

THE ULTIMATE INSTAR LARVAE OF THE CENTRAL AMERICAN
SPECIES OF *PROGOMPHUS* SELYS, WITH A DESCRIPTION OF
P. BELYSHEVI SPEC. NOV. FROM MEXICO
(ANISOPTERA: GOMPHIDAE)

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A survey is given of the ultimate instar larvae or exuviae of all *Progomphus* spp. known from Central America. The hitherto unknown exuviae are described and illustrated. — *P. belyshevi* sp. n. (holotype ♂, allotype ♀: Mexico, State of Morelos, Xochitepax, 7-VII-1987; deposited in FSCA) is described, illustrated and compared with *P. borealis* McLachlan, from which it strikingly differs by the much darker sides of the pterothorax, due to the occurrence of the midlateral stripe, which is conjoined with the femoral stripe. — *P. williamsi* Needham, 1943 is synonymized with *P. clendoni* Calvert, 1905.

INTRODUCTION AND ACKNOWLEDGEMENTS

In the following pages I present descriptions and figures of new larval material of *Progomphus* Selys from the Central American countries, and a key for species identification of the ultimate instars. The material which served NEEDHAM for his "Life history studies on *Progomphus*" of 1941 could not be located so that a direct study of this material was not possible. A new species, closely related to *P. borealis* McLachlan, is described, while *P. williamsi* Needham appears to be conspecific with *P. clendoni* Calvert.

It should be emphasized that this study was made possible solely thanks to the availability of regional material assembled by several fellow workers. From Dr Dennis R. Paulson (Seattle) I received on loan reared individuals of *P. anomalus* Belle, *P. clendoni* Cal. and *P. risi* Wllsn, as well as the supposed exuviae of *P. mexicanus* Belle, all gathered during his keen and energetic investigations in Central America. At my request, Rodolfo Novelo Gutiérrez, M. Sc. (Xalapa) sent me a number of reared individuals from the State of Morelos, Mexico,

referable to a new species, described here as *P. belyshevi* sp. n., in appreciation of the very significant contribution to odonatology, rendered by my colleague, Dr B.F. Belyshev (Novosibirsk). Enrique Gonzalez Soriano, M. Sc. (Mexico City) and Dr Rosser W. Garrison (Azusa) put at my disposal adult males of this new species, secured in the same State by the former. Dr Garrison also sent me adult specimens of *P. borealis* McL. collected by himself in Baja California. Professor Dr Minter J. Westfall, Jr (Gainesville, FL) loaned me his males of *P. clendoni*, taken in transformation in Guatemala. The (reared) female holotype of *P. williamsi*, along with the respective exuviae, I could borrow from the Cornell University (Ithaca) by the courtesy of Dr James K. Liebherr. Finally, two exuviae and a larva of an undescribed *Progomphus* species were sent to me by Dr Paulson and Mr González.

The illustrations were made from original camera lucida drawings (details completed by free hand). Not all were drawn on scale owing to the great difference of size between some details. The Jena oculars used are 6.3 and 12.5; the objectives 0.63, 1, 1.6 and 2.5. The combination is indicated in figure captions. The picture of the thoracic pattern is diagrammatic. Some exuviae were photographed in dorsal aspect; the reproductions of the photographs are on scale. The museum and institution acronyms used in the text of this paper have been proposed by HEPNER & LAMAS (1982).

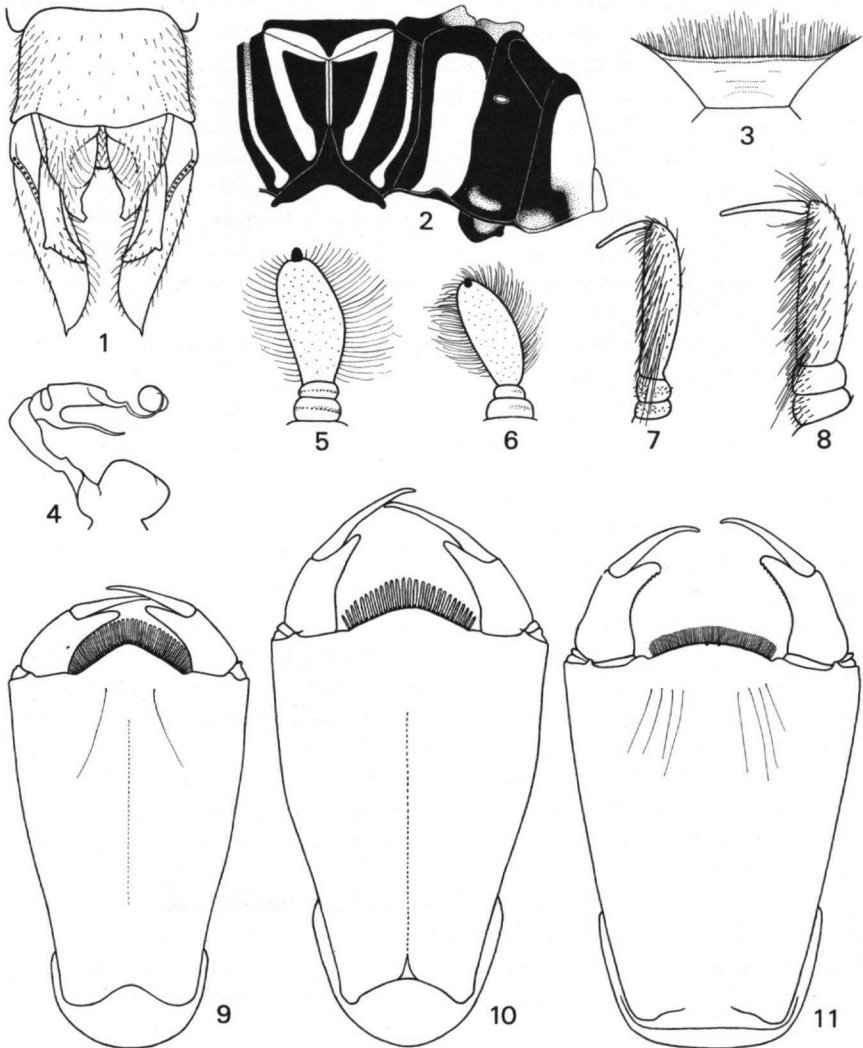
MORPHOLOGICAL FEATURES

The most useful reference work on the *Progomphus* immature stages is that by NEEDHAM (1941), where the *Progomphus* larva is characterized on pp. 238-242. The main characterization is based on the North American species. Larvae of South American species can considerably differ from those of this typical group as commented by Needham in the same paragraph.

