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Non-African representatives of the plesiomorphion Protopatellata (Ephemeroptera: Baetidae)

Внеафриканские представители плезиоморфона Protopatellata (Ephemeroptera: Baetidae)

Nikita J. Kluge
Н.Ю. Клюге

Department of Entomology, St. Petersburg State University, Universitetskaya nab., 7/9, St. Petersburg 199034, Russia. E-mail: kluge@FK13889.spb.edu. Website: http://www.insecta.bio.pu.ru

Кафедра энтомологии, биолого-почвенный факультет, С.-Петербургский государственный университет, Университетская наб., 7/8, С.-Петербург 199034, Россия.

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КЛЮЧЕВЫЕ СЛОВА: систематика, Ephemeroptera, Baetidae, Protopatellata, *Indocloeon*, *Anafroptilum*, новый вид.

ABSTRACT. *Indocloeon*, described as larvae of a single species from Sri Lanka, appears to belong to the plesiomorphon Protopatellata, which formerly was known from Africa only. *Indocloeon primum* is redescribed as larvae and male and female imagoes reared from larvae. A new species *Indocloeon indonesiae* **sp.n.** is described as male and female imagoes reared from larvae from Lombok Island in Indonesia. A new genus *Anafroptilum* **gen.n.** is establishes for the East-Palaearctoc species originally described as *Centroptilum kazlauskasi* Kluge, 1983 and some Nearctic species formerly attributed to the genus *Centroptilum*; their patella-tibial suture is developed on middle and hind legs only, that is characteristic for Protopatellata.

РЕЗЮМЕ. Установлено, что *Indocloeon*, описанный по личинкам одного вида из Шри Ланки, относится к плезиоморфону Protopatellata, ранее известному только из Африки. *Indocloeon primum* переописывается по личинкам и выведенным из личинок самцам и самкам имаго. По самцам и самкам имаго, выведенным из личинок с острова Ломбок в Индонезии, описывается новый вид *Indocloeon indonesiae* **sp.n.** Установлен новый род *Anafroptilum* **gen.n.**, включающий восточно-палеарктический вид, исходно описанный как *Centroptilum kazlauskasi* Kluge, 1983, и некоторые неарктические виды, ранее помещавшиеся в род *Centroptilum*; у них пателло-тибиальный шов развит только на средних и задних ногах, что свойственно Protopatellata.

Introduction

All Baetidae s.str., or Turbanoculata Kluge, 1997, are divided into a plesiomorphon Protopatellata Kluge & Novikova, 2011 and a holophyletic taxon Anteropatellata Kluge, 1997. The taxon Protopatellata is characterized by retaining the same primitive position of patella-tibial suture, which occurs in most Ephemeroptera: in all stages of both sexes this suture is developed on middle and hind legs, but absent on fore legs; in selected taxa patella-tibial suture is reduced on all legs, but it never appears on fore legs. The taxon Anteropatellata is characterized by an autapomorphy: patella-tibial suture is restored on fore legs, which become similar to middle and hind legs; only in male subimago and imago fore legs lack patella-tibial suture (see Table).

Table. Presence of patella-tibial suture in Protopatellata and Anteropatellata.
Таблица. Наличие пателло-тибиального шва у Protopatellata и Anteropatellata

		male			female		
		fore leg	middle leg	hind leg	fore leg	middle leg	hind leg
plesiomorphon Protopatellata	larva	–	+	+	–	+	+
	subimago	–	+	+	–	+	+
	imago	–	+	+	–	+	+
Anteropatellata	larva	+	+	+	+	+	+
	subimago	–	+	+	+	+	+
	imago	–	+	+	+	+	+

The taxon Protopatellata is abundant in Afrotropical region (including South Africa and Madagascar), where it is represented by more than 60 species forming a wide range of morphological forms. Non-African representatives of Protopatellata had been unknown yet. Three Asian baetid species with the primitive position of patella-tibial suture are described below.

Morphological terms used here, are explained in the previous paper [Kluge & Novikova, 2011].

All material, including holotypes and paratypes of the new species, is permanently deposited in the Zoological Institute of Russian Academy of Sciences (Saint

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Petersburg, Russia); temporarily locates in the Department of Entomology of Saint Petersburg State University. In the lists of material examined, the following arbitrary signs are used: L-S-I♂ — male imago reared from larva, with larval and subimaginal exuviae; L-S-I♀ — female imago reared from larva, with larval and subimaginal exuviae.

General classification of Baetidae

Here phylogenetic classification of Baetidae is accepted as the following (some poorly known taxa are not included):

1. **Turbanoculata** Kluge, 1997, or **Baetis/fg4** [f: Baetida Leach, 1815; g: *Baetis* Leach, 1815], or family Baetidae s.str. Characterized by a number of unique apomorphies [Kluge, 2004]. Distributed World-Wide, except New Zealand.

1.1. Plesiomorphion **Protopatellata** Kluge & Novikova, 2011, or **Afroptilum/f1=Centroptiloides/g1** [f: Afroptilinae Kluge, 1997; g: *Centroptiloides* Lestage, 1918], or subfamily Afroptilinae sensu Kluge 1997. Characterized by plesiomorphic absence of patella-tibial suture on fore legs. Distributed mainly in Ethiopian Region; a few species in Asia and North America (see below).

2.2. **Anteropatellata** Kluge, 1997, or **Baetis/fg5**. Characterized by restoring patella-tibial suture on fore legs of larva and female adults. Distributed World-Wide, except New Zealand.

2.2.1. **Cloeon/fg1** [f: Cloeonidae Newman, 1853; g: *Cloeon* Leach, 1815]. Characterized by presence of spines on lateral margins of last abdominal segments in larva and other characters. Distributed in Holarctic, Ethiopian, Oriental Regions and Australia.

2.2.1.1. Plesiomorphon **Similicloeon/g1** [g: *Similicloeon* Kluge & Novikova, 1992] (including *Intercloeon* Kluge & Novikova, 1992).

2.2.1.2. **Cloeon/fg2**. Characterized by strongly widened, double tergalii of peculiar shape in larva, triangular median projection of penial bridge of male imago, colored fore wing margin in female imago and viviparity. Distributed in Holarctic, Ethiopian, Oriental Regions and Australia.

2.2.1.3. **Procloeon/g1** [g: *Procloeon* Bengtsson, 1915]. Characterized by presence of one large spine on lateral side of each segment in distal part of larval cercus [Kluge & Novikova, 1992: Fig. 9:19]. Distributed in Holarctic, Ethiopian and Oriental Regions.

2.2.1.3.1. Plesiomorphon **Procloeon/g2**. Distributed in Holarctic, Ethiopian and Oriental Regions.

2.2.1.3.2. **Austrocloeon/g(1)** [g: *Austrocloeon* Barnard, 1940]. Characterized by a single vein in pterostigma and viviparity. Distributed in Ethiopian Region.

2.2.1.3.3. **Pseudocentroptiloides/g1** [g: *Pseudocentroptiloides* Jacob, 1987]. Characterized by peculiar modification of labium. Distributed in Holarctic, Ethiopian and Oriental Regions.

2.2.1.3.3.1. Plesiomorphon **Securiops/g(1)** [g: *Securiops* Jacobus et al., 2006]. Distributed in Ethiopian Region.

2.2.1.3.3.2. **Pseudocentroptiloides/g2**. Characterized by peculiar shape of labrum. Distributed in Holarctic and Oriental Regions.

2.2.2. **Centroptilum/g1** [g: *Centroptilum* Eaton, 1869] (see below).

2.2.3. **Baetopus/g1** [g: *Baetopus* Keffermuller, 1960]. Characterized by 2–segmented labial palp. Distributed in Holarctic and Oriental Regions.

2.2.3.1. Plesiomorphon **Baetopus/g2**. Distributed in Holarctic.

2.2.3.2. **Raptobaetopus/g(1)** [g: *Raptobaetopus* Müller-Liebenau, 1978]. Characterized by peculiar modification of mouth apparatus. Distributed in Palaearctic and Oriental Regions.

2.2.4. **Cheleocloeon/g(1)** [g: *Cheleocloeon* Wuillot & Gillies, 1993]. Characterized by paddle-shaped enlarged tergalius I and inner-apical projection on 2nd segment of labial palp. Distributed in Africa and Arabia.

2.2.5. **Afrobaetodes/g(1)** [g: *Afrobaetodes* Demoulin, 1970]. Characterized by ventral shifting of tergalii and adaptation for rheophilous inhabitance. Distributed in Ethiopian Region.

2.2.6. **Baetovectata** Kluge & Novikova, 2011, or **Baetis/fg6**. Characterized by peculiar structure of penial gonovectes, double intercalaries in each space of fore wing and non-lateral direction of 2nd segment subimaginal gonostylus when it develops under larval cuticle [Kluge & Novikova, 2011]. Includes most Baetidae; distributed World-Wide, except New Zealand.

Non-African taxa of Protopatellata

Out of Ethiopian Region, the plesiomorphon Protopatellata is represented by Oriental genus *Indocloeon* Müller-Liebenau, 1982 with two species — *I. primum* Müller-Liebenau, 1982 and *I. indonesiae* **sp.n.** and Amphipacific genus *Anafroptilum* **gen.n.** with a single East-Palaearctic species A. *kazlauskasi* (Kluge, 1983) **comb.n.** and several Nearctic species.

Indocloeon Müller-Liebenau, 1982
Figs 1–37.

TYPE SPECIES: *Indocloeon primum* Müller-Liebenau, 1982.

LARVA. Cuticle of abdominal terga nearly unicolor, without contrasting markings or blanks; cuticle of abdominal sterna nearly colorless. Cuticular pigmentation of other body parts species-specific.

Head rather narrow; frons between antennae forms elevation more or less narrowing anteriorly; margins of this elevation can somewhat overlap antennal bases (Fig. 1). Mandibles (Figs 16–17) [Müller-Liebenau, 1982: Fig. 1h]: Left mandible has incisor and kinetodontium fused up to apex; distalmost denticle of incisor turned ventrally and terminates far from apex; prostheca very massive; setae proximad of prostheca either present (in *I. indonesiae*) or absent (in *I. primum*). Right mandible has incisor and kinetodontium fused at most length; distalmost denticle of incisor turned ventrally and terminates far from apex; prostheca stick-like, pressed to kinetodontium; proximad of prostheca a row of setae. Hypopharynx with median tuft of stout setae-like spines, which are brought together, but not coalescent. Maxilla (Fig. 5) [Müller-Liebenau, 1982: Fig. 1e]: biting edge narrow; 3 canines and distal dentiseta teeth-like, curved at the same direction; middle and proximal dentisetae more slender; maxillary palp long and slender, differs in two species. Labium (Fig. 3) [Müller-Liebenau, 1982: Fig. 1b-d]: glossal and paraglossal muscles attached at one point near base of mentum; 2nd segment of labial palp has projected medio-apical angle and contains muscle moving 3rd segment.

