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Notes on the genus *Ctenoneura* Hanitsch, 1925 with description of six new species (Dictyoptera: Corydiidae)

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Abstract: Six new species of the genus *Ctenoneura* are presented: *C. complicata* sp. nov., *C. virgata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. orlovi* sp. nov. and *C. gorochovi* sp. nov. Morphology-based descriptions of the new species are given. Some questions concerning morphology and the taxonomic position of the genus *Ctenoneura* are briefly discussed. Changes in the method of working with small and weakly sclerotized cockroaches are proposed.

Keywords: Cockroaches - morphology - taxonomy.

INTRODUCTION

The genus *Ctenoneura* Hanitsch, 1925 includes small and morphologically very specialized cockroaches (Hanitsch, 1929, 1932; Princis, 1954, 1967; Bey-Bienko, 1957, 1969; Roth, 1993, 1995; Qiu *et al.*, 2017). At first glance, representatives of the genus are more similar to small ectobiids than to other members of the family Corydiidae. The genus is taxonomically very isolated, so at present it is impossible to identify the taxon which is closest to it. Molecular data may shed some light on the systematic position of the genus in the future.

The publications of Roth (1993) and Qiu *et al.* (2017) are especially valuable for the study of *Ctenoneura*. These cockroaches are rare in scientific collections, although they appear to be widespread in South-East Asia. Representatives of the genus are distributed from Burma and southern China via the Malay Peninsula, Sumatra and Java to Borneo (Beccaloni, 2014).

MATERIAL AND METHODS

In my opinion, the method of working with small and weakly sclerotized cockroaches should differ from the one currently in use. Such cockroaches should not be pinned and dried. Pinned and dried specimens are usually deformed and very difficult to study. I prefer to collect, study and keep such specimens and its body parts in alcohol or other kinds of fixing liquid. This applies to all small and delicate cockroaches, and even more so to very fragile representatives of the genus *Ctenoneura*. Also, I do not recommend mounting the structures of the genital complex (i.e. male genitalia, anal plate, hypandrium and other adjacent structures) on microscope slides because it makes them very difficult to study. First, because the structures of the genital complex are very often deformed on microscope slides. Second, because the slide-mounted genital structures are fixed and immovable, and therefore impossible to examine from all angles. All this makes it extremely difficult or impossible to reconstruct complex three-dimensional structures often formed by the sclerites of the genitalia of cockroaches.

The availability of only unique specimens limited my ability to dissect and study such complex structures, like the right phallomere of the male genitalia, in detail. Therefore I had to limit myself to simplified drawings only.

The material studied (specimens and dissected body parts) is kept in 70% ethanol. The morphological structures were dissected and examined in Petri dishes under alcohol. The structures of the male genitalia were treated with alkali using the standard technique for removing soft tissues (Anisyutkin *et al*., 2013).

The drawings were made by means of a drawing tube on a Leica MZ 16 binocular microscope and with an MBS-10 binocular microscope.

Rehn's (1951) terminology of tegmina and wing venation is used. The description of anterior margin of fore femur armament follows Bey-Bienko (1950) and Roth (2003). The terminology of male genital sclerites follows Klass (1997), with some modifications according to Qiu *et al.* (2017) and my previous papers. Terms introduced by the author are given in quotation marks.

The material studied is deposited in the Muséum

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d'histoire naturelle, Geneva, Switzerland (MHNG) and in the Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg, Russia (ZIN).

Abbreviation used in the figures (see text for further explanations):

1pl. - 1st plical vein of hind wing (terminology after Rehn, 1951);
2pl. - 2nd plical vein of hind wing (terminology after Rehn, 1951);
3pl. - 3rd plical vein of hind wing (terminology after Rehn, 1951);
1scl. - additional sclerite of male genitalia;
1st.pr., 2nd.pr., 3rd.pr., 4.pr., 5.pr., 6.pr. - outgrowths of posterior margin of hypandrium;
Ant.R.rami - area of anterior branches of radius vein of hind wing (terminology after Rehn, 1951);
CuA - area of cubitus anterior vein branches (terminology after Rehn, 1951);
CuP - cubitus posterior vein (= plical furrow *sensu* Rehn, 1951);
eds. - extending structure of subgenital sclerite of male genitalia (terminology after Qiu *et al.*, 2017);
f.scl. - "folded sclerite" (*ldp+lvp sensu* Qiu *et al.*, 2017) of male genitalia;
i.v. - intercalary vein of tegmen (terminology after Roth, 1993);
l.p.a. - left posterolateral corner of hypandrium;
l.sty. - left stylus;
L3 - sclerite of male genitalia;
M - area of media vein branches;
par. - paraproct;
pv. - pv-sclerite;
R - area of radius vein branches;
r.p.a. - right posterolateral corner of hypandrium;
r.sty. - right stylus;
R3 - sclerite of male genitalia;
Sc - area of subcosta vein branches;
scl. - additional sclerite of male genitalia;
sgs. - subgenital sclerite (terminology after Qiu *et al.*, 2017) of male genitalia;
t.o. - triangular outgrowth of hypandrium;
tvs. - transverse sclerite of male genitalia (terminology after Qiu *et al.*, 2017).

TAXONOMIC PART

Genus *Ctenoneura* Hanitsch, 1925

Type species: *Ctenoneura major* Hanitsch, 1925, by subsequent designation (Princis, 1950).

Remarks: The genus *Ctenoneura* was described by Hanitsch (1925) and revised by Roth (1993) and Qiu *et al*. (2017). It includes small cockroaches of untypical appearance for the family Corydiidae (Figs 1-12). These cockroaches are similar to small representatives of the family Ectobiidae. In fact, the placement in Corydiidae is supported by the presence of a folded anal area of the hind wing (Fig. 21). However, this character also occurs independently, as shown for the blaberid genus *Miroblatta* Shelford, 1906 (Grandcolas, 1993a). The male genitalia of *Ctenoneura* are so strongly reduced and modified (Figs 27, 34, 40, 47, 55, 63) that it is difficult to homologize its structures.

In this paper I principally follow Qiu *et al.* (2017), who first described the male genitalia of *Ctenoneura*, in naming the male genital sclerites. Nevertheless, in my opinion only the homology of the R3 sclerite is undisputed. The plate-like and curved sclerite R3 is common not only in species of the Corydiidae, for instance representatives of the genera *Polyphaga* Brullé, 1835, *Therea* Billberg, 1820 and *Tivia* Walker, 1869 (see Klass, 1997; Qiu *et al*., 2019), but also in species of the Cryptocercidae (see Klass, 1997), of Blattidae, for instance representatives of the genera *Periplaneta* Burmeister, 1838, *Macrostylopyga* Anisyutkin, Anichkin & Nguyen, 2013 and *Duchailluia* Rehn, 1933 (see Klass, 1997; Anisyutkin *et al*., 2013; Anisyutkin, 2014; Anisyutkin & Telnov, 2018), of Tryonicidae (see Klass, 1997), of Lamproblattidae (see Klass, 1997), of Anaplectidae (see Klass, 1997) and of Nocticolidae, for instance representatives of the genus *Nocticola* Bolivar, 1892 (see Andersen & Kjaerandsen, 1995). The homologization of the other structures of the male genitalia needs confirmation. To resolve the problem of homologization of male genitalia structures, intermediate forms between *Ctenoneura* and coridiids with more typical genitalia are required, if such taxa exist. It may also be possible to extract data from the ontogenetic development of these cockroaches.