The features discussed below hold only for the ultimate instar larvae or exuviae of the species occurring in Central America. In order to avoid unnecessary reiterations, repeated references are made to formerly published excellent depictions by diverse authors.

Size. — In terms of total length, i.e. the distance from the front border of the labrum to the tip of the caudal appendages, the larger species (21-30 mm) are *borealis*, *clendoni*, *mexicanus*, *zonatus*, *belyshevi* sp. n. and an unnamed one (spec. indet.), while to the smaller species (14-18 mm) belong *anomalous*, *longistigma*, *pygmaeus* and *risi*.

Labium. — The mentum of all species is widest anteriorly; the sides converge more or less regularly to the hinge. Species with a mentum that is widest near mid-length are found only in continental South America. There are two types of ligula (middle lobe of mentum): (a) ligula with a pair of minute submedium brown denticles at its apex (Fig. 11; also LIMONGI, 1985, Fig. 45) and (b) ligula without minute brown denticles on the front margin. A ligula of this latter type is found in the larger species and in *risi* (Figs 9-10). A ligula of type (a) is found in the



Figs 1-4. *Progomphus belyshevi* sp. n., adult ♂ [6.3x1.6, except diagram]: (1) tenth abdominal segment and caudal appendages, ventral; — (2) diagram of thoracic colour pattern; — (3) occipital plate; — (4) penis, right profile. — Figs 5-8. Right antenna of *Progomphus* larvae [6.3x2.5], dorsal: (5) *anomalus*; — (6) *pygmaeus*. — The same, right profile: (7) *risi*; (8) *clendoni* (holotype *williamsi*). — Figs 9-11. Mentum of labium of *Progomphus* larvae, ventral [12.5x1.6]: (9) *clendoni*; — (10) *risi*; — (11) *anomalus*.

other three smaller species. A more detailed description of the ligula of the larger species (*obscurus* and *borealis*) is given by NEEDHAM & HART (1901, p. 56) and KENNEDY (1917, pp. 527-529; 1921, pp. 595-596).

Antennae. — The third antennal segment is elongate, depressed and superiorly covered with lifting-bristles in the larger species and in *risi*; in the other smaller species it is fringed along the lateral sides with soft woolly hairs. The hirsute antennae have a fourth segment which is one-third to one-half the length of the third segment, almost cylindrical and slightly tapering to a blunt point (Figs 7-8; also DE MARMELS, 1990, Fig. 3). This fourth segment is often strongly recurved to lie (together with the bristles) on the dorsum of the third segment. The antennae with the soft woolly hairs have a fourth segment that is knob-like or hardly more than a small blunt cone (Figs 5-6).

Pronotum. — In the larger species and in *risi* the pronotum is flat, strongly rounded and shield-shaped; the mesostigmata are located close to the posterolateral angles. In the other smaller species the pronotum is subtriangular with swollen lateral edges; here the mesostigmata are situated at some distance behind the posterior border.

Legs. — The larger species and *risi* have very similar fossorial fore and middle legs (KENNEDY, 1917, Fig. 157). Their outer edges are heavily covered with bristle-like hairs. There are no burrowing hooks on the apices of the tibiae and the tarsal claws have some semblance of a chela. The remaining smaller species have moderately hairy legs and lack the bristle-like hairs. The fore and middle tibiae have burrowing hooks and the tarsal claws are of the ordinary divergent type. Attention should also be paid to the claws of the hind tarsi. NEEDHAM (1944, p. 210), when describing the larva of *Progomphus brachycnemis*, remarked that these claws bear a short seta close to the tip. DE MARMELS (1990, fig. 6) depicted very well the hind tarsal claws with the setae for the larva of the related *P. racenisi*. The United States *Progomphus* species surveyed normally have hind tarsal claws of the ordinary form but sometimes an inconspicuous subapical seta is discernible on one of the claws. The subapical seta is distinctive in the other species, with the claws suddenly decreasing in thickness beyond the site of the seta (Fig. 19; also DE MARMELS, 1990, fig. 6).

Abdomen. — The larvae of the larger species and *risi* have a well-developed, sharp, middorsal hook on segment 1; the other small species have no middorsal hook on this segment. All larvae have lateral spines on the segments 6 to 9; the presence or absence of lateral spines on the segments 2 to 5 is distinctive for some species. Of great relevance for the recognition of species is the relative length of the terminal segments in some species. A feature to which hitherto no attention has been paid within the classification of the *Progomphus* larvae, is the presence or absence of ventral longitudinal sutures (HAGEN, 1885, p. 274) on segment 9. The larger species have such sutures on segments 2 to 8 (Fig. 20; also KENNEDY, 1917, fig. 156), the smaller species on segments 2 to 9 (Figs 21-22). All species,

except *risi*, have inferior caudal appendages (paraprocts) with a straight ventral inner margin (KENNEDY, 1917, fig. 162). In the only exception, *risi*, the ventral inner margin of each inferior caudal appendage is strongly concave on the basal half; the concavities of both inferior caudal appendages are forming a ventro-basal anal hole (Fig. 21).

INFRAGENERIC RELATIONSHIPS

Based on the above mentioned features the ultimate instar larvae or exuviae of the Central American species of *Progomphus* can be categorized into three main groups which show some overlapping.

