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Oligineuria itayana sp.n. (Ephemeroptera: Oligoneuriidae) — a new mayfly species from Peruvian Amazonia

Oligineuria itayana sp.n. (Ephemeroptera: Oligoneuriidae) — новый вид поденок из Перуанской Амазонии

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KEY WORDS: Ephemeroptera, Oligoneuriidae, *Oligoneuria*, *Oligoneuria itayana* **sp.n.**, Peru, Amazonia.

КЛЮЧЕВЫЕ СЛОВА: Ephemeroptera, Oligoneuriidae, *Oligoneuria*, *Oligoneuria itayana* **sp.n.**, Перу, Амазония.

ABSTRACT. Larvae and adults of both sexes of a new mayfly species *Oligoneuria itayana* **sp.n.** are described. This is the first species of *Oligoneuria*, for which all stages of development are reliably associated. A new diagnosis of the genus *Oligoneuria* is given. A new synonym is established: *Oligoneuria* Pictet, 1843 = *Oligoneurioides* Demoulin, 1955, **syn.n**. In the new species (and probably in all other *Oligoneuria*) venation of larval protopteron is much more complete than venation of adult wing (unlike most other insects, whose protopteron venation is identical to wing venation). This means that the diminished number of wing veins, which formerly was regarded to be a generic character of *Oligoneurioides*, in the present case has no phylogenetic significance and because of this can not be used to establish a supra-species taxon.

РЕЗЮМЕ. Описываются личинки и взрослые особи обоих полов нового вида *Oligoneuria itayana* **sp.n.** Это первый вид *Oligoneuria*, для которого достоверно ассоциированы все стадии развития. Устанавливается новая синония: *Oligoneuria* Pictet, 1843 = *Oligoneurioides* Demoulin, 1955, **syn.n**. У нового вида (и, вероятно, у всех прочих *Oligoneuria*) жилкование личиночного протоптерона значительно более полное, чем жилкование имагинального крыла (в отличие от большинства других насекомых, у которых жилкование протоптерона идентично жилкованию крыла). Это значит, что уменьшение числа жилок крыла, которое прежде считалось родовым признаком *Oligoneurioides*, в данном случае не имеет филогенетического значения, и поэтому не может быть использовано для выделения надвидового таксона.

Introduction

The family-group names Oligoneurioidea, Oligoneuriidae and Oligoneuriinae are known to everybody who deals with mayflies; the holophyletic taxon often called superfamily Oligoneurioidea has world-wide distribution. However, nobody knows exactly, what is the genus *Oligoneuria*. Originally, the genus *Oligoneuria* Pictet, 1843 was characterized by a peculiar gemination of wing veins, and included the both known species, which had such venation; judging by its diagnosis, it was holophyletic and corresponded to the family Oligoneuriidae in the narrowest sense, or Geminovenata Kluge, 2004 in modern classification. When, in addition to the genus *Oligoneuria*, there were described other genera with the same type of vein gemination — *Lachlania* Hagen, 1868, *Elassoneuria* Eaton, 1881 and *Spaniophlebia* Eaton, 1881 — the genus *Oligoneuria* in a new sense became artificial (paraphyletic). Later, the former genus *Oligineuria* was divided into a genus *Oligoneuriella* Ulmer, 1924 (which includes the most common European species) and a genus *Oligoneuria* in restricted sense, in which it is accepted till recently.

In this modern sense, the genus *Oligoneuria* is regarded to be composed of a single species *O. anomala* Pictet, 1843, which is known as a single specimen — holotype, dry female adult from Brazil.

Spieth [1943] described and figured a single larval specimen (female larva of penultimate instar) from Surinam, which he determined as *Oligoneuria* sp. and assumed to be *O. anomala*. Demoulin [1955] regarded this larva to belong not to *Oligoneuria*, but to *Spaniophlebia*, basing on his interpretation of protoptera venation on the Spieth's drawing and on the fact, that larval paracercus is shorter than cerci. He also figured a young larva from Brazil, which he also regarded to belong to *Spaniophlebia*. Actually, the Spieth's drawing is not enough detailed to interpret venation, and in Geminovenata venation of protoptera can differ from venation of wings (see below and Figs 19–22). In *Spaniophlebia* paracercus of adult is completely absent; among Ephemeroptera, the same in *Lachlania* only; judging by the fact that in *Lachlania* larval paracercus is also absent, we can conclude that larva of *Spaniophlebia* (which is not described till now) also has no paracercus. In most Geminovenata (including the new species *O. itayana* described below), larval paracercus is shorter than cerci, while adult paracercus is equal to cerci; relative length of larval paracercus increases from instar to instar thanks to different mode of growth of cerci and paracercus (see below, the description of *O. itayana* **sp.n.** and Fig. 12). So the larvae figured by Spieth [1943] and Demoulin [1955] belong not to *Spaniophlebia*, but to *Oligoneuria*. Basing on a single specimen from unknown locality in Brazil, I figured a head of a young larva of "Oligoneuria/f5=g6 sp.O4" [Kluge, 2004: Fig. 51D].

Demoulin [1955] established a new genus *Oligoneurioides* for a single species *Oligoneurioides amazonicus*, which he described as male imagoes from Brazil. It is regarded to be different from *Oligoneuria* basing on less number of wing veins. As it will be shown below, in Oligoneuria/f5=g6 this character has no phylogenetic significance and because of this can not be used to establish supra-species taxa. Basing on a single specimen of male imago, collected by J.E. Fittkau in Brazil, I figured wings, head and genitals of another species, "Oligoneuria/f5=g6 sp.O5" [Kluge, 2004: Fig. 50].

In Peruvian Amazonia I collected all stages of development of a new species *Oligoneuria itayana*. Its female imago differs from *O. anomala*; male imago differs from *O. amazonicus* and the sp.O5; larva differs from the Spieth's larva, the Demoulin's larva and the sp.O4 (see comparison below). Thus, now there are known not less than four reliably different species of *Oligoneuria*.

Systematic position of *Oligoneuria*

In the modern phylogenetic system of mayflies [Kluge, 2004], *Oligoneuria* has the following position. The taxon Euplectoptera Tillyard, 1932 (which includes all recent mayflies) is divided into (1) Posteritorna Kluge, Studemann, Landolt & Gonser, 1995 and (2) Anteritorna Kluge, 1993. The taxon Anteritorna is divided into (1) a plesiomorphon Tridentiseta Kluge, Studemann, Landolt & Gonser, 1995 and (2) a holophyletic taxon Bidentiseta Kluge, 1993. The taxon Bidentiseta is divided into holophyletic taxa (1) Furcatergaliae Kluge, 1998 and (2) Branchitergaliae Kluge, 1998. The taxon Branchitergaliae (hierarchical name: Heptagenia/f1=Oligoneuria/g1) is divided into (1) Heptagennota Kluge, 2000 (hierarchical name: Heptagenia/f2=g1) and (2) Eusetisura Kluge, 1998 (hierarchical name: Oligoneuria/f1=g2). The taxon Eusetisura (sometimes named family Oligoneuriidae in the widest sense) is divided into three holophyletic taxa — (1) Coloburiscus/fg1 (i.e. Coloburiscidae, or Coloburiscinae), (2) Isonychia/fg1 (i.e. Isonychiidae, Isonychiinae, or *Isonychia*) and (3) Discoglossata Kluge, 2004 (hierarchical name: Oligoneuria/f2=g3). The taxon Discoglossata (or family Oligoneuriidae in a wide sense) is divided into (1) a monospecific taxon Pseudoligoneuria/f1=Chromarcys/g1 (i.e. Pseudoligoneuriidae, Pseudoligoneuriinae, or *Chromarcys*) and (2) a holophyletic taxon Geminovenata Kluge 2004 (hierarchical name: Oligoneuria/f3=g4). The taxon Geminovenata (or family Oligoneuriidae in the narrowest sense) includes several holophyletic taxa whose phylogenetic relationships are unclear — (1) Oligoneuriella/g1 (incl. *Oligoneuriopsis*), (2) Homoeoneuria/g1 (incl. *Oligoneurisca*), (3) Elassoneuria/g1 (incl. *Madeconeuria*), (4) *Fittkauneuria* and (5) Oligoneuria/f4=g5 (incl. *Lachlania*, *Spaniophlebia*).

