

Revision of the Genus *Cloeodes* Traver (Ephemeroptera: Baetidae)¹

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ABSTRACT A comprehensive revision of *Cloeodes* Traver, a genus clearly distinguished as larvae by the presence of ventral tufts of setae on abdominal segments 2-6, shows that species with hind wings and species without hind wings are included. Two major phyletic lineages within the genus are recognized as subgenera: the monotypic *Notobaetis* Morihara & Edmunds, n. status, including *C. penai* (Morihara & Edmunds) from Argentina; and *Cloeodes* sensu stricto (= *Centroptella* Braasch & Soldán [in part]) including *C. maculipes* Traver from Puerto Rico (the type species), *C. anduzei* (Traver), n. comb., from Venezuela, *C. aymara* (Traver), n. comb., from Uruguay, *C. consignatus* Traver from Puerto Rico, *C. excogitatus*, n. sp., from Arizona, *C. irvingi*, n. sp., from Paraguay, *C. longisetosus* (Braasch & Soldán) from China, *C. macrolamellus*, n. sp., from New Mexico, *C. peninsulus*, n. sp., from Baja California, *C. redactus*, n. sp., from Peru, and *C. soldani* (Müller-Liebenau) from Sri Lanka. Species are delineated primarily on the basis of larval structural characteristics, especially those of abdominal terga and armature associated with legs. Only *C. consignatus*, *C. anduzei*, and *C. aymara* are unknown as larvae, and these together with *C. penai* and *C. maculipes* are the only species presently known as adults. A key to the species in the larval stage is included.

KEY WORDS Ephemeroptera, Baetidae, *Cloeodes*, revision

THE GENUS *Cloeodes*, as originally conceived by Traver (1938), was a small group of poorly defined species of Baetidae from Puerto Rico. The genus as such was enigmatic because it was polyphyletic. Nominal species originally described as *Cloeodes* by Traver (1938) were *C. maculipes*, the type of the genus; *C. portoricensis*, which has since been transferred to the genus *Paracloeodes* by Day (1955); and *C. consignatus*, which unfortunately is known only from a female adult holotype that is inconsequential with regard to generic and specific level characteristics. *Cloeodes* sp. 1 (Traver 1938) is certainly not assignable to *Cloeodes*, as we redefine the genus herein. The type chosen for the genus, *C. maculipes*, does represent a grouping of Baetidae at the genus level that is distinct from other genera and clearly definable.

Until now, no subsequent reports of the genus have appeared, except the tentative assignment of a larval population from Peru as *Cloeodes* by Roback (1966). Some workers have, however, alluded to a possible occurrence of the genus in South and Central America (Traver 1943, Edmunds et al. 1976), but apparently without hard data.

Our revisionary studies of the family Baetidae and discovery of new characters of taxonomic value have revealed that *Cloeodes* is a widespread genus of Neotropical origin containing several species from South and Middle America as well as southwestern North America and Southeast Asia. Besides finding that a number of previously unstudied specimens are new species referable to

Cloeodes, we have found that certain specimens previously examined by other workers but identified variously are also clearly referable to *Cloeodes*. These include, in addition to the "Genus Poss. *Cloeodes*" of Roback (1966), *Pseudocloeon anduzei* Traver (1943), *Baetis aymara* Traver (1971), the "large-gilled baetid" of Edmunds et al. (1976, 156), the genus *Notobaetis* of Morihara & Edmunds (1980), the genus *Centroptella* Braasch & Soldán (1980) (in part), and the Genus *Incertae* of Allen & Murvosh (1983). We strongly suspect but cannot yet demonstrate unequivocally that some other records will also prove to be referable to *Cloeodes*. These include the South American larvae "A Nymph allied to *Centroptilum*, generis *incerti*" of Eaton (1883-88, 173), the *Baetis* sp. 1 of Traver (1938), as well as Baetine No. 2 and Baetine No. 4 of Traver (1944, 24).

Materials and Methods

To study properly the characters of most importance in *Cloeodes*, special care must be given to specimen preparation. Ultrastructural characters of armature and other cuticular surface differences require magnifications >100× and the use of properly cleared and slide-mounted specimens. Dissections should be performed on mature last instars or their exuviae. If exuviae are used, a clearing process is unnecessary.

The head, thorax, and abdomen should be carefully separated from one another and placed in a

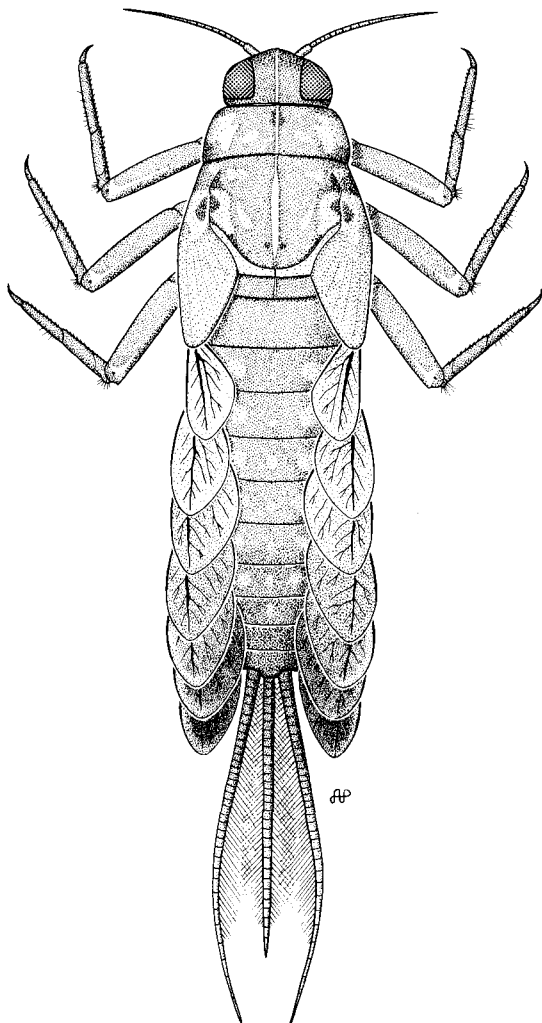


Fig. 1. *C. macrolamellus*, larva, dorsum.

macerating solution of cold 10% KOH. After ca. 15 min, the specimen should be moved to a distilled water rinse and rapidly rehydrated, permitting a controlled explosion of tissues. The following dissections should be performed while the specimen (or untreated exuviae) is in water: 1) separation of the mesotergum from the remainder of the thorax, 2) removal of the mouthparts from the head capsule, 3) bisection of the abdominal cavity along the pleural suture of one side so that the abdomen may be laid flat with both sterna and terga visible, and 4) removal of at least one paraproct. The dissected parts may be placed again in a 10% KOH solution to remove any remaining tissue. Once clean, the dissected parts should be moved to a water rinse containing a few drops of alcohol and through standard increasing concentrations of alcohol (and then xylene if using balsam as a mounting medium) before mounting slides. Caution should be used in the macerating process

because of the potential ruination of characters, especially of setae, scales, and spines.

The institutions housing materials used in this study and their acronyms appearing herein are as follows: Academy of Natural Sciences of Philadelphia (ANSP), Biological Inventory and National Museum of Natural History of Paraguay (BINMP), California Academy of Sciences (CAS), Cornell University (CU), Florida A&M University (FAMU), Purdue Entomological Research Collection (PERC), United States National Museum (USNM), and University of Utah (UU).

Genus *Cloeodes* Traver, 1938

Cloeodes Traver, 1938: 32. Type species: *C. maculipes* Traver, 1938: 32, by original designation. *Centroptella* Braasch & Soldán, 1980: 123 (in part).

Type species: *C. longisetosa* Braasch & Soldán, 1980: 123, by monotypy. As synonym of *Cloeodes*: Waltz & McCafferty (1987).

Type Species. *Cloeodes maculipes* Traver, 1938: 32, by original designation.

Mature Larva. Labrum (Fig. 2 and 25) slightly broader than long, clearly emarginate, with marginal shelf anteriorly. Left mandible (Fig. 4 and 26) with incisors fused apically; prosthema stout, digitate; no tuft of setae between incisors and molar area; thumb of molar area triangulate, elevated above plane of incisor base. Right mandible (Fig. 3 and 27) with incisors separated apically; prosthema reduced, slender, variably furcate. Maxilla (Fig. 5 and 28) with palp two-segmented or apparently three-segmented; palp variable in length; galealacinia with four apical denticles. Lingua of hypopharynx (figure 9 in Braasch & Soldán [1980]) apparently with eversible median region sometimes appearing excavate or slightly convex, without median tuft of setae. Labium (Fig. 6 and 29) with three-segmented palps; terminal segment rounded to oblique; segment 2 with weakly developed inner apical lobe; glossae subequal to paraglossae; paraglossae with subparallel margins. Intraantennal extension of frons broad distally (Fig. 35, 37, and 38) or narrowed (Fig. 36).

Femora (Fig. 7) parallel-sided, without ventral patch, with short to moderately elongate dorsal bristles, and similarly shaped distal bristles. Tibiae (Fig. 7) with subproximal arc of extremely long, fine setae. Claws (Fig. 8) ca. 0.33-fold tarsal length, with or without microspines basally.

Abdominal terga with broadly pointed, rectangular-based scales and fine setae; scales with median length subequal to basal width; with posterior marginal spines on all terga; abdomen ventrally with scales, fine setae, and prominent tufts (i.e., with contiguous setal bases) of long, fine setae on segments 2-6 (Fig. 9 and 44). Gills (Fig. 10) 1-7, asymmetrical, broadly pointed, without marginal spination or ciliation; each gill often 2-fold or more length of associated tergum. Median terminal filament subequal to cerci.

