NEW LARVAL DESCRIPTIONS AND COMPARISONS OF NORTH AMERICAN *CHOROTERPES* (EPHEMEROPTERA: LEPTOPHLEBIIDAE)

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ABSTRACT

Formal descriptions of larvae of the western North American species *Choroterpes albiannulata* and the eastern North American species *Choroterpes fusca* (Ephemeroptera: Leptophlebiidae) are given for the first time. Specimens, including reared adult and larval associations, of *C. albiannulata* were available from Nevada, Oregon, and Idaho, and rearings of *C. fusca* were made from the Huron Mountains in the Upper Peninsula of Michigan. Six of the nine species of North American *Choroterpes* (subgenus *Choroterpes*) are now known as larvae. Larval characteristics are compared, particularly with regard to similarities and differences between *C. albiannulata* and *C. fusca*, *C. albiannulata* and the western *C. inornata*, and *C. fusca* and the eastern *C. basalis*. *Choroterpes albiannulata* is distinct but shares gill morphology with *C. inornata*. *Choroterpes fusca* is quite similar to *C. basalis*, sharing gill morphology and color patterning, but with some apparent differences that may prove to be consistent. Certain *Choroterpes* larvae from Arkansas are probably *C. oklahomae* (known only as adults from Oklahoma) but cannot be associated at this time. Distributions of species of subgenus *Choroterpes* are updated, and a revision of the entire genus based on cladistic analysis is recommended.

Eaton (1892) described adults of *Choroterpes inornata* from Mexico, but it was not until 1973 that its larval stage was finally discovered and described (Kilgore and Allen 1973). This situation has typified the chronological gap between our knowledge of adults and larvae for many, if not most, species of Ephemeroptera and has contributed to the current need to re-evaluate the systematics of many genera. At the present, nine valid species of *Choroterpes* (subgenus *Choroterpes*) have been recognized in North America north of Mexico. Up to this point, descriptions of the larval stages of four species have been published: *C. basalis* (Banks) by Needham (1905), *C. terratoma* Seemann by Seemann (1927), *C. hubbelli* Berner by Berner (1946), and *C. inornata* Eaton by Kilgore and Allen (1973). The remaining five species are *C. albiannulata* McDunnough, *C. ferruginea* Traver, *C. fusca* Spieth, *C. nanita* Traver, and *C. oklahomae* Traver. In addition, three southwestern species of *Choroterpes* were described originally as larvae (remaining unknown as adults) but were placed in a separate subgenus *Neochoroterpes* by Allen (1974) on the basis of their gills having three well-developed terminal processes rather than having only the median process well developed, which distinguishes the subgenus *Choroterpes*.

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In much of the 1980's, I had the opportunity to extensively study the ecology and behavior of populations of *C. fusca* in the Huron Mountains of the Upper Peninsula of Michigan. As a result of making reared associations of larvae and adults, I present a description of the larvae of this species herein. In addition, I have studied larval and adult specimens of *C. albiannulata* from Nevada, Oregon, and Idaho that are housed in the Purdue Entomological Research Collection (PERC). Actually, G. F. Edmunds, Jr. associated larvae and adults of this latter species by rearing some from the Snake River near Blackfoot, Idaho in 1963; a brief description of those larvae appeared in a 1966 Master's thesis by S. L. Jensen on the mayflies of Idaho. No description of the larvae, however, has been published, and it seems propitious to do so herein. These descriptions should allow further comparative analyses of North American species of *Choroterpes*. However, three species will still remain unknown as larvae and any revision of *Choroterpes* will require more in-depth study in light of world-level generic concepts, as alluded to by Peters (1988).