In my opinion, the subgenital sclerite (Figs 27, 31, 40, 47, 49, 53, *sgs*.) is a structure of the male genitalia, not part of the hypandrium (subgenital plate after Qiu *et al.*, 2017). In the specimens I studied and in the drawings of Qiu *et al.* (2017) there is no evidence for an attachment of this structure to the hypandrium; only the distal part of the subgenital sclerite (*eds*. - extending structure after Qiu *et al.*, 2017) can be overlapped by outgrowths of the posterior margin of the hypandrium (Figs 31-33, 53-54, *eds*.). The subgenital sclerite is situated between other structures of the male genitalia and the dorsal wall of the hypandrium (= dorsal sclerotisation of subgenital plate *sensu* Klass, 1997). Similar structures are present in some Ectobiidae (for instance, "ventral structure" in *Nahublattella* Bruijning, 1959; see Anisyutkin, 2009) and evidently belong to the labile complex of the male genital structures (see Anisyutkin, 2011). The structures of the labile complex do not belong to the groundplan of male genitalia, but most likely represent secondary sclerotizations of the intersternal membrane (Anisyutkin, 2011). These structures can appear "de novo" and the homologization of such secondary sclerites is very difficult. After preparation, the subgenital sclerite can be tightly pressed against the dorsal wall of the hypandrium

(Figs 31, 53, *sgs*.) or it can be separated along with other structures of the male genitalia (Figs 27, 40, 47, *sgs*.). This depends on the strength of the membranes and on the dissecting skills of the researcher.

Small rod-like sclerites located near the "folded sclerite" (Figs 34, 40, 47, 55, 63, *1.scl.*, *scl.*) belong to the labile complex or are rudiments of sclerites of the groundplan of the male genitalia.

The left dorsal phallomere (*ldp*.) and the left ventral phallomere (*lvp*.) (*sensu* Qiu *et al.*, 2017) form a single "folded sclerite" (Figs 27, 34, 40, 47, 55, 64-65, *f.scl*.).

The complete reduction of sclerite L3 (genital hook) is unusual but not unique for Corydiidae. The almost complete reduction of L3 was noted in representatives of the genus *Therea* Billberg, 1820 by Grandcolas (1993b).

Sexual dimorphism in the genus is variable. All males are fully winged (forma euptera). Qiu *et al*. (2017) report completely wingless females (forma aptera) of *Ctenoneura heixuanfeng* Qiu, Che & Wang, 2017 and suggested that all earlier records of fully winged females (Hanitsch, 1925; Bey-Bienko, 1957) should be considered as doubtful.

In this paper I follow Beccaloni (2014) and Qiu *et al*. (2019) who consider *Ctenoneura* as Corydiidae *incertae sedis*. Clarification of the phylogenetic position of the genus requires further research.

Species included: At present 39 species are known: *Ctenoneura annulicornis* Princis, 1954, *C. biguttata* Hanitsch, 1932, *C. birmanica* Princis, 1954, *C. brunnea* Hanitsch, 1929, *C. crassistyla* Roth, 1993, *C. fulva* Hanitsch, 1925, *C. gigantea* Roth, 1993, *C. hanitschi* Princis, 1954, *C. kemneri* Princis, 1967, *C. kinabaluana* Roth, 1993, *C. luma* Roth, 1993, *C. major* Hanitsch, 1925, *C. misera* Bey-Bienko, 1969, *C. mjoebergi* Princis, 1954, *C. murudensis* Roth, 1993, *C. parascutica* Roth, 1993, *C. poringa* Roth, 1993, *C. propannulicornis* Roth, 1993, *C. scutica* Roth, 1993, *C. simulans* Bey-Bienko, 1969, *C. sipitanga* Roth, 1995, *C. spinastyla* Roth, 1993, *C. triprocessa* Roth, 1993, *C. tuberculata* Princis, 1954, *C. uncata* Roth, 1993 and *C. yunnanea* Bey-Bienko, 1957 [as given in Beccaloni, 2014 with the exception of *Beybienkonus acuticerca* (Bey-Bienco, 1957)], *C. bawangensis* Qiu, Che & Wang, 2017, *C. delicata* Qiu, Che & Wang, 2017, *C. elongata* Qiu, Che & Wang, 2017, *C. heixuanfeng* Qiu, Che & Wang, 2017, *C. helicata* Qiu, Che & Wang, 2017, *C. papillaris* Qiu, Che & Wang, 2017, *C. qiuae* Qiu, Che & Wang, 2017, *C. complicata* sp. nov., *C. virgata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. orlovi* sp. nov. and *C. gorochovi* sp. nov.

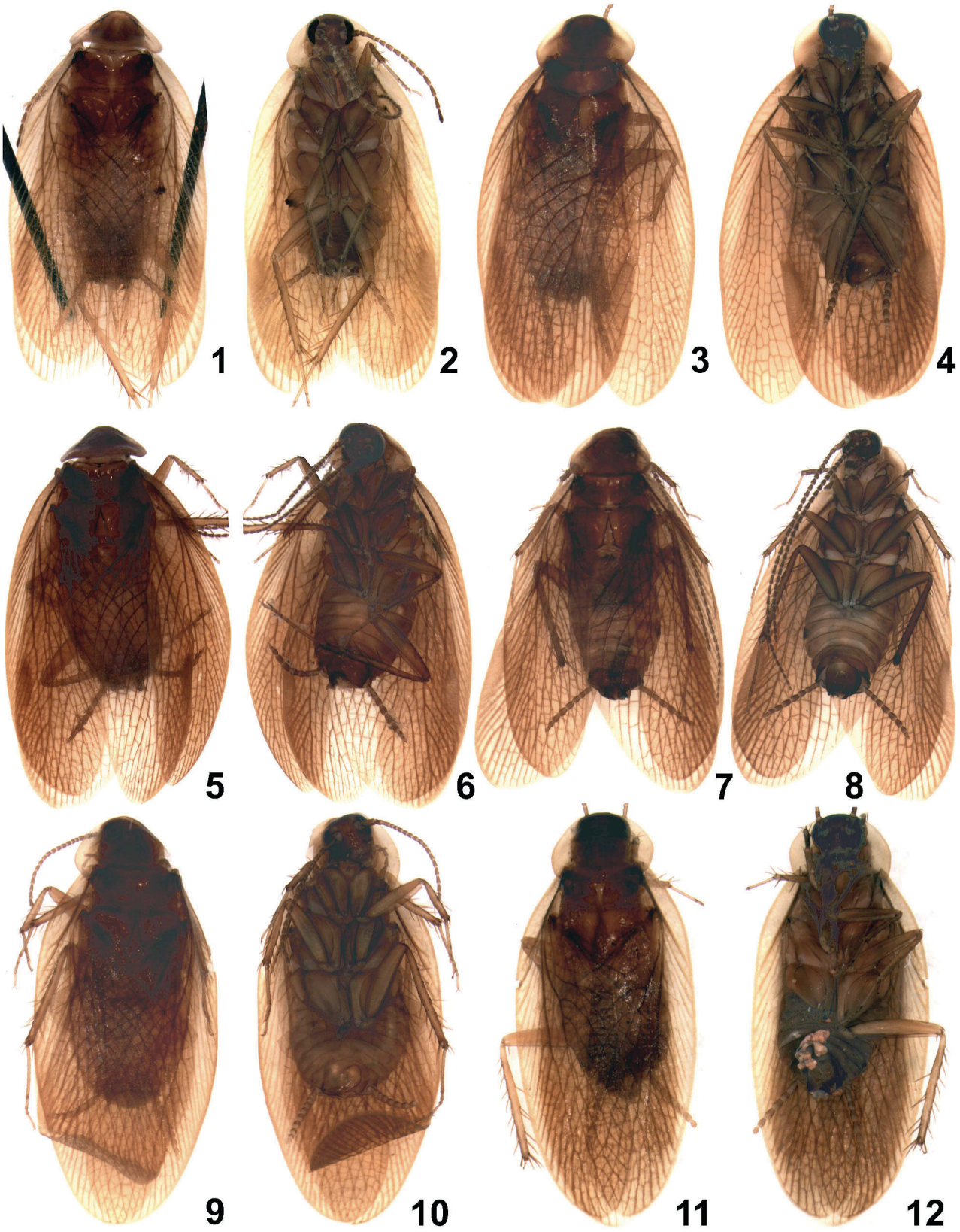
Ctenoneura complicata sp. nov.