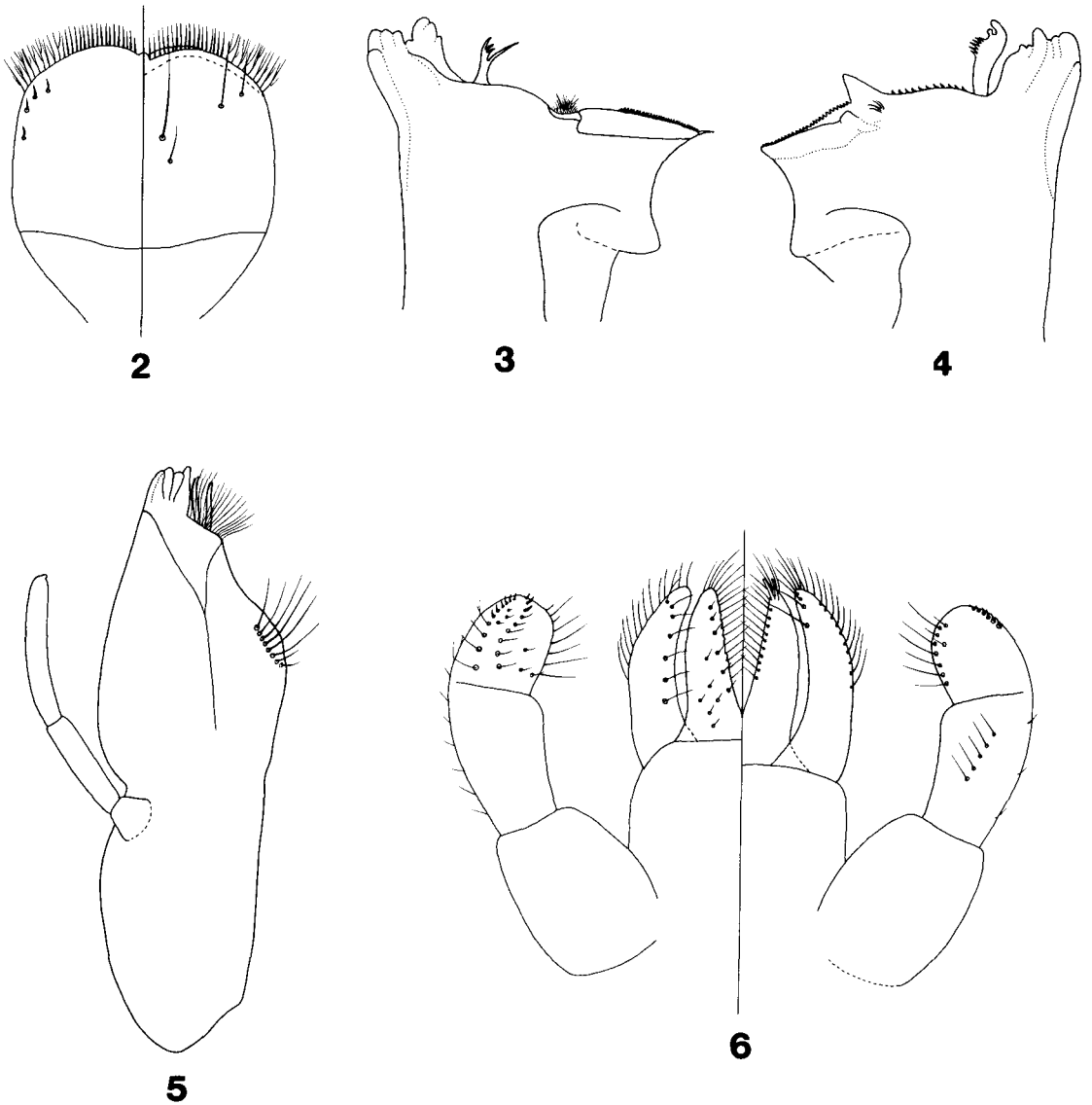


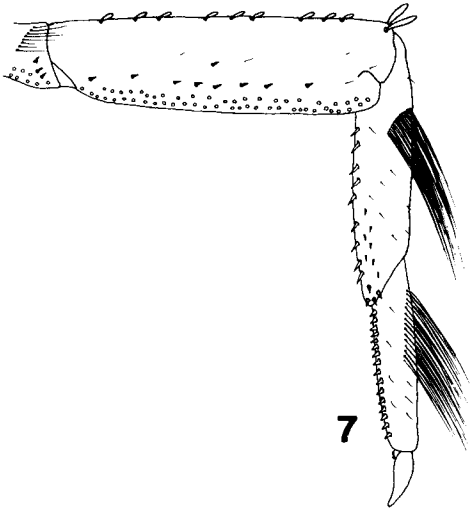
Fig. 2-6. *C. maculipes*: male larva. (2) Labrum (left, ventral; right, dorsal); (3) right mandible; (4) left mandible; (5) maxilla; (6) labium (left, ventral; right, dorsal).

Adult Male. Forewings (Fig. 16 and 22) with paired marginal intercalaries in most cells; detached base of vein MA_2 extending well beyond 0.5-fold distance between distal crossvein and proximal (= MA_1 - MP_1) crossvein. Hind wings present (Fig. 22 and 23) or absent; when present, with acute median costal process or distinctly hooked and proximal costal process. Posterior margin of metanotum (Fig. 14) deeply emarginate; metascutellar hump (Fig. 15) not flattened before apex but projecting dorsoposteriorly. Forceps (Fig. 34) four-segmented; segments 2 and 3 nearly fused and nonarticulating; segment 2 subequal to segment 1, with basal bulge bearing fine bristles; seg-

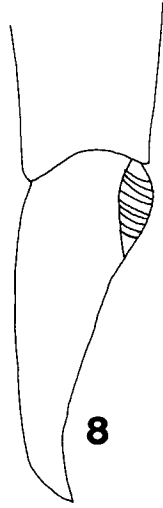
ment 3 ca. 2-fold length of segment 2; segment 4 ovoid. Genitalia without median spine or protuberance between forceps bases.

Adult Female. Marginal intercalaries of forewings (Fig. 18 and 19) paired or less often single. Posterior margin of metanotum not so deeply emarginate as in male; metascutellar process as in male. Subanal plate not developed.

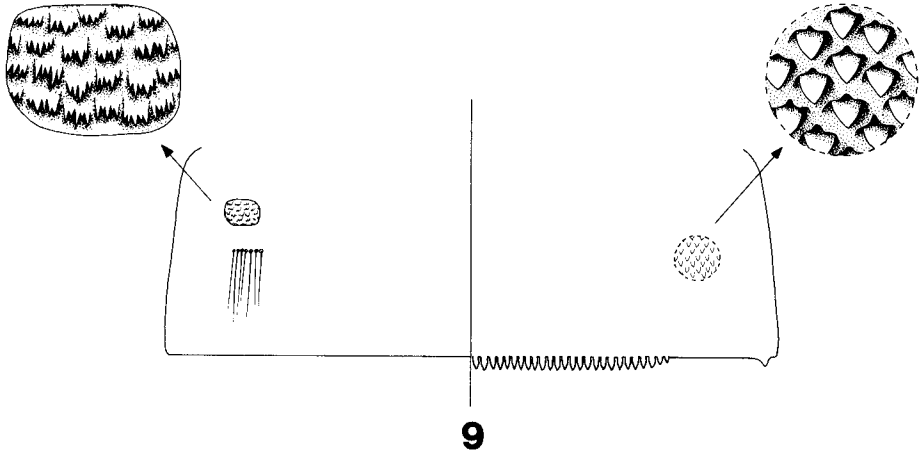
Discussion. We have seen South American *Cloeodes* from Argentina, Colombia (Fig. 32-34) (not yet placeable to species), Paraguay, Peru, and Venezuela. This and the strong possibility that it has been reported from Brazil as Baetine Nos. 2 and 4 by Traver (1944) indicate that it is probably



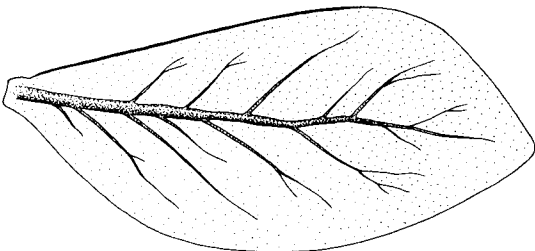
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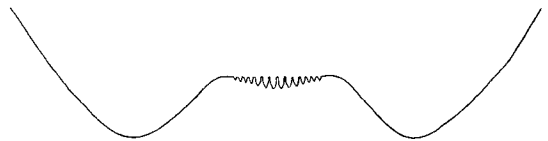
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Fig. 7-11. *C. maculipes*: male larva. (7) Foreleg; (8) claw; (9) abdominal segment 4 (left, ventral; right, dorsal); (10) abdominal gill; (11) apex of male sternite 9.

