum length: male 5.8–5.9 (5.9), female 6.0; pronotum width: male 7.5 (7.5), female 7.7; tegmen length: male 22.0–22.1 (22.1), female 22.0; tegmen width (in place where *CuP* running into anal margin of tegmen): male 5.8–6.0 (6.0), female 6.0. Holotype measurements in parentheses.

Comparison. Princis (1964, 1971) and Beccaloni (2015) listed 15 species of the genus *Paranauphoeta*: *P. circumdata* (de Haan, 1842); *P. vicina* Brunner von Wattenwyl, 1893 (with three subspecies: nominotypical one from Burma; *P. v. sinica* Bey-Bienko, 1958 from South China, Yunnan; *P. v. vietnamensis* Anisyutkin, 2003 from Vietnam); *P. lyrata* (Burmeister, 1838); *P. affinis* Shelford, 1906; *P. javanica* Saussure, 1873; *P. limbata* Saussure, 1869; *P. indica* Saussure et Zehntner, 1895; *P. basalis* (Serville, 1838); *P. adjuncta* (Walker, 1868); *P. formosana* Matsumura, 1913; *P. discoidalis* (Walker, 1868); *P. brunneri* Shelford, 1907; *P. rufipes* Brunner von Wattenwyl, 1865; *P. philippinica* Karny, 1915 and *P. nigra* Bey-Bienko, 1969.

The new species readily differs from *P. circumdata*, *P. vicina*, *P. lyrata*, *P. javanica*, *P. limbata*, *P. indica*, *P. adjuncta*, *P. formosana*, *P. discoidalis, P. brunneri*, *P. rufipes* and *P. philippinica* in the absence of well-developed light spots or bands on the tegmina (excepting very small and indistinct yellowish spots in the proximal parts), pronotum and head. *P. pullata* **sp. nov.** differs from *P. affinis* in a contrastingly coloured abdomen [in *P. affinis*, "abdomen beneath with no yellow spots, the last three segments of the abdomen above with very small yellow spots" (Shelford, 1906: 275)]. From *P. basalis*, the new species differs in having a uniformly black facial part of the head and lacking yellowish band between the eyes. *P. pullata* **sp. nov.** is somewhat similar to *P. nigra* in the pattern of colouration and the presence of preputial spines on the apical part of sclerite L2D of the male genita-

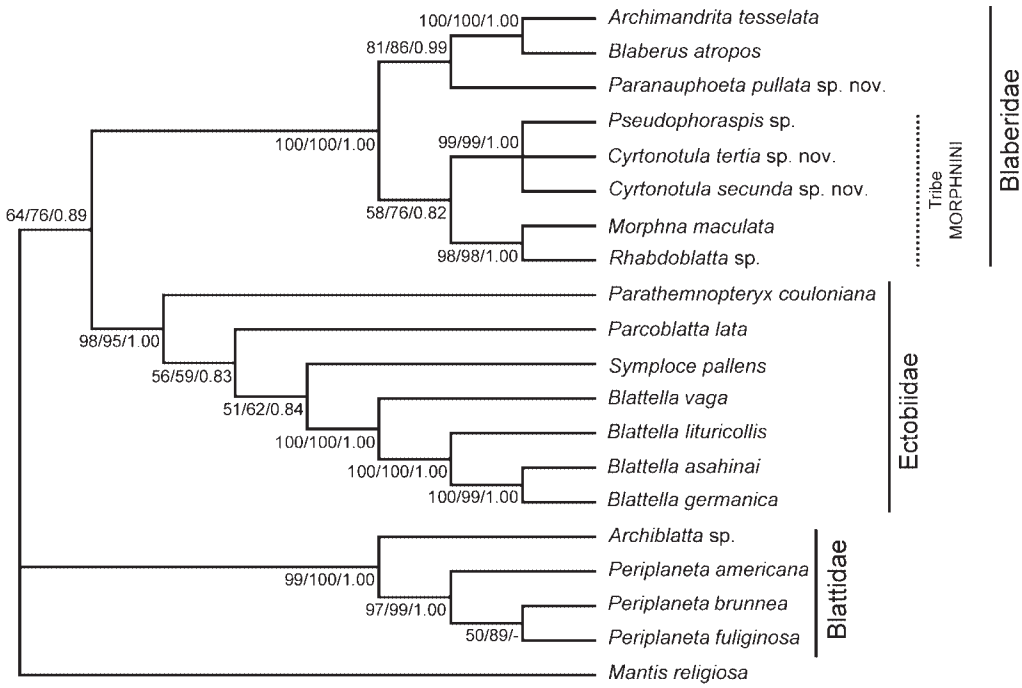

Fig. 5. Original cladogram reflecting phylogenetic relationships of Dictyoptera based on 28S rRNA gene fragment. Consensus cladogram inferred from 28S ribosomal DNA fragment sequence data of 19 Dictyoptera species using maximum likelihood (ML), maximum parsimony (MP), and Bayesian (MrBayes) analysis. *Mantis religiosa* was used as out group. Numbers indicating bootstrap value and Bayesian posterior probabilities are listed for ML/MP/MrBayes.

lia, but readily differs from it in the shape of apical sclerite L2D in the male genitalia [compare Fig. 3J, K and figures in Anisyutkin (2003a: figs 90, 91)].