Figs 1-2, 13-27

Material examined: MHNG; male holotype (No. 160920/01); East Malaysia, Borneo, Sabah, Mt Kinabalu (Fig. 13A), 1500 m, sample no. 9; 30.IV.1987; leg. D. Burckhardt & I. Löbl.

Etymology: The Latin adjective "complicatus, -a, -um" refers to the complicated shape of the posterior margin of the hypandrium.

Description of male holotype: General body colour yellowish brown (Figs 1-2); head, central part of pronotum, part of thorax, coxae, femora and abdominal apex darker; eyes black. Surfaces dull and lustrous, punctuation absent. Head slightly longer than wide, globular, vertex slightly uneven, area between antennal sockets slightly protruded, with sutures running from antennal sutures to clypeus (Fig. 14); ocellar spots small but distinct; eyes large, distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.3 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.8. Pronotum as in Fig. 15; anterior margin very weakly concave, nearly straight, posterior margin widely rounded. Tegmina and hind wings completely developed. Tegmina weakly sclerotized, translucent, venation partly reticulate and irregular (Fig. 20); *Sc* moderately thickened, with 1-3 anterior rami; *R* with 19-20 anterior and apical rami; intercalary vein present (Fig. 20, *i.v.*); *M* with 10-11 rami; *CuA* with 1 complete (reaching wing margin) or incomplete (not reaching wing margin) ramus; *CuP* thin, distinct, smoothly curved. Wings membranous, with exception of sclerotized area of anterior rami of *R* (Fig. 21); *Sc* simple; *RA* with about 11-13 anterior complete or incomplete rami; *M* with 4 rami; *CuA* pectinate, with 5-6 complete and 0-1 incomplete veins; a long and weak vein situated behind *CuA* (Fig. 21, *1pl.*), this probably corresponding to 1st plical vein *sensu* Rehn (1951) or to *CuP* [probably *CuP + A1 sensu* Bey-Bienko (1950)]; next vein not reaching wing margin and fused with previous one and with 1st anal vein (Fig. 21, *2pl.*), this probably corresponding to 2nd plical vein *sensu* Rehn (1951); 3rd vein weak and discernible only in proximal part (Fig. 21, *3pl.*), probably corresponding to 3rd plical vein *sensu* Rehn (1951); anal fan folded, consisting of 9 rami, first ramus proximally incrassated. Anterior margin of fore femora armed according to type C (*sensu* Bey-Bienko, 1950; Roth, 2003), with a single apical spine (Fig. 16). Fore tibiae not thickened distally; tibial spines weak (Figs 16-17). Structure of hind tarsi (Figs 18-19): metatarsus slightly longer than other segments combined; all euplantulae absent; spines along lower margins of tarsal segments arranged in single row; claws symmetrical, simple; arolium about half of claw length. Abdomen without visible glandular structure. Anal plate transverse (Fig. 22), with posterior margin medially protruded; dorsally with membranous spot. Paraprocts symmetrical, without armament, shaped like long trapezoid plates, with membranous pads at medial ends; *pv*-sclerites well developed (Fig. 23). Cerci with



Figs 1-12. *Ctenoneura* spp. Male holotypes. (1-2) *C. complicata* sp. nov. (3-4) *C. virgata* sp. nov. (5-6) *C. asymmetrica* sp. nov. (7-8) *C. emarginata* sp. nov. (9-10) *C. orlovi* sp. nov. (11-12). *C. gorochovi* sp. nov. (1, 3, 5, 7, 9, 11) Habitus, dorsal view. (2, 4, 6, 8, 10, 12) Habitus, ventral view. The black bars in Fig. 1 are insect pins fixing the specimen. Not to scale.

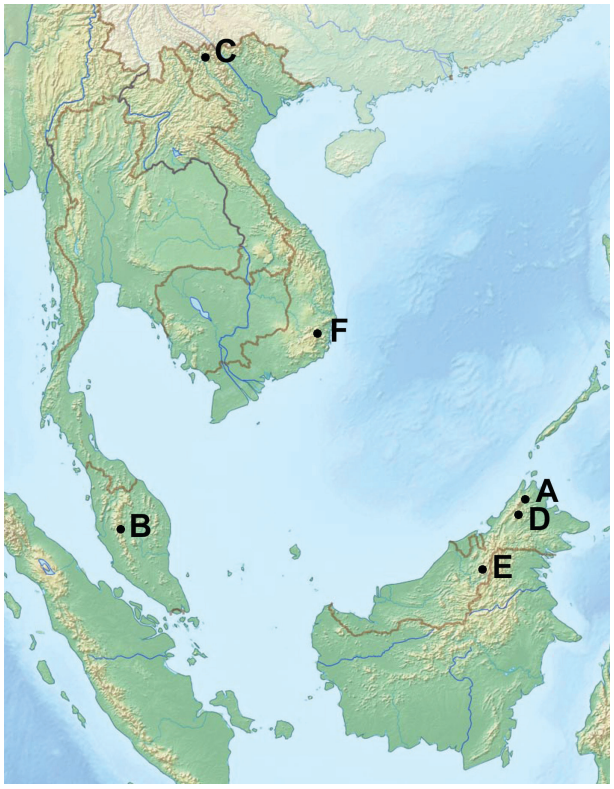


Fig. 13. Map of localities of *Ctenoneura* species described and discusses in this paper. (A) Borneo, Sabah, Mt Kinabalu: *C. complicata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. major*. (B) Peninsular Malaysia, Pahang, Cameron Highlands: *C. virgata* sp. nov. (C) Northern Vietnam, Lao Cai Prov., Sa Pa Distr., Mt Fan Si Pan: *C. orlovi* sp. nov. (D) Borneo, Sabah, Mt Trus Madi: *C. gorochovi* sp. nov. (E) Borneo, Sarawak, Mt Murud: *C. major*. (F) Southern Vietnam, Da Lat Plateau, Mt Lang Biang: *C. major*.

8 distinct segments (Fig. 22). Hypandrium broad and strongly asymmetrical (Figs 24-26); right anterolateral process larger than left one (Fig. 24); left posterolateral corner extended posteriorly, with small tooth at apex (Figs 24-26, *1st.pr.*); small and membranous left stylus situated medially (Fig. 24, *l.sty*.); 2 large curved outgrowths to their right (Figs 24-25, *2nd.pr.*, *3rd.pr.*); right posterolateral corner extended posterolaterally; between right large curved outgrowth and right posterolateral angle a small membranous outgrowth, probably the right stylus (Fig. 24, *r.sty.*); 3 complicated and strongly sclerotized outgrowths situated on posterodorsal side of hypandrium: the left one (Figs 25-26, *4.pr.*) dentate apically, the right one covered with long and curved bristles (Figs 25-26, *5.pr.*), cranial outgrowth shaped like a transverse plate, medially with thin curved process carrying a bristle (Figs 25-26, *6.pr.*). Male genitalia (Fig. 27): subgenital sclerite small and weakly sclerotized (Fig. 27, *sgs*.); "folded sclerite" (*ldp+lvp sensu* Qiu *et al*., 2017) large and well sclerotized (Fig. 27, *f.scl.*); right phallomere with thin transverse sclerite (Fig. 27, *tvs.*).