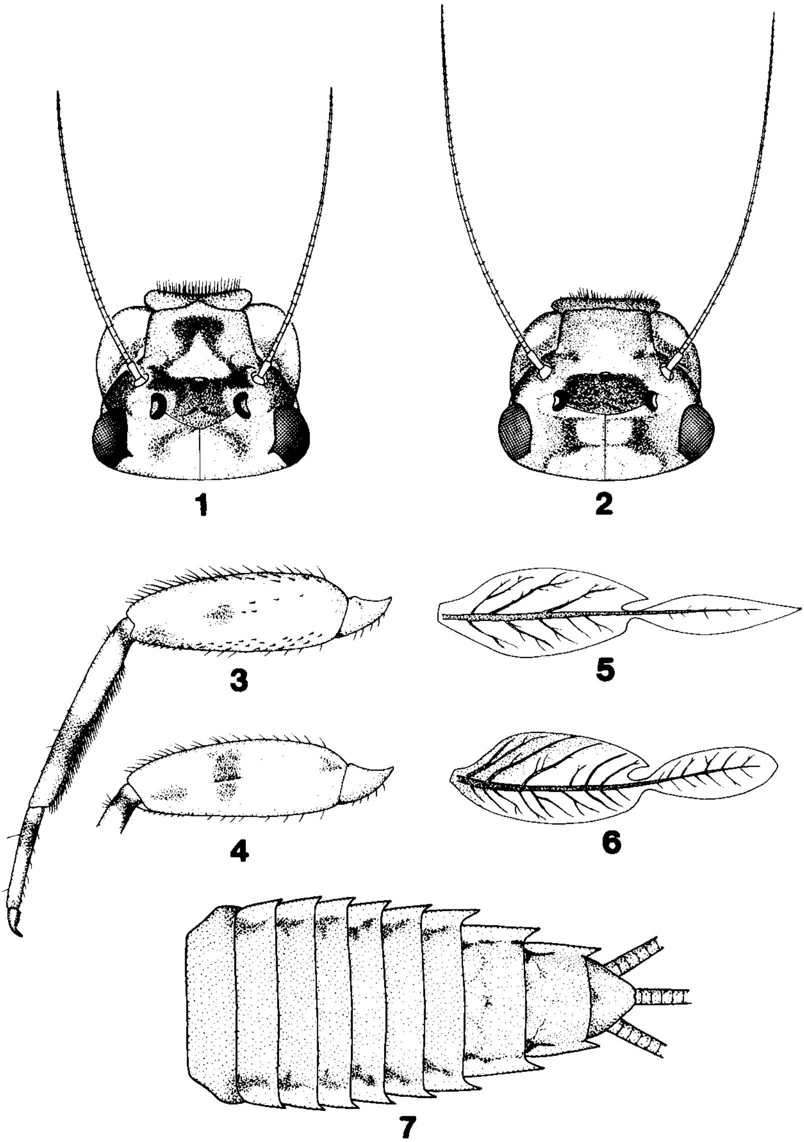
Choroterpes albiannulata McDunnough

Larva (in alcohol). Length of mature larvae, excluding caudal filaments: 7.4–7.8 mm (female), 6.3–6.5 mm (male). Caudal filaments subequal, 7.0–9.1 mm.

Head: Dorsal head capsule (Fig. 1) light brown with diffuse black markings as follows: one median dark blotch on frons narrowly connecting posterolaterally with a variable, darkened, more-or-less transverse marking extending from anterior of compound eyes and surrounding antennal bases to across vertex at level of ocelli, and in some individuals extending diffusely between and behind lateral ocelli (most distinct in females). Antennae pale, one and one half to twice as long as head. Compound eyes black, with upper portion rust colored in males. Clypeus with distinct transverse row of medium length setae subapically in median third, and much denser row of uniformly shorter setae apically at emargination in same area. Thick setal brush of galealaciniae light to golden brown; maxillary palpi distinctly three-segmented.

Thorax: Pronotum light brown with clear lateral flanges, and in some individuals with black, diffuse, longitudinal markings sublaterally and submedially behind lateral ocelli, and with somewhat shaded area medially. Mesonotum light brown, but with some dark penciling at sutures and taking on rufous coloration of adult in last instar. Legs light cream colored and generally lacking any conspicuous patterning, although some individuals with shading basally in femora and tibiae and also apically and medially on femora. Tarsal claws with 9–11 denticles.

Abdomen: Tergal pattern variable but generally consisting of dark brown or black granulation on light brown ground color; granulation weaker or less dense in some areas on some individuals, e.g., medially (giving allusion of very faint midlongitudinal stripe), at posterolateral corners, along anterior margin (especially of tergum 10), submedially at anterior margins, and sublaterally at anterior margins; tergum 10 mostly light except for posterior shading. Sterna cream colored to pale, lacking distinct maculations, although subcutaneous dark circle often evident on sternum 8 or around juncture of sterna 7 and 8. Gills with tracheae faint in median process of dorsal lamellae; median process of dorsal lamellae of gills 3 (Fig. 5) narrow leaf shaped, with acutely pointed apex. Caudal filaments pale except dark rings on basal 5 to 8 segments; basal third of segments with few spines and bristle-like setae at apex of each segment; middle and apical segments with mostly bristle-like setae at apex of every other segment.