The taxon with hierarchical name Oligoneuria/f4=g5 includes three taxa — (1) *Lachlania*, (2) *Spaniophlebia* and (3) Oligoneuria/f5=g6 (incl. *Oligoneurioides*). Characters of these three taxa contradict traditional principles of phylogenetic analysis: *Lachlania* and *Spaniophlebia* share a common apomorphy — complete loss of paracercus (not found in any other Ephemeroptera); *Spaniophlebia* and Oligoneuria/f5=g6 share another common apomorphy — presence of an unusual flat frontal projection, which in larva represents a large frontal continuation of the head shield, and in adult is small, soft and bent under the head; *Lachlania* and Oligoneuria/f5=g6 share the third apomorphy — on fore wing double vein RSa+iRS in proximal part is closely approximates with Sc+RA. Probably, all these three apomorphies appeared in the common ancestor of Oligoneuria/f4=g5 (i.e. represent autapomorphies of this taxon), and secondarily reversed in subordinated taxa.

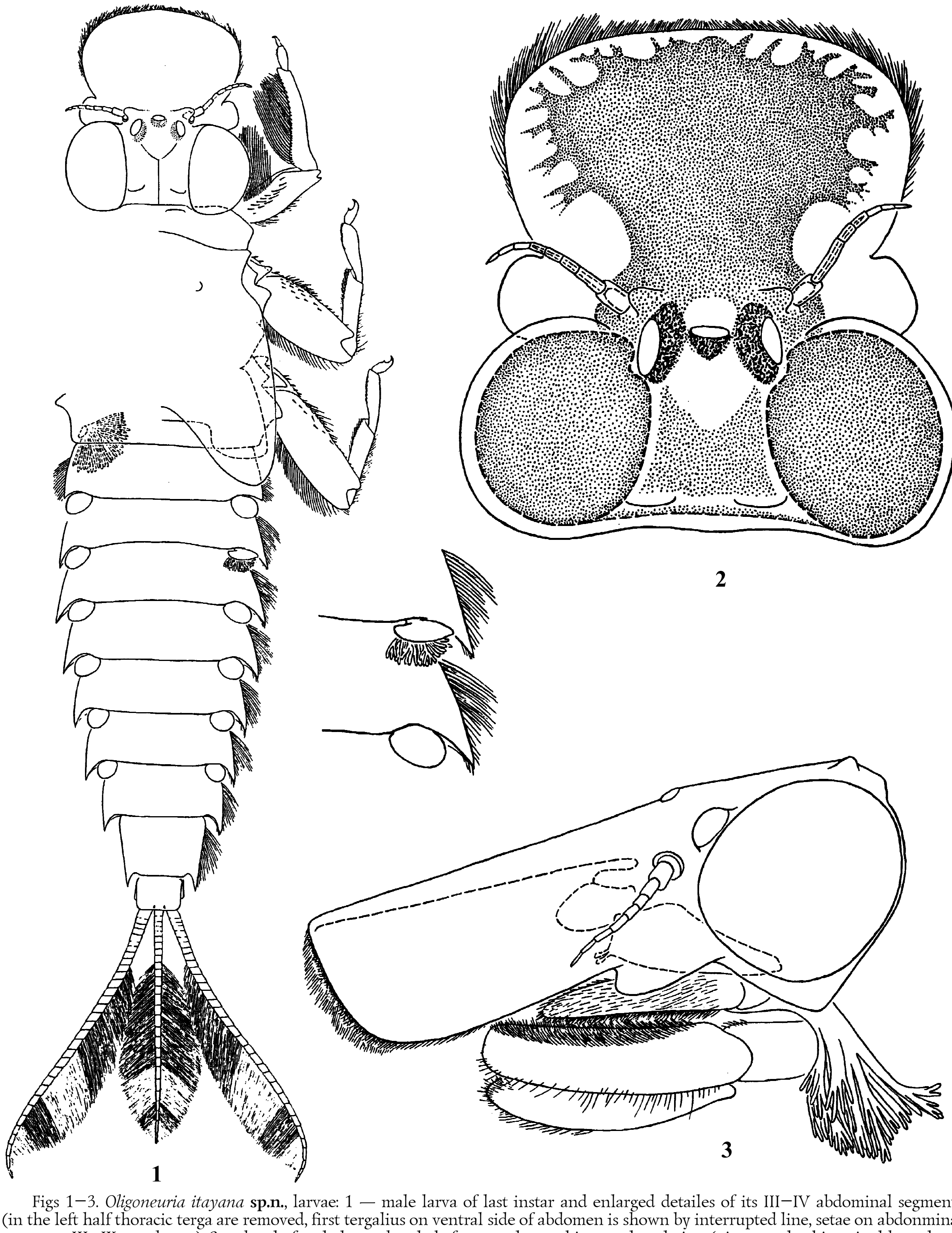
Genus ***Oligoneuria*** Pictet, 1843

Hierarchical name: Oligoneuria/f5=g6 (incl. *Oligoneurioides*)
Subjective synonym: *Oligoneurioides* Demoulin, 1955, **syn. n.**

Hierarchical genus-group name of this taxon is Oligoneuria/g6 ([2]sine *Heptagenia*; [3]sine *Coloburiscus, Isonychia*; [4]sine *Chromarcys*; [5]sine *Oligoneuriella, Homoeoneuria, Elassoneuria, Fittkauneuria*; [6]sine *Lachlania, Spaniophlebia*; incl. *Oligoneurioides*) [Kluge, 2004].

DIAGNOSIS. Head of larva and adult has a pair of lateral incisions by sides of eyes (as in other Oligoneuria/f4=g5) and has an anterior projection (the same in *Spaniophlebia* only) (Figs 1–3, 13, 17, 18). On fore wing double vein RSa+iRS in proximal part is closely approximated to Sc+RA (the same in *Lachlania* only); bifurcation of MA is situated near wing base (unlike Elassoneuria/g1) (Fig. 21). In male imago, on tarsus of middle and hind leg before the last (claw-bearing) segment, all three short segments are retained (if not take into account the 1st segment, which is fused with tibia, shortened and not expressed) (Fig. 6). Styliger has a pair of long processes between bases of gonostyli (Fig. 23; [Demoulin, 1955: Fig. 17e; Kluge, 2004: Fig. 50D]) (unlike *Lachlania* and *Spaniophlebia*). Gonostylus with one distal segment (as in other Oligoneuria/f4=g5). Bases of left and right penis lobes on their dorsal wall are articulated one with another by a median condylus; from this condylus toward anterior-lateral angles of sternite IX, goes a pair of strong muscles (unique structure, found in Oligoneuria/f4=g5 only) (Fig. 23; [Kluge, 2004: Fig. 50D]). Larval and imaginal paracercus is well-developed (unlike *Lachlania* and *Spaniophlebia*).