Pronotum short, without projected antero-lateral angles, with straight transverse ridge near anterior margin; mesonotum with hind margin projected between protoptera (Fig. 4). Metanotum without vestiges of hind protoptera [Müller-Liebenau, 1982: Fig. 1f]. Meso- and metathoracic pleura and legs bear

scales in angulate bases with opercula at angles (Fig. 15), similar to that on abdominal terga and sterna (Fig. 6). Legs slender; femora of all legs slender and parallel-sided, fore femur somewhat thicker and shorter than middle and hind femora; fore tibia somewhat shorter than middle and hind tibiae; fore tarsus somewhat longer than middle and hind tarsi (Figs 13–14). Patella-tibial suture present on middle and hind legs (Fig. 15), absent on fore legs. Femora, tibiae and tarsi have stout pointed bipectinate setae, which do not form regular rows; these bipectinate setae are most numerous on inner side of fore femur (Fig. 13), less numerous on inner side of middle and hind femora (not shown in Fig. 14). Outer margin of femur lacks longitudinal row of stout setae (in profile view irregular pectinate setae can be confused with such row — Fig. 14); apex of each femur with two stout blunt non-pectinate dark brown setae (Fig. 15). Claw slender, slightly bent, with 2 rows of denticles, among which 3–4 distalmost denticles larger and directed distally, and other denticles very small (Fig. 12) [Müller-Liebenau, 1982: Fig. 1j].

Abdomen narrow, equally convex dorsally and ventrally: being spread on slide, terga and sterna have equal width; tergum width between tergalii bases 2¼–2½ of tergim length; fore margins of terga and sterna strongly convex in middle part [Müller-Liebenau, 1982: Fig. 2]. Lateral margins of all abdominal segments lack spines or denticles (unlike Cloeon/fg1 and *Anafroptilum*). Terga and sterna covered by fine, longitudinally striated scales, situated in angulate nests, whose angles bear operculae (Fig. 6); in *Indocloeon primum* these scales can be arranged in irregular transverse rows [Müller-Liebenau, 1982: Fig. 3]. Denticles on hind margins of abdominal terga and sterna differ in *I. indonesiae* and *I. primum*. Paraprocts bear scales in angulate nests and regular denticles on medioposterior margin (Fig. 8). Tergalii able for rhythmical respiratory vibration. Tergalii I–VI with anal margin more convex than costal margin; tergalius VII with anal margin less convex than costal margin (Figs 9–11). Costal rib on tergalius I short, on tergalii II–VII long, terminate near tergalius apex and bear denticles in apical part. Anal rib on tergalius I absent, on tergalius II short, on next tergalii longer, on tergalius VII terminates near tergalius apex. All tergalii with tracheae dense and blackish. Cerci long, paracercus twice shorter than cerci. At proximal half of cercus (equal to paracercus length) swimming setae well developed; at distal half of cercus swimming setae absent. Paracercus has swimming setae nearly up to its tip, only several very thin apical segments lack setation. Each swimming seta is thick and pigmented in proximal half and thin and colorless in distal half (Fig. 7).

In mature male larva subimaginal gonostyli developing under larval cuticle are folded as following: 2nd segment bent laterally; 3rd segment bent medially and curved anteriorly (Fig. 35). This mode of folding corresponds to the «*Cloeon*-type» which is usual for Protopatellata, but it looks unusual due to the fact that 2nd segment is very short and 3rd segment is very long, as in imago.

SUBIMAGO AND IMAGO. Fore wings with no more than one marginal intercalary in each space. Hind wings absent. On middle and hind legs tibia slightly longer than femur; tarsus ½ of tibia length; proximal (1st+2nd) tarsal segment long; tarsus has one apical thorn on 3rd tarsomere only, while 1st+2nd and 4th tarsomeres lack apical-ventral thorns (Fig. 19). On fore leg of female tarsus also has one apical thorn on 3rd tarsomere only (Fig. 20). In subimago of both sexes all segments of all tarsi covered with pointed microlepides.

Male genitals have peculiar structure (Figs 23–25, 27–29, 32–33): Styligeral muscle wide, paired, its left and right halves convergent toward styliger (Figs 24, 32). Unistyligers (i.e., gonostyli pedestals, or lateral parts of styliger containing styligeral muscles) widely separated and poorly expressed. Proximal (1st+2nd) segment of gonostylus unusually short. Distal (3rd) segment of gonostylus unusually long; in subimago nearly as long as in imago (compare Figs 23 and 24, 27 and 28, 32 and 33), develops under larval cuticle without crumpling (Fig. 35). Penial bridge with wide rectangular median projection; gonovectes of penis short, at most membranous.

COMPARISON. As in most Protopatellata, all stages (larva, subimago and imago) of both sexes of *Indocloeon* have patella-tibial suture developed only on middle and hind legs and absent on fore legs (Figs 13–14) . Probably, Müller-Liebenau [1982: Fig.1i] wrongly indicated a larval leg with developed patella-tibial suture as "1st leg".

Indocloeon differs from all known baetids by genital structure with wide styliger, short 1st+2nd segments of gonostyli and long 3rd segments of gonostyli (Figs 24, 28, 32). Unlike most Protopatellata, gonovectes are vestigial and membranous (Figs 24, 29, 32).

Larva of *Indocloeon* resembles *Cheleocloeon* in having slender legs (Figs 13–14) combined with chelate labial palp (Fig. 3); it differs from *Cheleocloeon* by absence of patella-tibial suture on fore legs (Fig. 13), elevated frons (Fig. 1), and non-enlarged first tergalii (Fig. 9).

DISTRIBUTION. Oriental Region: known from Sri Lanka and Lombok.

SPECIES COMPOSITION. *Indocloeon primum* Müller-Liebenau, 1982 (Sri Lanka) and *I. indonesiae* **sp.n.** (Lombok).

SYSTEMATIC POSITION. *Indocloeon* undoubtedly belongs to Turbanoculata, or Baetidae s.str., but has no synapomorphies with any other group within Turbanoculata. Symplesiomorphy with Protopatellata (presence of patella-tibial suture only on middle and hind legs of all stages of both sexes) allows to attribute it to the plesiomorphon Protopatellata.

Indocloeon indonesiae Kluge, **sp.n.**
Figs 1–30.

MATERIAL. Holotype: L-S-I♂ {specimen [XL](7)}: Indonesia, Island Lombok, Senaru, 25.IX.2009, coll. N. Kluge and L. Sheyko. Paratypes: the same locality, 19–26.IX.2009: 1 L-S-I♂, 1 L-S-I♀, 2 larvae.

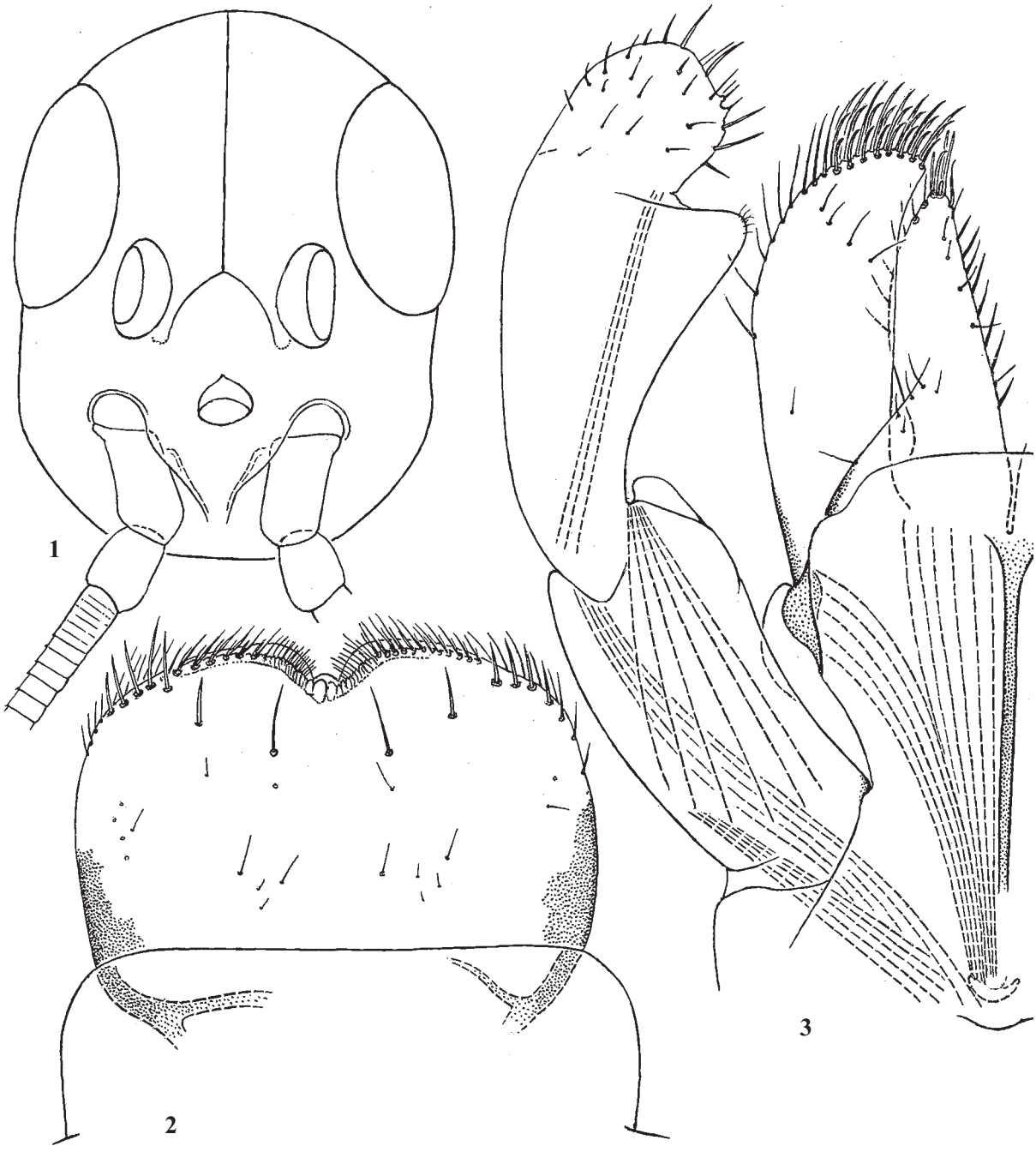
LARVA. Cuticular coloration: Cuticle of head brown, with blanks in front of median ocellus and between eyes and lateral ocelli. Pronotum and mesonotum brown, sometimes with diffusive lighter and darker markings; median longitudinal molting suture light; protoptera with darker and lighter stripes along some longitudinal veins. Thoracic sclerites brown, sterna lighter. Legs have diffusive lighter and darker areas: femur in proximal half light, distally with dark band, apex light, apical flaps dark; tibia in proximal half dark (on middle and hind legs with contrasting light patella-tibial suture), in distal part light; tarsus at most part dark, apex and claw light. All abdominal terga I–IX nearly uniformly brown, sometimes with small diffusive light blanks near anterior margin; tergum X lighter, with hind margin dark. Abdominal sterna lighter than terga. Caudalii nearly uniformly brown.