Figs. 1–7. *Choroterpes* larvae. 1–2. Head of female larva, dorsal: (1) *C. albiannulata*; (2) *C. fusca*. 3. Dorsal foreleg, *C. fusca*. 4. Ventral forefemora, *C. fusca*. 5–6. Dorsal lamella, gill 3: (5) *C. albiannulata*; (6) *C. fusca*. 7. Ventral abdomen, *C. fusca*.

Material examined: Twenty-one larvae were studied from the Koss Collection at PERC as follows: Nevada, Elko Co., Humbolt River at Elko, VII-29-1965; Oregon, John Day River, Kimberley, IX-5-1933; and Idaho, Bingham Co., Snake River at Blackfoot, VIII-7-1963.

Choroterpes fusca Spieth, 1938

Larva (in alcohol). Length of mature larvae, excluding caudal filaments: 5.8–6.5 mm (female), 5.8–6.3 mm (male). Caudal filaments subequal, 9.5–11.5 mm.

Head: Dorsal head capsule (Fig. 2) medium brown with light patches as follows: one immediately anterior to median ocellus, variously extended between antennae and tending to narrow anteriorly (appearing triangular in well-marked individuals), pair of somewhat rounded or hemispherical, conspicuous patches on dorsally visible mandibles and anterior to antennae, and pair of lightened areas each continuous from laterad of lateral ocelli, anterior to compound eyes, and posterior to antennae; vertex dark brown or darkest between lateral ocelli and in areas directly posterior to lateral ocelli and extending slightly medially from there; median two-thirds of posterior edge of vertex variously mottled. Antennae light, about twice length of head. Compound eyes black, with upper portion rust-colored in males. Clypeus dorsally colored as dorsal head capsule, with dorsal subapical row of medium length setae in median third and with row of short, thick setae prominent along well-developed anterior emargination. Thick setal brush of galealaciniae dark brown; maxillary palpi three-segmented but with segments 2 and 3 partially fused and often appearing fused under low magnification in some individuals.

Thorax: Pronotum either patterned or diffuse medium brown, always with light to transparent lateral flanges; if patterned, darker or dark brown sublaterally and submedially (submedial marks narrow-elongate anteriorly and broadening posteriorly), and with lighter area anteromedially. Mesonotum lighter brown to yellowish with some dark markings laterally near base of forewingpads (some individuals with penciling transversely at middle third of suture separating pronotum and mesonotum, and longitudinally at lateral notal sutures). Legs light tan to yellow; claws with 10–12 denticles. Forefemora dorsally (Fig. 3) with weak or diffuse maculation medially, not extending from anterior to posterior margins and with shaded area apically in some individuals; ventrally (Fig. 4) similarly placed markings are more distinct, and medial maculation broader, nearly transverse and often divided into two spots. Foretibiae (Fig. 3) diffusely darkened at base and with light brown shading (difficult to see in some individuals) from about midlength to near apex. Foretarsi (Fig. 3) with diffuse brown area beginning subbasally to about midlength, and with small dark maculation ventrally at tarsus-claw articulation. Midlegs and hindlegs with markings generally similar to forelegs, except hindlegs with dorsal maculation extending diffusely from midlength to apex in some individuals.

Abdomen: Tergal pattern quite variable but generally with dark brown granular appearance (darkest at posterior and posterolateral region of each tergum) with variously discernible lighter or less densely granulate markings, including midlongitudinal line and somewhat ill-defined large round areas laterally on most terga, but in some individuals additional more defined, small light spots sublaterally at anterior margin of terga and larger ones at base of gills, and pair of small, light, triangular areas submedially at anterior margins, becoming more elongate in more distal terga. Sterna (Fig. 7) light to medium brown, sometimes with general indistinct mottling, usually with slightly darker markings sublaterally, more continuous in basal sterna but more separated and defined in distal sterna (sternum 9 often with distinct dark markings sublaterally at anterior margin). Gills with distinct, dark tracheae, with lateral tracheae well developed in median process of at least gills 2–4; median process of dorsal lamellae of gills 3 (Fig. 6) relatively broad and with bluntly pointed apex. Caudal filaments light; basal segments with whorls of spines at apex of each segment; middle segments with whorls of bristle-like setae and spines at apex of every other segment; distal segments with whorls of bristle-like setae at apex of every other segment.