Female: Unknown.

Measurements (in mm): Head length 1.3; head width 1.2; pronotum length 1.7; pronotum width 2.2; tegmen length 7.2; tegmen width 2.4.

Comparison: *Ctenoneura complicata* sp. nov. is somewhat similar to *C. yunnanea,* described from Yunnan, China (Bey-Bienko, 1957), in the presence of a rounded hollow on the posterior margin of the hypandrium, but both species clearly differ in general shape of the hypandrium (Fig. 24 cf. Bey-Bienko, 1957: fig. 1). The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. presence of two curved outgrowths on posterior margin and three complicated outgrowths situated on posterodorsal side of hypandrium (Figs 24-26). *Ctenoneura complicata* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly widely rounded and protruded pronotum (Fig. 15 cf. Roth, 1993: fig. 2A).

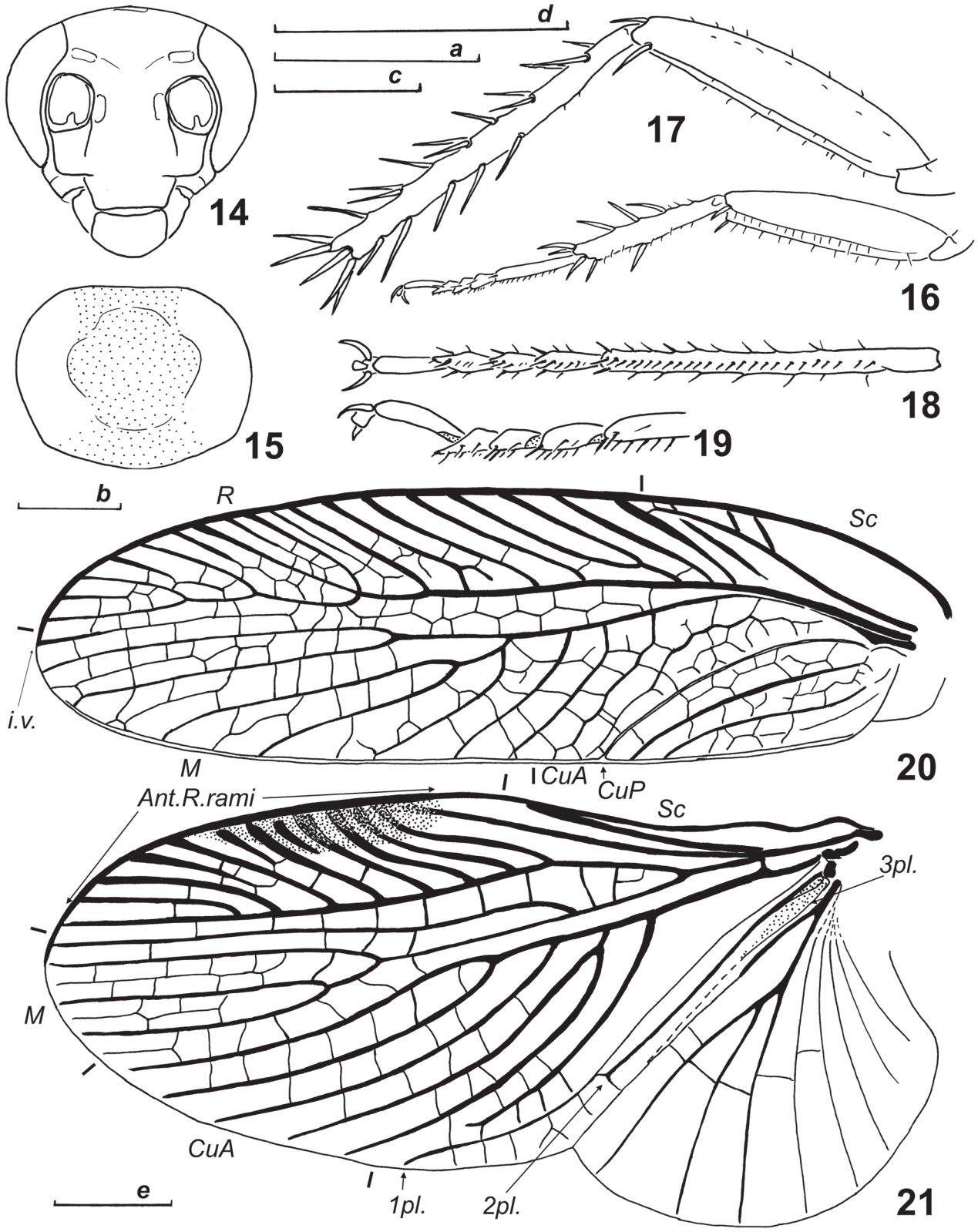
Ctenoneura virgata sp. nov.

Figs 3-4, 13, 28-34

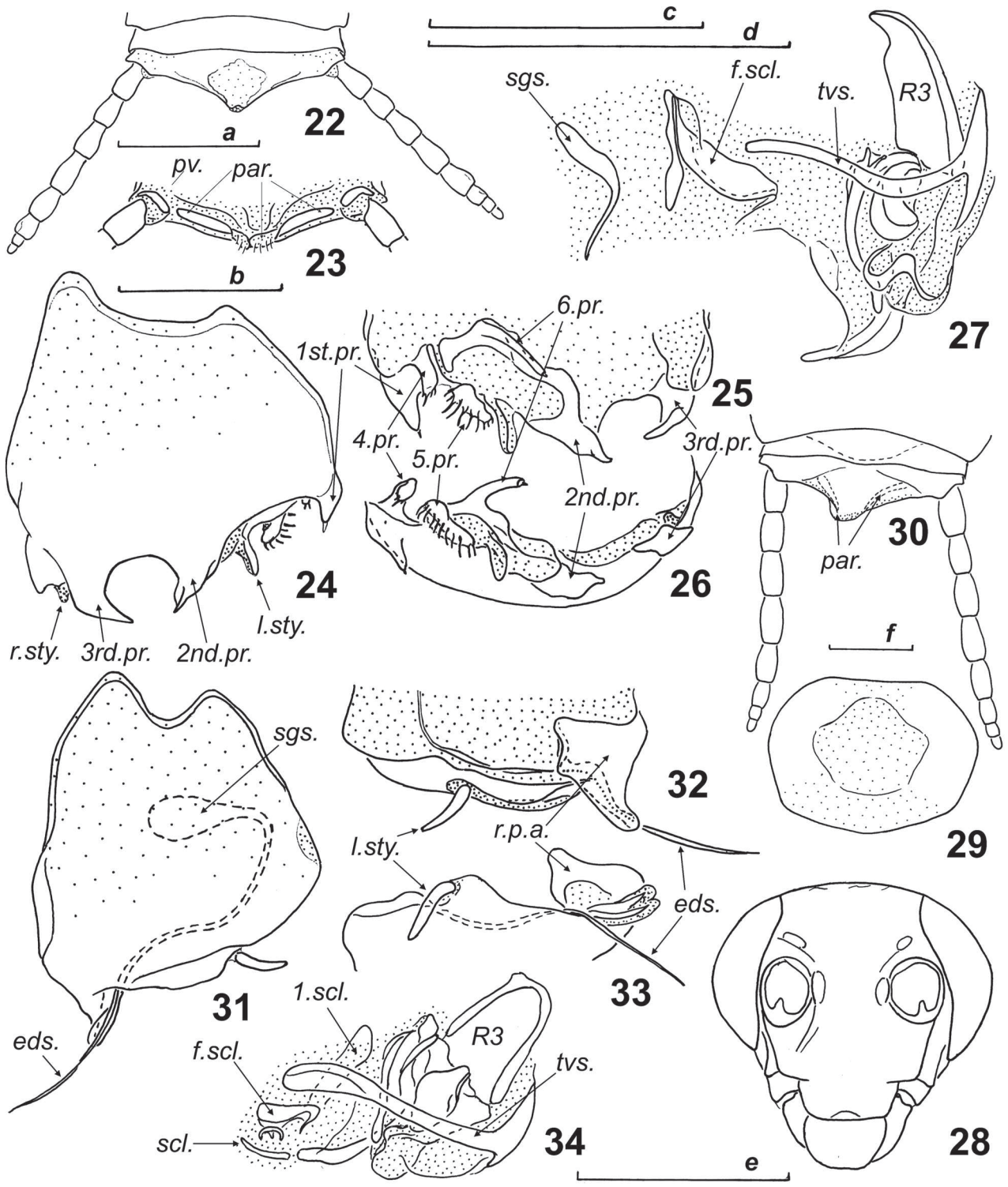
Material examined: MHNG; male holotype (No. 160920/02); West Malaysia, Pahang, Cameron Highlands, Ringlet (Fig. 13B), 4200 feet; 7.VIII.1972; leg. T. Jaccoud.