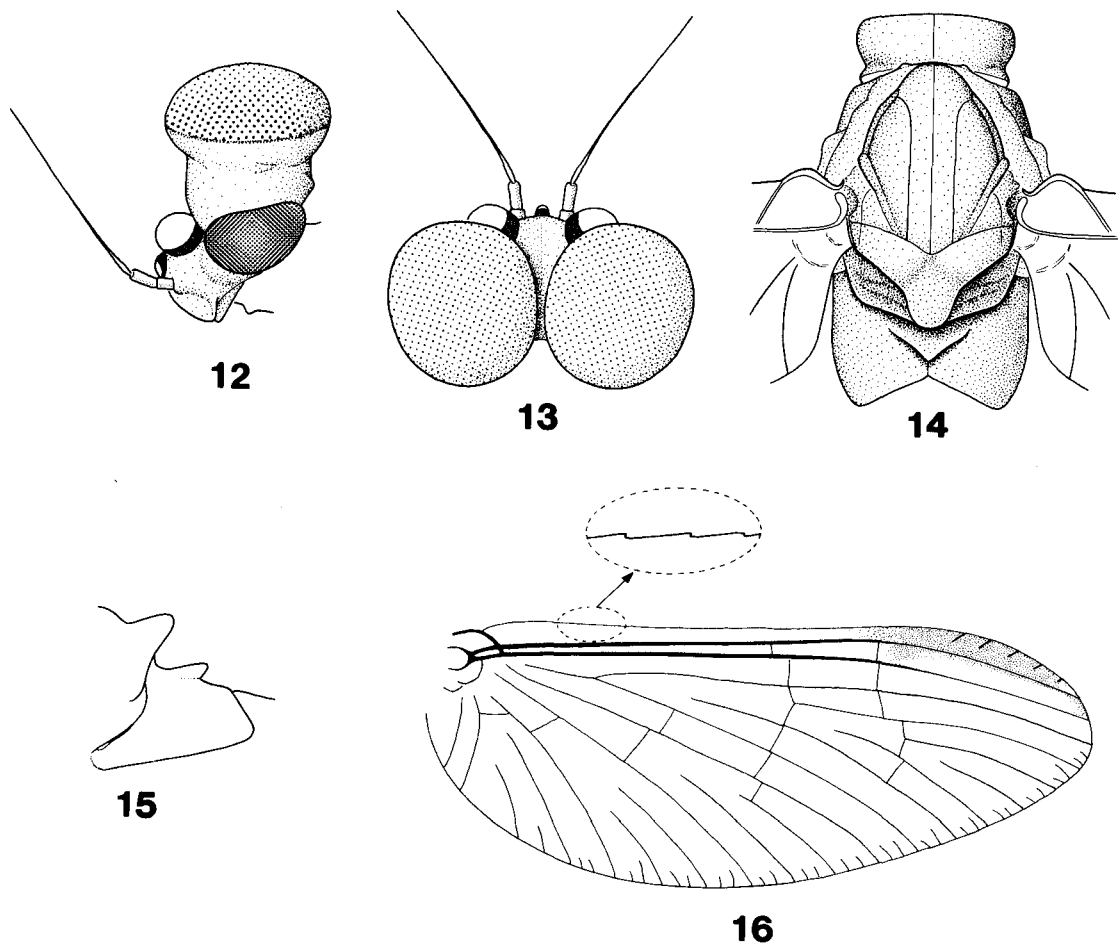


Fig. 12-16. *C. maculipes*: male adult. (12) Head capsule (lateral); (13) head capsule (dorsal); (14) thorax (dorsal); (15) metanotum (lateral); (16) forewing.

found throughout that continent, with the probable exception of the Chilean-Patagonian area. In Middle America, *Cloeodes* is well documented from Puerto Rico, and we have also seen adults from Panama that we cannot yet place to species. There is no reason not to expect *Cloeodes* to exist throughout Central America and other West Indian islands. We have *Cloeodes* from Baja California, Arizona, and New Mexico and expect it to be restricted in North America to this southwestern region, as is typical of many Holoamerican mayfly genera of Neotropical origin (McCafferty et al. 1987). The close relationship of *Cloeodes* with another South American genus of Baetidae (Waltz & McCafferty 1987) further supports a theory of Neotropical (most likely South American) origin.

As larvae, *Cloeodes* can be recognized from other baetid genera that possess tapering edentate claws (Fig. 8) by the asymmetry of the left and right mandibular incisors (Fig. 3, 4, 26, and 27), the reduction of the right mandible prostheca (Fig. 3 and 27), a prominent arc of extremely long, fine

setae subproximally on the tibiae (Fig. 1 and 7), simple gills on abdominal segments 1-7 (Fig. 1 and 10), a median terminal filament subequal to the cerci (Fig. 1), and the presence of prominent setal tufts on abdominal segments 2-6 (Fig. 9 and 44). Couplet 42 of Edmunds et al. (1976, 67) requires modification to allow recognition of this genus in the Western Hemisphere. In this instance, at least, the presence or absence of hind wings (or hind-wing pads) is not of generic importance.

The identification of larval *Cloeodes* species relies on various characters of the armature of legs, posterior marginal spines of the tergum, and paraprocts. Mouthpart characters, as used in the genus *Baetis* Leach and some other Baetidae, were not found to be useful in differentiating species of *Cloeodes* larvae. Although slight differences in shape of the labial palps and, in two described species, the number of maxillary palp segments are notable exceptions, the remaining mouthpart characters are remarkably similar in structure. Color patterns as illustrated are helpful but should not be regarded as diagnostic.

The few known *Cloeodes* male adults are distinguishable from other adult male baetids as follows: *Cloeodes* males have paired marginal intercalaries in the forewings. If hind wings are present (Fig. 22 and 23), then the costal projection of those wings is either simple and acute with a broad base and located at about midlength of the costal margin, or the costal process is hook-shaped and located more basally, as in species generally assigned to *Centropilum* (see figure 5 of Traver 1971). Couplet 35 in the generic key of Edmunds et al. (1976, 98) requires modification to accommodate these *Cloeodes*. If hind wings are absent, *Cloeodes* can be told from *Paracloeodes*, with which it shares a number of key characteristics, by the presence of an inner basal bulge of forceps segment 2 (Fig. 34) and eyes that are nearly contiguous basally. Couplet 40 of Edmunds et al. (1976, 100) has to be modified to accommodate these *Cloeodes*.

Subgenus *Notobaetis* Morihara & Edmunds,
n. status

Notobaetis Morihara & Edmunds, 1980: 606. Type species: *Notobaetis penai* Morihara & Edmunds, 1980: 606, by original designation. As synonym of *Cloeodes*: Waltz & McCafferty (1987).

Type Species. *Notobaetis penai* Morihara & Edmunds, 1980: 606.

Diagnosis. *Mature Larva.* Antennae (Fig. 35) long but <0.5-fold length of body; scape and pedicel occasionally with small spines. Maxilla with palp subequal to or exceeding apex of galealacinia and with indication of third segment. Labium (figure 7 of Morihara & Edmunds 1980) with segment 3 of palp obliquely truncate. Femora with stout serrate-margined bristles.

Adult Male. Turbinate portion of eyes (Fig. 20 and 21) on low stalks. Forewings (Fig. 22) with stigmatic veinlets complete, marginal intercalaries uniformly paired and present in R_1 - R_2 cell (first cell posterad of subcostal cell). Hind wings with a medially situated costal process.

Remarks. The unique condition of the hind wings—i.e., bearing a medially situated costal process—is diagnostic for this subgenus.

Species Included. *C. penai* (Morihara & Edmunds).

***Cloeodes penai* (Morihara & Edmunds)**

Notobaetis penai Morihara & Edmunds, 1980: 606. *Cloeodes penai*: Waltz & McCafferty (1987).

Mature Larva. Body 7–10 mm long. Head capsule (Fig. 35) lightly pigmented. Labrum (figure 4 of Morihara & Edmunds 1980) with 8–10 ventral spines. Left mandible (figure 6 of Morihara & Edmunds 1980) with thumb triangular and narrow basally. Right mandible as in figure 5 of Morihara

& Edmunds (1980). Maxilla with palp subequal to or exceeding apex of galealacinia; palp with indication of third segment and protuberance apically; galealacinia with 1+6–7 basal setae. Labium (figure 7 of Morihara & Edmunds 1980) with segment 2 of palp having 6–7 dorsal setae; segment 3 obliquely truncate; paraglossa with 4–5 inner dorsal marginal setae medioapically and 5–6 long, ventral inner marginal setae; glossa with 22–25 stout inner marginal setae.

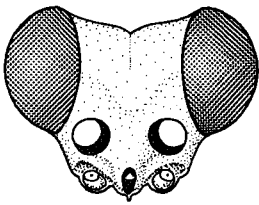
Thorax unicolorous tan; hind wing pads present. Legs (figure 8 of Morihara & Edmunds 1980) uniformly tan, darker dorsally than ventrally; trochanter without bristles or long setae; femora with 15–20 stout dorsal bristles, bristles more numerous ventrally, apically with 4–6 sublanceolate blunted distal bristles; tibiae with fine setae, lanceolate stout bristles with serrate margins (abundant ventrally, less abundant dorsally), one sublanceolate, blunted subtending bristle; tarsi with long, fine setae and bristles (abundant ventrally, less abundant dorsally).

Abdominal tergum 3 with 30–40 posterior marginal spines (both sexes with smaller, minor spines in series on either side of median) with bases ca. 0.5-fold height. Paraprocts with 20–30 long, sharp spines. Posterior margin of male sternite 9 with 18–20 median spines.

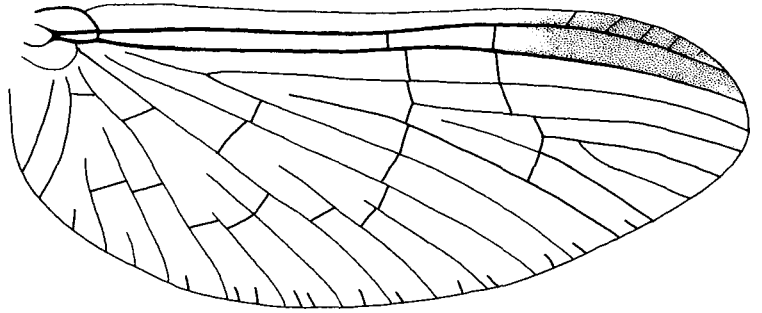
Adult. Adults of *C. penai* have been adequately characterized by Morihara & Edmunds (1980). We add here figures of the male wings (Fig. 22 and 23), head capsule (Fig. 20 and 21), and female hind leg (Fig. 24) for comparative purposes.

Material Examined. *Notobaetis penai* Morihara & Edmunds: Paratypes: male larva, Argentina, Tucuman NW of San Miguel de Tucuman, 25-I-1969, W. L. & J. G. Peters, slidemounted in balsam (solvent: xylene), PERC; female larva, Argentina, Cordoba Prov., Copina (ca. 25 km WNW Alta Garcia), elev. 1,650 m, 11/14-IV-1969, L. Peña, slidemounted in balsam, PERC; female adult, legs slidemounted in balsam, same data as above, PERC; male adult, wings slidemounted, same data as above, PERC; 3 whole larvae (in alcohol), same data as above, FAMU; 2 adult males and 1 subimago male and 2 associated larval exuviae (in alcohol), same data as above, UU.

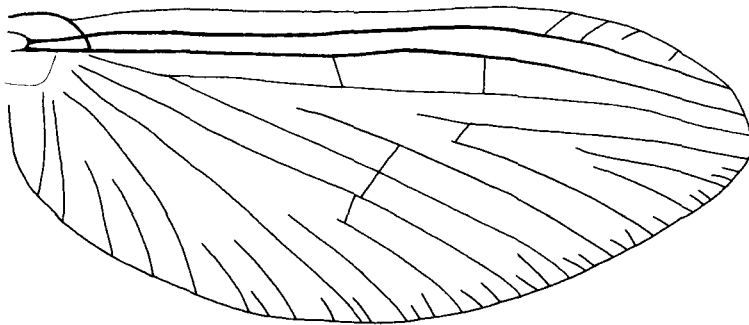
Remarks. *C. penai* is easily distinguished in the larval stage from other known *Cloeodes* by the presence of obliquely truncate apices of the labial palps, elongate antennae (ca. 0.5-fold body length), and apparently three-segmented maxillary palps. Hind wing pads will distinguish it from most but not all other known larvae of *Cloeodes*. At present, adults of *C. penai* may be separated from other known adults of *Cloeodes* by their hind wings with a costal projection medially along the margin, distinctive abdominal color pattern, and turbinate portion of eyes situated on short stalks. On the basis of larvae, *C. irvingi*, n. sp., also possesses hind wings as an adult, but we do not know yet the position of the costal projection.



