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ABSTRACT The Nearctic stonelly genus *Perlinella* Banks is reviewed; three valid species are recognized. *Perlinella drymo* (Newman) and *Perlinella ephyre* (Newman) are widespread east of the Rocky Mountains, whereas *Perlinella zwicki*, n. sp. (*P. fumipennis* of Zwick 1971), is restricted to the southeastern Coastal Plain. *Perlinella fumipennis* (Walsh) is replaced as a synonym of *Perlinella ephyre*. Keys for adults and nymphs are provided, and the nymph of *P. zwicki* is described for the first time. Male drumming calls of *Perlinella drymo* and *Perlinella ephyre* are described.

KEY WORDS Insecta, Perlinella, taxonomy, drumming calls

THE GENUS Perlinella was erected by Banks (1900) for Perla trivittata Banks, a species he described from Michigan in 1895, Needham & Claassen (1925) regarded Perla elongata Walsh and P. trivittata as synonyms of Perlinella drymo (Newman), and Illies (1966) considered Perlinella a monotypic genus endemic to the Nearctic region. Zwick (1971) reviewed Perlinella, included Atoperla Banks as a new junior synonym, and recognized three rather widespread geographical species, P. drymo, P. =Atoperla) ephyre (Newman), and P. (=Atoperla) fumipennis (Walsh). His revalidation of the name fumipennis for a species described originally from Illinois was based only on specimens from Florida. Because Hitchcock (1974) and Stark & Gaufin (1976) have questioned Zwick's (1971) concept of P. fumipennis, we re-evaluate the status of the species included in Perlinella, and we provide descriptions of all life stages using current techniques in stonefly systematics.

Stewart & Zeigler (1984b) discussed the use of stonefly drumming behavior as evidence for solving systematic questions and reconstructing phylogeny. One objective of our study was to include as much behavioral information as possible to help delineate *Perlinella* species and determine if they have a generically distinct drumming pattern.

Materials and Methods

Adult male and female terminalia were examined using the methods of Stark & Szczytko (1981). Eggs were removed from gravid females and prepared for SEM, using the technique of Stark & Szczytko (1981). The following museums, institutions, and individuals provided material for this study: R. W. Baumann, Brigham Young University; O. S. Flint, Jr., United States National Museum of Natural History; D. G. Huggins, State Biological Survey of Kansas; P. K. Lago, University of Mississippi; A. Provonsha, Purdue University; B. P. Stark, Mississippi College; J. D. Unzicker, Illinois Natural History Survey; C. Vogt, Museum of Comparative Zoology, Harvard University; and J. R. Voshell, Jr., Virginia Polytechnic Institute and State University.

Methods of recording and oscilloscope analysis of drumming followed Stewart & Zeigler (1984a) and Maketon & Stewart (1984). We attempted to rear nymphs of *P. ephyre* and *P. zwicki* for recording and comparison with signals of *P. drymo* (Zeigler & Stewart 1977); however, suitable nymph populations of the two species were not found during the two years of the study, and a few *P. ephyre* rearings were unsuccessful. Recordings of male drumming calls (n = 27) were obtained from two wild males of *P. ephyre* collected from Arkansas, Stone County, Blanchard Springs, 2 mi NE of Hwy. 56, 19-III-1985, by B. C. Poulton.

Perlinella Banks

- Perlinella Banks, 1900: 242. Type-species, Perla elongata Walsh = Perlinella drymo (Newman) (type by monotypy).
- Atoperla Banks, 1905: 56 (syn. Zwick, 1971: 316). Type species Perla producta Walsh = Atoperla ephyre (Newman) (type by monotypy).
- Atoperla: Illies, 1966: 325.
- Perlinella: Illies, 1966: 348; Zwick, 1973: 278; Stark & Gaufin, 1976: 34.

