NEW SPECIES, REDESCRIPTIONS, AND CLADISTICS OF THE GENUS PSEUDOCENTROPTILOIDES (EPHEMEROPTERA: BAETIDAE)

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Abstract.—Two new species of the baetid genus Pseudocentroptiloides Jacob are described: P. usa from the Nearctic, and P. christineae from the Orient. The genus and its type species P. shadini (Kazlauskas) are redescribed in a comparative format, and larval keys to species are provided. The Oriental species P. christineae and P. ceylonica Glazaczow are sister species with several synapomorphies. The Palearctic species P. shadini is the most closely related to this pair, sharing certain other apomorphies with them. The most basally derived species is P. usa. Neither cladistic nor phenetic relationships of species support subgeneric classification as previously proposed.

Larvae of the genus *Centroptilum* Eaton are poorly known in North America, as only seven of the 25 recognized species are known as larvae. Comparative larval descriptions are nonexistent, rendering specific diagnosis of this stage virtually impossible. A review of Nearctic larvae that have been placed in *Centroptilum*, together with larva to adult rearings conducted at Purdue University, revealed a new genus and species distinct as both larva and adult from *Centroptilum* and other Baetidae. We then found that certain larvae collected by G. F. and C. H. Edmunds in Maylasia represented an additional species belonging to this new genus. Meanwhile, the genus *Pseudocentroptiloides* Jacob (Jacob and Glazaczow, 1986) was established, based on a Palearctic species and a new Oriental species. It was apparent when the description became available in 1987 that our distinctive new material was assignable to that genus.

We here describe our two new species. Also, as part of our ongoing revision of baetid genera, we comparatively redescribe *Pseudocentroptiloides* and its type species *P. shadini* (Kazlauskas), provide larval keys to all species, and discuss cladistic relationships within the genus. Jacob and Glazaczow (1986) and Keffermüller and Sowa (1984) (as *Centroptilum*) presented useful figures of *Pseudocentroptiloides*. We include citations of these as JG and KS respectively in our descriptions.

Pseudocentroptiloides Jacob

Description. Larva. Labrum (Figs. 1, 13; KS 29; JG 1a, 2a) deeply and triangularly notched on anterior margin. Mandibles (Figs. 2, 3, 14, 15; KS 30; JG 2b, c) with incisors widely separated apically; tuft of setae present between prostheca and molar region; thumb of left mandible parallel to slightly elevated above plane of incisor bases. Hypopharynx as in Figures 19; KS 32; JG 1b, 2d. Maxillae (Figs. 4, 16, 17;

KS 31; JG 2e) with broadened galealacinea and prominent crest of setae proximal to outer margin of apical denticles. Labium (Figs. 5, 18; KS 33; JG 1c, 3) with three-segmented palps; terminal segment of palps very broad distally and truncate; palpal segment 2 without inner apical lobe; glossae truncate distally, with numerous setae, and shorter than paraglossae; paraglossae truncated distally, with numerous setae apically, and with subparallel margins.

Margins of femora (Figs. 6, 7; JG 4) subparallel, without ventral femoral patch and without long, dorsal bristles; stout ribbed bristles sometimes present ventrally and laterally; vertical row of long, fine setae (Fig. 6) present on posterior face. Tibiae (Figs. 6, 7) with subproximal arc of long, fine setae. Claws (Figs. 6, 7, 20; KS 28; JG 4) edentate and elongate, $0.5 \times$ or more length of respective tarsi.

Abdominal terga (Fig. 21) with fine setae and broadly pointed, cresentic based scales with median length subequal to basal width; posterior marginal spines (Figs. 21; JG 7) present on all terga, alternately large and small in series, widely spaced and spike-like. Sternal surfaces with fine setae and scales similar to tergal scales. Pleural spines as in Figure 22. Gills (Figs. 23; KS 27; JG 5) 1–7 asymmetric, ovate and simple in presently included species. Median terminal filament subequal to cerci.

Adult Male. Forewings (Fig. 8) with single marginal intercalaries and relatively few crossveins. Hindwings (Figs. 9; KS 25) elongate, fore and hind margins subparallel or somewhat broadened medially and with distinctly hooked costal process. Genitalia (Figs. 12; KS 26; JG 1d) with forceps segments 2–3 fused, appearing three segmented; (in presently included species, forceps with distinct inner tubercle on segment 2); penes plate between forceps bases broad and flattened apically.