(I) The *OBSCURUS* GROUP (= typical group of NEEDHAM, 1941, p. 231). — The larval type of this group has been photographed (Fig. 31; also NEEDHAM & WESTFALL, 1955, fig. 43). The species composing this group are *belyshevi* sp. n., *borealis*, *clendoni*, *mexicanus*, *zonatus* and a spec. indet. Their larvae share the following 10 characters:

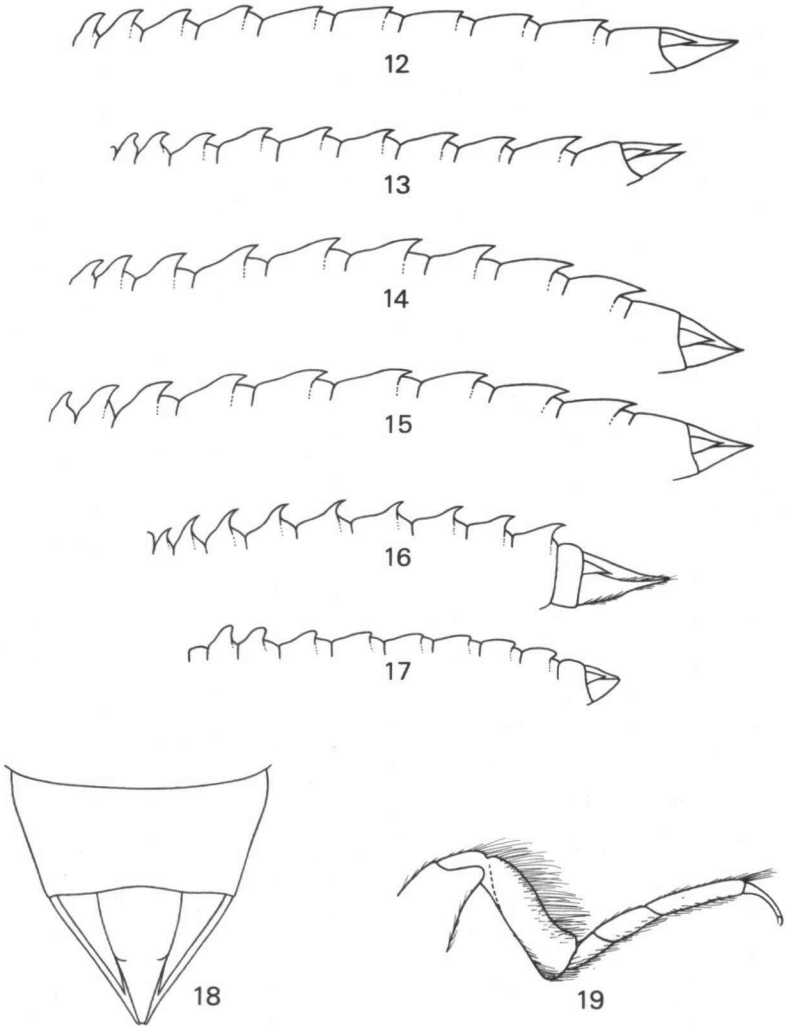
- (1) larva of large size (total length 21-30 mm);
- (2) abdomen regularly tapering to the end;
- (3) abdominal segment 9 without ventral longitudinal sutures;
- (4) anal pyramid about as long as the tenth abdominal segment;
- (5) pronotum rounded and flat, the mesostigmata next to its postero-lateral angles;
- (6) ventral inner margins of inferior caudal appendages straight;
- (7) fore and middle tibiae without burrowing hooks;
- (8) fore and middle tarsal claws cheliform;
- (9) third antennal segment superiorly covered with bristle-like hairs, the fourth antennal segment one-third to half as long as third segment, almost cylindrical but slightly tapering to a blunt point;
- (10) front margin of ligula without a pair of submedian minute brown denticles.

(II) The *RISI* GROUP. — In Central America represented by *risi* only. Other members pertaining to this group such as *P. brachycnemis* Needham and *P. racenisi* De Marmels, are found in continental South America. Figure 32 is a reproduction of a photograph of the larval type of this group. The characters (5), (7), (8), (9) and (10) given for the *obscurus* group are identical with those of the *risi* group. The other distinguishing characters are:

- (1) larva of small size (total length 14-18 mm);
- (2) abdomen long-pointed;
- (3) abdominal segment 9 with a pair of ventral longitudinal sutures;
- (4) anal pyramid about three to four times as long as tenth abdominal segment;
- (6) ventral inner margins of inferior caudal appendages strongly concave on basal halves.

(III) The *PYGMAEUS* GROUP. — Into this group I placed the remaining three Central American species *pygmaeus*, *longistigma* and *anomalus*. The larval type of this group has been photographed (Figs 33-34). The larvae agree with the characters (1) and (3) of the *risi* group and with the characters (4) and (6) of the *obscurus* group. The differential characters of the *pygmaeus* group are:

- (2) abdomen beyond middle segments quickly tapering to the end;
- (5) pronotum subrectangular with swollen lateral edges, the mesostigmata at some distance from posterior margin;
- (7) fore and middle tibiae with burrowing hooks;



Figs 12-17. Outline of abdomen of *Progomphus* larvae, left profile [6.3x0.63]: (12) *belyshevi* sp. n.; — (13) *mexicanus* (supposition); — the same [6.3x1]: (14) *clendoni* (Guatemala); — (15) *clendoni* (Veracruz, Mexico); — (16) *risi*; — (17) *anomalous*. Fig. 18. *Progomphus pygmaeus*, larva from Mexico, tenth abdominal segment and caudal appendages, dorsal [6.3x4]. — Fig. 19. *Progomphus risi* larva, left hind tibia, tarsus and claws, left profile [6.3x1.6].

- (8) fore and middle tarsal claws of the ordinary divergent type;
- (9) third antennal segment with soft woolly hairs along lateral sides, the fourth antennal segment knob-like or merely a small blunt cone;
- (10) front margin of ligula with a pair of submedian minute brown denticles.