Stark & Gaufin (1976) provided a generic description of all life stages of *Perlinella*. Kirchner & Kondratieff (1985) added the following two characters which help distinguish *Perlinella* nymphs from all other Nearctic Perlidae: 1) legs with a ventral and dorsal fringe of long silky hairs, and

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² The views of the author do not purport to reflect the position of the Department of the Army or the Department of Defense.

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Fig. 1-4. Perlinella adult head and pronotum: (1) P. drymo, (2) P. ephyre, (3) P. ephyre, (4) P. zwicki.

2) mandibles with 4 teeth, right mandible with teeth ¼ subparallel (Fig. 23). Shepard & Stewart (1983) illustrated the gills of the nymphs.

Adults are separated from other sympatric perlids by their distinct elongate habitus and in having one or more crossveins between A1 and A2 of the forewings. Adult males are distinguished from other Nearctic Acroneuriini by the combination of 1) paired aedeagal sclerites, 2) large oval hammer on sternum 9, and 3) spinules present on tergum 10. Adult females are recognized by the short, bilobed subgenital plate.

Perlinella cinctipes Banks (1905) is a species of Perlesta (Needham & Claassen 1925; B. Stark, personal communication).

Keys to Species of Perlinella

Males

- 1. A dark triangular spot in front of clypeus and pronotum with dark median stripe bordered by pale areas (Fig. 1); aedeagus as Fig. 11; 3 ocelli drymo (Newman)



Fig. 5-10. Male terminalia, dorsal view: (5) P. drymo; (6) P. ephyre; (7) P. zwicki. Male paraproct, lateral view: (8) P. drymo; (9) P. ephyre; (10) P. zwicki.

 Lateral sclerites of aedeagus with a sharp sclerotized hook (Fig. 12)ephyre (Newman) Lateral sclerite of aedeagus without a hook (Fig. 13) .. zwicki Kondratieff et al., n. sp.

Females

- Three ocelli; subgenital plate with broad median notch (Fig. 14) drymo (Newman) Two ocelli; subgenital plate otherwise (Fig. 15 and 16) 2
- Subgenital plate truncately bilobed, usually strongly produced posteriorly, with deep medium notch (Fig. 15); head usually with dark pigmentation extending to clypeus (Fig. 2); distribution widespread east of Rocky Mountains ephyre (Newman)

Preliminary Key to Mature Nymphs

- 1. Anterior ocellus present in mature nymphs; head and thorax usually with discernible dark and light pattern (Fig. 22)
 - drymo (Newman) Anterior ocellus absent; head and body light or dark brown, without distinct pattern on pronotum (Fig. 21) 2
- 2. Body yellowish brown; distribution widespread east of Rocky Mountains

Body dark brown; head with paler shading (Fig. 21); distribution southeastern U.S.

..... zwicki Kondratieff et al., n. sp.

Perlinella drymo (Newman) Fig. 1, 5, 8, 11, 14, 17, 18, 22–26

- Isogenus drymo Newman, 1839: 86. Type locality, Georgia (lectotype des. Kimmins 1970: 341). Type in BM(NH), not examined.
- Perla elongata Walsh, 1862: 366. Type locality, Rock Island, Illinois (syn. Needham & Claassen, 1925: 164). Type lost.
- Perla trivittata Banks, 1895: 313. Type locality, Michigan (syn. Needham and Claassen, 1925: 164). Type in MCZ (MCZ #11332), examined.
- Perlinella drymo: Illies, 1966: 348; Zwick, 1973: 279; Hitchcock, 1974: 163; Stewart et al., 1976: 381; Stark & Gaufin, 1976: 36; Szczytko & Stewart, 1977: 372; Stark & Gaufin, 1979: 420; Zeigler & Stewart, 1977: 497.