Hypodermal coloration: Not expressed.

Shape and setation: Labrum with paired anterior-lateral row of setae located close to anterior margin, one seta locates between this row and submedian seta (Fig. 2). Left mandible proximad of prostheca has a small bunch of setae directed proximally (Fig. 16). Maxillary palp indistinctly 3–segmented, with 3rd segment long (Fig. 5). Glossa apically somewhat

wider than in *I. primum*, with three rows of apical setae, ventrally with oblique row of 4 setae; projected medio-apical angle of 2nd segment of labial palp not pointed (Fig. 3). Hind margin of each tergum bears regular row of sclerotized triangular denticles, which are long on posterior terga (Fig. 6) and shorter on anterior terga, so that on tergum I they are equilateral. Hind margins of sterna I–III lack denticles; sternum IV with small denticles; each sternum V–VIII of male and each sternum V–IX of female with regular long triangular sclerotized denticles similar to denticles on terga. Sternum IX of male bears long triangular denticles by sides of protogonostyli and very thin and dense denticles between protogonostyli. At proximal half of cercus (which bears swimming setae — see characteristics of *Indocloeon*) each 4th segment bears several stout spines on lateral side, other segments have smaller spines (Fig. 7); at distal half of cercus (which lacks swimming setae) all segments have no lateral spines.

SUBIMAGO. Cuticular coloration: Cuticle of head and prothorax colorless. Cuticle of mesonotum nearly colorless, only lateral sclerite of parascutellum brown. Cuticle of



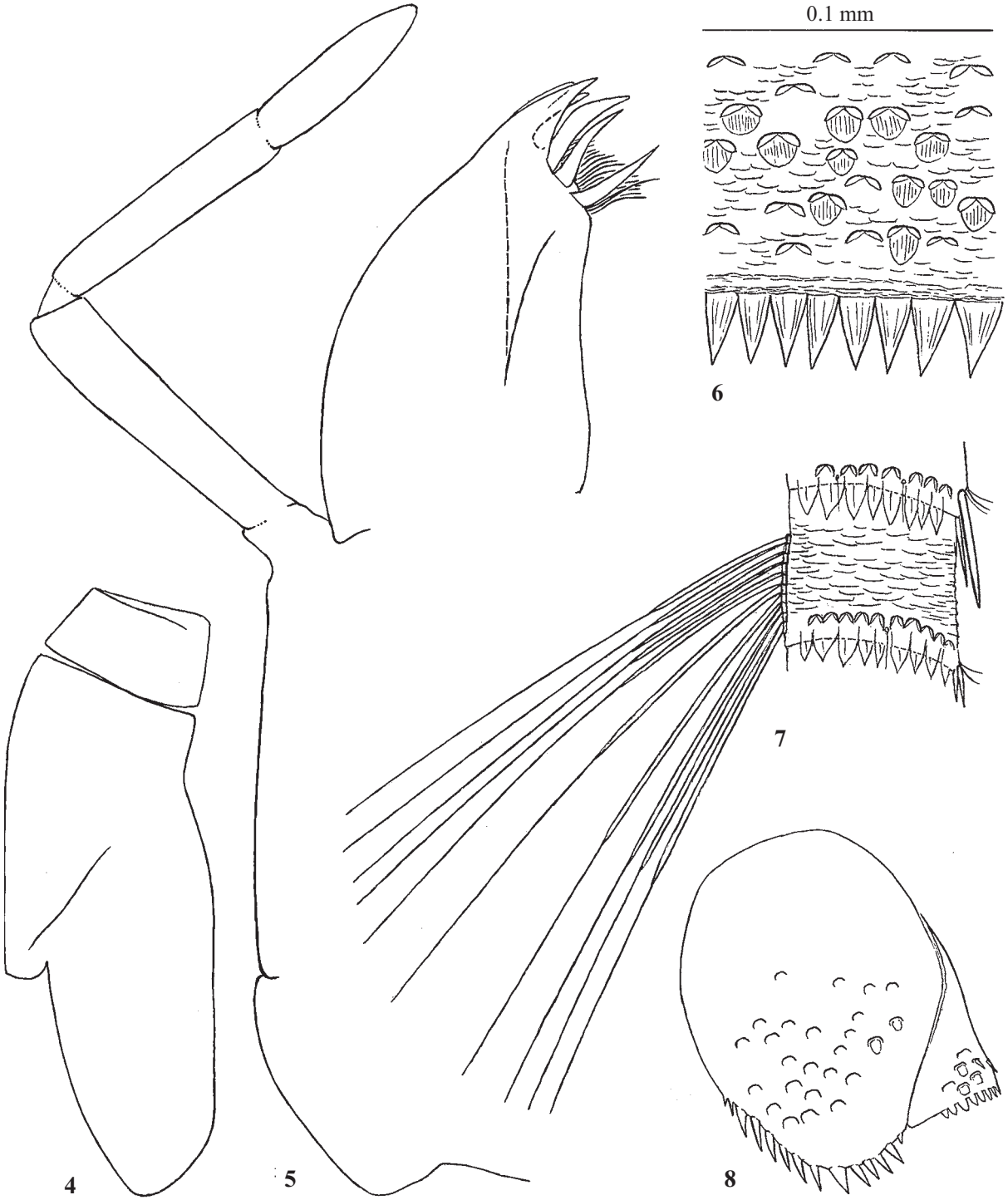
Figs 1–3. *Indocloeon indonesiae* **sp.n.**, last instar larva: 1 — head of female larva, front view; 2 — labrum; 3 — half of labium, ventral view (muscles and setae on dorsal side of 2nd palpomere shown by interrupted lines).

Рис. 1–3. *Indocloeon indonesiae* **sp.n.**, личинка последнего возраста: 1 — голова личинки самки, вид спереди; 2 — верхняя губа; 3 — половина нижней губы, вентрально (мышцы и щетинки на дорсальной стороне второго членика щупика показаны прерывистыми линиями).

pleura at most colorless, with a few brownish stripes; postsubalar sclerite brown, high and short, with antero-dorsal angle stretched and curved, postero-dorsal angle shortly stretched (Fig. 26). Legs colorless. Wings light. Cuticle of abdomen colorless or tinged with pale brownish. Cerci colorless.

Hypodermal coloration: As in imago.

IMAGO, MALE. Head pale ocher. Antennae pale; scapus with dark brown spot near apex, pedicellus with distal half brown (Fig. 30). Turban eyes large (Fig. 30); facetted surface yellow; stem in proximal part light red, in distal part lighter. Medionotum of mesothorax light brown; other parts of thorax at most pale ocher, with a few small brown markings;



Figs 4–8. *Indocloeon indonesiae* **sp.n.**, last instar larva: 4 — exuviae of right half of pronotum and mesonotum (holotype); 5 — maxilla; 6 — hind margin of abdominal tergum VII; 7 — segment of cercus about 1/3 from cercus base, the same scale; 8 — paraproct.

Рис. 4–8. *Indocloeon indonesiae* **sp.n.**, личинка последнего возраста: 4 — экзувий правой половины пронотума и мезонотума (голотип); 5 — максилла; 6 — задний край VII тергита брюшка; 7 — членик церка около 1/3 от основания церка, в том же масштабе; 8 — парапокт.

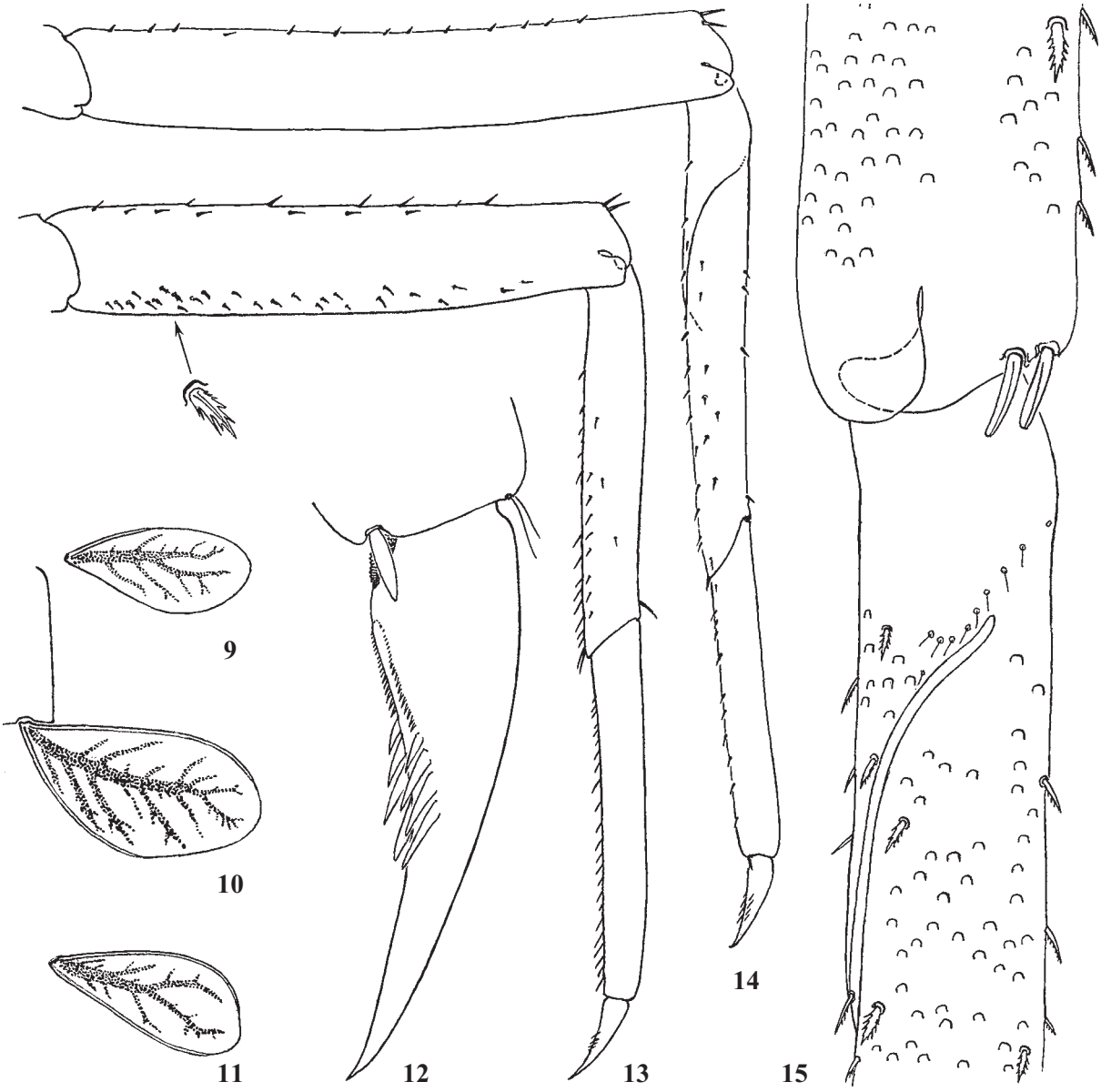
ventral part lighter (Fig. 30). Legs colorless. Wings colorless, all veins pale; pterostigma with 3 crossveins; short single marginal intercalary in some spaces (Fig. 18). Abdominal segments I–VII translucent and colorless, with dark lateral tracheal trunks; terga VIII and IX reddish medially, with white lateral parts; segment X light. Cerci colorless.