MOLECULAR PHYLOGENETIC ANALYSIS

It was shown previously that the analyzed 28S gene fragment is excellent for higher-level phylogenetic studies in cockroaches (Mukha et al., 2002). In the current research, we define the phylogenetic position of the newly described cockroaches. For the 19 cockroach species, the length of the 28S gene fragments used for phylogenetic analysis is ranged between 848 and 949 bp. The length of the 28S gene fragment of *Mantis religiosa* used as the out group is 922 bp.

The cladogram based on the comparison of the 28S gene fragments (Fig. 5) generally corresponds to the phylogeny of the analyzed species based on the morphological analyses. Similar topologies and levels of support at most nodes were obtained for all 28S phylogenetic trees constructed using the ML, MP and MrBayes methods. The specimens belonging to the Dictyoptera with high bootstrap support formed three major clades on the tree corresponding to Blattidae, Ectobiidae and Blaberidae families. Ectobiidae and Blaberidae clades are clustering together separately from Blattidae clade (Fig. 5).

Newly described species of the genera *Cyrtonotula* (*C. tertia* **sp. nov.** and *C. secunda* **sp. nov.**), *Pseudophoraspis* sp. and *Rhabdoblatta* sp. are clustering together into a separate subclade which also includes

Morphna maculata, type species of the genus *Morphna*. Unexpectedly, the newly described *Paranauphoeta pullata* **sp. nov.** with high bootstrap support is clustered with representatives of the subfamily Blaberinae (Fig. 5).

DISCUSSION

The structures of the male genital complex (*sensu* Anisyutkin, 1999), including the male genitalia itself, are crucial for phylogenetic reconstruction in the order Dictyoptera (McKittrick, 1964; Klass, 1997; Roth 2003). These structures are described for the genus *Cyrtonotula* for the first time and undoubtedly testify that this genus belongs to the subfamily Epilamprinae. Structure of the male genitalia, namely right phallomere (large and subrectangular sclerite R4, shape of sclerites R2 and R3, presence of bristles; see Figs 1G–I, 2F–H) and hook *hla* (strongly elongated, with folded structures well developed, and with sclerite L3 lacking median incision; see Figs 1K–N, 2L–O), gives evidence of belonging of *Cyrtonotula* to the tribe Morphnini McKittrick, 1964. The representatives of the genera *Pseudophoraspis* and *Rhabdoblatta* are characterized by a similar structure of the male genitalia (Anisyutkin, 1999, 2000, 2003b) and undoubtedly belong to the tribe Morphnini too. This attribution is supported by our molecular data (Fig. 5).

The systematic position of the subfamily Paranauphoetinae with the single genus *Paranauphoeta* is unclear. There is no doubt that this genus belongs to the family Blaberidae, but its more precise position has not yet been determined. This genus was described in the family Panesthiidae by Brunner von Wattenwyl (1865). Later, it was placed into the subfamilies Perisphaeriinae (Saussure & Zehntner, 1895; Kirby, 1904; Hanitsch, 1915) or Gyninae (Princis, 1960, 1964). Roth (2003) placed *Paranauphoeta* in Blaberidae as the genus with an undetermined or uncertain position. Rehn (1951) ascribed the genus *Paranauphoeta* to the monotypical tribe Paranauphoetini. Later, Anisyutkin (2003a) proposed to raise the rank of Paranauphoetini up to a subfamily.

The grouping of the genus *Paranauphoeta* with representatives of the subfamily Blaberinae is rather unexpected according to our molecular data (Fig. 5). Nevertheless, there are morphological similarities between these taxa. There are similarities in the shape of the hypandrium and in the male genitalia structure: right phallomere comparatively weakly sclerotized, with somewhat similar shape of sclerites R2 and R4 [compare Fig. 3I and figures in Roth (1969: figs 13–24)]; shape of apical part of sclerite L2D and presence of preputial spines [compare Fig. 3J, K: *pr.s.* and figures in Roth (1969: figs 28–40 etc.; 1970: 32, 35, 38, 41, 44–56 etc.); shape of sclerite L3 [compare Fig. 3L–O and figures in Roth (1969: figs 1–12; 1970: 33, 36, 39, 60, 63 etc.)]. Of course, further investigations based on more representative material, both morphological and molecular, are needed to elucidate the relationships in the genus *Paranauphoeta*.

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