Included species. Pseudocentroptiloides usa (Nearctic), P. christineae (Oriental), P. shadini (Kazlauskas 1964) (type species by original designation) (Palearctic), and P. ceylonica Glazaczow (Oriental).

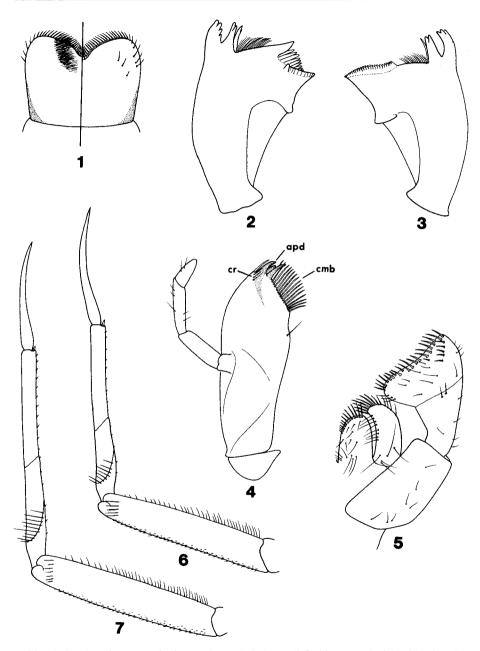
Pseudocentroptiloides usa, new species

Diagnosis. Larva. Body length 7-8 mm. Terminal filaments ca. 2 mm. Antennae extend to middle coxae. Labrum (Fig. 1) slightly wider than deep. Mandibles (Figs. 2, 3) with relatively broad bases (compared to *P. ceylonica*). Maxillae (Fig. 4) with crest of fine setae restricted to apical width of galealacineal crown and shorter in height than galealacineal denticles; broad, digitate setae of galealacineal comb not present. Maxillary palp three segmented. Labium as in Figure 5. Claws (Figs. 6, 7) subequal in length to respective tarsi.

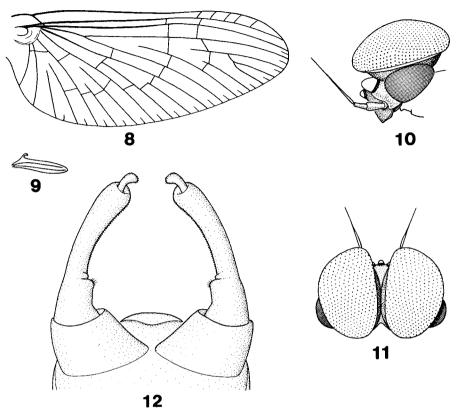
Adult male. Body length ca. 5 mm. Forewing (Fig. 8) length 4.5 mm. Hindwings (Fig. 9) with fore and hind margins subparallel. Turbinate eyes (Fig. 10), yellow to yellow-orange, slightly divergent anteriorly, and on low stalks. In dorsal view, turbinate eyes (Fig. 11) ca. $2.0 \times$ longer than wide, hemispherical with medial margin relatively straight. Genitalia as in Figure 12.

Holotype. USA, Indiana, Pulaski Co., Tippecanoe River at Co. Rd. 1.5 mi S Tippecanoe River St. Prk., VI-30-1978, A. V. Provonsha, D. Bloodgood, H. Hollis, male larval exuviae (slidemounted in euparal; solvent abs. alc.) and its reared male adult (body stored in alcohol; forewing, hindwing, foreleg, and genitalia slidemounted on one slide; foreleg and genitalia in euparal).

Paratypes. USA, Indiana, Pulaski Co., Tippecanoe River at Co. Rd. 1.5 mi S Tippecanoe River St. Prk., VI-30-1978, A. V. Provonsha, D. Bloodgood, and H.



Figs. 1-7. Pseudocentroptiloides usa, larva. 1. Labrum (left side, ventral; right side, dorsal). 2. Left mandible. 3. Right mandible. 4. Maxilla (cr—crest of setae; cmb—galealacineal comb; apd—apical denticles). 5. Labium. 6. Foreleg. 7. Hindleg.



Figs. 8–12. *Pseudocentroptiloides usa*, male imago. 8. Forewing. 9. Hindwing. 10. Turbinate eyes, lateral view. 11. Turbinate eyes, dorsal view. 12. Genitalia, ventral view.