SPECIES KEY TO THE ULTIMATE INSTAR LARVAE

- 1 Total length < 20 mm; abdominal segment 9 with a pair of ventral longitudinal sutures 2
- Total length > 20 mm; abdominal segment 9 without ventral longitudinal sutures (larvae of the *obscurus* group) 5
- 2(1) Pronotum flat and shield-shaped, the mesostigmata close to its postero-lateral angles; anal pyramid about three to four times as long as abdominal segment 10; ventral inner margins of inferior caudal appendages strongly concave on basal half; no burrowing hooks on tibiae (larvae of the *risi* group) *risi*
- Pronotum subrectangular with swollen lateral edges, the mesostigmata placed outside of its hind margin; anal pyramid about as long as abdominal segment 10; ventral inner margins of inferior appendages straight; fore and middle tibiae with burrowing hooks (larvae of the *pygmaeus* group) 3
- 3(2) Dorsal hooks of abdominal segments 5 to 9 low, that on segment 6 almost lacking (Fig. 17) *anomalus*
- Dorsal hooks of abdominal segments 5 to 9 well developed 4
- 4(3) Dorsal hooks of abdominal segments 7 to 9 regularly increasing in height rearwards; hind femur 2.5 mm *pygmaeus*
- Dorsal hooks of abdominal segments 7 to 9 regularly diminishing in height; hind femur 4 mm *longistigma*
- 5(1) Dorsal hooks of abdomen highest on segments 1 and 2, then diminishing in size, being very small and low on segments 6, 7 and 8, the one on segment 9 slightly larger 6
- Dorsal hooks of abdomen well developed on all segments 1 to 9 7
- 6(5) Midventral length of abdominal segments 8, 9 and 10 approximately in ratio 10: 9:8, with the inferior caudal appendages 11 on the same scale *borealis*
- Midventral length of abdominal segments 8, 9 and 10 approximately in ratio 10:12:11, with the inferior caudal appendages 11 on the same scale *belyshevi* sp. n.
- 7(5) Lateral spines on abdominal segments 4 or 5 to 9 8
- Lateral spines on abdominal segments 6 to 9 *zonatus*
- 8(7) Abdominal segment 10, in ventral view, as long as wide anteriorly; hind tarsi pale whitish from base to near apex 9
- Abdominal segment 10, in ventral view, longer than wide anteriorly, hind tarsi entirely brownish *mexicanus* (supposition)
- 9(8) Total length 21-22 mm; colour pattern of abdomen shaped as shown in NEEDHAM's (1941) Fig. 10a *clendoni*
- Total length 24-25 mm; colour pattern of abdomen shaped as shown in Figures 26-27 spec. indet.

SYSTEMATIC ACCOUNT OF THE SPECIES

The groups are treated in the same sequence in which they are mentioned in the key. Within each group the larvae are discussed, as much as possible, in such a sequence as to allow expression of apparent relationships. Under each species are

given the main references, the data on the material studied, and a description or descriptive notes.

The predicate "reared" following a species name means that the larva of the species involved has been taken in transformation or has been caged until the imago emerged, while the predicate "supposition" following a species name means that the larva of the species involved has never been reared. In the latter case the specific identification of the exuviae is on grounds of size, appearance and known distribution.

The term "width of head" means "the width of the head across the compound eyes". The term "width of abdomen" means "the greatest width of the abdomen"; this is generally the width of the sixth abdominal segment.

Obscurus group

PROGOMPHUS BOREALIS McLACHLAN, reared

Figure 28

HAGEN, 1885: 275-276 (under "32. *Progomphus* spec.", cf. BYERS, 1939: 57); — KENNEDY, 1917: 527-529, figs 155-163 (larva & larval struct.); — SEEMANN, 1927: 19 (under "*Progomphus obscurus*", cf. BYERS, 1939: 58); — NEEDHAM, 1941: 234, 241 (tab.), pl. 20, fig. 2 (profile abd.).

Material. — USA: (Arizona, San Pedro River, 30-VII-1956, 1 ♂, 1 ♀ (both taken in transformation), M.J. Westfall, Jr, FSCA; — California, Napa Co., Pope Creek (in sand near shore line 600 ft), 20-IV-1975, 1 ♂ (larva), J.A. Garrison, RNHL.

P. borealis belongs to the Mexican fauna. Adult specimens of this species from Baja California were sent to me for study by Dr Garrison. I have serious doubt about the occurrence of the species in the region of Mexico below the 25th degree of latitude (cf. BELLE, 1977; p. 11). I have not seen CALVERT's specimens of *borealis* reported from central Mexico (*Biologia cent.-am.*, 1905; p. 151), but I believe that they belong to the below described *P. belyshevi* sp. n., since his "Guadalajara male has a brown stripe on the partly obsolete first lateral thoracic suture", a colour feature that is typical of the new species.

The larvae of *borealis* have lateral spines on the abdominal segment 3 (NEEDHAM & WESTFALL, 1955; p.96) but sometimes also on the abdominal segment 2. The male exuviae from Arizona and the male larva from California have no lateral spines on the abdominal segment 2. The colour pattern of the dorsal side of the abdomen is weakly developed and shaped as shown in Figure 28.

Measurements (in mm). — Total length 27, — abdomen 18 (incl. caud. app. 2.1), — width of abdomen 6, — width of head 5, — hind femur 3.7.

PROGOMPHUS BELYSHEVISP. N., reared

Figures 1-4, 12, 20, 29

Material: adults. — Mexico: State of Morelos, km 18.3 Carretera 95, 5 km S of Acatlipa, Municipality of Xochitepex, 26-VII-1985, 2 ♂ (holotype and paratype), — 1 ♂, 1 ♀ in cop. (paratype and allotype, respectively), all G. González; — 7-VII-1987, 2 ♂ (paratypes), V. García, E. González & R. Novelo. — Holotype in FSCA, allotype and 2 paratypes in coll. González, 1 paratype in coll. Garrison and 1 paratype in RNHL.

Larvae. — Mexico: State of Morelos, Municipality of Jojutla, San Rafael Vicente Aranda (800 m), Río Amacuzac (on sand bank), 3-IV-1985, 1 ♀ (taken in transformation), — 14-IV-1985, 2 ♂, both emerged on 24-V-1985 (in aquarium), — 2-VI-1985, 1 ♂ (larva), 1 ♂, 1 ♀ (both exuviae), all R. Novelo.

Independently of the author, Mr E. González discovered that the present species was unnamed. In the belief that, in connection with my current studies on allied larval material, it would be better to leave its description to me, he kindly placed all his adult material at my disposal.

Etymology. — This species is named in honour of the nestor of the Russian odonatology, Dr B.F. BELYSHEV, on the occasion of the celebration of his 80th birthday.

MALE (holotype). — Total length (in mm) 55.5, — abdomen 43.5, — hind wing 32, — costal edge of pterostigma of fore wing 4.4.