Etymology: The Latin adjective "virgatus, -a, -um" (= shaped like a twigs or rod) refers to the peculiar structure of the subgenital sclerite.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters: Head with only one suture running from right antennal suture to clypeus (Fig. 28); distance between antennal sockets about 0.9 times scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.4. Tegmina and hind wing venation principally similar to that of *C. complicata* sp. nov.; tegmina with intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 30), mostly membranous (paraprocts clearly visible through anal plate; Fig. 30, *par.*), with posterior margin medially protruded. Hypandrium asymmetrical (Figs 31-33), with posterior margin folded up and roundly protruded medially; right posterolateral corner with folded-up outgrowth (Figs 32-33, *r.p.a.*) enclosing extended structure of subgenital sclerite (Figs 31-33, *eds.*); left stylus large (Figs 31-33, *l.sty.*), right one absent.



Figs 14-21. *Ctenoneura complicata* sp. nov., male holotype. (14) Facial part of head. (15) Pronotum, dorsal view. (16) Right fore leg, proventral view. (17) Right hind leg (tarsus not shown), proventral view. (18) Right hind tarsus, retroventral view. (19) Apical part of right hind tarsus, proventral view. (20) Left tegmen, dorsal view. (21) Left hind wing, dorsal view. Dotted areas indicate dark colour (15), sclerotized areas or strongly reduced part of 3rd plical vein (21). Abbreviations are explained in the paragraph "Material and methods". Scale bars 1 mm: a (14), b (15), c (16-17), d (18-19), e (20-21).



Figs 22-34. (22-27) *Ctenoneura complicata* sp. nov., male holotype (28-34) *C. virgata* sp. nov., male holotype. (22, 30) Abdominal apex, dorsal view. (23) Paraprocts and adjacent structures, ventral view. (24, 31) Hypandrium, ventral view. (25, 32) Posterior margin of hypandrium, dorsal view. (26, 33) Same, posterior view. (27, 34) Male genitalia, dorsal view. (28) Facial part of head. (29) Pronotum, dorsal view. Dotted areas indicate membranous parts (22-27, 30-34) or dark colour (29). Abbreviations are explained in "Material and methods". Scale bars 1 mm: a (22, 30), b (23), c (24-26, 31-33), d (27, 34), e (28), f (29).

Male genitalia (Figs 31-34): subgenital sclerite looped, large and well sclerotized (Fig. 31, *sgs*.), extending structure of subgenital sclerite long (Figs 31-33, *eds.*); "folded sclerite" (*ldp+lvp sensu* Qiu *et al*., 2017) small (Fig. 34, *f.scl.*); right phallomere with well sclerotized transverse sclerite (Fig. 34, *tvs.*); weakly sclerotized trapezoidal structure situated below "folded sclerite" (Fig. 34, *1.scl.*) and small rod-like sclerite situated near "folded sclerite" (Fig. 34, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.3; head width 1.2; pronotum length 1.8; pronotum width 2.5; tegmen length 8.4; tegmen width 2.4.

Comparison: The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. posterior margin folded up and protruded medially, right posterolateral corner with folded-up outgrowth (Figs 31-33). *Ctenoneura virgata* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and of a posteriorly rounded pronotum.
A similar switch-like extended structure of the subgenital sclerite is present in *C. orlovi* sp. nov. (see below) and *C. triprocessa* Roth, 1993, but these species can be readily distinguished by the structure of their hypandria (Fig. 31 cf. Roth, 1993: fig. 19A-E).

Remark: The asymmetrical suture running from the right antennal suture to the clypeus (Fig. 28) may be due to damage to the larva. To resolve the question of whether this character has a taxonomical value, it is necessary to examine additional material.

Ctenoneura asymmetrica sp. nov.
Figs 5-6, 13, 35-40

Material examined: MHNG; male holotype (No. 160920/03); East Malaysia, Borneo, Sabah, Mt Kinabalu National Park (Fig. 13A), 1500 m, collected by interception trap; 8.-16.V.1987; leg. A. Smetana.