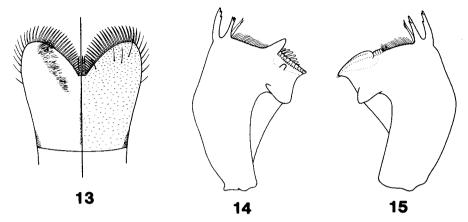
Hollis. 1 female exuviae (slidemounted as above) and its reared female adult (in alcohol); 3 larvae, same locale as holotype, VIII-4-1976, A. V. Provonsha and M. Minno. Holotype and paratypes deposited at Purdue University Entomological Research Collection, West Lafayette, Indiana.

Etymology. The species epithet, usa, is an arbitrary combination of letters based on the acronym for the United States of America.

Pseudocentroptiloides shadini (Kazlauskas)

Pseudocentroptilum shadini Kazlauskas, 1964. Centroptilum shadini, Keffermüller and Sowa, 1984. Pseudocentroptiloides shadini, Jacob and Glazaczow, 1986.

Diagnosis. Larva. Body length 5-6 mm. Antennae elongate, reaching to middle coxae. Labrum (figs. KS 29; JG 1a) slightly wider than deep. Hypopharynx as in figs. KS 32 and JG 1b. Mandibular incisors (fig. KS 30) broad based (compared to *P. christineae*). Maxillae (fig. KS 31) with crest of fine setae extended beyond ga-



Figs. 13-15. *Pseudocentroptiloides christineae*, larva. 13. Labrum (left side, ventral; right side, dorsal). 14. Left mandible. 15. Right mandible.

lealacineal crown, and longer than galealacineal denticles; broad, digitate setae of galealacineal comb present and well developed. Maxillary palp three segmented, segment 3 poorly differentiated. Labium as in figs. KS 33 and JG 1c. Claws (fig. KS 28) subequal in length to, or longer than, respective tarsi.

Adult male. Body length 5.0-5.5 mm, cerci ca. 9 mm. Turbinate eyes, yellow-orange, slightly divergent anteriorly; oval, ca. 1.5×10 longer than broad, in dorsal view. Hindwings (fig. KS 25) concave from wing base to costal process, convex from costal process to wing apex. Forceps (figs. KS 26; JG 1d) with segment 1 broad, slightly tapered distally; segments 2 and 3 fused, with prominent inner tubercle at base and distally swollen; segment 4 broad apically with narrow base.

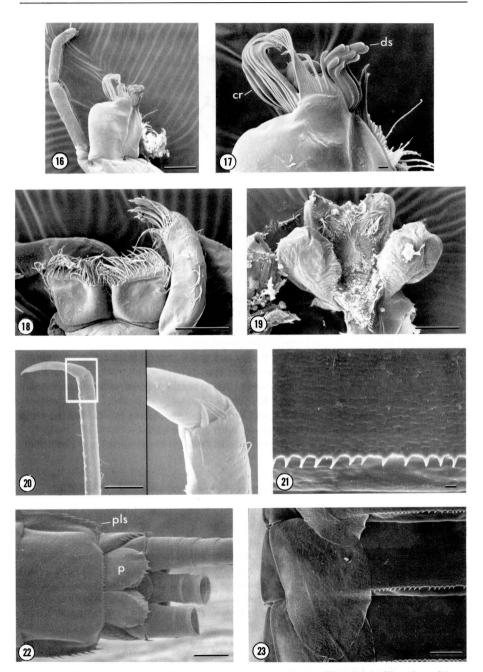
Distribution. USSR (Oka River) and Poland (Warta River and Bug River) (Keffermüller and Sowa, 1984).

Pseudocentroptiloides christineae, new species

Diagnosis. Larva. Body length 4–5 mm. Length of terminal filaments 1.0–1.5 mm. Antennae shortened (compared to *P. shadini* and *P. usa*), extend to vertex of head capsule. Labrum (Fig. 13) elongated, ca. 2.0× deeper than wide. Mandibles (Figs. 14, 15) with incisors narrowly based (compared to *P. shadini* and *P. usa*). Maxillae (Figs. 16, 17) very broad, subquadrate, with crest of fine setae distinctly longer than galealacineal denticles; broad, digitate setae of galealacineal comb highly developed and apparent. Maxillary palp three segmented, segment 3 poorly differentiated. Labium as in Figure 18. Hypopharynx as in Figure 19. Claws (Fig. 20) shorter in length than respective tarsi, ca. 0.5× length of tarsi. Hindwing pads absent (as in fig. JG 6a).

Adult. Unknown.