Male. Body length 10-19 mm; forewing length 10-19 mm. General color dark brown to brownish yellow, patterned with yellow. Head with dark ocellar triangle, a pale M-line, a dark triangular spot in front of clypeus, 3 ocelli; pronotum with a dark median stripe (sometimes reduced to a narrow streak) bordered by pale areas (Fig. 1). Abdomen often with middorsal dark stripe or dashes. Paraprocts sclerotized (Fig. 8), with hooklike apex recurved over posterior margins of tergum 10 (Fig. 5). Aedeagus with lateral sclerites expanded over distal half, serrated laterally (usually with 12-16 teeth) along expanded lobe, usually truncated apically and terminating in an acute point mesoapically (Fig. 11); base of lateral sclerites divergent. Spinules distributed over expanded membranous sac apically.

Female. Body length 11-21 mm; forewing length 11-21 mm. General color similar to male (Fig. 1). Subgenital plate bilobed (Fig. 14). Vagina with patches of golden brown spinulae. Spermathecum membranous, 6 accessory glands typically present.

Egg. Outline oval, often more narrowly rounded posteriorly (Fig. 17); surface often shallowly punctate; circular in cross section. Collar stalked, umbrellalike tuberculate anchor plate stalked (Fig. 18). Micropyles near posterior pole just above subequatorial ridge; orifices oval, canals distinct. Nymph. Claassen (1931) and Frison (1935) have described this species in detail. Body length 10–22 mm. General color yellowish brown to brown. Head and thorax usually patterned as in Fig. 22. Three ocelli present (mature nymphs). Subanal gills usually long, conspicuous, and consisting of several filaments (Fig. 25).

Type Material. Ricker (1938) examined the female types of *Isogenus drymo*, and Kimmins (1970) designated one of these females as the lectotype. Newman's (1839) original description, Ricker's redescription and sketches of the lectotype sent by S. Brooks (British Museum) clearly establish the identification of this species. The types of *Perla elongata* are presumed lost (Frison 1935), and from Walsh's (1862) original description (especially the prothorax) and geographical locality, we follow the Needham & Claassen (1925) and Frison (1935) synonymy. Our examination of the types of *Perla trivittata* Banks confirmed Needham & Claassen's (1925) synonymy.

Remarks. *P. drymo* is a species variable in size and color intensity; however, adults are easily recognized by the pronotal stripe, dark triangular spot on the clypeus, lateral aedeagal sclerites, and the short bilobed subgenital plate of the female with a broad median notch. Nymphs are recognized by the distinctive color pattern and the conspicuous long, branched subanal gills.

A few much paler and smaller individuals were examined from several southeastern states. Examination of the aedeagus, egg, and the few nymphs available revealed no consistent characters for separation from typical *P. drymo*. In series of specimens from Alabama and South Carolina, intergrades of color and size with this "southern form" were found. These paler and smaller forms appear to be merely ecophenotypes.

The only other sympatric perlid with habitus similar to that of adults and nymphs of *P. drymo* is *Hansonoperla appalachia* Nelson. However, the rectangular hammer of the male, the deeply punctate egg, the slightly produced subgenital plate of the female, the nymphal legs which have only a dorsal hair fringe, the right mandible with 5 teeth, and the subanal gills absent (Kirchner & Kondratieff 1985), distinguish *Hansonoperla* from all *Perlinella* species.

Material Examined. CANADA: Nova Scotia (5 $\delta\delta$, 2 \mathfrak{P} , 1 N); UNITED STATES: Alabama (22 $\delta\delta$, 16 \mathfrak{P}) Clarke Co., Mobile Co.; Arkansas (1 N) Craighead Co.; Florida (5 $\delta\delta$, 1 \mathfrak{P} , 14 N) Leon Co., Liberty Co., Okaloosa Co., Walton Co.; Georgia (3 $\delta\delta$, 4 \mathfrak{P}) Bryan Co., Chattooga Co., Evans Co.; Illinois (3 $\delta\delta$, 6 \mathfrak{P} , 24 N) Champaign Co., Pope Co., Rock Island Co., Union Co.; Indiana (22 $\delta\delta$, 30 \mathfrak{P} , 20 N) Crawford Co., Dubois Co., Daviess Co., Martin Co., Monroe Co., Perry Co., Tippecanoe Co.; Kansas (2 $\delta\delta$) Chase Co.; Maine (1 \mathfrak{P}) Piscataquis Co.; Maryland (1 \mathfrak{P}) Plummers Island; Michigan (3 \mathfrak{P}) Arenac Co., Baraga Co.; Minnesota (2 \mathfrak{P}) Washington Co.; Missouri (3 $\delta\delta$, 1 N) ChrisANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA



Fig. 11-13. Male aedeagus: (11) P. drymo, a, ventral view, b, laterial view; (12) P. ephyre, a, ventral view, b, lateral view; (13) P. zwicki, a, ventral view, b, lateral view.

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tian Co., Taney Co., Oregon Co.; Mississippi (1 å, 1 ?) Claiborne Co.; New York (2 ??, 2 N) Deer River; Ohio (1 ?) Athens Co.; Oklahoma (6 ??) Murray Co.; Pennsylvania (1 ?) Northampton Co.; South Carolina (5 $\delta\delta$, 4 ??, 3 N) Aiken Co.; Barnwell Co.; Saluda Co.; Texas (2 $\delta\delta$, 6 ??, 4 N) McLennon Co.; Virginia (5 $\delta\delta$, 9 ??, 2 N) Fairfax Co., Madison Co., Smyth Co.; West Virginia (4 ??) Hampshire Co.; Wisconsin (1 δ) Washburn Co.; District of Columbia (1 ?).

а

Perlinella ephyre (Newman) Fig. 2, 3, 6, 9, 12, 15, 19, 27

- Chloroperla ephyre Newman, 1839: 87. Type locality, Georgia. Holotype female. Type in BM(NH), not examined.
- Perla producta Walsh, 1862: 365. Type locality, Rock Island, Illinois (syn. Needham & Claassen, 1925: 161). Type in MCZ (#10130), examined.
- Perla fumipennis Walsh, 1862: 366. Type locality, Rock Island, Illinois (syn. Needham & Claassen, 1925: 161). Type lost. New Synonymy.

Atoperla consors Banks, 1948: 123. Type locality, Kingston, Rhode Island (syn. Ricker, 1963: i.1. in Illies, 1966: 325). Type in MCZ (#27722), examined.

b

- Atoperla ephyre: Illies, 1966: 325.
- Perlinella ephyre: Zwick, 1971: 319; Zwick, 1973: 279; Hitchcock, 1974: 164.

Male. Body length 7-11 mm; forewing length 7-10 mm. General color brown to dark brown. Head with 2 ocelli, occasionally with faint impression at location of anterior ocellus; dorsum of head with dark pigmentation usually extending to anterior margin of frons (Fig. 2), but sometimes limited to ocellar region (Fig. 3). Prothorax usually without middorsal stripe (Fig. 2), but if no dark clypeal coloration, prothorax often with pale middorsal streak (Fig. 3). Paraprocts sclerotized, sharply pointed apex (Fig. 9) recurved over posterior margin of tergum 10 (Fig. 6). Aedeagal sclerites expanded ventrally into rounded lobe in distal ¼, serrated laterally along expanded lobe, terminating in sharp downturned darker hook on inner margin, resulting in claw-hammer shape in lateral aspect



Fig. 14-16. Female terminalia, ventral view: (14) P. drymo, (15) P. ephyre, (16) P. zwicki.

(Fig. 12); spinules distributed over membranous sac apically.

Female. Body length 9–13 mm; forewing 10–14 mm. Color similar to that of male (Fig. 2 and 3). Subgenital plate bilobed, lobes usually obliquely truncated, produced toward midline posteriorly, forming deep membranous notch (Fig. 15). Vagina with patches of golden brown spinulae. Spermathecum membranous, typically with 4 short accessory glands.