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Fig. 17-19. (17 and 18) *C. maculipes*: adult female. (17) Head capsule (frontal); (18) forewing; (19) *C. consignatus*: adult female. Forewing.

Subgenus *Cloeodes* sensu stricto

Type Species. *Cloeodes maculipes* Traver, 1938: 32.

Diagnosis. Mature Larva. Antennae shorter than length of thorax, often little longer than 1.5-fold length of head capsule; scape, pedicel without small spines. Maxilla (Fig. 5 and 28) with palp subequal to or not attaining apex of galealacinia, apparently three- or two-segmented. Labium (Fig. 6 and 29) with segment 3 of palp rounded to slightly quadrate. Femora without stout serrate-margined bristles.

Adult Male. Turbinate portion of eyes (Fig. 12 and 32) on stalks of various lengths. Forewings (Fig. 16, 18, 19, and 33) with stigmatic veinlets complete or incomplete with tendency for reduction; marginal intercalaries relatively shortened, uniformly paired in males and absent from R_1 - R_2 cell. Hind wings with basally situated costal process (*C. aymara*) or hind wings absent.

Species Included. *C. anduzei* (Traver), n. comb.; *C. aymara* (Traver), n. comb.; *C. consignatus* Traver; *C. excogitatus*, n. sp.; *C. irvingi*, n. sp.; *C. longisetosus* (Braasch & Soldán); *C. macrolamelus*, n. sp.; *C. maculipes* Traver; *C. peninsulus*, n.

sp.; *C. redactus*, n. sp.; and *C. soldani* (Müller-Liebenau).

***Cloeodes anduzei* (Traver), n. comb.**

Pseudocloeon anduzei Traver, 1943: 88.

Mature Larva. Unknown.

Adult. Adequately characterized and illustrated by Traver (1943). Hind wings absent.

Remarks. The description, illustrations, and discussion of this Venezuelan species by Traver (1943) leave no doubt as to its reassignment to *Cloeodes*.

***Cloeodes aymara* (Traver), n. comb.**

Baetis aymara Traver, 1971: 60.

Mature Larva. Unknown.

Adult. Adequately characterized and illustrated by Traver (1971). Hind wings present.

Material Examined. Holotype: male adult (legs missing), Uruguay, Province Treinta y Tres, Quebrada de los Cuervos, 17-XII-1952, C. S. Carbonell, UU. Paratypes: 2 male adults (wings, legs, and genitalia removed) and 1 female adult (wings and legs removed), same data as holotype, UU.

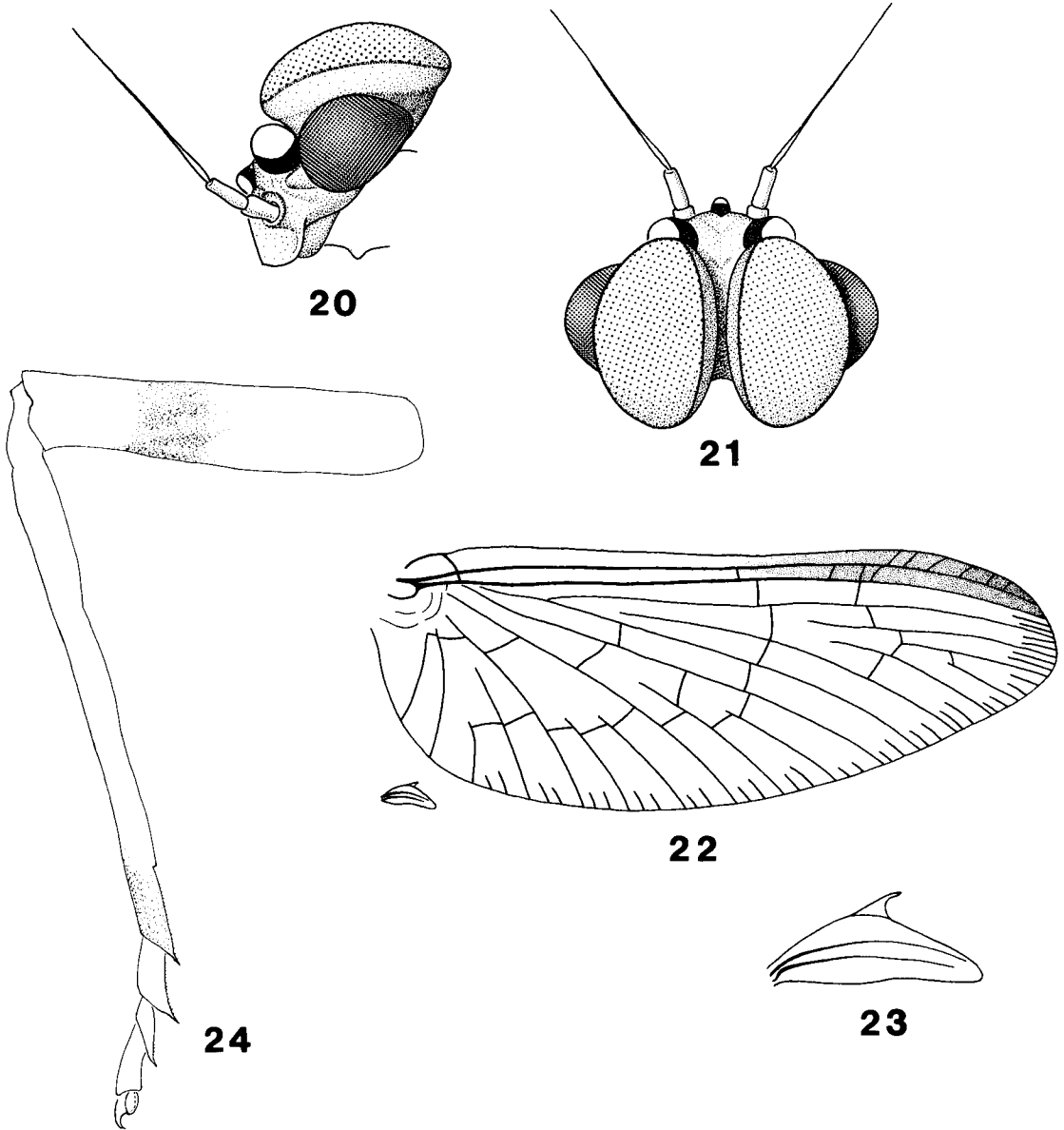


Fig. 20-24. *C. penai*: adults. (20) Male head capsule (lateral); (21) male head capsule (dorsal); (21) male wings; (23) male hind wing (enlarged); (24) female hind leg.

The published record of type depositions for this species (Traver 1971) is in error. All the above type material is deposited in the J. R. Traver collection, % G. F. Edmunds, Jr., University of Utah, Salt Lake City, Utah.

Remarks. Of the type material cited above, we examined only the material preserved in alcohol. The dissected body parts have been slidemounted and are also deposited at the University of Utah.

The distinct shape of the genitalia, the congruence of thoracic characters (compared with the type species of the genus, *C. maculipes*) with known *Cloeodes* species, and agreement in wing

characters justify the transfer of this species to *Cloeodes*. The presence of hind wings in *Cloeodes* s.s. is known in only one other species, *C. irvingi*, n. sp., from Paraguay (known only as larvae and described below). It is possible that larvae we are calling *C. irvingi*, n. sp., are the as yet unassociated larvae of *C. aymara*.

***Cloeodes consignatus* Traver**

Cloeodes consignatus Traver, 1938: 37.

Mature Larva. Unknown.

Adult. Female characterized by Traver (1938).