DISCUSSION. Till now, *Oligoneuria* (known as a single type species *Oligoneuria anomala* Pictet 1843) and *Oligoneurioides* Demoulin 1955 (known as a single type species *Oligoneurioides amazonicus* Demoulin 1955) were regarded



Figs 1–3. *Oligoneuria itayana* **sp.n.**, larvae: 1 — male larva of last instar and enlarged detailes of its III–IV abdominal segments (in the left half thoracic terga are removed, first tergalius on ventral side of abdomen is shown by interrupted line, setae on abdonminal segments III–IX not shown); 2 — head of male larva shortly before moult to subimago, dorsal view (pigmented subimaginal hypoderm, visible through larval cuticle, is dotted; cuticular pigmentation is not shown); 3 — head of female larva of last instar, lateral view; parts, hidden by frontal shield (clypeus, labrum and left mandible) are shown by interrupted line.

Рис. 1–3. *Oligoneuria itayana* **sp.n.**, личинки: 1 — личинка самца последнего возраста и увеличенные детали III–IV сегментов брюшка (на левой половине тергиты груди удалены, первая тергалия на вентральной стороне брюшка показана прерывистой линией, щетинки на III–IX сегментах брюшка не показаны); 2 — голова личинки самца незадолго до линьки на субимаго, дорсально (субимагинальная гиподерма, просвечивающая сквозь личиночную кутикулу, пунктирована; кутикулярная пигментация не показана); 3 — голова личинки самки последнего возраста, латерально; части, скрытые лобным щитом (клипеус, верхняя губа и левая мандибула) показаны прерывистой линией.

as two different genera. Separation of these genera was based on venation of fore wing of adults [Dominguez et al., 2006]: In adult *Oligoneurioides amazonicus* crossveins are present only in anteriormost fields, in front of double vein RSa+iRS; intercalary iMP is absent. In adult *Oligoneuria anomala* crossveins are present, besides these fields, in some fields behind RSa+iRS; iMP is present. Actually, this difference exists in venation of adult wings only, but not in venation of larval protoptera. In some Geminovenata, unlike other winged insects, venation of larval protoptera is not identical to venation of adult wings, being more complete [Kluge, 2004: 140]. Particularly, in the new species *O. itayana*, larval fore protopteron has numerous crossveins in all fields; its iMP is well-developed and bears a trachea (Fig. 19); such venation corresponds to the diagnosis of *Oligoneuria*; adult wings of the same species have no crossveins behind RSa+iRS and have no iMP (Fig. 21), that corresponds to the diagnosis of *Oligoneurioides*. Probably, all species of this group have in larval stage complete venation; when larva transforms to adult, most part of crossveins and iMP either disappear (in *itayana* [*Oligoneuria*], *amazonicus* [*Oligoneurioides*] and the sp.O5), or are retained (in *anomala* [*Oligoneuria*]). In course of evolution, the crossveins and iMP of adult wing can appear or disappear repeatedly, because in all cases they are retained in larval stage, and genetic program which encodes them, is not lost. So presence or absence of these veins in adult is neither apomorphy, nor plesiomorphy of any taxon in this group. This means, that this character can not be used as a diagnostic character of a genus or any other supra-species taxon, because all supra-species systematics is based on phylogeny only. We do not know if this character is poorly individual, or species-specific, because a single specimen with adult venation of the *anomala*-type is known. Even if this adult venation will appear to be peculiar for certain species, it does not mean that all species with such adult venation constitute a natural group.

Oligoneuria itayana Kluge, **sp.n.**
Figs 1–23

MATERIAL EXAMINED. PERU, Rio Itaya, above Puente Itaya (57 km by road from Iquitos), near Omaguas, 1–15.II.2006 (N. Kluge): Holotype — ♂, died when moulted from larva to adult, with subimaginal and imaginal cuticle completely developed. Paratypes: 1 ♂ larva ready to moult to adult; 1 ♀, died when moulted from larva to adult, with subimaginal cuticle of abdomen detached; 25 ♂♂ larvae and 70 ♀♀ larvae of various instars; 4 ♀♀ adults collected at light.

Larva. Coloration. Cuticle in most part is non-pigmented, dull-yellowish, with a few paired diffuse brownish pigmented marks on dorsal side of head, pronotum, mesonotum, metanotum and each abdominal segment; cuticle of caudalii is nearly unicolour with sharply coloured swimming setae (see below). Hypodermal pigmentation is well visible through cuticle. Hypoderm of frontal shield is in most part unicolourous dark brown (sometimes with fine light net-like pattern), lateral sides colourless. Hypoderm of the rest of head and on thorax with composite maculation. Legs with variable hypodermal brown maculation: femur either with several brown maculae or irregular bands on light background, or with light blanks on brown background; tibia are either colourless, or with transverse brown maculae, or with brown band(s). Abdomen with intensive hypodermal pigmentation similar to that of adult (Fig. 14): usually with light median stripe, bordered by dark areas, with diffuse maculation repeated on segments I–IX. Hypoderm of caudalii is pigmented in proximal half, light in apical half.

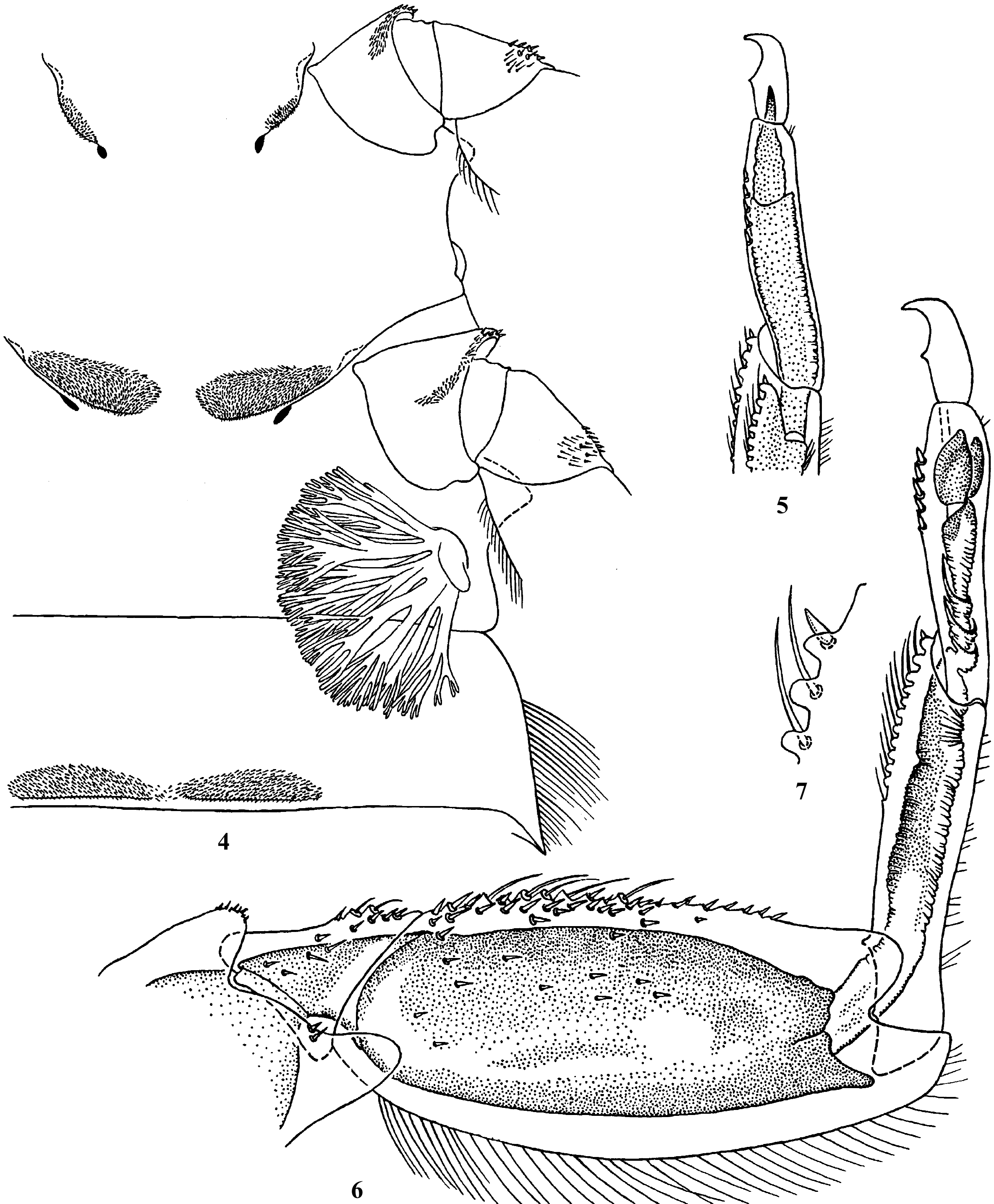
Head (Figs 1–3). Anterior projection of frontal shield is large; its anterior margin is wide and blunt, nearly straightly truncate (unlike other known species); it bears dense, irregularly situated, rather long, pointed setae. Near bases of antennae there is a pair of projected plates, which partly cover from above scapus and base of pedicellus. Near posterior margin of head, between eyes, at the area of attachment of posterior cranio-mandibular muscles (mandibular adductors), there is a pair of transverse ridge-like protuberances, pointed in lateral view (Fig. 3) and roundish in front or hind view. Antennae are short, segments of flagellum are simple, without processes (unlike *Lachlania*). Mouth parts have the same structure as in other Discoglossata [see Kluge, 2004: 136]; thanks to long anterior projection of head shield, mouth apparatus locates far from anterior margin of head (Fig. 3).