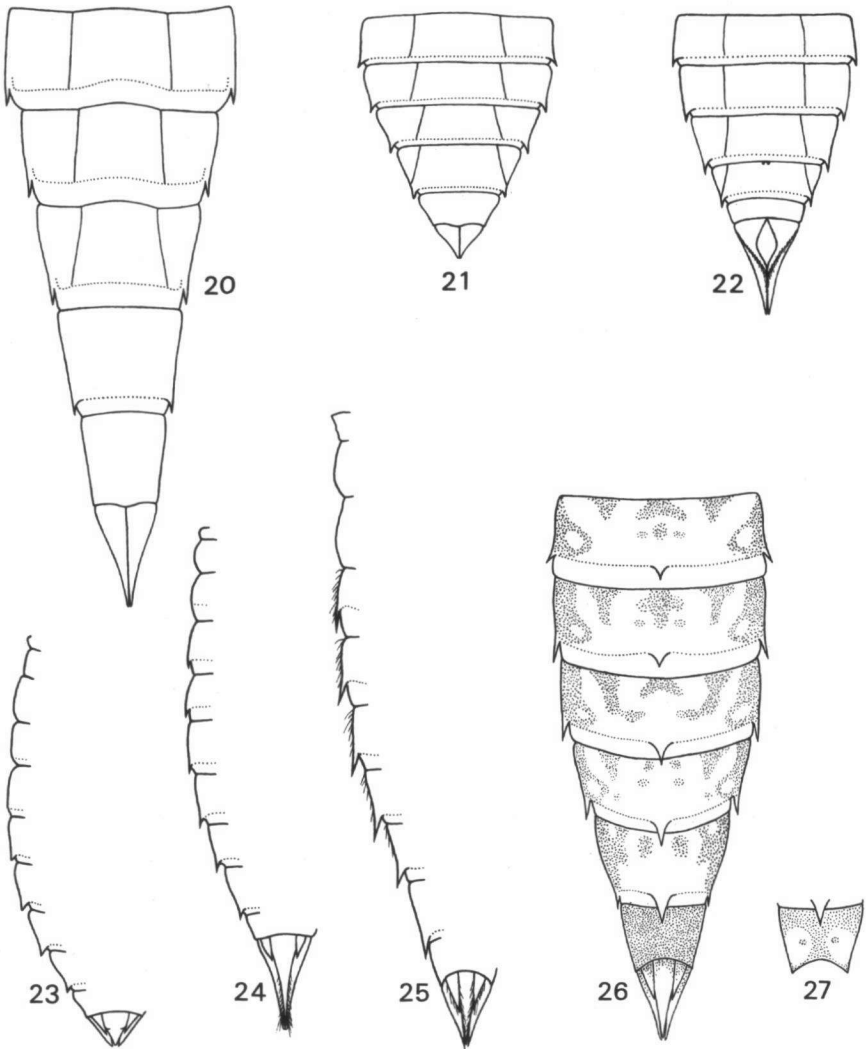
Closely allied to the northern *P. borealis* and having also a well-developed middorsal spine on the abdominal segment 1 (cf. DUNKLE, 1984, p. 479), but notably differing in the following particulars: (1) sides of pterothorax with midlateral stripe well developed and conjoined with femoral stripe, a pale spot near subalar carina (Fig. 2); in *borealis* midlateral stripe undeveloped, a dark spot at spiracle; — (2) occipital plate narrower than in *borealis* (Fig. 3); — (3) caudal appendages more slender than in *borealis* (Fig. 1); — (4) accessory genitalia similar to that of *borealis*, but ventral spine of penile median segment slightly diverging from the latter towards apex (Fig. 4).

FEMALE (allotype; abdomen broken between segments 4 and 5). — Total length (in mm) 55.5, — abdomen 43.5, — hind wing 33, — costal edge of pterostigma of fore wing 4.9.

Similar to male holotype in characters other than those of sex but with larger wings and pterostigma. Vulvar lamina not remarkably different from that of *borealis*.

LARVA (described from the exuviae of one of the reared males). — Total length (in mm) 29, — abdomen 21 (incl. caud. app. 2 mm), — width of abdomen 5, — width of head 4.5, — hind femur 3.3.

The exuviae are more slender than those of *borealis*. The abdomen has relatively longer end segments. The midventral length of the abdominal segments 8, 9 and 10 are approximately in ratio 10:10:9, with the inferior caudal appendages 9 on the same scale; in *borealis* 10:9:8, with the inferior caudal appendages 11 on the same scale. The colour pattern of the abdomen is better



Figs 20-22. Apical half of abdomen in *Progomphus* larvae, ventral, showing longitudinal sutures [6.3x1]: (20) *belyshevi* sp. n., — (21) *anomalus*; — (22) *risi*. — Figs 23-25. Left margin of abdomen and caudal appendages in *Progomphus* larvae, dorsal [6.3x1]: (23) *anomalus*; — (24) *risi*; — (25) *clendoni* (holotype *williamsi*). — Figs 26-27. Larva of spec. indet. [6.3x1]: (26) colour scheme of dorsum of abdomen in Apotla specimens; — (27) colour scheme of dorsum of tenth abdominal segment in Cintalapa specimen.

developed than in *borealis* with the greatest colour difference for segment 7. The dorsal side of this segment has longitudinal dark bands (Fig. 29), in *borealis* a pair of semicircular dark bands (Fig. 28). In contrast to the larva of *borealis* the abdominal segment 3 does not always have lateral spines. Of the six exuviae of *belyshevi* sp.n. here recorded, two have the abdominal segment 3 without lateral spines, two with a minute lateral spine on one side only, and two with a minute lateral spine on either side.

PROGOMPHUS CLENDONICALVERT, reared

Figures 8-9, 14-15, 25, 31

NEEDHAM, 1941: 235 (under "*Progomphus clendoni*?"), 241 (tab.), pl. 20, fig. 10 (labial palp., profile & pattern abd.); 237-238 (under "Nymph No. 15", 241 (tab.), pl. 20, fig. 15 (profile abd.); — 1943: 202-205 (under *Progomphus williamst*).

Material. — Mexico: State of Veracruz, stream 16.9 mi SW of Coatzacoalcos (at Mex. 180, 200 ft), 2-VII-1965, 1 ♀ (exuviae); — State of Chiapas, Rio Arenas (21 mi SE of Pijijiapan, 150 ft), 1-VIII-1965, 1 ♂ (emerging), both D.R. Paulson. — Guatemala: Dept. Escuintla, Finca El Salto, 1-VII-1977, 2 ♂ (both emerging), M.J. Westfall, Jr, FSCA.

P. clendoni is reported from all Central American countries with the exception of Honduras and Panama, but its occurrence in these countries may certainly be expected. The exuviae of all reared specimens here listed are very similar and do not show morphological or colour differences.

Measurements (in mm). — Total length 21.5, — abdomen 14.5 (incl. caud. app. 1.4), — width of abdomen 3.8-4.1, — width of head 3.6, — hind femur 2.4, — third antennal segment 1.4.