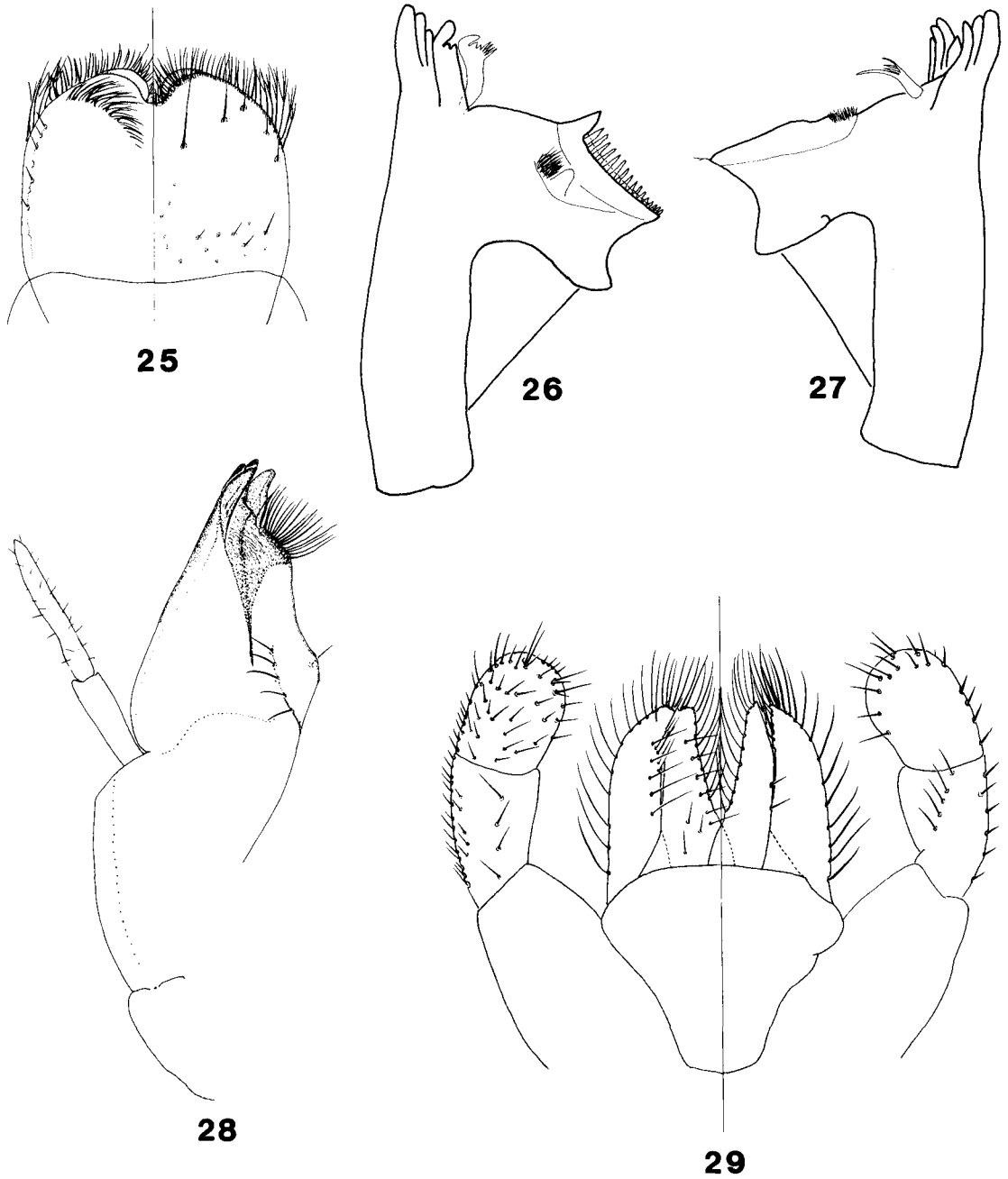


Fig. 25-29. *C. excogitatus*: male larva. (25) Labrum (left, ventral; right, dorsal); (26) left mandible; (27) right mandible; (28) maxilla; (29) labium (left, ventral; right, dorsal).

Material Examined. Holotype: female adult, Puerto Rico, Yunez River, 21-VI-1935, J. Garcia-Diaz. CU Type No. 1403.1 (female preserved in alcohol; one wing slidemounted), CU.

Remarks. This species is known only from the holotype. We found this specimen to have been cleared in a caustic solution and, thus, significantly altered from its original state. It appears to belong

to *Cloeodes* based on the structure of the thorax, metanotum, and wing venation (Fig. 19); however, this species cannot at this time be distinguished from other species.

Female adult *Cloeodes*, even in excellent condition, lack known diagnostic features and cannot be distinguished as species from one another. This fact and the poor condition of the single holotype

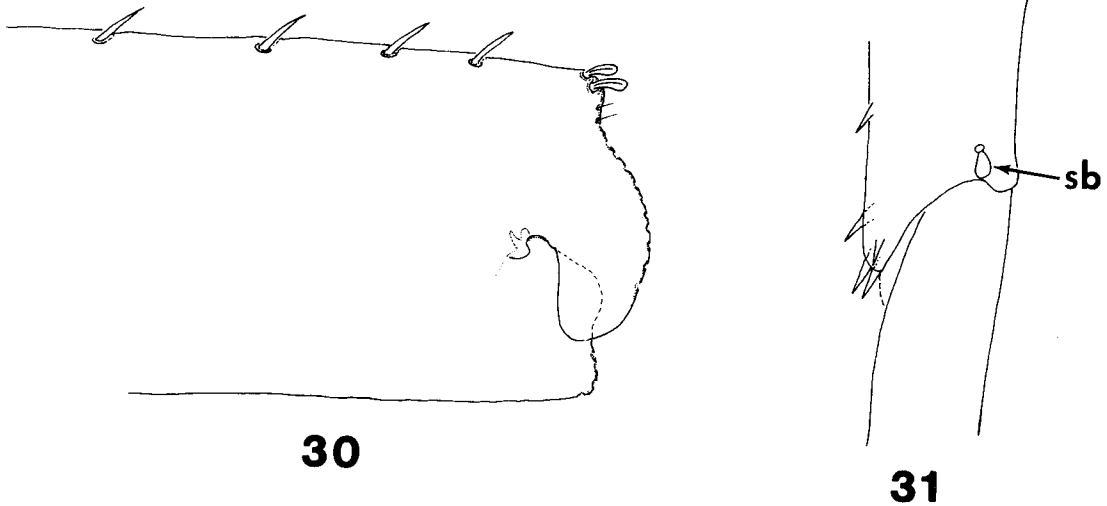


Fig. 30, 31. *C. excogitatus*: male larva. (30) Apex of femur; (31) apex of tibia (sb, subtending bristle).

specimen make it virtually impossible ever to deal further taxonomically with *C. consignatus* although the name must remain occupied. We have no opinion as to its actual validity.

Cloedes excogitatus
Waltz & McCafferty, n. sp.

Mature Larva. Body 4.5–6.0 mm long. Head capsule (Fig. 36) light brown with cream lateral genal spot above mandibular base and 2 cream longitudinal marks frontally between antennal bases and base of labrum. Antennae pale, subequal to head capsule in length; pedicel slightly longer than scape. Labrum (Fig. 25) with 8–10 ventral marginal spines (weakly developed). Left mandible (Fig. 26) with thumb stout, triangulate. Right mandible as in Fig. 27. Maxilla (Fig. 28) with palp shorter than galealacinia, two-segmented; galealacinia with moderately elongated apical dentes and 1+4–5 basal setae. Labium (Fig. 29) with segment 2 of palp having 5 or 6 dorsal setae; segment 3 of palp rounded, ovoid, with apical inner stout bristles; paraglossa with 5–6 ventral medioapical setae and 4–5 stouter dorsal medioapical setae; glossa with ca. 15 inner marginal setae. Intraantennal extension of frons narrowed distally (Fig. 36).

Thorax with brown and white mottling. Hindwing pads absent. Legs unicolorous, tibiae and tarsi slightly darkened; trochanters with 3–4 ventral stout setae; femora (Fig. 30) with 2–3 lanceolate distal bristles; tibiae with seam weakly defined, subtending bristle (Fig. 31) apically broadened; tarsi with dorsal row of long, fine setae in shape of inverted "V" and ca. 0.5– to 0.66-fold tarsal length; 12–14 ventral bristles (fewer on meso- and metatarsi).

Abdominal terga (Fig. 40) 1–3 and 5–7 with 3

pale spots (medial spot smaller than adjoining spots); segments 4 and 8 similar to preceding segments but with more broken pattern; segment 9 pale; segment 10 brownish with median pale spot. Abdominal sterna pale. Tergum 3 with 30–35 posterior marginal spines on either side of midline, bases of spines ca. 0.33-fold height. Paraprocts with scales, fine setae, 12–15 marginal spines. Distal margin of sternum 9 of male with ca. 12 median spines with basal width ca. 0.33-fold spine height.

Adult. Unknown.

Type Material. Holotype: male larva, USA, Arizona, Oak Creek Canyon, 12-IV-1968, R. W. Koss & R. Baumann, PERC. Paratype: male larva, same data and deposition as holotype, slidemounted in euparal (solvent: absolute alcohol).

Etymology. Latin: ex (out) and cogitato (to think), an allusion to the thought-provoking discovery of this North American representative of the genus.

Remarks. In many ways, this species resembles the larva of *C. maculipes* but is distinct from that species and all other described larvae by the distinctly narrowed intraantennal extension of the frons (Fig. 36), by the apically broadened subtending bristle, and by the relatively narrow (spine width at base subequal to 0.33-fold spine length) posterior marginal spines of abdominal tergum 3.

Cloedes irvingi
Waltz & McCafferty, n. sp.

Mature Larva. Body ca. 5.5 mm. Head capsule as in Fig. 36; light brown with pale border distally and laterally on frons. Antennae pale above, brownish below, ca. 1.5-fold length head capsule; pedicel longer than scape. Labrum with 5–7 ventral marginal spines. Left mandible with thumb stout and blunted. Right mandible similar to Fig.

4. Maxilla with palp subequal to galealacinia, apparently three-segmented; galealacinia with 1+5-6 basal setae. Segment 2 of labial palp with 5 or 6 dorsal bristles; segment 3 unevenly truncate with apical inner stout bristles; paraglossae with 5 or 6 ventral medioapical bristles, and 4 or 5 stouter dorsal bristles; glossae with ca. 14-15 inner marginal setae.

Thorax uniformly tan. Hind wing pads present, prominent. Legs pale brown, darkened at joints; meso- and metafemora with 6-8 dorsal bristles and 2 lanceolate distal bristles; tibiae with distinct tibial seam, subtending bristle lanceolate but broader than in *C. maculipes*; tarsi with dorsal row of long, fine setae in shape of inverted "V" and ca. 0.5- to 0.66-fold tarsal length, and 7-8 ventral spines on meso- and metatarsi.

Abdomen as in Fig. 41, irregularly mottled, appearing brown dorsally and pale ventrally. Tergum 3 with 20-25 posterior marginal spines on either side of median, basal spine width ca. 0.5-fold height. Paraprocts with scales, fine setae, ca. 12 marginal spines. Distal margin of male sternum 9 with ca. 15 median spines, their basal width ca. 0.5-fold height.

Adult. Unknown.

Type Material. Holotype: male larva, Paraguay, Paraguari, Parque Nacional Ybycui, Arroyo Mina, edge, 2-X-1984, R. T. Bonace, whole specimen in alcohol, PERC. Paratypes: male larva, Paraguay, Dep. Amambay, P.N., Cerro Corá, riffle sample, Arroyo Panambay, 5-IX-1983, T. Bonace, slide-mounted specimen in euparal (solvent: absolute alcohol), head capsule and foreleg missing, PERC; 1 male and 1 female larva, Paraguay, Paraguari, Parque Nacional Ybycui, Arroyo Mina, edge, 18-VIII-1985, R. T. Bonace, whole specimens in alcohol with male mouthparts slidemounted in Gisin's medium (solvent: water), PERC; 14 larvae, Paraguay, Dep. Neembucu Pilar, Rio Neembucu, 23-IX-1985, R. T. Bonace, whole specimens in alcohol, 5 larvae, PERC and 9 larvae, BINMP.