Thorax (Fig. 1). Pronotum has angle-like projected lateral margins; near anterior margin it bears a pair of dorsal submedian transverse ridge-like protuberances. Lateral margin of mesonotum has a small angle-like projection anteriorly and a roundish incision behind it; dorsal surface of pronotum has a pair of shallow protuberances. Each pleuron has two angle-like flat projections by sides of pleuro-coxal articulation; each coxa has two angle-like flat projections by sides of anterio-dorsal coxo-trochanteral articulation.

Sterna of thorax and abdomen (Fig. 4). Ventral side of body bears 6 pairs of convex spiny fields: a pair on mesosternum, a pair on metasternum and 4 pairs on abdominal sterna II–V; first abdominal sternum (which is fused with metasternum) lacks such spiny field. Each spiny field is densely covered by short, straight, spiniform setae, directed mainly medio-posteriorly. Spiny fields on mesosternum are small, widely separated, have a form of narrow oblique ridges; each has its latero-anterior end near sternal articulation of middle leg and medio-posterior end near mesosternal furcal pit. Spiny fields on metasternum are the largest, rounded-triangular, nearly transverse and brought together medially; each located in front of metasternal furcal pit, has its acutest angle near articulation of hind leg and shortest side near median line. Spiny fields on abdominal sterna II–V are transverse, oval, brought together medially; each locates submedially on posterior margin of abdominal sternum; spiny fields of the last pair (on abdominal sternum V) are smaller than previous ones. Besides spiny fields on sterna, there are similar spiny fields on ventral side of coxa of middle and hind legs (see below).

Fore leg. Smaller than others, with filtering specialization typical for Eusetisura [Kluge, 2004: 125]; tarsus bears a few small setae near apex; claw is similar to claws of middle and hind legs, but much smaller, with the same small 1–2 denticles on inner margin.

Middle and hind legs (Figs 4–7). Coxa ventrally bears a spiny field — a band of densely situated short straight spiniform setae. Femur on its outer margin bears a regular row of long setiform setae. Inner margin of femur, at its proximal half, bears a row of peculiar setae: cuticular collar which surrounds base of each seta, on its proximal side is produced into a prominent protuberance; in front view of leg (Fig. 6) these protuberances look as a row of denticles. Near this setal row there are irregularly situated setiform setae and shorter spiniform setae. Outer margin of tibia bears irregular slender setiform setae. Inner margin of tibia, at its distal half, bears a peculiar setal row: one distalmost seta of this row is spiniform, short and very stout; other setae are setiform, much more long and slender; cuticular collar which surrounds base of each seta, on its anterior-proximal side, is produced into a prominent protuberance; in front view of leg (Figs 6–7) these protuberances look as a regular row of blunt warts in



Figs 4–7. *Oligoneuria itayana* **sp.n.**: 4 — ventral side of larval mesothorax, metathorax and abdominal sterna I–II; 5 — hind tarsus of male larva of penultimate instar; under larval cuticle there is shown a fully-developed crumpled tarsus of next (the last) larval instar; 6 — middle right leg of last instar male larva when it moults to subimago (holotype), anterior view; under larval cuticle there is shown a fully-developed subimaginal leg with crumpled tibia and tarsus (in Figs 5 and 6 hypodermal pigmentation is shown by dots, cuticular pigmentation is not shown); 7 — enlarged setae-bearing protuberances on inner side of larval tibia.

Рис. 4–7. *Oligoneuria itayana* **sp.n.**: 4 — вентральная сторона среднегруди, заднегруди и I–II сегментов брюшка личинки; 5 — задняя лапка личинки самца предпоследнего возраста; под личиночной кутикулой показана полностью развитая смятая лапка следующего (последнего) личиночного возраста; 6 — средняя правая нога личинки самца последнего возраста при линьке на субимаго (голотип), вид спереди; под личиночной кутикулой показана полностью развитая субимагинальная нога со смятой голенью и лапкой (на рис. 5 и 6 гиподермальная пигментация показана пунктировкой, кутикулярная пигментация не показана); 7 — увеличенные щетинконосные бугорки на внутренней стороне личиночной голени.

front of setal bases. Tarsus at distal half of inner margin bears dense pressed short spiniform setae. Claw is at most part light, only apex is strongly sclerotized and brown, strongly hooked; inner margin with one (Figs 5–6) or two small sclerotized brown denticles.

Sexual dimorphism in leg structure. In male larva of the last instar, tarsi of all legs are somewhat clavate, being swollen in distal part (Fig. 1); when larva transforms to adult, this swelling serves as a case for developing adult claws (Fig. 6). In male larvae of previous instars, as well as in female larvae of all instars, tarsi are nearly parallel-sided, without swelling (Fig. 5). This is connected with the fact that claws of adult male are large (Fig. 6), while claws of adult female are vestigial (Fig. 13) (as in all other Geminovenata).

Abdomen (Figs 1, 4, 8–10). Abdominal segment I has posterolateral angles rectangular, not stretched into spines. Abdominal segments II–IX have large posterolateral spines. Each of abdominal segments II–IX on lateral margin bears a regular row of long pointed setae, which become smaller toward tip of posterolateral spine; posterior margin of posterolateral spine with several setae of similar size. Posterior margins of abdominal terga and sterna are smooth, without any denticles. Sternum IX has bipointed process projected backward; in mature male larva protogonostyly are developed as projections by sides of this process (Figs 8–10, see below).