Genitals as characterized for *Indocloeon* (Figs 23–25, 27–29). Styliger colorless. 1st+2nd segment of gonostylus has proximal swollen part colorless and covered by small spine-like microtrichiae; distal narrow part brown, covered with brown blunt microlepides, which are longer on inner side. Shape of this segment is quite variable, being different in two specimens examined (Figs 24 and 28). Distal (3rd) segment of gonostylus straight, brown, covered with brown blunt microlepides, which are longer on inner side. Penis brown.

IMAGO, FEMALE. Head pale ocher with brown markings between eyes; antennae as in male (Fig. 22). Pronotum with ornament of contrasting ocher and brown areas. Mesonotum pale ocher, with medionotum slightly darker. Thoracic pleura with ocher and brownish maculation. Ventral part of thorax pale. Legs colorless. Wings as in male. Abdomen with intensive pigmentation: terga I–IX brown, with median part darker, lateral parts pale ocher and contrastingly outlined; tergum X light with posterior margin brown; pleura II–VIII pale ocher, each with a pair of contrasting brown wedge-formed stripes by sides; sternum IX at most brownish; tracheal trunks bordered by blackish (Fig. 21).

EGG. Oval, about 0.15 mm length; surface without regular relief.

DIMENSION. Fore wing length 4–5 mm.



Figs 9–15. *Indocloeon indonesiae* **sp.n.**, last instar larva: 9–11 — tergalii I, IV and VII; 12 — claw (holotype); 13 — fore leg, front view and enlarged bipectinate seta on ventral side of femur; 14 — hind leg, front view; 15 — femoro-tibial articulation of hind femur.

Рис. 9–15. *Indocloeon indonesiae* **sp.n.**, личинка последнего возраста: 9–11 — тергалии I, IV и VII; 12 — коготок (голотип); 13 — передняя нога, вид спереди, и увеличенная двоякогребенчатая щетинка на вентральной стороне бедра; 14 — задняя нога, вид спереди; 15 — сочленение бедра и голени задней ноги.

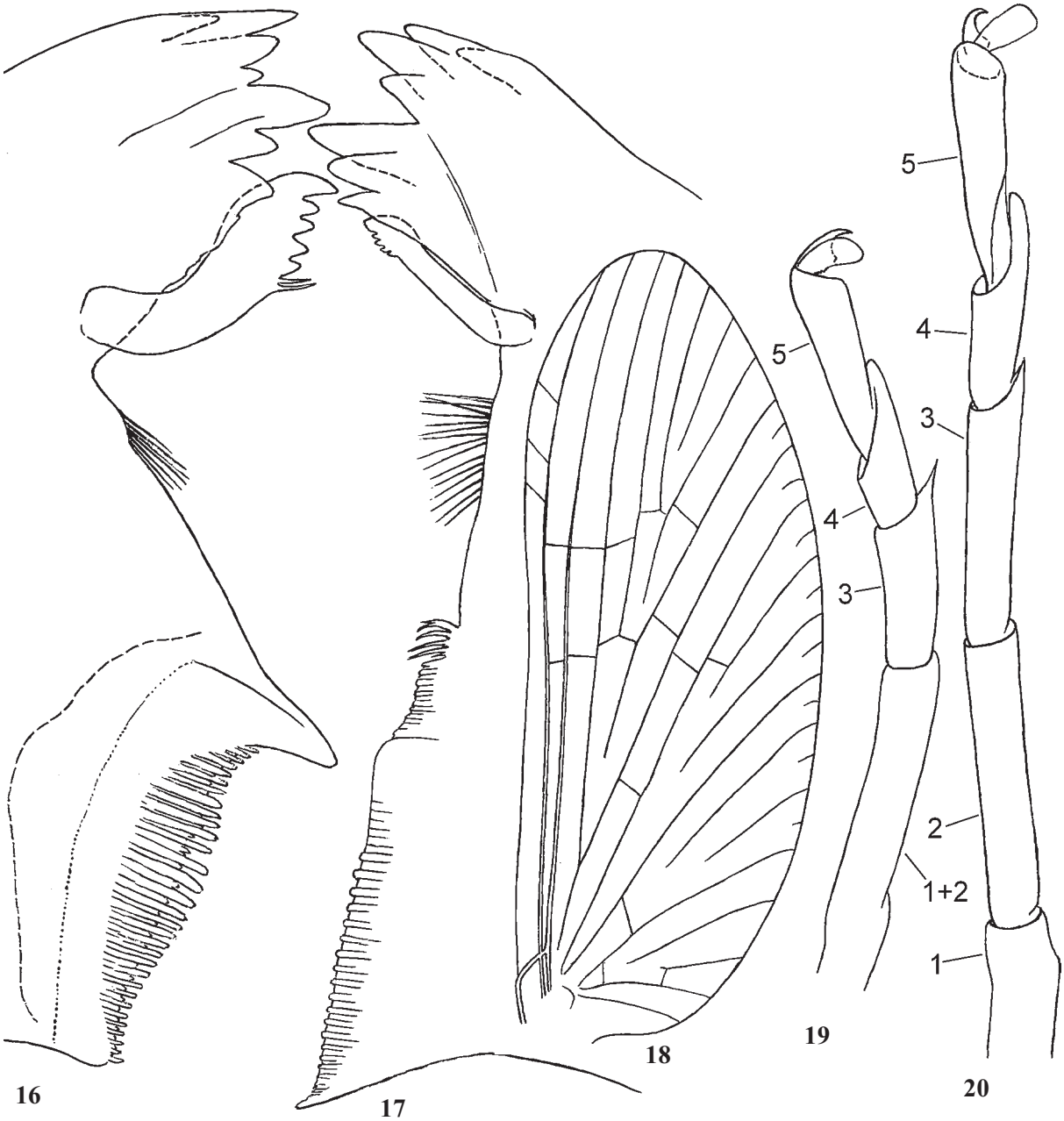
DISTRIBUTION. Known from a single point in Island Lombok (Indonesia).

COMPARISON. Larva of new species differs from *I. primum* by absence of dark brown boundary between frons and clypeus, more intensive cuticular coloration of head, thorax and legs, presence of setae on left mandible, absence of point on labial palp, non-fused denticles on abdominal terga and sterna, and enlarged spines on lateral sides of cerci.

Subimago and imago differ from *I. primum* by shape of postsubalar sclerite and by coloration: peculiar coloration of antennae, darker mesonotum and absence of reddish transverse stripes on abdominal terga. Subimago also differs from *I. primum* by pigmentation of postsubalar sclerite and lateral sclerite of postscutellum. Female imago also differs from *I. primum* by non-darkened crossveins and brown pigmentation of abdomen. Male imago also differs from *I. primum* by reddish tergum IX, brown gonostyli and penis and by absence of semicircular concavity on styliger.

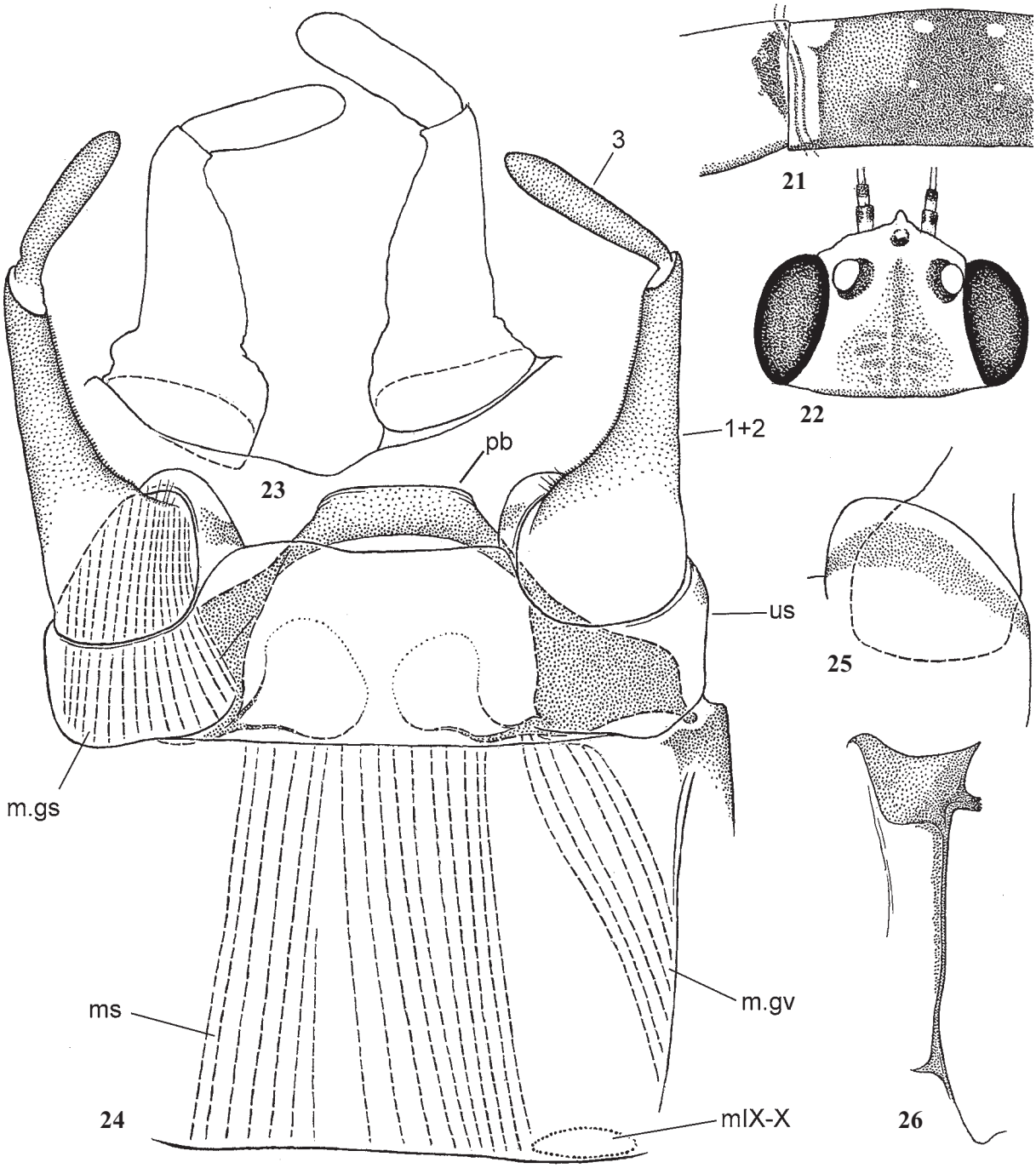
Indocloeon primum Müller-Liebenau, 1982
Figs 31–37.