Etymology. irvingi, in honor of the American author, Washington Irving.

Remarks. This species is clearly a member of *Cloeodes* s.s. as defined herein. However, it retains several plesiomorphic characters (e.g., hind wings and an apparently three-segmented maxillary palp) not found in any other known *Cloeodes* s.s. larvae (with the possible exception of *C. aymara*).

Cloeodes longisetosus (Braasch & Soldán)

Centropptella longisetosa Braasch & Soldán, 1980: 123.

Cloeodes longisetosus: Waltz & McCafferty (1987).

Mature Larva. Adequately characterized and illustrated by Braasch & Soldán (1980).

Adult. Unknown.

Material Examined. Paratype: male larva, People's Republic of China, Liu Chui, Kuj Fon Shan

River, 11-XII-1959, I. Hrđy, in alcohol, from the collection of T. Soldán, PERC.

Remarks. The paratype, newly deposited in the Purdue University Entomological Research Collection, was received in the following condition: head capsule detached from body, mouthparts intact, all legs missing but one middle leg (right side), cerci and median filament broken and lost, and the specimen had absorbed the ink used in labeling and is entirely black and devoid of pattern. In spite of the relatively poor condition of this paratype, the diagnostic presence of prominent abdominal setal tufts on sterna 2-6, the form of the gills, and the setation of the legs in conjunction with published descriptions of the species clearly establish this species as belonging to *Cloeodes* s.s.

C. longisetosus's apparent sister species is *C. soldani*; they share the synapomorphies, elongate dorsal femoral bristles relative to other *Cloeodes* s.s., and a more elongated arc of subproximal setae extending to 0.33-fold the length of the tibia in *C. longisetosus* and ca. 0.75-fold the length of the tibiae in *C. soldani*. The secondary row of tibial setae as illustrated for *C. soldani* (figure 3 i and j of Müller-Liebenau 1983) is not present in *C. longisetosus* contrary to the data indicated in table 2 of Müller-Liebenau 1983).

Cloeodes macrolamellus

Waltz & McCafferty, n. sp.

Mature Larva. Body 6-8 mm long. Head capsule (Fig. 37) brown-tan, light areas bordering antennal bases, ocelli, eyes, and sutures. Antennae slightly longer than head capsule. Labrum with 12-14 small ventral marginal spines. Left mandible with thumb triangulate and pointed. Maxilla with palp shorter than galealacinia and two-segmented; galealacinia with 1+5-6 basal setae. Labium with segment 2 of palp having 4-6 dorsal setae; segment 3 of palp rounded apically; paraglossae with 6-7 ventral interomarginal setae and 3-4 dorsal marginal setae medioapically; glossa with 9 or 10 stout inner marginal setae.

Thorax mottled. Hind wings pads absent. Legs dark brown, lighter at segmental junctures and medial area of tibiae; trochanters with ca. 12 ventral bristles; femora dorsally with 8-10 stout bristles and 3 or 4 distal bristles; tibiae with lanceolate subtending bristle, 5-8 ventral bristles; tarsi with dorsal row of long, fine setae in shape of inverted "V" and ca. 0.5- to 0.66-fold tarsal length, and 14-15 ventral bristles (fewer on meso- and metatarsi).

Abdominal terga (Fig. 1) 2-6 with circular pale spots, medial spots sometimes forming weakly defined medial stripe. Tergum 3 with ca. 30-40 posterior marginal spines on either side of midline. Posterior marginal spines subequal, broadly pointed, much shorter than in other known *Cloeodes* species (basal width subequal to height, becoming slightly more elongate and acute on posterior ter-

ga). Paraprocts with 20–22 elongate marginal spines. Gills 1–7 asymmetric, broadly pointed, each ca. 2.5- to 3.0-fold length of respective tergum; gill 7 extending well beyond posterior margin of tergite 10 (Fig. 1).

Adult. Unknown.

Type Material. Holotype: female larva, USA, New Mexico, Grant County, N of Silver City, Cherry Creek, 2.4 mi N of Cherry Crk. Campground, 7-VII-1969, R. W. Koss, W. P. McCafferty, A. V. Provonsha, body and head capsule in alcohol, mouthparts and foreleg slidemounted in euparal (solvent: absolute alcohol), PERC. Paratypes: 10 larvae, same data as holotype; 4 PERC; 3 USNM; 3 CAS. All specimens in alcohol except two slidemounted paratypes, PERC.

Etymology. Latin: macro (large), lamellus (lamella or plate), in reference to the relatively large gills of this species.

Remarks. This species is evidently the large-gilled baetid mentioned by Edmunds et al. (1976, 156). Among *Cloeodes* it is distinctive as a larva because of its large gills (Fig. 1) and many but short posterior marginal spines on the abdominal terga. Cherry Creek at the type locality of this species is a small, midelevation, temporary stream consisting mostly of pools in summer.

Cloeodes maculipes Traver

Cloeodes maculipes Traver, 1938: 33.

Mature Larva. Body 5.0 mm in length. Head capsule brown, pale markings medially and laterally, pale horizontal band between eyes and bases of antennae. Antennae longer than head capsule, pale basally; scape subequal to pedicel. Labrum (Fig. 2) with submarginal setal pattern 1+2–3 and 8–10 weakly developed ventral marginal spines. Left mandible (Fig. 4) with thumb broadly triangulate. Right mandible as in Fig. 3. Maxilla (Fig. 5) with palp shorter than galealacinia, two-segmented; galealacinia with 1+5–6 basal setae. Labium (Fig. 6) with segment 2 of palp having 5–6 dorsal setae; segment 3 ovoid with conical inner margin and 4 or 5 inner marginal stout bristles; paraglossa with 5 or 6 ventral interomarginal setae, and 2 or 3 dorsal medioapical setae (stouter than ventral setae).

Hind wing pads absent. Legs (Fig. 7) pale; femora with 12–20 dorsal bristles, and 2 or 3 distal bristles; subtending bristle elongate, narrow, lanceolate; tarsi with dorsal row of long, fine setae in shape of inverted "V" and ca. 0.5-fold length of tarsus, and with 18–20 ventral spines.

Abdominal terga brown; segments 1–3 with pair of small pale yellow submedian spots; segments 4, 7, and basal half of segment 9 yellowish with brown patterning; segments 5, 6, and apical half of segment 9 smoky brown (often darker apically than basally); segment 10 smoky brown. Tergum 3 with 20–25 posterior marginal spines on either side of

median, basal spine width ca. 0.5-fold spine height. Paraprocts with 12–15 marginal spines. Distal margin of sternite 9 of male with 12–14 median spines, basal spine width ca. 0.5-fold height.

Adult Male. Body ca. 5.0 mm long. Wing 5.5 mm long. Turbinate eyes on high stalks (Fig. 12), nearly circular in dorsal view (Fig. 13). Thorax (Fig. 15) pale, yellowish tan. Foreleg slightly shorter than body; segment 1 of tarsus very short; segment 2 subequal to 3 and 4 combined; order of segments by decreasing length: 2, 3, 4, 5, 1. Abdominal terga 2–6 pale, without maculation; terga 7–10 same color as thorax. Forceps (Fig. 34) long, four-segmented; segment 2 subequal to 1, with distinct inner basal bulge bearing fine bristles; segment 3 ca. 2.5-fold length of 2; segment 4 attached subapically, basally narrowed, ca. 0.25-fold length of segment 3.

Material Examined. Holotype: male adult, Puerto Rico, Ludillo Mtns., camp lab 46 (107), 14-VI-1935, J. Garcia-Diaz, adult in alcohol, genitalia slidemounted in balsam (solvent: xylene); larval exuviae of holotype male slidemounted in euparal (solvent: absolute alcohol), CU Type No. 1402.1, CU. Paratype: male adult (genitalia missing), subimago exuviae, larval exuviae (missing), same data and deposition as above; female adult (allotype) in alcohol; wing slidemounted, Puerto Rico, Trout's pool, El Yunque Trail, 12-VI-1935, J. Garcia-Diaz, CU Type No. 1402.2, same deposition as holotype.

Remarks. Traver (1943) stated that the swollen basal area of the male forceps is lacking in *C. maculipes*. Actually, we found that the holotype's slidemounted genitalia do have the swollen basal areas of the male forceps, but these have been rotated back in an unnatural position and are difficult to discern.

Cloeodes peninsulus

Waltz & McCafferty, n. sp.

Genus *Incertae* Allen & Murvosh, 1983: 427.

Mature Larva. Body 2.5–4.0 mm. Head capsule (Fig. 38) uniformly brown. Antennae pale brown, subequal in length to head capsule; pedicel longer than scape. Labrum with 5 or 6 small, weakly developed ventral marginal spines. Left mandible (similar to Fig. 4) with thumb elongate and triangulate. Right mandible similar to Fig. 3. Maxilla (similar to Fig. 5) with palp shorter than galealacinia, two-segmented; galealacinia with 1+5–7 basal setae. Labium (Fig. 6) with segment 2 of palp having 4 or 5 dorsal setae; segment 3 rounded, with apical inner stout bristles; glossa subequal to paraglossa; paraglossa with 6–8 ventral interomarginal setae, dorsally with 3–5 stouter medioapical setae; glossa with ca. 15–20 inner marginal setae.