Holotype. West Malaysia, Trengganu Kampong Sungai Tong, 9-IX-1978, G. F. and C. H. Edmunds, male larva, in alcohol. Holotype deposited at the Purdue University Entomological Research Collection (PERC), West Lafayette, IN.



Figs. 16–23. *Pseudocentroptiloides christineae*, larva. 16. Maxilla. 17. Maxilla enlarged (crcrest setae; ds—digitate setae). 18. Labium (dorsal view). 19. Hypopharynx. 20. Claw. 21. Tergal surface. 22. Ventral abdomen (p—paraprocts; pls—pleural spines). 23. Gill (Abd. 4). Figs. 16, 18–20, 22, 23 scale bar = 100μ ; Figs. 17, 21 scale bar = 10μ .

Paratypes. West Malaysia, Trengganu Kampong Sungai Tong, 9-IX-1978, G. F. and C. H. Edmunds, 3 larvae: 1 (in alcohol) deposited at PERC (mouthparts slide-mounted); 1 (on SEM stub used for SEM studies) deposited at PERC; 1 (in alcohol) deposited United States National Museum.

Etymology. This species is named in honor of Christine Edmunds, who along with her husband, the renowned ephemeropterist George F. Edmunds, Jr., collected the material upon which this species is based.

LARVAL KEY TO THE SPECIES OF PSEUDOCENTROPTILOIDES

1.	Labrum (Fig. 13) elongated, clearly longer than wide and deeply notched distally; maxillae with crest of setae highly developed as in Figures 16, 17
1'	Labrum (Fig. 1) length subequal to width and not notched as deeply as above; maxillae
	with crest of setae not so prominently developed (Fig. 4)
2.	Maxillae quadrate (Fig. 16), galealacineal width subequal to length. Crest of setae on
	maxillae strongly hooked distally (Fig. 17)
2'	Maxillae not so quadrately formed as above (fig. JG 2e). Crest of setae on maxillae not
	hooked distally P. ceylonica
3.	Maxillae (Fig. 4) with crest of setae restricted to crown of galealacinea, shorter in length
	than denticles of galealacinea; broad, digitate setae of galealacineal comb not developed
	P. usa
3′	Maxillae (fig. KS 31) with crest of setae extending basally beyond crown of galealacinea,
	subequal to or longer than denticles of galealacinea; broad, digitate setae of galealacineal
	comb well developed

DISCUSSION

Pseudocentroptiloides is most similar to complexes within the large genus Centroptilum, as the latter is currently composed. Centroptilum is used as the outgroup for proposing apomorphies for cladistic analysis. Thus, the apomorphic character states common to all Pseudocentroptiloides and its hypothetical common ancestor are 1) labrum triangularly and deeply notched, 2) maxillae broadened, 3) prominent crest of setae present on the crown of the galealacinea, 4) segment 3 of labial palps greatly broadened, 5) glossae truncate and shorter than paraglossae, 6) paraglossae truncate, subparallel, 7) glossae and paraglossae with numerous apical setae, 8) claws edentate, and 9) claws subequal to or greater than $0.5 \times$ length of respective tarsi.

The above synapomorphies clearly show *Pseudocentroptiloides* to be monophyletic. We propose cladistic interrelationships of *Pseudocentroptiloides* species based on several additional larval apomorphies and one adult apomorphy. The earliest derived species within the group is *P. usa*, which remains essentially similar to the hypothetical ancestor of the genus. The remaining three species share further apomorphies of increased development of the maxillary crest, extension of the line of crown setae basally on the galealacinea, and a galealacineal comb consisting of digitate setae. The ancestor with these character states gave rise to one lineage leading to *P. shadini* and one leading to the common ancestor of *P. ceylonica* and *P. christineae*. These sister species share apomorphic elongation of the labrum and a more deeply recessed labral notch, further elongation of the crest of setae of the maxillae, and loss of the hind wings (wingpads in larvae).

Jacob and Glazaczow (1986) proposed two subgenera for the two species of Pseu-

docentroptiloides known to them based only on the presence or absence of hindwings. Ironically, in this same paper these authors rejected this character for generic criteria, citing observations of its taxonomic unreliability by Edmunds et al. (1976). Although we have presented characters, including the loss of hindwings, that show *P. ceylonica* along with *P. christineae* to be a derived sister pair, the intermediate phyletic position of *P. shadini* between them and *P. usa*, and the gradational differences within the genus, do not support a subgeneric division.

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