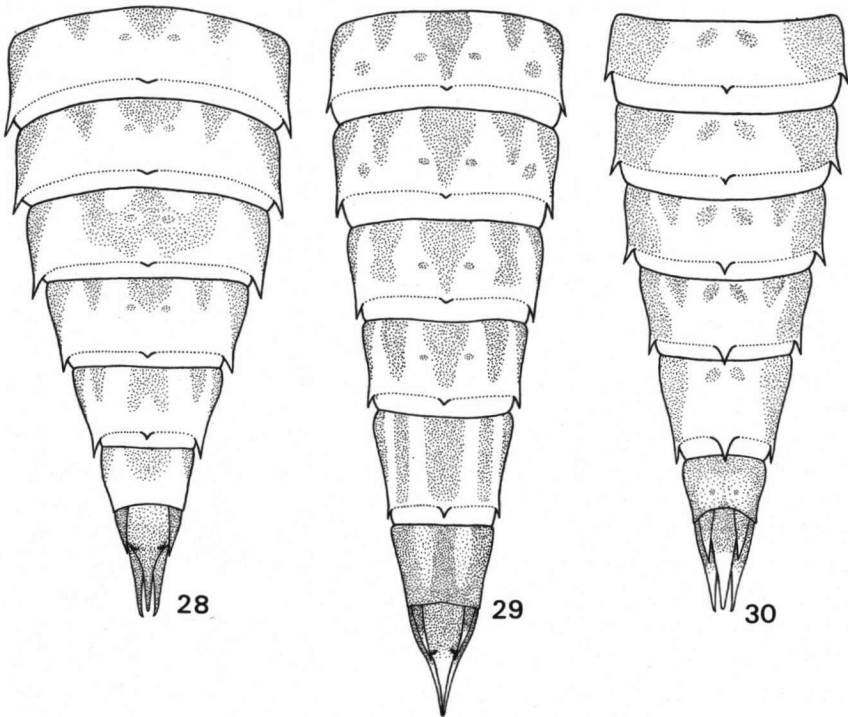
Antenna shaped as shown in Figure 8. Labium extending back to posterior margin of procoxae; it is shaped as shown in Figure 9. Distance between left and right coxa of the first, second and third pair of legs approximately in ratio 3:1:6. Hind tibiae as long as hind tarsi. Abdomen with lateral spines on segments 4 or 5 to 9; they are sub-equal and thorn-like. Dorsal hooks on segments 1 to 9; they are well developed and acute, those on basal segments more erect, the others becoming more strongly inclined rearwards, successively (Fig. 14). Ventral side of abdominal segment 9 with two symmetrical pairs of basal tufts of hairs. Mid-ventral length of abdominal segments 8, 9 and 10 approximately in ratio 8:10:8, with the inferior caudal appendages 8 on the same scale. Caudal appendages pale on apical half, the superior (epiproct) a trifle shorter than the inferiors and the laterals (cerci) somewhat more than half of the inferiors.

The exuviae from Veracruz do not differ in size from the exuviae of the reared individuals but the dorsal hooks on the abdominal segments 4 to 9 are somewhat smaller and less erect (Fig. 15). The colour scheme of the dorsum of the abdomen resembles that of NEEDHAM's (1941) larva No. 10 (depicted in his Fig. 10a), but his No. 10 seems to have a larger size and a much shorter fourth antennal

segment. Could the given relative length 2 for the fourth antennal segment in NEEDHAM's (1941) table be a lapsus calami pro 5?

In 1943 NEEDHAM described *Progomphus williamsi* from Guatemala on the basis of a female taken in transformation. A study of the exuviae of the holotype enabled me to make some corrective notes in the lines 18 to 21 on p. 204 of NEEDHAM's 1943 paper. Firstly, the "6th abdominal segment" should be the "4th abdominal segment". The statement, "they are absent from one side of the exuvium of the reared specimen and from both sides of the nymph", is confusing. With "nymph" cannot be meant Needham's "*Progomphus* nymph No. 15" since this skin has a spine on each side of the abdominal segment 4 (NEEDHAM, 1941, tab. on p. 241). The exuviae of the holotype have a very small and inconspicuous lateral spine on the right side of the abdominal segment 4; the lateral spine on the left side of the abdominal segment 4 is better developed and undoubtedly the one to which Needham referred (Fig. 25).

I have directly compared the adult female holotype of *P. williamsi* and the exuviae from which it came with the two reared males of *P. clendoni* and their exuviae from the same (type) locality. The three larval skins have the same size (total length 21.5 mm). This is contrary to NEEDHAM's (1943) statement that the larva of *williamsi* is his larva No. 15 because from his verification table it follows that the length of larva No. 15 is 28 mm. For the rest, the three cast skins are very similar in their morphology except for the following minor characters: One of the two larval skins of *clendoni* has very small and inconspicuous lateral spines on the abdominal segment 4. These spines are similar to that on the right side of abdominal segment 4 of the exuviae of *williamsi*. The other larval skin of *clendoni*, from the same locality, has a slightly shorter fourth antennal segment and an abdominal segment 4 without lateral spines. The cast skin of the reared male of *clendoni* from Mexico has also an abdominal segment 4 without lateral spines, but it does agree with that of *williamsi* in having the antennal segment 4 half as long as antennal segment 3. The colours of the *williamsi* exuviae are largely faded, but from the remaining dark markings we can conclude that the colour pattern of the abdomen is similar to that of the two cast skins of *clendoni* from the same *williamsi* locality. The adult female holotype of *P. williamsi* agrees with the two reared adult males of *clendoni* in non-sexual characters. Obviously, the adult holotype of *williamsi* is the (firstly described) female of *clendoni*. The latter was unknown at the time that Needham described his *williamsi*. In 1973 I described a fully mature adult female of *clendoni*. This specimen shows some differences in colouration and proportions with the adult female of *williamsi*, but these differences I would (in retrospect) credit to the immature condition of the type.



Figs 28-30. Colour scheme of dorsum of abdomen in *Progomphus* larvae [6.3x1]: (28) *borealis*; — (29) *belyshevi* sp. n.; — (30) *mexicanus* (supposition).

PROGOMPHUS SPEC. INDET.

Figures 26-27

Material. — Mexico: State of Chiapas, Río Cintalapa (at Mex. 190, 1800 ft), 24-VII-1965, 1 ♂ (exuviae), D.R. Paulson; — State of Morelos, Municipality Xochitepec, Río Apotla (920 m), 24-VII-1985, 2 ♀ (larva and exuviae), R. Novelo.