MATERIAL. Sri Lanka, coll. N. Kluge and L. Sheyko: Uva province, Badulla district, Haputale, small stream in tea plantation, running from Haputale Forest, 15–23.I.2011: 19 L-S-I♂, 12 L-S-I♀, 3 L-S♂, 3 L-S♀, 128 larvae; Central province, Nuwara Elya district, Dalhausie (nr. Maskelya), very small stream close to hotel “Green



Figs 16–20. *Indocloeon indonesiae* **sp.n.**: 16–17 — cutting edges of left and right mandibles; 18 — fore wing (holotype); 19–20 — hind and fore tarsus of female imago; 1, 2, 3, 4, 5 — 1st, 2nd, 3rd, 4th and 5th tarsomeres; 1+2 — completely fused 1st and 2nd tarsomeres.

Рис. 16–20. *Indocloeon indonesiae* **sp.n.**: 16–17 — режущий край левой и правой мандибул; 18 — переднее крыло (голотип); 19–20 — задняя и передняя лапки самки имаго; 1, 2, 3, 4, 5 — 1–й, 2–й, 3–й, 4–й и 5–й тарсомеры; 1+2 — полностью слитые 1–й and 2–й тарсомеры.



Figs 21–26. *Indocloeon indonesiae* **sp.n.** 21 — parts of abdominal tergum and sternum VIII of female imago, spread on slide; 22 — head of female imago; 23–25 — genitals of male, holotype; 23 — subimaginal exuviae of genitals; 24 — imaginal genitals, ventral view (hidden parts and muscles shown by interrupted lines; right gonostylar muscle and left retractor of gonovectis not shown); 25 — dorsal view of imaginal unistyliger; 26 — subimaginal exuviae of left postsubalar sclerite and lateropostnotal crest; 1+2 — fused 1st and 2nd segments of gonostylus; 3 — 3rd segment of gonostylus; m.IX-X — area of anterior attachment of right intersegmental ventral muscles going from base of 9th segment to base of 10th abdominal segment; m.gs — gonostylar muscle, located in unistyliger; m.gv — muscle-retractor of gonovectis; m.s — median sterno-styligeral muscle; pb — penial bridge; us — unistyliger.

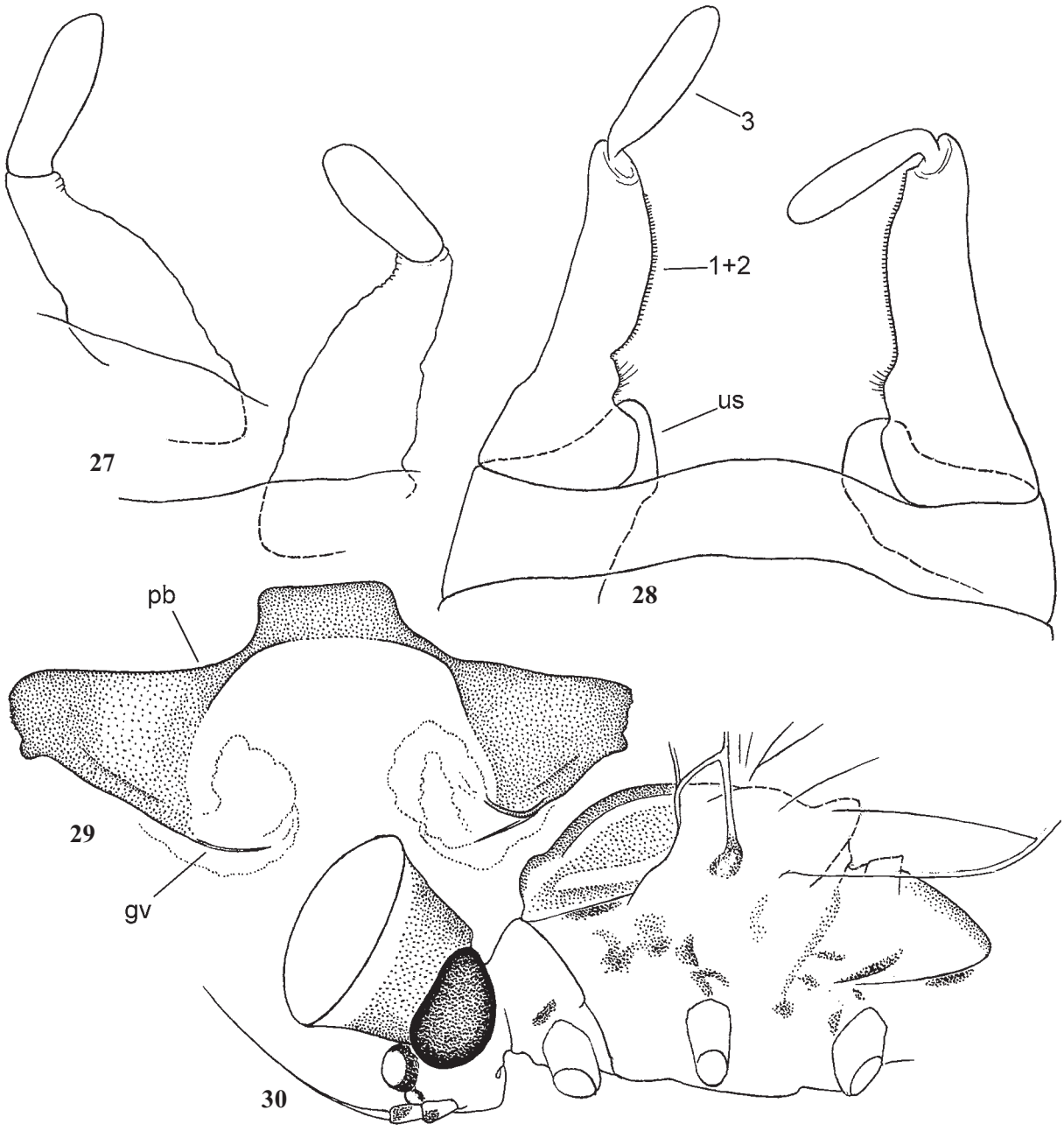
Рис. 21–26. *Indocloeon indonesiae* **sp.n.** 21 — части VIII тергита и стернита брюшка самки имаго, расправлены на препарате; 22 — голова самки имаго; 23–25 — гениталии самца, голотип; 23 — субимагинальный экзувий гениталий; 24 — имагинальные гениталии, вентрально (скрытые части и мышцы показаны прерывистыми линиями; правая гоностилярная мышца и левый ретрактор гоновектиса не показаны); 25 — имагинальный унистилигер, дорсально; 26 — субимагинальный экзувий постсубалярного склерита и латеропостнотального гребня; 1+2 — слитые 1–й и 2–й членики гоностиля; 3 — 3–й членик гоностиля; m.IX-X — область переднего прикрепления правой межсегментарной мышцы, идущей от основания 9–го к 10–му сегменту брюшка; m.gs — гоностилярная мышца, находящаяся в унистилигере; m.gv — мышца-ретрактор гоновекитиса; m.s — медиальная стерно-стилигеральная мышца; pb — мост пениса; us — унистилигер.

House" near beginning of way to Sri Pada (Adam's Peak), 24–26.I.2011: 3 L-S-I♀, 1 S-I♂, 1 S-I♀, 1 ♀ imago, 6 larvae; Central province, Matale district, Sigiriya, 28–30.I.2011: 1 S-I♂.

LARVA. Cuticular coloration: Cuticle of head at most light brownish, with contrasting dark brown boundary between frons and clypeus. Pronotum and mesonotum light brownish, with diffusive lighter and darker markings; mesonotum with diffusive darker wide longitudinal median stripe; protoptera with darker and lighter stripes along some longitudinal veins. Thoracic pleura and sterna colorless. Legs colorless. All abdominal terga I–X nearly uniformly brown. Abdominal sterna lighter than terga [Müller-Liebenau, 1982: Fig. 2]. Caudalii nearly uniformly brown.

Hypodermal coloration: Each abdominal tergum can have more or less expressed reddish transverse band on posterior margin, as in imago.

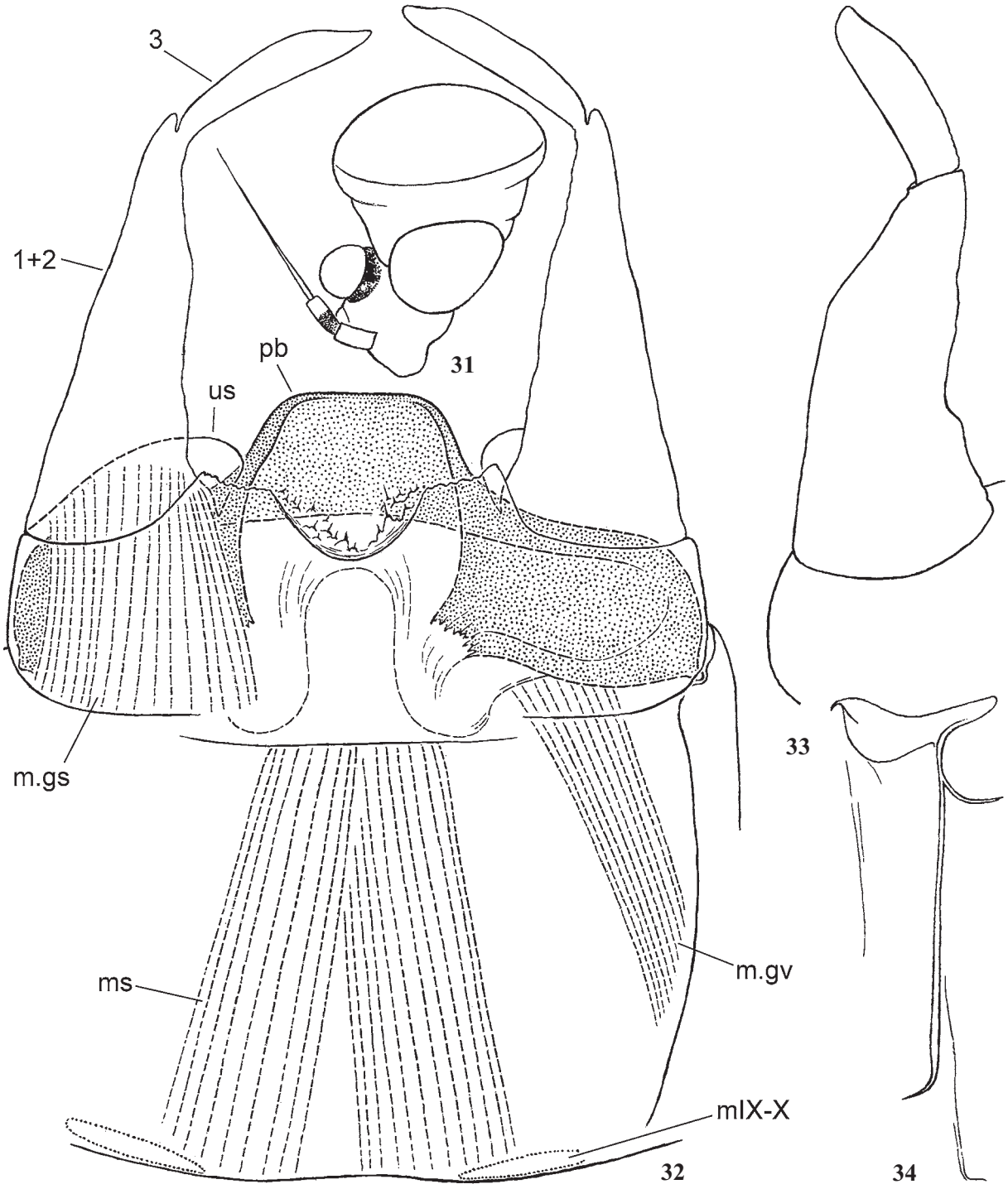
Shape and setation: Labrum usually with a paired row of several setae stretching from submedian seta to anterolateral