Material examined: Over 50 larvae were studied from Michigan, Marquette Co., Ives Lake, VIII-25, IX-6-1985, VIII-3-1986, PERC.

DISCUSSION

Spieth (1938) indicated that *C. albiannulata* and *C. fusca* were most closely related to each other (on the basis of adults) among the species of *Choroterpes*. Therefore a comparative analysis of their larvae would appear to be of some importance. A direct comparison of the larvae of the two indicates a number of diagnostic characteristics that serve to distinguish them, and at the same time a number of characteristics in common, some of which appear to be uniform throughout the subgenus in North America. The most obvious differences include the dorsal color pattern of the head (including the exposed dorsal surfaces of the mandibles). While all North American species of the subgenus *Choroterpes* may have a central white or pale patch located directly in front of the median ocellus, the black patch forward on the frons of *C. albiannulata* (Fig. 1) may be unique. The head patterning of *C. fusca* (Fig. 2) appears much like that drawn for *C. inornata* by Kilgore and Allen (1973), particularly with regard to light mandibular patches and the dark brown area between the lateral ocelli described for other species.

The setal brushes on the galealaciniae of *C. albiannulata* are light relative to the much darker ones found in *C. fusca*, and whereas the maxillary palpi are distinctly three-segmented in *C. albiannulata*, the distinction between segments two and three in *C. fusca* can sometimes be difficult to discern. Leg and ventral abdominal patterning in the two species is quite different, with *C. albiannulata* lacking the maculations of *C. fusca* (Figs. 3, 4 and 7). The claws of both species possess approximately the same number of denticles. This character is often difficult to use in species diagnoses of mayflies because of its known variability in species of certain genera (e.g., Bednarik and McCafferty 1979), however it should be noted that Kilgore and Allen (1973) reported 14–18 such spines in *C. inornata*. Given the variability of dorsal body patterning in both species and evidently in others as well, it is impossible to draw conclusions about the usefulness of such patterning in formulating diagnoses of species. I suspect that the patterning is generally similar throughout the subgenus in North America and may vary somewhat with age and habitat of the larvae [see also plate 7, Fig. 2. in Needham (1905) and Fig. 1 in Kilgore and Allen (1973)].

The median process of the dorsal lamellae of gills is distinctly different in *C. albiannulata* (lanceolate and sharply pointed) and *C. fusca* (broad and blunt), as is clearly shown in Figs. 5 and 6. This process in the gills of *C. hubbelli* [Fig. 3, Berner (1946)] has aspects of both, in that it is broad like that of *C. fusca*, but with a sharper apex, more similar to that of *C. albiannulata*. There may also be differences in the caudal filaments in that some dark annulations are found basally in *C. albiannulata* but not in *C. fusca*, and segmental spination may be better developed in *C. fusca*. Also, the caudal filaments appear to be somewhat longer in proportion to the body in *C. fusca* than they are in *C. albiannulata*, where the tails are not much longer than the body. The latter situation is apparently also found in *C. hubbelli* and *C. inornata*. Finally, there appears to be some difference in body size between the two and in the degree of sexual dimorphism with respect to size in the two species. In *C. fusca*, the mature larvae range from 5.8 to 6.5 mm with little difference in the size of the males and females. However, in *C. albiannulata*, the range is 6.5 to 7.8 mm., but the females are always distinctly larger than the males. I have found this to be true also for species of the subgenus *Neochoroterpes*.

Since Traver (1935), on the basis of adult comparisons, concluded that *C. albiannulata* was most closely related to *C. inornata*, a reiteration of the larval differences in those two appears pertinent. Both of these species are found only in the West, with *C. inornata* known from Arizona and New Mexico (Kilgore and Allen 1973), Colorado (B. C. Kondratieff, pers. comm.), and Mexico (Eaton 1892), and *C. albiannulata* known from Alberta (McDunnough 1924), Saskatchewan (Lehmkuhl 1976), Oregon (Allen and Edmunds 1956), Idaho, and Nevada (herein), and Utah (Edmunds 1954). The only other species of the subgenus known from the far West is *C. terratoma*, from southern California (Seemann 1927, Traver 1935), although *C. oklahomae* and *C. nanita* are known from Oklahoma and Texas, respectively (Traver 1934).