Tergalii. Tergalius I (attached ventrally, as in all Geminovenata) is vestigial, with a very large dense fibrillar gill (Fig. 4). Tergalii II–VII are small, oval, with fibrillar gills subequal to tergalius (Fig. 1). Cuticle of tergalii is light, but tergalii looks dark thanks to intensive hypodermal pigmentation.

Caudalii. Caudalii (cerci and paracercus) are not long, with very long dense primary swimming setae. Swimming setae of mature larva are coloured as the following: on proximal half of caudalii — darkened; from 1/2 to 3/4 of caudalii length — light; more distally — darkened; on several apical segments — light (Fig. 1). Young larva has no darkening on proximal half (Fig. 12). In mature larva, paracercus is only slightly shorter than cerci, with swimming setae as long and dense as on cerci (Fig. 1). In young larva, paracercus is much shorter than cerci (about 1/2 of cerci length), with a few short swimming setae (Fig. 12). At each moult, total number of segments of cerci increases: number of segments which are added (because of growth and division of proximalmost segments) is more than number of segments which are lost (because tissues of distalmost segments die and shed together with cuticle). In young larva segments of paracercus are only added, but not lost (Fig. 12), so their number increases more rapidly. In older larva segments of paracercus are both added and lost, like segments of cerci; the same during moult from larva to adult.

Adult. Both male and female, when moult from larva to subimago, already have imaginal cuticle developed, being ready to the next moult — from subimago to imago. In course of the moult from subimago to imago, subimaginal cuticle is shed from the whole abdomen and partly from thorax, but not from wings and legs.[1] Subimaginal cuticle is colourless.

Head (Figs 13, 17, 18). Head is entirely coloured by intensive dark gray hypodermal pigment; frons and its projections are dark gray (as in Fig. 2). Anterior projection of frons (developed inside larval anterior projection of frontal shield — Fig. 2) is bent down and backward, so that is pressed to ventral side of head (Fig. 13); sides and apex of this projection bear numerous irregular branched and non-branched thin processes. Lateral projections of frons (developed inside larval lateral projections of frontal shield — Fig. 2) have margins either smooth (Fig. 18) or bearing a finger-like processes (Fig. 17). Eyes of male are not large, only slightly larger than in female.

Thorax (Fig. 13). Thorax is partly pale yellowish, partly with diffuse gray pigmented marks on hypoderm; this hypodermal pigmentation (not shown in Fig. 13) does not correspond to sclerites or membranes and completely masks shape of sclerites. Cuticle with membranes colourless, sclerites light brown. Plumidia are short. In mature adult wings are nearly colourless; double longitudinal veins of fore wing are coloured by brownish at anterior-proximal part and are light at distal and posterior parts; veins of hind wing are colourless. When adult emerges from larval skin, its fore wings are coloured by brownish at anterior half and whitish at posterior half, hind wings are entirely whitish. About wing venation see below.

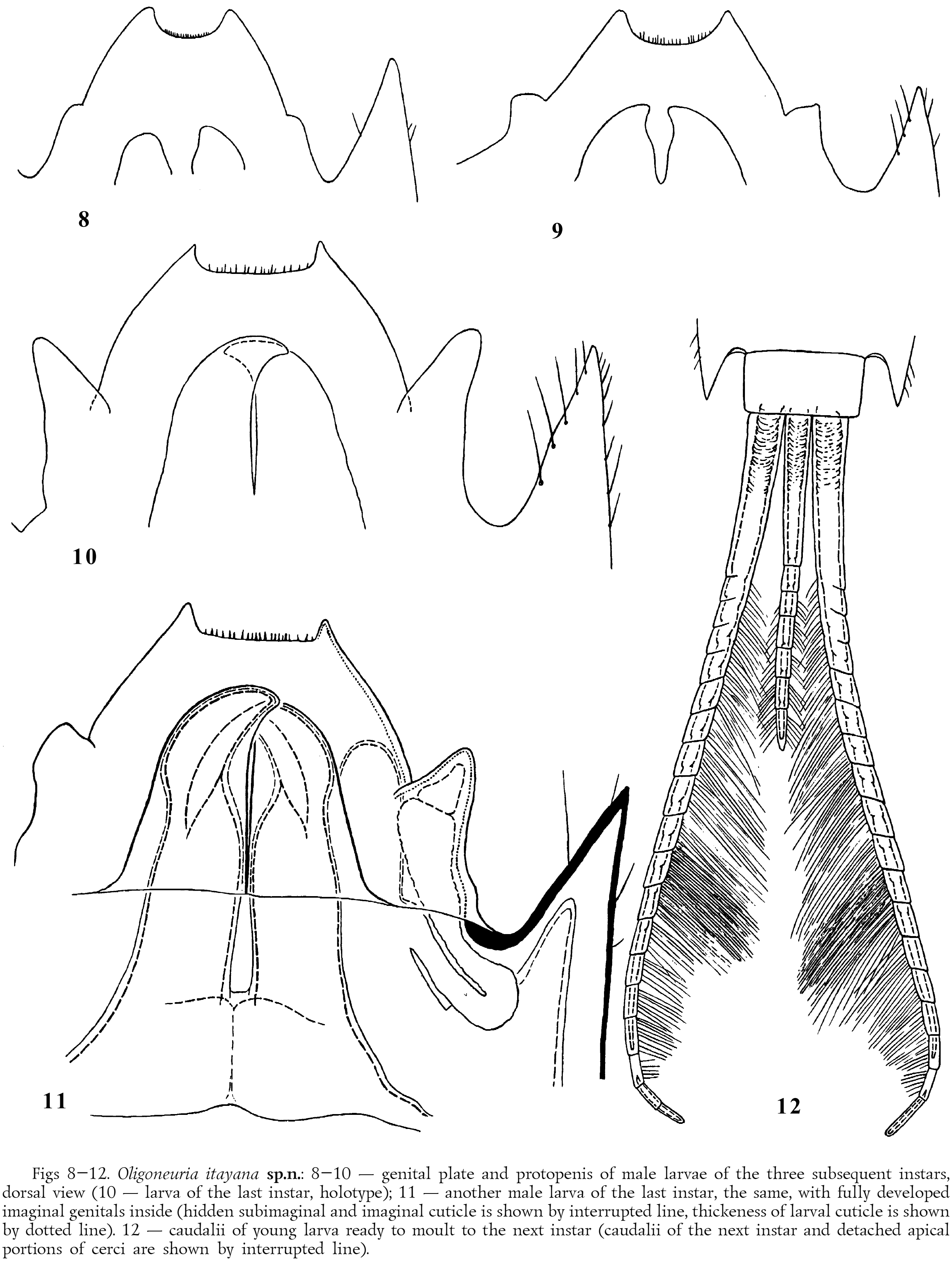
Abdomen (Figs 14–16). Coloration of abdomen is the same in male and female: terga have intensive hypodermal gray pigmentation, sterna are lighter; colour pattern repeats on terga I–IX: medially there is a light longitudinal stripe, bordered by a pair of dark submedian longitudinal stripes; on background of these dark submedian stripes, there is a pair of roundish light spots, each bordered by dark from behind (Fig. 14); on posteriormost segments these light spots become smaller and indistinct. Posterolateral spines of segments II–VII are soft, crumpled; in male imago and subimago they are prominent (Fig. 15), in female imago and subimago — small (Fig. 14). Posterolateral spines of segment IX in imago and subimago of both sexes are larger and keep their shape (Figs 16, 23). All three caudalii (cerci and paracercus) have subequal length. Their hypodermal colour pattern: in proximal part gray, in middle part with alternating gray and colourless rings, apically colourless. Subimaginal caudalii of male and female are as short as larval ones, cerci have oblique segment boundaries (as in larva); inner margin of each cercus and each lateral margin of paracercus bears a row of long setae (arranged as in larva, but not so long). Imaginal caudalii of male and female bear whorls of long setae; caudalii of female imago are as short as in larva and subimago, caudalii of male imago are many times longer.