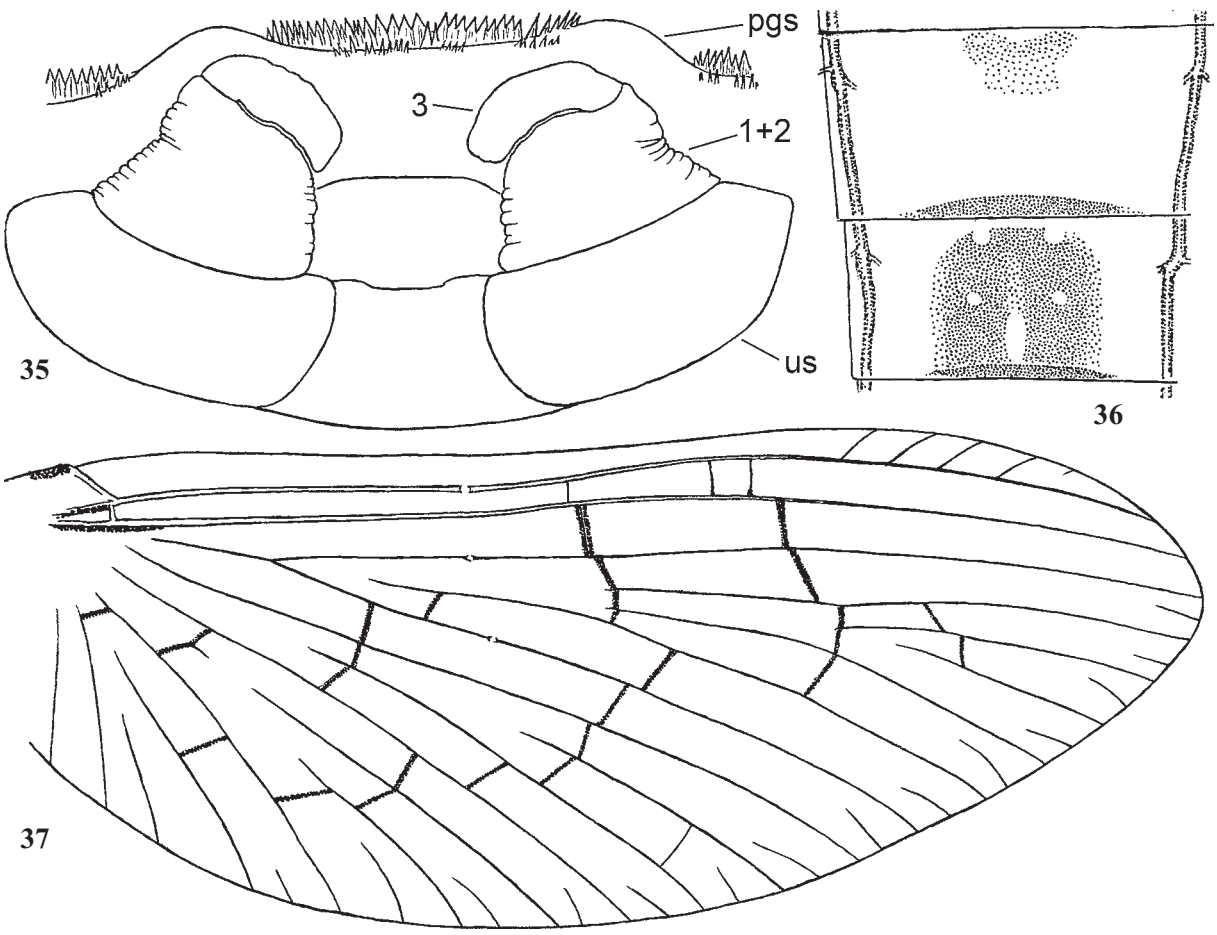
Figs 27–30. *Indocloeon indonesiae* **sp.n.**: 27–29 — genitals of male, paratype; 27 — subimaginal exuviae of left and right gonostyli; 28 — imaginal styliger and gonostyli, ventral view (dorsal outlines of unistyligers shown by interrupted lines); 29 — imaginal penis, ventral view; 30 — head and thorax of male imago (holotype); 1+2 — fused 1st and 2nd segments of gonostylus; 3 — 3rd segment of gonostylus; gv — gonovectis; pb — penial bridge; us — unistyliger.

Рис. 27–30. *Indocloeon indonesiae* **sp.n.**: 27–29 — гениталии самца, паратип; 27 — субимагинальные экзувии левого и правого гоностилей; 28 —имагинальный стилигер и гоностили, вентрально (дорсальные очертания унистилигеров показаны прерывистыми линиями); 29 — имагинальный пенис, вентрально; 30 — голова и грудь самца имаго (голотип); 1+2 — слитые 1–й и 2–й членики гоностиля; 3 — 3–й членик гоностиля; gv — гоновектис; pb — мост пениса; us — унистилигер.

margin [Müller-Liebenau, 1982: Fig. 1a]. Maxillary palp indistinctly 3–segmented, with remnant of 3rd segment very short and bent inward [Müller-Liebenau, 1982: Fig. 1e]. Glossa narroved apically [Müller-Liebenau, 1982: Fig. 1d]. Projected medio-apical angle of 2nd segment of labial palp sharply pointed [Müller-Liebenau, 1982: Fig. 1b, c]. Hind margin of tergum I lacks denticles; hind margin of each tergum II–IX bears regular row of denticles fused together [Müller-Liebenau, 1982: Fig. 3]. Hind margins of sterna I–II lack denticles; each sternum III–VIII of male and each sternum V–IX of female



Figs 31–34. *Indocloeon* primum: 31 — head of male imago, lateral view; 32 — genitals of male imago, ventral view (hidden parts and muscles shown by interrupted lines; right gonostylar muscle and left retractor of gonovectis not shown); 33 — subimaginal exuviae of right gonostylus, the same individual; 34 — subimaginal exuviae of left postsubalar sclerite and lateropostnotal crest; 1+2 — fused 1st and 2nd segments of gonostylus; 3 — 3rd segment of gonostylus; m.IX-X — area of anterior attachment of right intersegmental ventral muscles going from base of 9th segment to base of 10th abdominal segment; m.gs — gonostylar muscle, located in unistyliger; m.gv — muscle-retractor of gonovectis; m.s — median sterno-styligeral muscle; pb — penial bridge; us — unistyliger.



Figs 35–37. *Indocloeon* primum: 35 — subimaginal genitals folded under larval cuticle in mature male larva ready to molt to subimago (left gonostylar muscle shown by interrupted lines); 36 — abdominal terga VII and VIII of female imago, spread on slide; 37 — wing of female imago; 1+2 — fused 1st and 2nd segments of subimaginal gonostylus; 3 — 3rd segment of subimaginal gonostylus; pgs — larval protogonostylus; us — subimaginal unistyliger.

Рис. 35–37. *Indocloeon* primum: 35 — субимагинальные гениталии, сложенные под личиночной кутикулой у зрелой личинки самца, готовой линять на субимаго (левая гоностилярная мышца показана прерывистыми линиями); 36 — VII и VIII тергиты брюшка самки имаго, расправлены на препарате; 37 — крыло самки имаго; 1+2 — слитые 1–й и 2–й членики субимагинального гоностиля; 3 — 3–й членик субимагинального гоностиля; pgs — личиночный протогоностиль; us — субимагинальный унистилигер.

with fused denticles similar to denticles on terga. Sternum IX of male bears long thin pointed denticles by sides of protogonostyli and between protogonostyli. Unlike *I. indonesiae*, cerci have no long spines on each 4th segment.

SUBIMAGO. Cuticular coloration: Cuticle nearly completely colorless, only margin of scutellum and knees tinged with brownish. Postsubalar sclerite colorless, with antero-dorsal angle stretched and curved and postero-dorsal angle stretched to a long projection (Fig. 34). Wings light.

Hypodermal coloration: As in imago.

IMAGO, MALE. Head pale (ocher or white), sometimes with small brown dot(s). Antennae pale; scapus entirely pale, pedicellus with basal half brown (Fig. 31). Lateral eyes pale grayish. Turban eyes large, rounded (Fig. 31). Stems of turban eyes pale grayish; facetted surfaces vary individually from colorless whitish or yellowish to dull red or brownish. Thorax entirely pale (ocher or white), with a few small brown markings; sometimes medioscutum and scutellum slightly tinged with pale brownish. Legs colorless. Wings colorless; all veins pail, only junction of Sc, RA and costal brace tinged with brown; pterostigma with 2–5 crossveins; single marginal intercalary in each space (as in Fig. 37). Unlike female, crossveins thin and light; one non-reared specimen from Dalhausie has crossveins bordered by brown as in female. Abdominal segments I–VII translucent and colorless, with dark lateral tracheal trunks; each tergum II–VII with contrasting red or brown narrow transverse stripe on posterior margin, laterally these stripes are pointed and do not reach tracheal trunks (as in Fig.

←

Рис. 31–34. *Indocloeon* primum: 31 — голова самца имаго, латерально; 32 — гениталии самца имаго, вентрально (скрытые части и мышцы показаны прерывистыми линиями; правая гоностилярная мышца и левый ретрактор гоновектиса не показаны); 33 — субимагинальный экзувий правого гоностиля, тот же экземпляр; 34 — субимагинальный экзувий постсубалярного склерита и латеропостнотального гребня; 1+2 — слитые 1–й и 2–й членики гоностиля; 3 — 3–й членик гоностиля; m.IX-X — область переднего прикрепления правой межсегментарной мышцы, идущей от основания 9–го к 10–му сегменту брюшка; m.gs — гоностилярная мышца, находящаяся в унистилигере; m.gv — мышца-ретрактор гоновектиса; m.s — медиальная стерно-стилигеральная мышца; pb — мост пениса; us — унистилигер.

36); tergum VIII reddish medially, with white lateral parts; segments IX and X light. Cerci colorless.

Genitals as characterized for *Indocloeon* (Fig. 32), entirely colorless. Styliger medially with large concavity, which in ventral view looks as semicircular incision. Proximal (1st+2nd) segment of gonostylus entirely covered with spine-like microtrichiae, which are longer on its inner side. Distal (3rd) segment of gonostylus with outer side convex and inner side straight or slightly concave, entirely covered with colorless blunt microlepides, which are longer on its inner side.