Differences in the head patterning between *C. inornata* and *C. albiannulata* are distinct as mentioned above. The leg markings are apparently very different also, with broad, almost transverse maculae on the femora of *C. inornata* and little, if any, maculation in *C. albiannulata*. If the number of denticles on the tarsal claws proves to be a valid specific character, then differences reported for the two species are significant. It is not clear whether or not the shape of the median process of the dorsal lamellae of the middle gills is different or not in the two species. From the habitus drawing of Kilgore and Allen (1973) of *C. inornata*, the process appears very narrowly leaf shaped and almost lanceolate; this is in general agreement with *C. albiannulata* (Fig. 5), although the latter may be even broader; gills of both species are sharply pointed apically. Also, it is not clear whether or not larvae of *C. inornata* and *C. albiannulata* share the presence of a few dark annulations on the basal segments of the caudal filaments.

Burian and Gibbs (1991) suggested that *C. fusca* and *C. basalis* were probably synonymous. Therefore, I have compared larval collections of *C. basalis* present in the PERC with those of *C. fusca*. The former species apparently is widespread throughout northeastern and midwestern North America, and I have studied larval specimens from Indiana. *Choroterpes fusca*, however, is known only from Ontario (Spieth 1938) and the Upper Peninsula of Michigan (herein). Burian and Gibbs (1991) reported *C. fusca* from Maine, but since they suggested its equivalency to *C. basalis*, it is not clear as to which of these names their populations actually refer. *Choroterpes ferruginea* is known only from New York, but little is known of this species, and it may represent a color morph of *C. basalis*. *Choroterpes hubbelli*, the only other eastern species, is known only from Florida, Alabama, and South Carolina, and possibly North Carolina.

Larvae that I have examined of *C. basalis* and *C. fusca* are quite similar. I can find no consistent differences in the color patterns, although leg and head patterning appears to be extremely variable among *C. basalis*, with legs of a large proportion of individuals lacking medial femoral markings dorsally but not ventrally. Also the white medial patch anterior to the median ocellus is never very well developed in *C. basalis* as it is in some *C. fusca* (Fig. 2). There is usually a small, distinct, dark spot at the tibia-tarsus articulation of *C. basalis* that I did not find in *C. fusca*. The sometimes weak articulation of segments 2 and 3 of the maxillary palpi described above for *C. fusca* is also found in *C.*

basalis. Needham (1905) had reported the maxillary palpi of *C. basalis* to be two-segmented, most probably for this reason.

The shape of the gills is similar in *C. basalis* and *C. fusca* (Fig. 6), particularly with regard to the shape of the median process of the dorsal lamellae of the middle gills, however, the median process does not appear to have lateral tracheation as well defined as in *C. fusca*. Claw denticles numbered 10–12 in *C. fusca*, but I have found only 8–10 in about 30 specimens of *C. basalis* that were examined for this character. The length of the antennae relative to the head and the length of the caudal filaments relative to the body are within the same range in both species.

It remains to be seen if the above stated differences are consistent and diagnostic of two discrete species, or if they are due to variability of individuals or populations among one widespread species. This will have to be ascertained within the context of a revisionary study of the genus as intimated above. From the diverse opinions about North American species of the subgenus *Choroterpes* and their relationships (Traver 1935, Spieth 1938, Burian and Gibbs 1991), it is clear that only a cladistically based revision will resolve questions of species integrity and relationships.

Larval specimens I have seen from Arkansas and that were tentatively identified as *C. basalis* in the PERC are quite different from what I consider to be typical *C. basalis*, discussed above, in that they have gills essentially of the *C. inornata-C. albiannulata* type (Fig. 5), discussed above, and have some other characteristics that do not seem to fit any of the presently described species of *Choroterpes* in North America. They may, in fact, prove to represent a new species, but I rather suspect they are the larvae of *C. oklahomae* (presently known only as adults from Oklahoma). Since they are not associated with adults by rearing, it is difficult to make a definitive assessment at this time.

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