These exuviae and larva possibly belong to the new species recently detected at a sulphur stream near Ciudad de Valles (State of Oaxaca) by Mr E. González and Dr K.J. Tennessen (communicated by the former, 27 August 1990). The skins differ strikingly from *clendoni* by the larger size and by the reduced dark colours on the dorsum of the abdomen.

Measurements (in mm). — Total length 24-26, — abdomen 16.5-18 (incl. caud. app. 1.6-2), — width of abdomen 4.2-5, — width of head 4.2-4.4, — hind femur 2.8-2.9, — third antennal segment 1.5.

Profile of abdomen identical in shape to that of typical *clendoni* larva. Colour

pattern of abdomen of the Apotla specimens shaped as shown in Figure 26, that of the Cintalapa specimen differs from it by the much paler dorsum of the tenth abdominal segment (Fig. 27).

PROGOMPHUS MEXICANUS BELLE, supposition
Figures 13, 30

Material. — Costa Rica: Prov. Guanacaste, Hacienda Tabo Taboga, Rio Higueron (100 ft), 7-VII-1966, 1 ♀ (exuviae), D.R. Paulson, CP.

P. mexicanus has been described from Mexico and Costa Rica (BELLE, 1973). Surely this species will be found in the interjacent countries. The above recorded specimen, being a cast-off skin left behind at emergence, is described below.

Measurements (in mm). — Total length 27, — abdomen 19 (incl. caud. app. 1.6), — width of abdomen 4.5, — width of head 4.2, — hind femur 2.8, — third antennal segment 1.9.

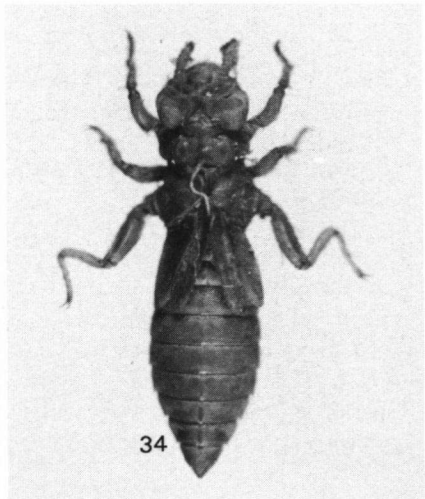
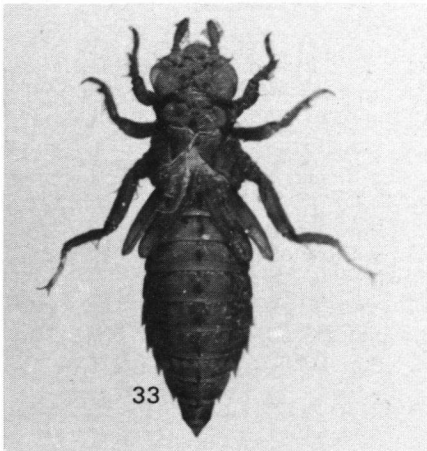
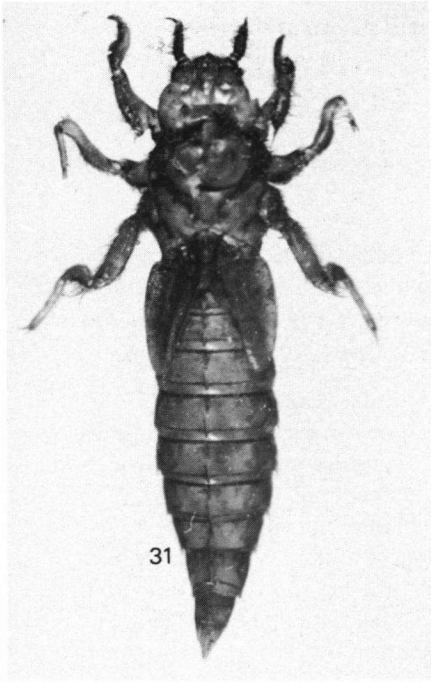
This skin resembles in its morphology that of the spec. indet. but is distinguished from it by the particulars given in the key, by the larger size, by having the fourth antennal segment a trifle longer than half the length of the third segment, and by having the middorsal hooks on the apical abdominal segments somewhat smaller (Fig. 13). The colour pattern of the abdomen is hardly discernible and approaches somewhat that of the Cintalapa specimen of the spec. indet. (Fig. 30). The relative distances between the respective coxae are the same. The midventral length of the abdominal segments 8, 9 and 10 is approximately in ratio 10:14:10, with the inferior caudal appendages 9 on the same scale. There are well developed lateral spines on the abdominal segments 4 to 9.

I have risked the supposition that this is the cast larval skin of *P. mexicanus* on the slender basis of facts communicated by Dr D.R. Paulson. He wrote from Seattle on 13 April 1980: "I am assuming the exuviae from Taboga, Costa Rica, is *mexicanus* as that species was common there and was the only species of the genus I collected". But compared with the exuviae of its nearest relative *clendoni* the size of the skin is too large to be in agreement with such a supposition since the adult specimens of *mexicanus* are smaller than those of *clendoni*, judging from the specimens I have studied. The Taboga cast skin agrees with the features of NEEDHAM's (1941) larva No. 15 except for the colour pattern of the abdomen which is not developed in Needham's larva.

PROGOMPHUS ZONATUS HAGEN, supposition

NEEDHAM, 1941: 234-235, 241 (tab.), pl. 20, fig. 9 (pattern abd.).

P. zonatus is reported from Mexico and Guatemala (BELLE, 1973). Its larva is recognizable in not having lateral spines on the abdominal segments 1 to 5.



Figs 31-34. *Progomphus* exuviae in dorsal aspect (from photographs): (31) *clendoni*; — (32) *risi*; — (33) *pygmaeus*; — (34) *anomalus*.

Risi group*PROGOMPHUS RISI* WILLIAMSON, reared

Figures 7, 10, 16, 19, 22, 24, 32

Material. — Mexico: State of Chiapas, Rio Cuil (1.9 mi NW of Huixtla), 31-VII-1965, 1 ♂, 1 ♀ (both emerging), M.L. Paulson.