IMAGO, FEMALE. Head and thorax pale (ocher or white); head with yellow markings between eyes; antennae as in male; Pronotum with contrasting paired brown or reddish maculae. Legs colorless or diffusively tinged with reddish or yellowish. Behind anterior radial vein crossveins bordered by brown (Fig. 37) (in contrast to male). Coloration of abdomen similar to that of male: segments I–VII colorless, with dark lateral tracheal trunks; each tergum I–VII with contrasting red or brown narrow transverse stripe on posterior margin, laterally these stripes are pointed and do not reach tracheal trunks; tergum VIII reddish medially, with colorless lateral parts (Fig. 36); segment IX usually entirely colorless; tergum X reddish. One non-reared specimen from Dalhausie has, in addition to transverse stripes, a longitudinal median stripe on abdominal terga III–VI.

EGG. Oval, about 0.15 mm length; surface without macrorelief, with dense even punctuation, about 3–4 elements per 0.01 mm.

DIMENSION. Fore wing length 5–6 mm.

Anafroptilum Kluge, **gen.n.**
Figs 38–55.

TYPE SPECIES: *Centroptilum kazlauskasi* Kluge, 1983.

ETYMOLOGY. Neutral gender. Can be interpreted either "non-*Afroptlilum*", or "non-African *Centroptilum*".

LARVA. Cuticle of abdominal terga with contrasting markings and blanks, which are species-specific and vary individually; tergum VI usually has most intensive dark markings [Lowen & Flannagan, 1991: Fig. 13]; cuticle of abdominal sterna nearly colorless.

Head not wide; frons between antennae forms parallel-sided elevation, whose margins can somewhat overlap antennal bases (Fig. 55). Both mandibles have incisor and kinetodontium separated nearly up to base; prostheca of left mandible has moderate width, terminates by several slender denticles; prostheca of right mandible very slender, terminates either by single point (*kazlauskasi* [*Centroptilum*]), or by two slender denticles (*bifurcatum* [*Centroptilum*]); setae proximad of prostheca present [Kluge, 1983: Figs115–116; Lowen & Flannagan, 1991: Figs 17–18]. Median setae-like spines of hypopharynx very short. Maxilla has biting edge rather wide; 3 canines and distal dentiseta teeth-like, curved at the same direction; middle and proximal dentisetae more slender; maxillary palp long and slender, consists of 3 segments of subequal length [Kluge, 1983: Fig. 117; Lowen & Flannagan, 1991: Fig. 19; Kluge & Novikova, 1992: Fig. 3]. Labium has paraglossal muscle fan-formed; 2nd segment of labial palp narrower than 3rd segment and contains muscle moving 3rd segment; 3rd segment strongly widened apically and truncate (Fig. 46) [Kluge, 1983: Fig. 118; Lowen & Flannagan, 1991: Fig. 20; Kluge & Novikova, 1992: Fig. 6]. Pronotum short, without projected antero-lateral angles [Kluge, 1983: Fig. 120], with straight transverse ridge near anterior margin; mesonotum with hind margin projected between protoptera. Metanotum with hind protoptera. Legs (Figs 38–40): Slender; femora of all legs slender and parallel-sided, fore femur somewhat thicker and shorter than middle and hind femora; fore tibia somewhat shorter than middle and hind tibiae; fore tarsus somewhat longer than middle and hind tarsi. Patella-tibial suture present on middle and hind legs (Fig. 39), absent on fore legs (Fig. 38). Femora, tibiae and tarsi have small stout pointed setae, which do not form regular rows; outer margin and apex of femur lack stout setae. Claw slender, slightly bent, with 2 rows of small denticles (Fig. 40).

Abdomen narrow, equally convex dorsally and ventrally: being spread on slide, terga and sterna have equal width. Lateral margins of abdominal segment IX and more anterior ones have pointed denticles (Fig. 41). Terga and sterna covered by fine scales situated in wide semicircular nests lacking operculae (Fig. 44). Tergalii able for rhythmical respiratory vibration. Tergalii I–VI with anal margin more convex than costal margin; tergalius VII with anal margin less convex than costal margin; costal rib far not reaching tergalius apex, anal rib less developed (Figs 47–53) [Lowen & Flannagan, 1991: Fig. 21]. Cerci and paracercus have subequal length, not long, bear swimming setae nearly up to apex, in middle part have dark rings at apex of each 4th segment [Lowen & Flannagan, 1991: Fig. 13]; hind margin of each segment with denticles, no one of each reaches ½ of segment length (unlike Procloeon/g1).

In mature male larva subimaginal gonostyli developing under larval cuticle are folded by "*Cloeon*-type": 2nd segment bent laterally, 3rd segment bent medially (Fig. 54).

SUBIMAGO AND IMAGO. Fore wings with no more than one marginal intercalary in each space. Hind wing more or less narrow, with curved costal projection [Kluge, 1983: Fig. 126; Lowen & Flannagan, 1991: Fig. 5]. On middle and hind legs tibia slightly longer than femur; tarsus ½ of tibia length; proximal (1st+2nd) tarsal segment long; tarsus either has one apical thorn on 3rd tarsomere only, while 1st+2nd and 4th tarsomeres lack apical-ventral thorns (*kazlauskasi* [*Centroptilum*]), or has two apical thorns — on 1st+2nd and on 3rd tarsomeres (*bifurcatum* [*Centroptilum*]); the same on fore leg of female. In subimago all segments of all tarsi covered with pointed microlepides. Male genitals similar to that of Cloeon/fg1 (Fig. 45): styligeral muscle well-developed; 2nd segment of gonostylus (fused with 1st segment) narrower than 1st segment, widened apically; distal (3rd) segment petiolate; penial bridge with wide median projection; gonovectes completely fused with penial bridge.

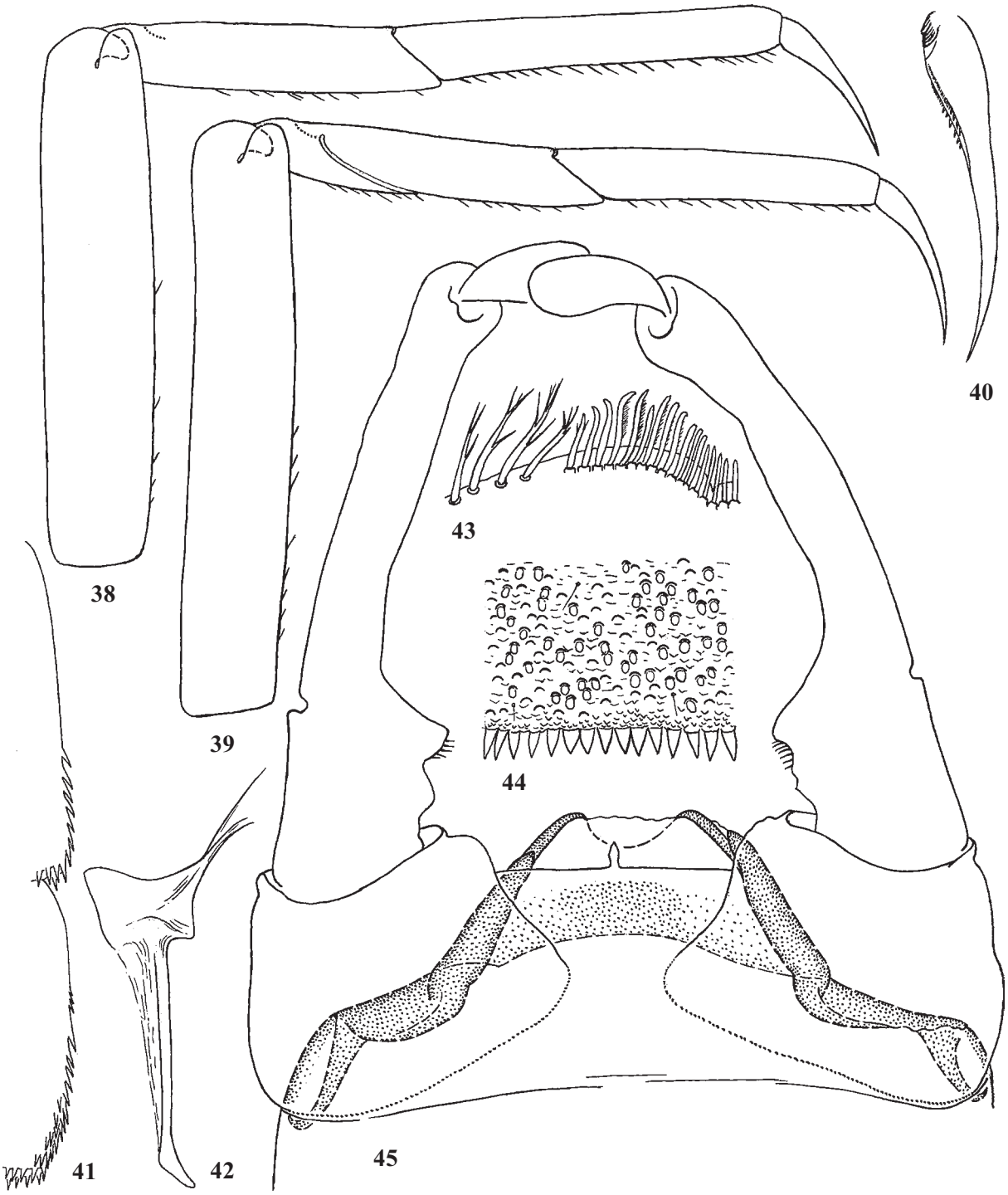
COMPARISON. Formerly representatives of *Anafroptilum* were attributed to *Centroptilum*. In contrast to *Centroptilum* and other Anteropatellata, *Anafroptilum* has primitive position of patello-tibial suture, characteristic for Protopatellata: In larva, subimago and imago of both sexes patella-tibial suture is developed only on middle and hind legs, being absent on fore legs (Figs 38, 39).

The following characters of *Anafroptilum* are in common with *Centroptilum* and Cloeon/fg1 (incl. *Procloeon*): Labial palp has 3rd segment truncate and 2nd segment non-projected. Larval legs slender; femur parallel-sided, without row of setae on outer margin and without two apical setae; claw slender, with two rows of denticles. Larval abdominal terga with scales situated in semicircular nests lacking operculae at angles. Larval caudalii in middle part with dark rings at apex of each 4th segment.

The following characters of *Anafroptilum* are in common with Cloeon/fg1 (incl. *Procloeon*): Segments VIII and IX with spines forming longitudinal rows on lateral margins. Gonovectes fused with penial bridge (in contrast to *Centroptilum*).