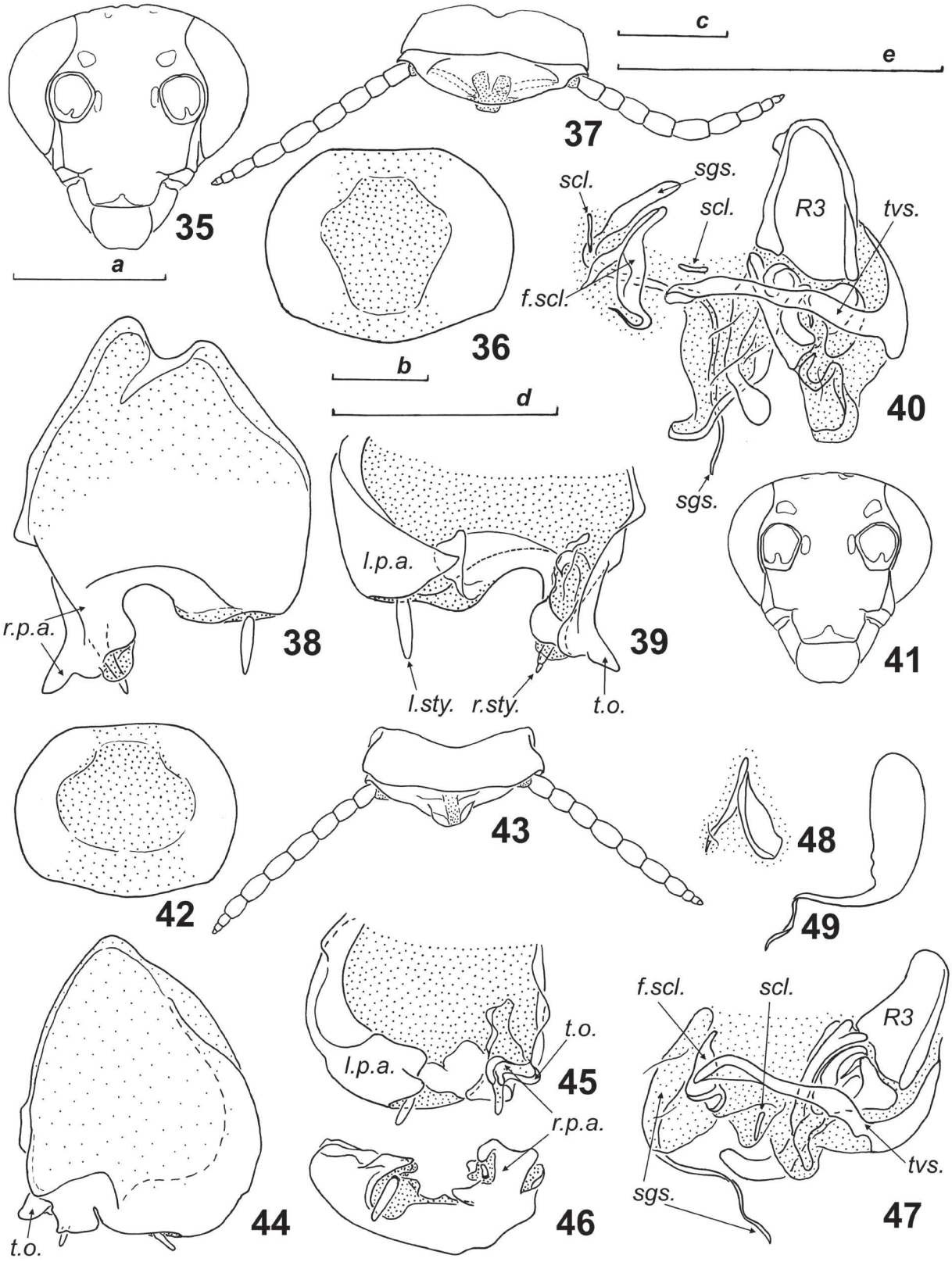
Etymology: The Latin adjective "asymmetricus, -a, -um" (= asymmetrical) refers to the strongly asymmetrical shape of the hypandrium of this species.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but larger and darker, additionally different in the following characters: Head longer than wide, without sutures below antennal sockets (Fig. 35); distance between eyes about 0.9 times eye length; distance between antennal sockets about equal to scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.3, 1.0, 1.6. Pronotum as in Fig. 36. Tegmina and hind wing venation largely similar to that of *C. complicata* sp. nov.; tegmina with intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 37), dorsally with medial membranous spot. Cerci with 10 distinct segments, apical segment very small (Fig. 37). Hypandrium strongly asymmetrical (Figs 38-39); left posterolateral corner folded up (Fig. 39, *l.p.a.*); left stylus large (Figs 38-39, *l.sty.*); posterior margin medially emarginated; right posterolateral corner protruded into large and complicated outgrowth (Fig. 38, *r.p.a.*) with triangular outgrowth at outer side (Figs 38-39, *t.o.*), apically with distinct right stylus (Figs 38-39, *r.sty.*).
Male genitalia (Fig. 40): subgenital sclerite long and somewhat coiled (Fig. 40, *sgs*.); "folded sclerite" (*ldp+lvp sensu* Qiu *et al*., 2017) large and well sclerotized (Fig. 40, *f.scl.*); right phallomere with large and well sclerotized transverse sclerite (Fig. 40, *tvs.*); two small rod-like sclerites situated near "folded sclerite" (Fig. 40, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.7; head width 1.4; pronotum length 2.0; pronotum width 2.6; tegmen length 9.8; tegmen width 2.9.

Comparison: The new species can be readily distinguished from all other congeners, with the exception of *C. major*, by the peculiar shape of its hypandrium, i.e. presence of a folded left posterolateral corner and of a large and complicated right outgrowth (Figs 38-39). *Ctenoneura asymmetrica* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly rounded pronotum.
Ctenoneura asymmetrica sp. nov. and *C. major* have a hypandrium of somewhat similar shape (Figs 38-39 cf. Roth, 1993: fig. 9D-E). The new species differs from *C. major* in the following characters: (1) interocular space wider than distance between ocellar spots, about equal to distance between antennal sockets (Fig. 35) (in *C. major* "interocular space less than distance between ocellar spots and antennal sockets"; see Roth, 1993: 96); (2) cerci with 10 segments (Fig. 37) (8 in *C. major*; see Hanitsch, 1925); (3) right posterolateral process of hypandrium with distinct, well sclerotized triangular outgrowth (Figs 38-39, *t.o.*) (in *C. major* outgrowth absent; Figs 38-39 cf. Roth, 1993: fig. 9D-E).
Remarks: *Ctenoneura major*, probably the species most closely related to *C. asymmetrica* sp. nov., was described from Mt Murud (Sarawak, Borneo) (Hanitsch, 1925) (Fig. 13E). Later this species was also discovered in Sabah (Mt Kinabalu; see Roth, 1995) (Fig. 13A) and in southern Vietnam, on the Da Lat Plateau [5500-7500 feet, Langbian Peaks (= Mt Lang Biang), S. Annam; see Hanitsch, 1927] (Fig. 13F). The most important



Figs 35-49. (35-40) *Ctenoneura asymmetrica* sp. nov., male holotype. (41-49) *C. emarginata* sp. nov., male holotype. (35, 41) Facial part of head. (36, 42) Pronotum, dorsal view. (37, 43) Abdominal apex, dorsal view. (38, 44) Hypandrium, ventral view. (39, 45) Posterior margin of hypandrium, dorsal view. (46) Same, posterior view. (40, 47) Male genitalia, dorsal view. (48) "Folded sclerite" of male genitalia. (49) Subgenital sclerite of male genitalia, ventral view. Dotted areas indicate dark colour (36, 42) or membranous parts (37-40, 43-48). Abbreviations are explained in "Material and Methods". Scale bars 1 mm: a (35, 41), b (36, 42), c (37, 43), d (38-39, 44-46), e (40, 47-49).

characters for species determination in *Ctenoneura* are characters of the hypandrium. Hanitsch (1925, 1927) described species mainly on the base of tegmina and wing venation, paying little attention to the structure of the hypandrium. In the original description of *C. major* characters of the hypandrium are not mentioned at all (Hanitsch, 1925). Taking this into account, the record from southern Vietnam needs confirmation. However, a similar range, including Sabah and southern Vietnam, is known, for example, for the praying mantis *Ceratocrania macra* Westwood, 1889 (Shcherbakov & Anisyutkin, 2018).

Ctenoneura emarginata sp. nov.

Figs 7-8, 13, 41-49

Material examined: MHNG; male holotype (No. 160920/04); East Malaysia, Borneo, Sabah, Mt Kinabalu National Park (Fig. 13A), 1500 m, collected by interception trap; 25.-30.IV.1987; leg. A. Smetana.

Etymology: The Latin adjective "emarginatus, -a, -um" (= notched) refers to the shape of posterior margin of the hypandrium.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters.