Wing venation (Figs 19–22). On fore wing double vein RSa+iRS in proximal part is closely approximated to Sc+RA (as in other *Oligoneuria*); crossveins are retained only between C and Sc+RA and between Sc+RA and RSa+iRS; intercalaries other than iRS are absent; instead of iMP only an indistinct trace of degenerated trachea can be visible (not shown in Fig. 21). Unlike adult fore wing, larval fore protoptera have numerous anastomosed crossveins in all fields and a distinct straight iMP with trachea (Fig. 19).

On hind wing longitudinal veins are weak and do not reach wing margin; RS is absent; MP_1 and CuP are short; intercalaries and crossveins are absent (Fig. 22). Unlike adult hind wing, larval hind protoptera can have long longitudinal veins, intercalary iMP and crossveins in many fields (Fig. 20).

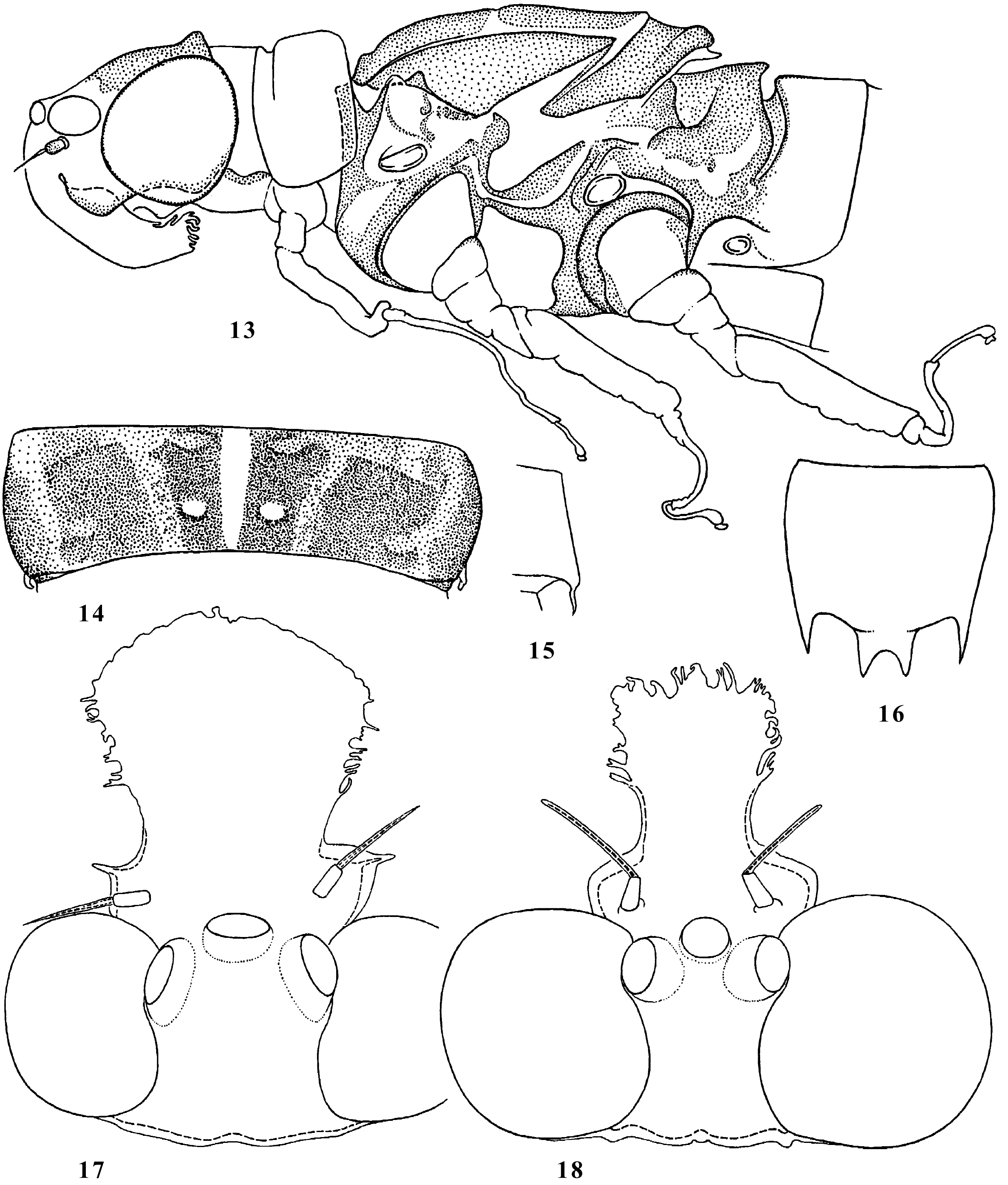
Male genitals (Fig. 23). Styliger bears a pair of long projections between gonostyli; these projections are directed caudally, flat, with rounded apices; hind margin of styliger between projections is slightly convex. Styliger and its projections have no distinct cuticular pigmentation, only pale grayish hypodermal maculation; posterior margin of styliger and its projections represents sclerotized yellowish flange. Gonostyli are non-sclerotized and non-pigmented, whitish;

[1] In the book about mayfly system [Kluge, 2004], I wrongly wrote that in Geminovenata the moult from subimago to imago occurs in males only. Probably, in all Geminovenata males and females have the same partial moult.