Thorax uniformly tan with few pale spots on pro- and mesothorax. Hind wing pads absent. Legs unicolorous pale brown; trochanters with 6–8 ventral bristles; femora with 5–10 stout dorsal bristles

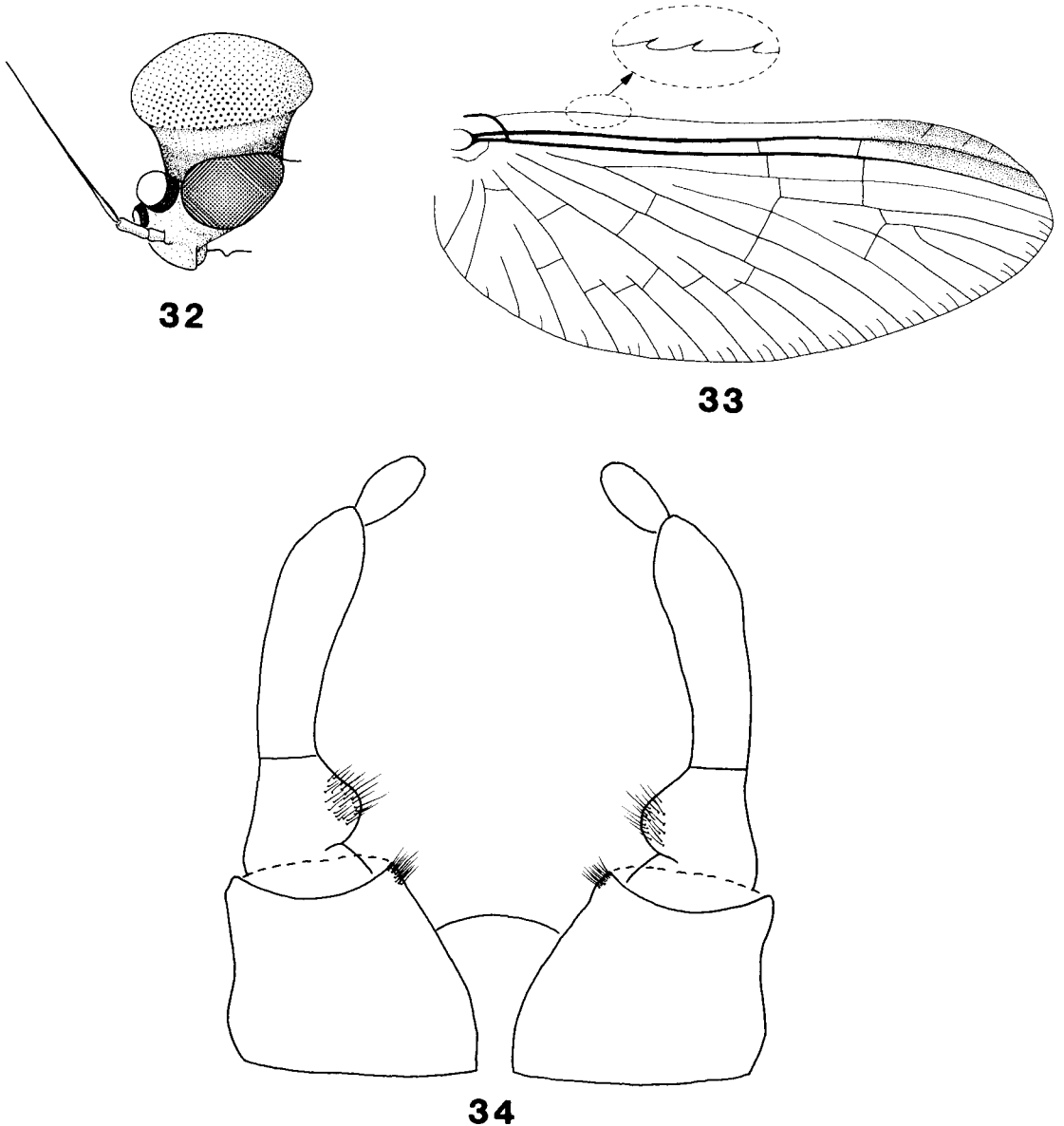


Fig. 32-34. *Cloeodes* sp.: male adult from Colombia. (32) Head capsule (lateral); (33) forewing; (34) genitalia (ventral).

and 2 or 3 lanceolate distal bristles; lateral femoral bristles subequal to dorsal bristles, but ventral femoral bristles smaller than dorsal bristles; tibiae with 8-12 ventral bristles, and easily discernible tibial seam; subtending bristle lanceolate; tarsi with row of long, fine dorsal setae 0.5-fold length of tarsus, and 10-15 ventral tarsal bristles on foreleg (fewer on middle and hind tarsi).

Abdomen (Fig. 42) uniformly brown with medially darkened posterior borders. Posterior marginal spines of tergum 3 all subequal in female, with interspersed smaller spines in male; 30-36 posterior marginal spines on either side of midline;

basal width of major spines ca. 0.5-fold length. Paraprocts with 15-20 marginal spines, scales, and fine setae. Posterior margin of sternum 9 of male with ca. 12 median spines, basal spine width ca. 0.33-fold height.

Adult. Unknown.

Type Material. Holotype: male larva, Baja California Sur, Rio Poza, 10 mi SW Loreto on road to San Javier, 6-VI-1978, 600 ft elev., R. K. Allen, whole specimen in alcohol, CAS. Paratypes with same data as holotype, 3 female larvae, whole specimens in alcohol, CAS; 2 female larvae, whole specimens in alcohol, 1 male and 1 female larva,

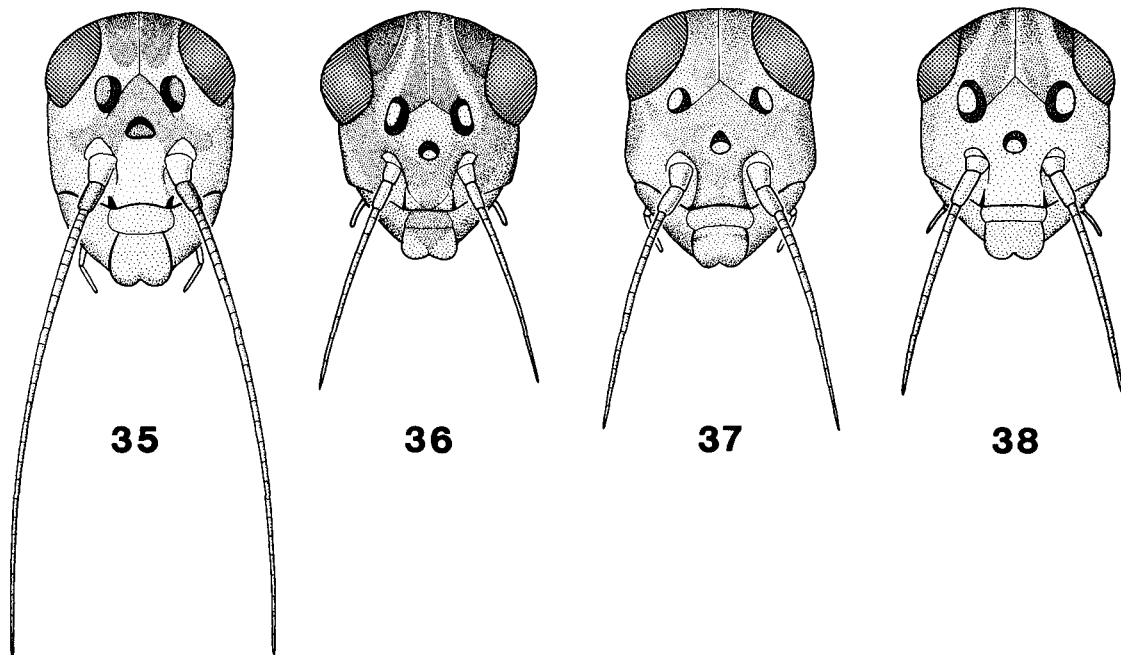


Fig. 35-38. *Cloeodes* spp.: larval head capsules. (35) *C. penai* (female); (36) *C. excogitatus* (male); (37) *C. macrolamellus* (female); (38) *C. peninsulus* (male).

slidemounted in euparal (solvent: absolute alcohol), PERC. Additional paratypes: 8 larvae, Baja California Sur, Arroyo Agua Caliente, 3 mi E Ejido Agua Caliente off Hwy. #1, 4-VI-1978, R. K. Allen, whole specimens in alcohol, CAS; 2 male larvae slidemounted in balsam (solvent: xylene) and 3 female larvae slidemounted in euparal, PERC.

Etymology. *peninsulus*: a reference to the type locale, the Baja California peninsula.

Cloeodes redactus

Waltz & McCafferty, n. sp.

Genus Poss. *Cloeodes* Traver. Roback, 1966: 133.

Mature Larva. Body ca. 4.0 mm long. Head capsule brown. Antennae brown, longer than head capsule; scape ca. 1.5-fold length of pedicel. Labrum (Fig. 2) with 8-10 weakly developed ventral marginal spines. Left mandible (Fig. 4) with thumb large, triangulate, and blunted. Right mandible as in Fig. 3. Maxilla (Fig. 5) with palp subequal to galealacinia, two-segmented; galealacinia with 1+6-7 basal setae. Labium (Fig. 6) with segment 2 of palp having 3 or 4 dorsal setae; segment 3 rounded ovoid; paraglossa with 7-8 ventral medioapical setae, and 2 or 3 medioapical dorsal setae; glossa with 9-10 inner marginal setae.

Thorax with brown and white mottling. Hind wing pads absent. Tibiae lighter than femora and tarsi, with distinct tibial seam; femora with 2 or 3 distal bristles; tarsi with dorsal row of long, fine setae ca. 0.5-fold length of tarsus and 8-10 ventral spines on foretarsi (fewer on remaining tarsi).

Abdomen (Fig. 43) with tergum 1 brown with paler lateral areas; terga 2 and 3 brown each with anteromedial pale spot and pair of submedian posterior spots, laterally pale; tergum 4 pale with diffuse brown; terga 5-7 brown with medial pale spot on posterior margin; tergum 8 pale with diffuse brown; tergum 9 brown with 2 mediolateral pale spots; tergum 10 brown. Abdomen pale ventrally. Tergum 3 with 15-20 posterior marginal spines on either side of midline, basal spine width ca. 0.5-fold height (spination uniform in both sexes). Paraprocts with 7-12 large teeth marginally.

Type Material. Holotype: male larva, Peru, Puente Perez River nr. Tingo Maria, 1/2-X-1955, S. S. Roback, slidemounted in euparal (solvent: absolute alcohol), ANSP. Paratype: female larva, same locale and data as for holotype, slidemounted in euparal, PERC.

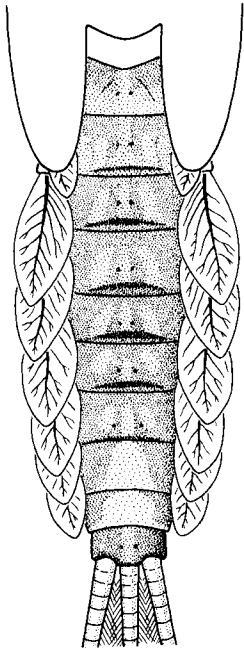
Etymology. Latin: *redactus* (reduced), in reference to the reduced size and specialized nature of characters in this species.