Head without sutures below antennal sockets (Fig. 41); distance between eyes about 0.9 times eye length; distance between antennal sockets about equal to scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.6. Pronotum as in Fig. 42. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with very short intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 43), well sclerotized, with only a longitudinal stripe of weak sclerotization, its posterior margin medially rounded and protruded. Cerci with 10 distinct segments, apical segment very small (Fig. 43). Hypandrium asymmetrical (Figs 44-46); left and right anterolateral processes fused; left posterolateral corner folded up, bifurcated apically (Fig. 45, *l.p.a.*); posterior margin medially rounded, with deep and narrow notch; right posterolateral corner of complicated shape (Figs 45-46, *r.p.a.*), with a triangular outgrowth on its outer side (Figs 44-45, *t.o.*); left and right syli distinct.

Male genitalia (Figs 47-49): subgenital sclerite long and slightly coiled (Figs 47, 49, *sgs.*); "folded sclerite" (*f.scl.*, corresponding to *ldp+lvp* of Qiu *et al*., 2017) as in Figs 47-48; right phallomere with distinct transverse sclerite (Fig. 47, *tvs.*); small rod-like sclerite situated near "folded sclerite" (Fig. 47, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.4; head width 1.3; pronotum length 1.8; pronotum width 2.3; tegmen length 8.9; tegmen width 3.2.

Comparison: *Ctenoneura emarginata* sp. nov. can be readily distinguished from all other congeners by the shape of its hypandrium, i.e. left posterolateral corner folded up and bifurcated apically, posterior margin of hypandrium deeply notched, right posterolateral corner complicated, with outer triangular outgrowth (Figs 44-46). The new species differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly rounded pronotum (see Fig. 42 and Roth, 1993: fig. 2A).

Ctenoneura orlovi sp. nov.

Figs 9-10, 13, 50-55

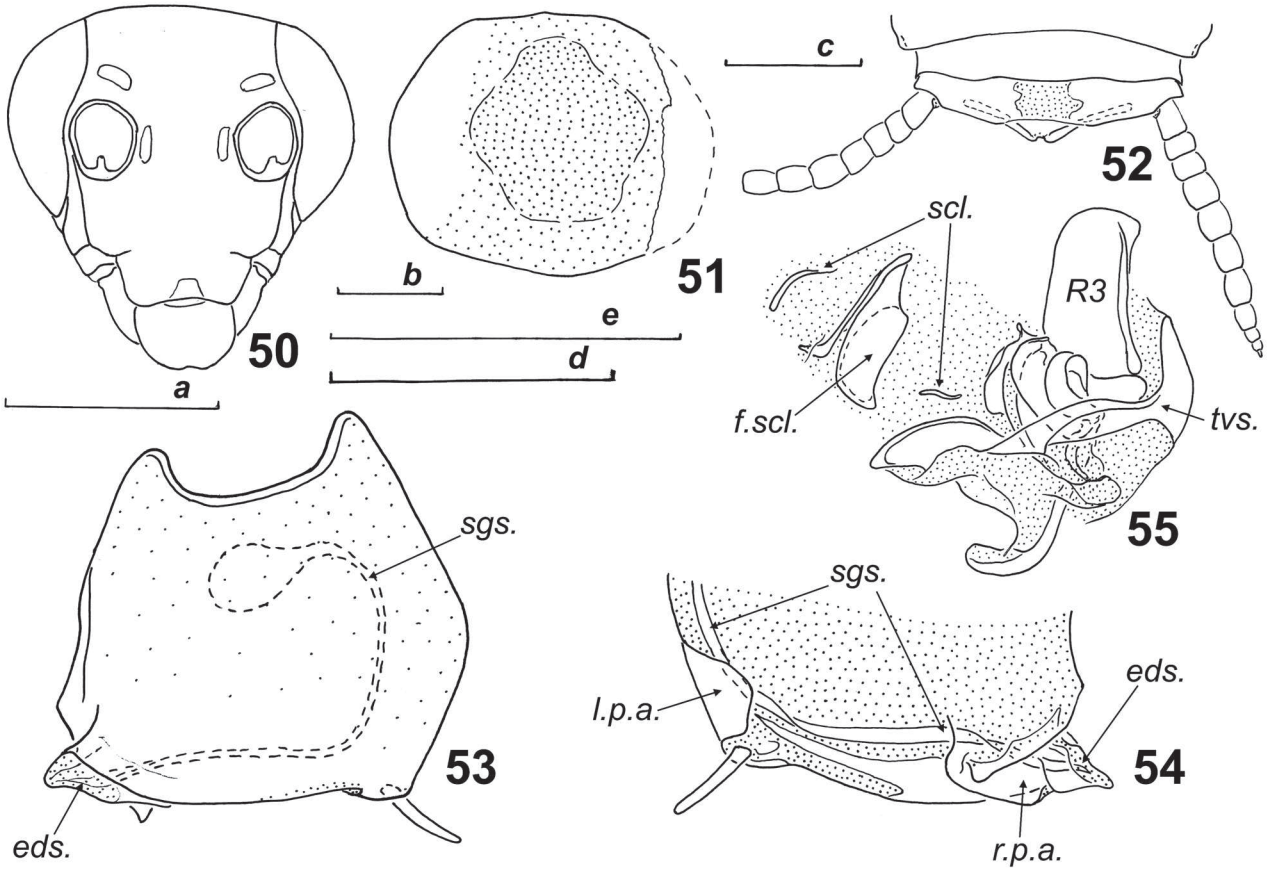
Material examined: ZIN; male holotype (No. 160920/05); Vietnam, Lao Cai Prov., Sa Pa Distr., Mt Fan Si Pan (Fig. 13C), 1400-1500 m, 22°8'56"N, 103°49'35"E; 26.V.-6.VI.1999; leg. N.L. Orlov.

Etymology: This species is named in honour of the collector of the holotype, the famous Russian herpetologist Dr Nikolai L. Orlov.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but larger, additionally different in the following characters.

Head without sutures below antennal sockets (Fig. 50); distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.5 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.4, 1.0, 1.5. Pronotum as in Fig. 51, anterior margin very weakly protruded; right paranotalium broken off. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with a very short intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins indiscernible. Anal plate transverse (Fig. 52), its posterior margin medially protruded and separated by a transverse fold; dorsally with a membranous spot. Right cercus with 11 distinct segments, the apical one very small; left cercus partly broken off, with 7 basal segments remaining (Fig. 52). Hypandrium broad and asymmetrical (Figs 53-54); left anterolateral process larger than right one; left posterolateral corner folded up (Fig. 54, *l.p.a.*), posterior margin widely rounded; right posterolateral corner of complicated shape (Fig. 54, *r.p.a.*), with an outgrowth directed postero-dorsal, this outgrowth forming fold and supporting extended structure of subgenital sclerite (Figs 53-54, *eds.*); left stylus large, right one absent.

Male genitalia (Figs 53-55): subgenital sclerite long and strongly curved (Figs 53-54, *sgs.*); "folded sclerite" (corresponding to *ldp+lvp* of Qiu *et al*., 2017) large and well sclerotized (Fig. 55, *f.scl.*); right phallomere with



Figs 50-55. *Ctenoneura orlovi* sp. nov., male holotype. (50) Facial part of head. (51) Pronotum, dorsal view. (52) Abdominal apex, dorsal view. (53) Hypandrium, ventral view. (54) Posterior margin of hypandrium, dorsal view. (55) Male genitalia, dorsal view. Dotted areas indicate dark colour (51) or membranous parts (52-55). Abbreviations are explained in "Material and Methods". Scale bars 1 mm: a (50), b (51), c (52), d (53-54), e (55).

wide transverse sclerite (Fig. 55, *tvs.*); two small rod-like sclerite located near "folded sclerite" (Fig. 55, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.7; head width 1.6; pronotum length 2.5; pronotum width ~3.0 (right paranotalium broken off); tegmen length 10.2; tegmen width 3.1.