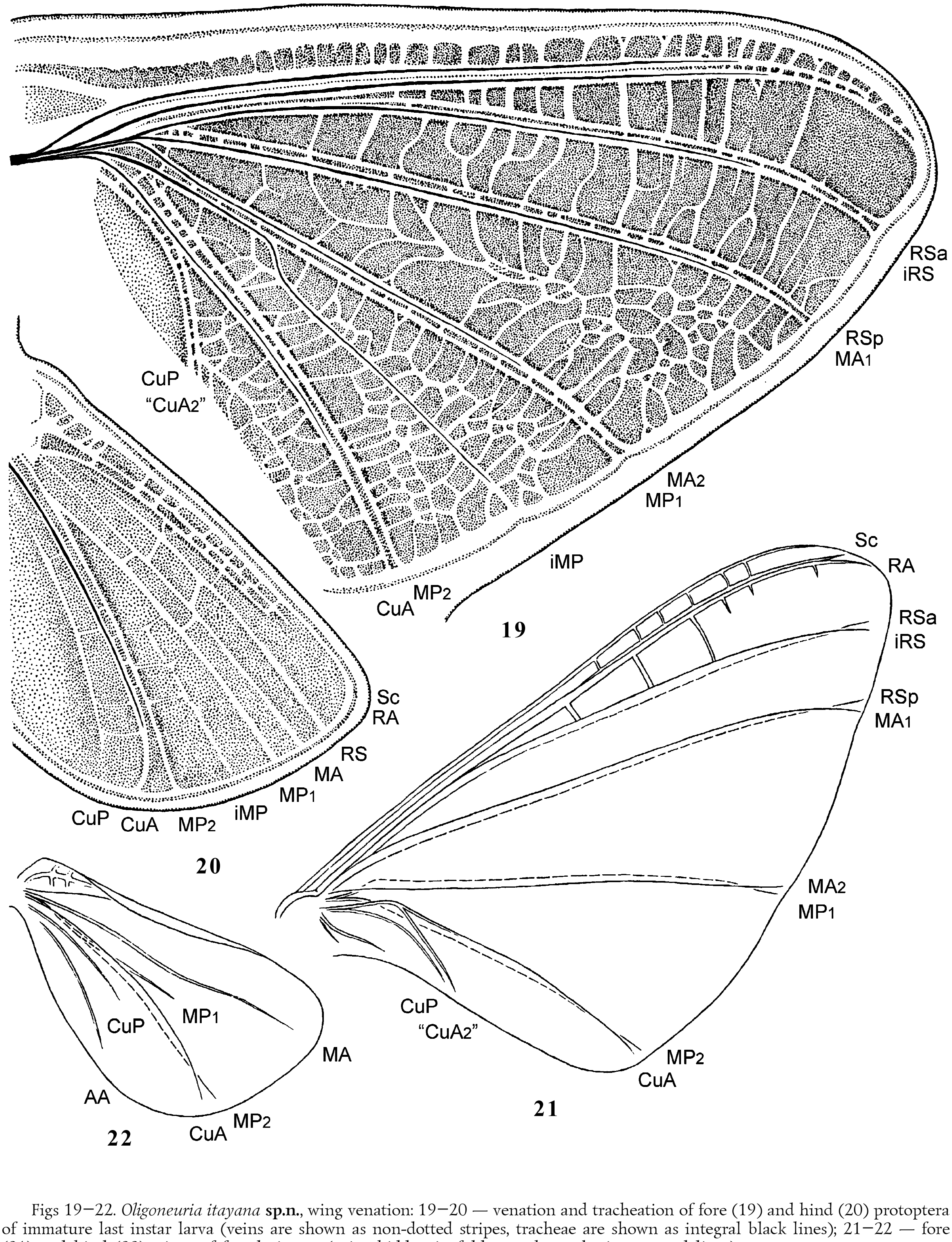
Figs 8–12. *Oligoneuria itayana* **sp.n.**: 8–10 — genital plate and protopenis of male larvae of the three subsequent instars, dorsal view (10 — larva of the last instar, holotype); 11 — another male larva of the last instar, the same, with fully developed imaginal genitals inside (hidden subimaginal and imaginal cuticle is shown by interrupted line, thickeness of larval cuticle is shown by dotted line). 12 — caudalii of young larva ready to moult to the next instar (caudalii of the next instar and detached apical portions of cerci are shown by interrupted line).

Рис. 8–12. *Oligoneuria itayana* **sp.n.**: 8–10 — генитальная пластинка и протопенис личинок самцов трёх следующих друг за другом возрастов, дорсально (10 — личинка последнего возраста, голотип); 11 — другая личинка самца последнего возраста, то же, с полностью развитыми имагинальными гениталиями внутри (срытая субимагинальная и имагинальная кутикула показана прерывистой линией, толщина личиночной кутикулы показана точечной линией). 12 — каудалии молодой личинки, готовой к линьке на следующий возраст (каудалии следующего возраста и отделившиеся концевые части церков показаны прерывистой линией).



Figs 13–18. *Oligoneuria itayana* **sp.n.**, adults: 13 — head and thorax of female imago (cuticular pigmentation is shown by dots; hypodermal pigmentation, which is much darker and masks it, is not shown); 14 — spread 5th abdominal tergite of female imago (hypodermal pigmentation is shown by dots); 15 — posterolateral spine of 5th abdominal segment of male imago (holotype); 16 — ventral side of 9th abdominal segment of female imago; 17 — head of female subimago just after hatching from larva (imaginal cuticle is shown by interrupted line); 18 — the same, male (holotype).

Рис. 13–18. *Oligoneuria itayana* **sp.n.**, взрослые: 13 — голова и грудь самки имаго (кутикулярная пигментация показана пунктировкой; гиподермальная пигментация, которая значительно темнее и маскирует её, не показана); 14 — расправленный 5-й тергит брюшка самки имаго (гиподермальная ригментация показана пунктировкой); 15 — постеролатеральный шип 5-го сегмента брюшка самца имаго (голотип); 16 — вентральная сторона 9-го сегмента брюшка самки имаго; 17 — голова самки субимаго сразу после вылупления из личинки (имагинальная кутикула показана прерывистой линией); 18 — то же, самец (голотип).



Figs 19–22. *Oligoneuria itayana* **sp.n.**, wing venation: 19–20 — venation and tracheation of fore (19) and hind (20) protoptera of immature last instar larva (veins are shown as non-dotted stripes, tracheae are shown as integral black lines); 21–22 — fore (21) and hind (22) wings of female imago (veins hidden in folds are shown by interrupted lines).

Рис. 19–22. *Oligoneuria itayana* **sp.n.**, жилкование крыльев: 19–20 — жилкование и трахеация переднего (19) и заднего (20) протоптеронов незрелой личинки последнего возраста (жилки показаны как непунктированные полосы, трахеи — как сплошные чёрные линии); 21–22 — переднее (21) и заднее (22) крылья самки имаго (жилки, скрытые в складках, показаны прерывистыми линиями).