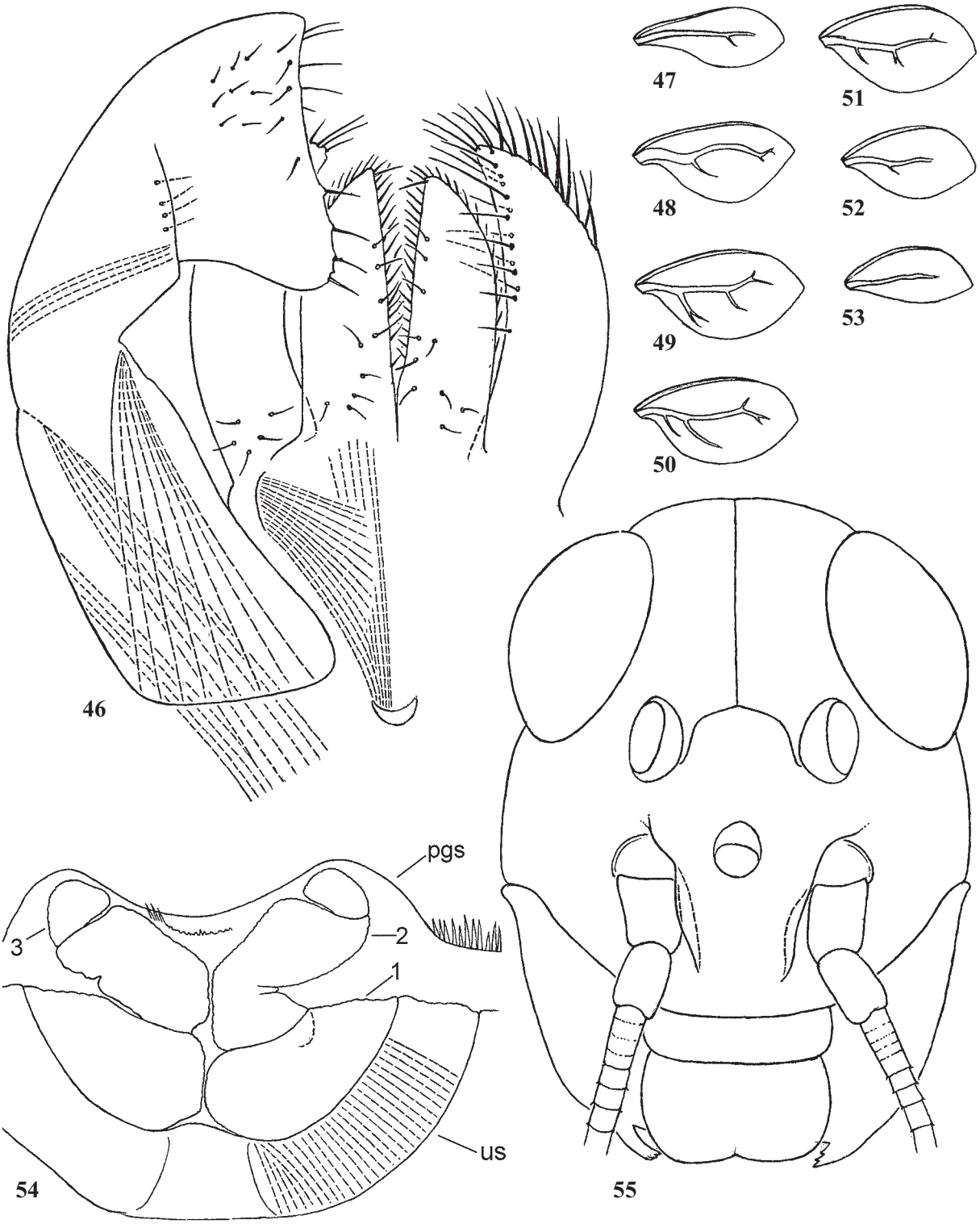
DISTRIBUTION. East Palaearctic and Nearctic.

SPECIES COMPOSITION. Includes a single East-Palaearctic species *Anafroptilum kazlauskasi* (Kluge, 1983) **comb.n.** and several Nearctic species, among which only *Anafroptilum bifurcatum* (McDunnough, 1924) **comb.n.** is examined by me.



Figs 38–45. *Anafroptilum kazlauskasi*: 38 — larval fore leg, front view; 39 — larval hind leg, front view; 40 — claw; 41 — lateral margins of larval abdominal segments VIII and IX; 42 — subimaginal exuviae of left postsubalar sclerite and lateropostnotal crest; 43 — setae on fore margin of labrum; 44 — hind margin of larval abdominal tergum; 45 — genitals of male imago, ventral view (hidden parts of penis shown by interrupted lines).

Рис. 38–45. *Anafroptilum kazlauskasi*: 38 — передняя нога личинки, вид спереди; 39 — задняя нога личинки, вид спереди; 40 — коготок; 41 — латеральные края VIII и IX сегментов брюшка личинки; 42 — субимагинальный экзувий постсубалярного склерита и латеропостнотального гребня; 43 — щетинки на переднем крае верхней губы; 44 — задний край тергита брюшка личинки; 45 — гениталии самца имаго, вентрально (скрытые части пениса показаны прерывистыми линиями).



Figs 46–55. *Anafroptilum kazlauskasi*: 46 — half of labium, ventral view (muscles and setae on dorsal side of 2nd palpomere shown by interrupted lines); 47–53 — tergalii I–VII; 54 — subimaginal genitals folded under larval cuticle in mature male larva ready to molt to subimago (right gonostylar muscle shown by interruptede lines); 55 — head of female larva, front view; 1, 2, 3 — 1st, 2nd and 3rd segments of subimaginal gonostylus; pgs — larval protogonostylus; us — subimaginal unistyliger.

Рис. 46–55. *Anafroptilum kazlauskasi*: 46 — половина нижней губы, вентрально (мышцы и щетинки на дорсальной стороне второго членика щупика показаны прерывистыми линиями); 47–53 — тергалии I–VII пар; 54 — субимагинальные гениталии, сложенные под личиночной кутикулой у зрелой личинки самца, готовой линять на субимаго (правая гоностилярная мышца показана прерывистыми линиями); 55 — голова личинки самки, вид спереди; 1, 2, 3 — 1–й, 2–й и 3–й членики субимагинального гоностиля; pgs — личиночный протогоностиль; us — субимагинальный унистилигер.

Anafroptilum kazlauslasi (Kluge, 1983) **comb.n.**
Figs 38–55.

Centroptilum kazlauskasi Kluge, 1983.

Cloeon (*Centriptilum*) *kazlauskasi*: Kluge & Novikova, 1992.

MATERIAL. RUSSIA, Promorskiy Territory: river Sidime (= Narva) near natural reserve «Kedrovaya Pad'», 13–21.VII.1980, coll. N. Kluge: 2 L-S-I♂ (holotype and paratype), 3 L-S-I♀ (paratypes), 3 L-S♀ (paratypes), 2 larvae (paratypes); river Serebryanka near Terney, 15–19.VIII.1990, coll. N. Kluge: 2 L-S-I♂, 3 L-S♂, 3 L-S-I♀, 8 larvae.

Imago and larva are described in my previous peper [Kluge, 1983]. Larva and female imago (as well, as male imago) have patella-tibial suture absent on fore leg and present on hind legs (Figs 38–39) (as in other Protopatellata, unlike *Centroptilum*). Penis has gonovectes completely fused with penial bridge (Fig. 45) (as in other *Anafroptilum*, unlike *Centroptilum*).

Anafroptilum bifurcatum (McDunnough, 1924) **comb.n.**

Centroptilum bifurcatum McDunnough, 1924.

MATERIAL. USA, Nebraska, Cherry Co., R+61, Snake River, 6.VI.1995, coll. B. Kondratieff: 4 I♂, 1 S♂, 3 I♀, 4 larvae, 2 larval exuviae.

Male imago is described by McDunnough [1924, 1929] and Lowen & Flannagan [1991]; larva is described by Lowen & Flannagan [1991]. Basing on the material examined, it should be added, that larva and female imago (as well, as male imago) have patella-tibial suture absent on fore leg and present on hind legs (as in other Protopatellata, unlike *Centroptilum*). Penis has gonovectes completely fused with penial bridge (as in other *Anafroptilum*, unlike *Centroptilum*).

Systematic position of *Anafroptilum* and status of *Centroptilum*

Till present, all species of *Anafroptilum* were attributed to the genus *Centroptilum* Eaton, 1869. Traditionally, the genus *Centroptilum* was acceped in wide sense and included all baetid species, which do not belong to Baetovectata and retain hind wings. Later the genus *Centroptilum* was restricted to exclude African species belonging to Protopatellata [Gillies, 1990] and to exclude Holarctic species related to *Procloeon* [McCafferty & Waltz, 1990; Kluge & Novikova, 1992].

Formerly we assumed that in such restricted sense the taxon *Centroptilum* should be represented in Palaearctic by 3 species: (1) *luteolua* Müller, 1776 [*Ephemera*] (the type species of *Centroptilum*), (2) *kazlauskasi* Kluge, 1983 [*Centroptilum*] and (3) undescribed species named "*Cloeon* (*Centroptilum*) **sp.n.**1" [Kluge & Novikova, 1992]. But the last one, as appears from newly collected material, actually belongs not to *Centroptilum*, but to Procloeon/g1 (see classification above). The species *kazlauskasi* [*Centroptilum*] is moved now to *Anafroptilum*. Thus, *Centroptilum* is represented in the Old World by a single species *Centroptilum luteolum* (Müller, 1776).

Centroptilum differs from Cloeon/fg1 (see classification above) and *Anafroptilum* by retention of free gonovectes, which are not fused with penial bridge [Grandi, 1960: Fig. XI.3]. In contrast to Cloeon/fg1 and *Anafroptilum*, larva of *Centroptilum* has no longitudinal rows of spines on lateral margins of last abdominal segments; instead of it, in *Centroptilum luteolum* the whole surface of all abdominal segments is evenly and densely covered by minute spines.

Systematic position of *Anafroptilum* is vague: On the one hand, it has apomorphies of Cloeon/fg1: longitudinal rows of spines on larval abdominal segments VIII and IX (sometimes also on previous segments) are present in *Anafroptilum* and Cloeon/fg1, being not found in other taxa; truncate labial palp and dark rings on each 4th segment of caudalii are characteristic for *Anafroptilum* and Cloen/fg1, being found in some other taxa; fusion of gonovectes with penial bridge, besides *Anafroptilum* and Cloeon/fg1, is known for Rhithrocloeon/g1 [g: *Rhithrocloeon* Gillies, 1985] (including *Mutelocloeon* Gillies & Elouard 1990, *Bugilliesia* Lugo-Ortiz & McCafferty, 1996 and *Kivuiops* Lugo-Ortiz & McCafferty, 2007), which belongs to Protopatellata. On the other hand, all representatives of Cloeon/fg1 have patella-tibial suture equally developed on all legs of larva and female adult, that is an autapomorphy of Anteropatellata, while *Anafroptilum* has a primitive position of patella-tibial suture on middle and hind legs only, as in the plesiomorphon Protopatellata. Such characters as two rows of denticles on larval claws and single marginal intercalaries of fore wings, are symplesiomorphies of Protopatellata and Cloeon/fg1. Scales in semicircular nests are found in various non-related taxa, including all Cloeon/fg1, but they are not characteristic for Protopatellata, which often have scales in angulate nests with operculae (Fig. 6).

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