P. risi was described from Gualán, Guatemala, and recorded from Mexico by PAULSON (1982). The larva resembles much those of *P. brachycnemis* and *P. racenisi*, but the size is smaller and the caudal appendages are longer than in these two South American species. The female larval skin is described below.

Measurements (in mm). — Total length 16, — abdomen 10.5 (incl. caud. app. 2), — width of abdomen 4, — width of head 3.3, — hind femur 2, — third antennal segment 1.5.

Mentum of labium very long, shaped as shown in Figure 10, the hinge reaching backward well between the middle coxae. Ligula occupying half the front border of mentum and fringed with about 25 spaced long slender scales. Terminal portion of lateral labial lobe slender and bluntly tipped. Movable hook about three times as long as portion of lateral lobe beyond base of movable hook; it is slender and has an unusual twist inwards just beyond the tip of the terminal portion of the lateral lobe. Inner margin of lateral lobe smooth. Third antennal segment shaped as shown in Figure 7. Distance between left and right coxa of first, second and third pair of legs approximately in ratio 5:3:10. Hind tibiae notably shorter than the tarsi they bear (Fig. 19).

Abdomen sandy brown, without colour pattern and without definite scars. It is widest on segment 6 and its lateral sides have long, rearwardly directed, pale brownish hairs (for clarity's sake these hairs not drawn in Fig. 24). Dorsal hooks on segments 1 to 9, small on segment 1, increasing in size on segments 1 to 3, on segments 3 to 9 erect, sharp, of nearly equal height and reaching farther to rearward on successive segments (Fig. 16). Midventral length of abdominal segments 8, 9 and 10 approximately in ratio 20:15:8, with the inferior caudal appendages 40 on the same scale. Inferior appendages very acutely pointed, the ventral inner margins concave on basal half and heavily hairy along a line from outer basal angle to apex of concavity at middle of inner margin (Fig. 22). Superior appendage also very acutely pointed and as long as inferiors. Lateral appendages one-fourth as long as inferiors.

Pygmaeus group

PROGOMPHUS PYGMAEUS SELYS, reared
Figures 6, 18, 33

LIMONGI, 1985: 114-117, figs 40-45 (larva & larval struct.).

Material. — Mexico: State of Chiapas, Río Huehuetan (15.0 mi NW of Tapachula, 200 ft), 28-VII-1965, 1 ♂ larva, emerged 1-VIII-1965, D.R. & M.L. Paulson.

P. pygmaeus is recorded from Costa Rica, Guatemala and Mexico (PAULSON, 1982) but the occurrence in whole Central America can be expected. The ultimate instar larval skin has been described from Venezuela by LIMONGI (1985), the identification being based on a reared individual (Mr J. De Marmels 1990, pers. comm.). Assuming that the details are exactly figured, the cast skin from Mexico differs slightly in the configuration of the antennae and caudal appendages. The present skin has the outer lateral side of the third antennal segment more strongly convex and the lateral caudal appendages more acute and longer, being five-sixths the length of the inferior caudal appendages. The differences may be seen by comparing my Figures 6 and 18 with Limongi's corresponding illustrations (his figs 44 and 42, resp.).

The dimension 16.5 for the "total length" given in the description of the cast skin is apparently derived from the figure of the entire skin in dorsal aspect (Limongi's fig. 40). From the accompanying 10 mm scale follows that the distance from the apex of the anal pyramid to the tips of the stretched fore legs measures 16.5 mm but to the front border of the labrum 14.6 mm. The latter number is in agreement with the proportions of the Mexican skin.

PROGOMPHUS LONGISTIGMA RIS, reared

NEEDHAM, 1941: 231-232, 241 (tab.), pl. 20, fig. 8 (lat. lobe labium).

P. longistigma was described from Costa Rica, but PAULSON (1982) collected the species in Mexico so its occurrence in the interjacent countries can be expected. The ultimate instar larval skin was described by NEEDHAM (1941).

PROGOMPHUS ANOMALUS BELLE, reared
Figures 5, 11, 17, 21, 23, 34

Material. — Costa Rica: Prov. Puntarenas, Rincón de Osa, Quebrada Aguabuena, 13-III-1970, 1 ♂ (emerging), D.R. Paulson.

P. anomalus is here recorded from Costa Rica for the first time. The species

has been described from Peru, Ecuador and Panama (BELLE, 1973). The present raised adult male is peculiar in having the anal triangle of the hind wings one-celled (that of the right hind wing with a partly developed cross-vein); it is normally two-celled in this species. The larva resembles that of *P. pygmaeus*, from which it is easily discerned in having the dorsal hooks of the middle segments of the abdomen very low (Fig. 17). The larval cast-off skin is described below.

Measurements (in mm). — Total length 15, — abdomen 9 skin (incl. caud. app. 0.7), — width of abdomen 4, — width of head 3.5, — hind femur 2.3, — hind tibia 2.5, — hind tarsi 2, — third antennal segment 1.1.

Antennal segment 3 depressed-oval, widest on basal half, strongly convex on outer lateral side (Fig. 5). Fourth antennal segment dark brown, conical, erect, one-eighth as long as third segment. Labium extending back to anterior margin of middle coxae, shaped as shown in Figure 11. Ligula slightly produced and evenly convex, with a submedian pair of minute brown denticles on the front margin, the left denticle being less developed; its free border densely fringed with scale-like hairs. Lateral labial lobe finely serrated along its slightly concave inner margin. Movable hook strongly curved inward at tip and twice as long as the portion of lateral lobe beyond base of movable hook. Distance between left and right coxa of the first, second and third pair of legs approximately in ratio 6:5:10. Abdomen widest on segment 6, almost bare, the lateral margins scarcely provided with pale brown hairs. Lateral spines on segments 6 to 9, longest on segments 7 and 8, smaller on segments 6 and 9, those on segment 6 smaller than those on segment 9 (Fig. 23). Dorsal hooks on segments 2 to 9, largest on segment 2, becoming smaller on segments 3 to 5 successively, very low on segment 6, becoming again slightly larger on segments 7, 8 and 9 successively (Fig. 17). Abdomen sandy brown, without colour pattern but with clusters of weakly discernible scars on upper sides of segments 5 to 8. Midventral lengths of segments 8, 9 and 10 approximately in ratio 8:10:7; with the inferior caudal appendages 7 on the same scale. Superior caudal appendage a trifle shorter than inferior appendages, the laterals three-fifths as long as the inferiors.

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