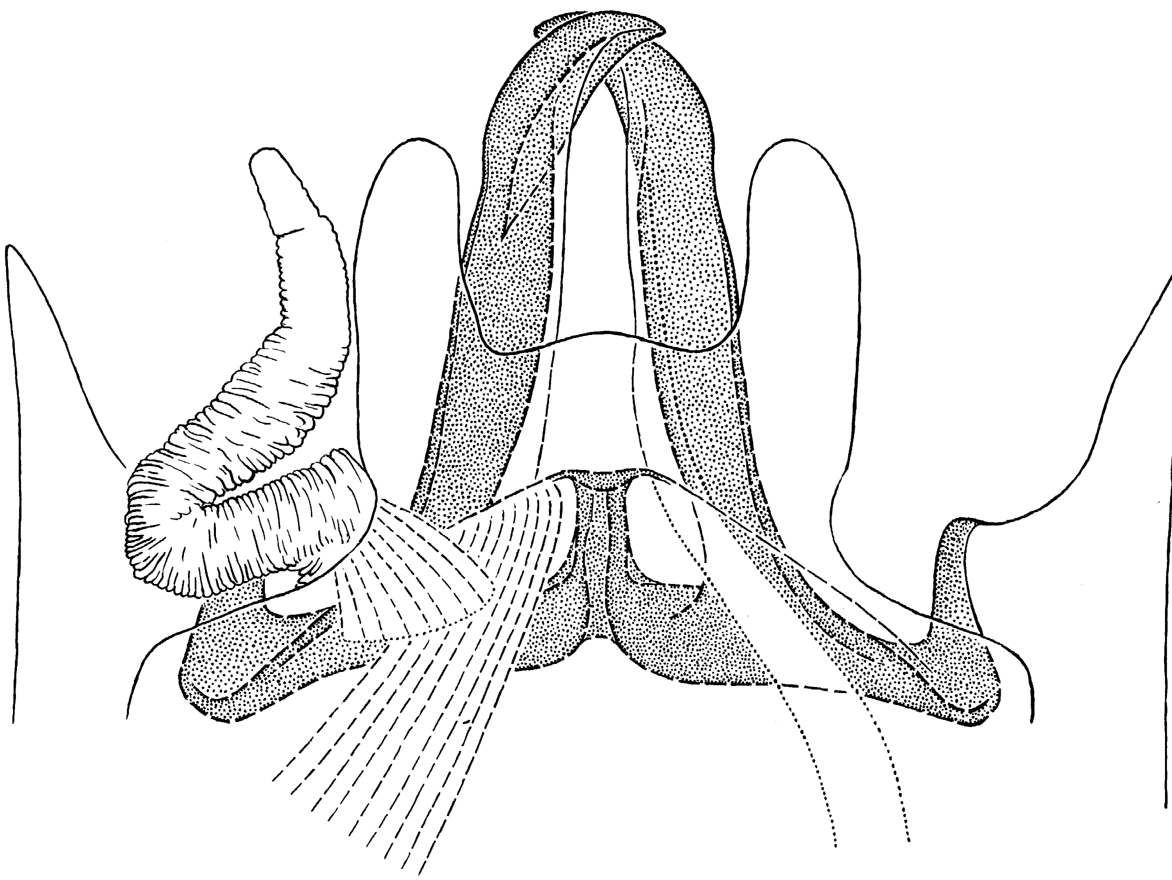


Fig. 23. *Oligoneuria itayana* **sp.n.**, holotype, genitals of male imago, extracted from larva which started to moult to subimago, ventral view; in right half gonostylus and muscles are not shown, to show basal part of penis and gonoduct (muscles are shown by interrupted lines, gonoduct — by dotted line, sclerotized areas of penis are dotter, other sclerites are not dotted). At this stage gonostyli are crumpled, but penis and styliger have definite imaginal shape.

Рис. 23. *Oligoneuria itayana* **sp.n.**, голотип, гениталии самца имаго, отпрепарированные из личинки, начавшей линять на субимаго, вентрально; на правой половине гоностиль и мышцы не показаны, чтобы показать базальную часть пениса и гонодукт (мышцы показаны прерывистыми линиями, гонодукт — точечной линией, склеротизованные участки пениса пунктированы, прочие склериты не пунктированы). На этой стадии гоностили смяты, но пенис и стилигер имеют окончательную имагинальную форму.

proximal segment is long (its definite shape is unknown, probably arched); single apical segment has lenght exceeding width. Sclerotized parts of penis are yellowish, apices are light brownish. Penis lobes are connected basally, area of their connection represents a ventro-median sclerotized projection directed caudally; near apex of this projection, a thick paired muscle-retractor is attaches. Paired lobes of penis are long, pointed, with apices strongly bent medially, so that cross one another; each lobe is apically widened, with a dorso-median flap.

Development of male genitals (Figs 8–11). Larval protogonostyli are distinguishable not less than in three last larval instars and have a form of small projections by sides of posterior outgrowth of sternum IX. Larval protopenis has characteristic shape, with apices bent medially; in last larval instar its apices overlap one another. Imaginal penis has the same shape and size of apices, but is much longer and has middle part narrowed. When subimaginal and imaginal cuticles of penis develop under larval cuticle, they are not crumpled and get the definitive shape at early stages of this process; instead of crumpling (which takes place in most mayflies), future imaginal penis shifts its base anteriorly (Fig. 11). Thanks to this, it is possible to study definitive shape of imaginal penis, examining mature larva. Unlike penis, subimaginal/imaginal gonostyli are strongly crumpled under larval cuticle, and get definitive shape only after the moult from larva to subimago. Subimaginal cuticle of genitals is very thin, non-sclerotized and colourless; cuticle of subimaginal styliger is hard enough to keep its shape, but, unlike imaginal cuticle of styliger, has no posterior sclerotized flange.

Egg. Structure of chorion is the same as described by Koss & Edmunds [1974] for Oligoneuriidae.

Dimensions. Body length 10–16 mm, fore wing lenght 10–12 mm.

BIOLOGY. Larvae were collected from branches of a large tree which was sinked at the middle of river Itaya, at the place with the strongest water current. Larva of *O. itayana* sits on the tree branch directing by its head against the water current and pressing its frontal shield upon the substrate. When larva sits in such a pose, the enlarged frontal shield helps it to keep itself on the tree branch. While the population consists of both sexes, females distinctly dominate upon males.

COMPARISON. Besides *O. itayana*, there are known several other forms of Oligoneuria/f5=g6 sensu Kluge, 2004 (or the genus *Oligoneuria*), each of which is known as a single stage and was not sufficiently described. Each of these forms is not conspecific with *O. itayana* and differs from it by the following characters.

Oligoneuria anomala Pictet, 1843. The species is known as a single female adult from Rio de Janeiro; deposited in Natural History Museum in Vienna. Described by Pictet [1843] and redescribed by Hagen [1855], Ulmer [1921] and Pescador [in Dominguez et al., 2006: 548]. Unlike *O. itayana*, female adult has thorax and abdomen at most part light [Pictet, 1843]; crossveins between iRS and PSp, intercalary iCu and crossveins in cubital field are somewhat expressed in adult [Dominguez et al., 2006: Fig. 208A].

Some other female adult specimens were determined as *Oligoneuria anomala* by Needhan & Murphy [1924] and Puthz [1973]; their real systematic position is unknown.

***Oligoneuria* sp.**: Spieth, 1943. A single female larva of penultimate instar from Surinam [Spieth, 1943: 12, Figs 2–4, 7, 8, 10, 21]; the specimen is missing [Dominguez et al., 2006]. Length 20 mm, plus cerci 5 mm (that is much larger than *O. itayana*); unlike *O. itayana*, anterior projection of frontal shield is distinctly pointed anteriorly [Spieth, 1943: Fig. 21].

*"**Spaniophlebia** **sp.**"*: Demoulin, 1955. Young larva collected in Brazil, Asaihsal-Jutahy, 8.II.1923, was figured by Demoulin [1955: Figs 18a–g]. Unlike *O. itayana*, anterior projection of frontal shield is rounded anteriorly; claw lacks denticle on inner margin [Demoulin, 1955: Figs 18a, 18c–d]. Probably, this larva belongs to *O. amazonica*, which was described as imagoes from the same locality (see below).

Oligoneuria amazonica (originally *Oligoneurioides amazonicus* Demoulin 1955). The species was described as two male imagoes collected in Brazil, Asaihsal-Jutahy, 8.II.1923. Unlike *O. itayana*, styliger is concave medially, its paired processes are slender and diverge; penis lobes are not so strongly bent apically, more slender [Demoulin, 1955: Fig. 17e].

Oligoneuria/f5=g6 sp.O4: Kluge, 2004**.** A single young larva from Brazil, "A463", with label "*Spaniophlebia*? det. G.F. Edmunds" was examined. Unlike *O. itayana*, frontal shield is distinctly pointed anteriorly [Kluge, 2004: Fig. 51D]. Like *O. itayana*, there are convex paired fields with spiniform setae on metasternum, mesosternum and abdominal sterna; but unlike *O. itayana*, setal fields on mesosternum are similar to that on metasternum — wide and brought together medially; besides paired setal fields near posterior margins of abdominal sterna II–V, there is a pair of smaller setal fields on abdominal sternum I, at a distance from posterior margin. Unlike *O. itayana*, abdominal segment I has posterolateral angles stretched into short spines. Unlike *O. itayana*, on middle and hind legs all setae on inner margins of femora and tibiae are short and stout, protuberances at their bases are not so prominent.

Oligoneuria/f5=g6 sp.O5: Kluge, 2004. A single male imago from Brazil, Amazonas st., Rio Hazania, Taparuquaza, 22.I.1963 (coll. J.E. Fittkau), with label "*Oligoneuria*, T. Soldan det.", was examined and figured [Kluge, 2004: Figs 50A–D]. Unlike *O. itayana*, paired processes of styliger are soft and diverge; penis lobes are not so strongly bent apically, more slender, without apical flaps [Kluge, 2004: Fig. 50D]. Genitals resemble that of *O. amazonicus*, but styliger is much shorter.

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