Remarks. *C. redactus*, with respect to all characteristics, is the most derived member of the genus. Because the derivations are autapomorphies, precise sister relationships are unknown.

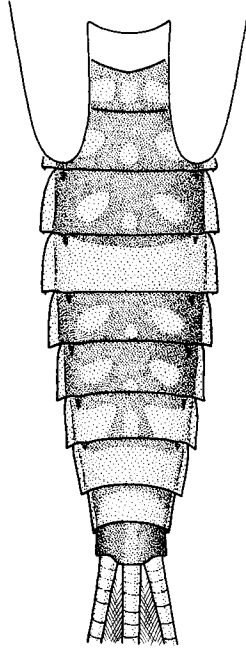
***Cloeodes soldani* (Müller-Liebenau)**

Centroptella soldani Müller-Liebenau, 1983: 491
Cloeodes soldani: Waltz & McCafferty (1987)

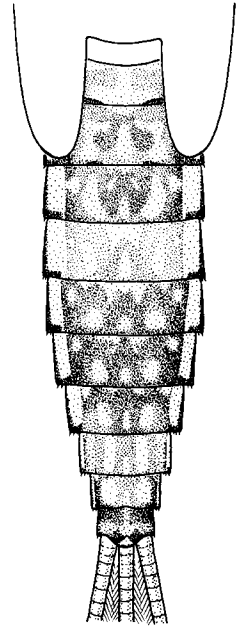
Mature Larva. Body 3.8 mm long. Head capsule uniformly cream. Antennae pale, subequal to head capsule length; pedicel slightly longer than scape.



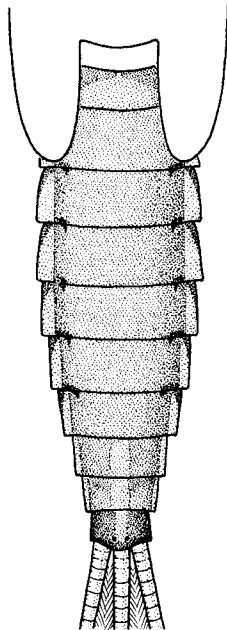
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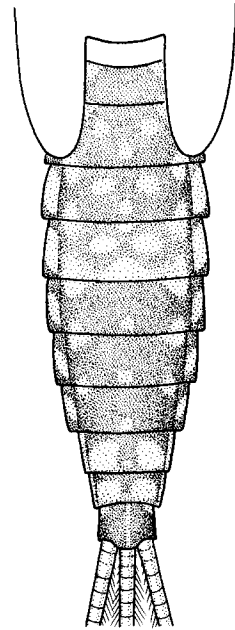
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Fig. 39-43. *Cloeodes* spp.: larval abdominal patterns (dorsal). (39) *C. penai*; (40) *C. excogitatus*; (41) *C. irvingi*; (42) *C. peninsulus*; (43) *C. redactus*.

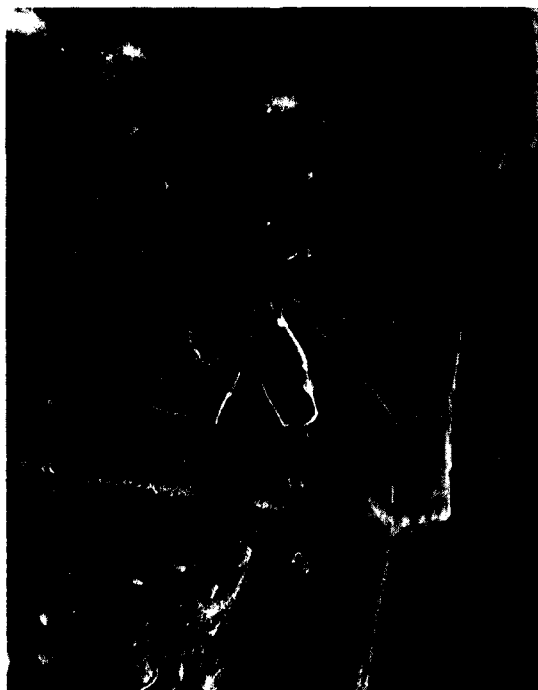


Fig. 44. *C. peninsulus*: scanning electron micrograph (470 \times) of larval abdominal segment 4 (ventral).

Labrum (figure 3a of Müller-Liebenau 1983) with 1+3-5 submarginal setae. Left mandible (figure 3e of Müller-Liebenau 1983) with stout and triangulate thumb. Right mandible as in figure 3e of Müller-Liebenau (1983). Maxilla (figure 3d of Müller-Liebenau 1983) with palp acute apically, shorter than galealacinia and two-segmented. Labium (figure 3b of Müller-Liebenau 1983) with segment 2 of palp having 4 dorsal setae; segment 3 of palp broadly truncate, somewhat quadrate, with apical inner stout bristles; paraglossa with 3 or 4 stout dorsal medioapical setae; glossa with ca. 15 inner marginal setae.

Thorax pale cream, without distinct pattern. Hind wing pads absent. Legs (figure 3 i and j of Müller-Liebenau 1983) pale cream; femora with elongate and subclavate dorsal bristles, and 2 or 3 distal bristles; tibia without tibial seam on foreleg (present on meso- and metatibiae) and with elongated subproximal arc of long, fine setae.

Abdomen without distinct pattern (figure 8 of Müller-Liebenau 1983). Terga 1-10 with posterior marginal spines (figure 10 of Müller-Liebenau 1983); spines with basal width subequal to height. Paraprocts (figure 3g of Müller-Liebenau 1983) with 12-13 marginal spines.

Adult. Unknown.

Material Examined. Paratype: 1 larva (in alcohol), Ceylon, FC/11/c Rasanawa-Fall, Ratnapura, 19-XI-1970. F. Starmühlner, FAMU.

Remarks. The presence on the paratype of clearly delineated ventral setal tufts on abdominal

segments 2-6, the form of the gills, claws, and mouthparts, along with the tergal characters illustrated by Müller-Liebenau (1983), clearly place this species in *Cloeodes* s.s.

Key to the Larvae of *Cloeodes*

1. Labial palps with obliquely truncate apical segment; maxillary palp subequal to or exceeding apex of galealacinia and apparently three-segmented; larger bristles of femora laterally serrate (Argentina) *penai* (Moriyama & Edmunds)
- 1'. Labial palps with rounded or with truncate apical margin; maxillary palp shorter than or attaining apex of galealacinia and apparently two- or three-segmented; larger bristles of femora never laterally serrate (widespread) 2
2. Hind wing pads present, prominent; maxillary palp apparently three-segmented (Paraguay) *irvingi* Waltz & McCafferty, n. sp.*
- 2'. Hind wing pads absent or greatly reduced; maxillary palp two-segmented 3
3. Subproximal arc of setae on tibiae extending to ca. 0.33-fold or more length of tibia (Oriental) 4
- 3'. Subproximal arc of setae on tibiae extending much less than 0.33-fold length of tibia (often <0.20-fold length of tibia) (Western Hemisphere) 5
4. Maxillary palp ca. 0.5-fold length galealacinia (China) *longisetosus* (Braasch & Soldán)
- 4'. Maxillary palp subequal to length of galealacinia (Sri Lanka) *soldani* (Müller-Liebenau)
5. Gills of 7th segment extending well beyond apex of 10th tergum (Fig. 1) (southwestern United States) *macrolamellus* Waltz & McCafferty, n. sp.
- 5'. Gills of 7th segment not extending beyond apex of tergum 10 6
6. Posterior marginal spines of tergum 3 with 15-18 spines each side of midline; paraprocts with 7-12 marginal spines (Peru) *redactus* Waltz & McCafferty, n. sp.
- 6'. Posterior marginal spines of tergum 3 with 20-40 each side of midline; more than 12 paraproct spines 7
7. Posterior marginal spines of tergum 3 with basal width of spines ca. 0.33-fold spine height; subtending bristle truncate and broadened apically (Fig. 31); intraantennal extension of frons narrowed distally (Fig. 36) (southwestern United States) *excogitatus* Waltz & McCafferty, n. sp.

* The larva of the Uruguayan species *C. aymara* (Traver) also presumably keys here. The larva of *C. aymara* is unknown.

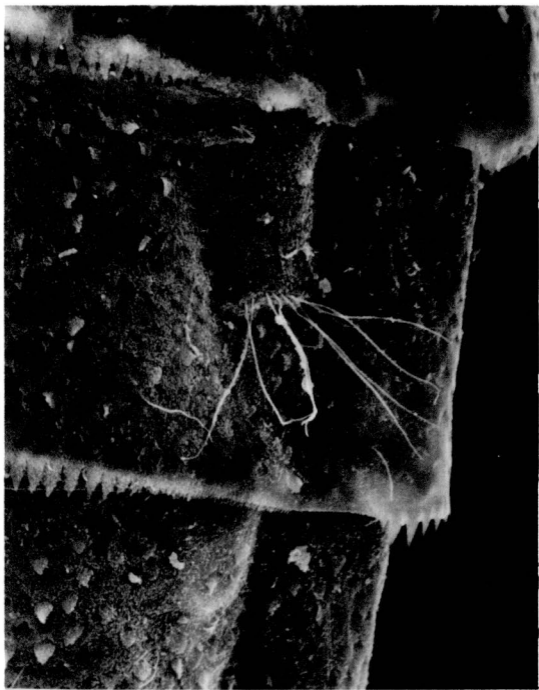


Fig. 44. *C. peninsulus*: scanning electron micrograph (470 \times) of larval abdominal segment 4 (ventral).

- 7'. Posterior marginal spines of tergum 3 with basal width of spines ca. 0.5-fold spine height; subtending bristle of tibia lanceolate; intraantennal extension of frons broad distally (Fig. 35, 37, and 38) 8
- 8. Body length 2.5–4.0 mm; abdomen uniform brown (Fig. 42) (Baja California Sur) ...
..... *peninsulus* Waltz & McCafferty, n. sp.
- 8'. Body length 5.0 mm; abdomen with distinct color pattern (Puerto Rico)
..... *maculipes* Traver

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