Comparison: The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. presence of a folded up left posterolateral corner, widely rounded posterior margin, complicated outgrowth at right posterolateral corner and large left stylus (Figs 53-54). *Ctenoneura orlovi* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and an angular, protruded posterior margin of the pronotum.

***Ctenoneura gorochovi* sp. nov.**

Figs 11-13, 56-65

Material examined: ZIN; male holotype (No. 160920/06); East Malaysia, Sabah, Mt Trus Madi (Fig. 13D), about 1000 m, partly primary / partly secondary forest; 13.-25.V.2007; leg. A.V. Gorochov.

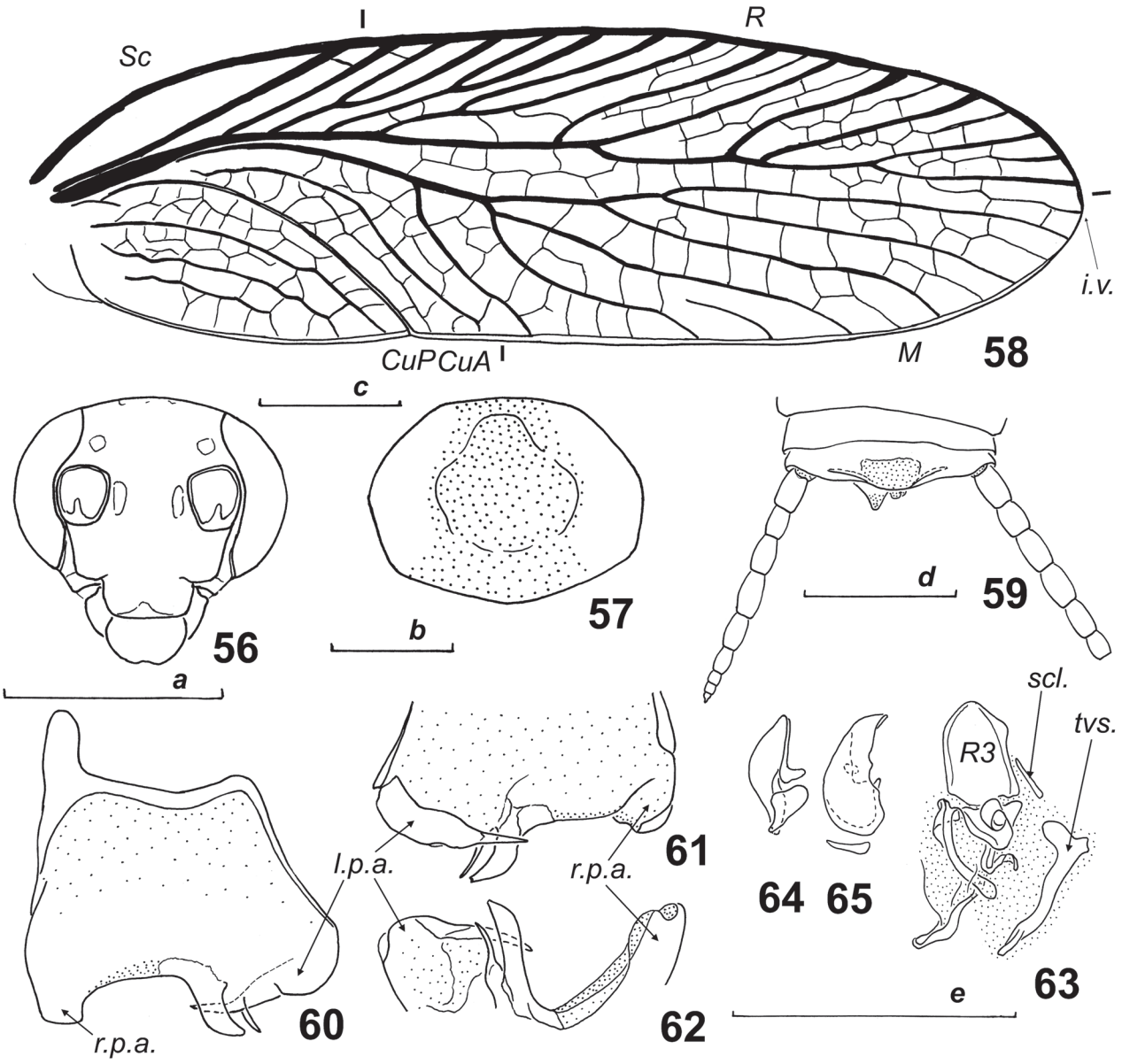
Etymology: This species is named in honour of the collector of the holotype, the famous Russian orthopterologist Dr Andrey V. Gorochov.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters.

Head about as long as wide, without sutures below antennal sockets (Fig. 56); distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.3 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.4, 1.0, 1.3. Pronotum as in Fig. 57. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with very short intercalary vein (Fig. 58, *i.v.*); hind wings with moderately sclerotized area of

anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 59), its posterior margin medially protruded and separated by transverse fold; dorsally with a membranous spot. Left cercus with 9 distinct segments, the apical one very small, with attenuate apex; the right cercus partly broken off, with 6 basal segments remaining (Fig. 59). Hypandrium broad (Figs 60-62); right anterolateral process larger than left one; left posterolateral corner drawn out into mediad-directed spine (Figs 60-62, *l.p.a.*); strongly sclerotized tooth-like process situated near middle of posterior margin of hypandrium; a small sclerotized spine to the left of tooth-like process; a wide and rounded notch with weakly sclerotized edges situated to the right of these spines; right posterolateral corner in the shape of an obtuse unarmed outgrowth (Figs 60-62, *r.p.a.*); styli absent.

Male genitalia (Figs 63-65): subgenital sclerite absent; "folded sclerite" (corresponding to *ldp+lvp* of Qiu *et al*., 2017) well sclerotized (Figs 64-65); right phallomere



Figs 56-65. *Ctenoneura gorochovi* sp. nov., male holotype. (56) Facial part of head. (57) Pronotum, dorsal view. (58) Right tegmen, dorsal view. (59) Abdominal apex, dorsal view. (60) Hypandrium, ventral view. (61) Posterior margin of hypandrium, dorsal view. (62) Same, posterior view. (63) Right phallomere of male genitalia, dorsal view; structures partly disarticulated. (64) "Folded sclerite" of male genitalia. (65) Same at different angle of view plus small accessory sclerite. Dotted areas indicate dark colour (57) or membranous parts (59-63). Abbreviations are explained in "Material and methods". Scale bars 1 mm: a (56), b (57), c (58), d (59), e (60-65).

with well sclerotized transverse sclerite (Fig. 63, *tvs.*); two small rod-like sclerites situated near "folded sclerite" (Fig. 65) and near right phallomere (Fig. 63, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.2; head width 1.2; pronotum length 1.7; pronotum width 2.2; tegmen length 7.4; tegmen width 2.3.

Comparison: *Ctenoneura gorochovi* sp. nov. can be readily distinguished from all other congeners by the shape of its hypandrium, i.e. mediad-directed spine present at posterolateral corner, tooth-like process situated near middle, posterior margin of hypandrium with wide and rounded notch, styli absent (Figs 60-62). The new species differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by smaller size and by the presence of an intercalary vein and a posteriorly rounded pronotum (see Fig. 57 and Roth, 1993: fig. 2A).

Remark: The abdomen of the holotype is damaged (Fig. 12) and therefore the genitalia sclerites are distorted and disarticulated (Figs 63-65).

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