Egg. Outline oval, circular in cross section, surface smooth (Fig. 19). Collar stalked, umbrellalike tuberculate anchor plate stalked; micropyles near posterior pole just above subequatorial ridge (Fig. 19).

Nymph. Claassen (1931) and Frison (1935) described the nymph in detail. Body length 6–13 mm. Body uniformly yellowish brown. Two ocelli. Subanal lobe gills small and inconspicuous (may be broken off).

Type Material. Ricker (1938) examined the holotype female and confirmed the usage proposed by Needham & Claassen (1925) and Frison (1935). We examined the types of *P. producta*, a female specimen determined by Walsh as *P. producta* Walsh, and types of *P. consors*, but the type of *P. fumipennis* is no longer in existence (Frison 1935).

In agreement with Needham & Claassen (1925) and Frison (1935), we consider P. fumipennis Walsh a synonym of P. ephyre, rather than Zwick's (1971) use of the name for "very dark specimens" from Florida. Walsh (1862) described Perla fumipennis from an adult male collected from Rock Island, Illinois. It differed from P. producta by "the anterior and posterior wings being distinctly and equally subfumose" and "head bright clay-yellow, the spot enclosing the ocelli black." Walsh (1863) further supplemented his original description with the following points: "head bright or obscure luteous [brownish-yellow]" and "wings equally tinged with fuscous [dark brown]." Conspicuously darker specimens matching Walsh's (1862, 1863) (fumose wings and unmarked frons) descriptions were examined from Illinois, Kansas, Missouri, South Carolina, and Virginia. The aedeagi of these specimens all have the sharp sclerotized hooks typical of all other P. ephyre populations examined throughout its geographical range. Frison (1935: 378) previously concluded: "upon the basis of comparisons of Illinois material with the original description and our intimate knowledge of the Illinois fauna which does not indicate the existence of another species closely allied to ephyre." Because the characters mentioned by Walsh in his original description fall



Fig. 17-20. Scanning electron photomicrographs of eggs: (17) P. drymo, $276 \times$; (18) P. drymo, egg collar, $680 \times$; (19) P. ephyre, $312 \times$; (20) P. zwicki, $230 \times$.

within the range of the color variation of this species, and on the basis of the above evidence, we synonymize *P. fumipennis* with *P. ephyre*.

Material Examined. Arkansas (1 ?) Washington Co.; Connecticut (3 88, 1 ??) Lorain Co., Tolland Co.; Florida (75 $\delta\delta$, 5 \mathfrak{P} , 1 N) Okaloosa Co.; Georgia (3 \mathfrak{P}) Burke Co.; Illinois (5 $\delta\delta$, 12 \mathfrak{P} , 4 N) Daviess Co., Ogle Co., Rock Island Co., Winnebago Co., Vermilion Co.; Indiana (2 $\delta\delta$, 2 \mathfrak{P} , 1 N) Dubois Co.; Kansas (1 δ) Cherokee Co.; Louisiana (1 \mathfrak{P} , 2N)



Fig. 21. Mature nymph habitus, P. zwicki.

Washington Parish; Maryland (2 ठठ, 19) Plummers Island; Massachusetts (51 ठठ, 87 99, 1 N) Hampshire Co.; Maine (1 9) Valley Grove; Minnesota (6 ठठ, 3 99) Hennepin Co.; Missouri (4 ठठ, 27 99) Dallas Co., McDonald Co., Taney Co.; New Jersey (1 ठ, 2 99) Gloucester Co., Ocean Co.; New York (3 99) Tompkins Co.; Ohio (1 ठ) Franklin Co.; Oklahoma (3 ठठ, 3 99) Ottawa Co., Sequoyah Co.; Pennsylvania (2 ठठ, 5 99) Cumberland Co.; South Carolina (5 ठठ, 34 99) Aiken Co.; Tennessee (3 ठठ, 3499) Marshall



Fig. 22-25. (22) Nymph head and pronotum, *P. drymo;* (23) nymphal mandibles, *P. drymo;* (24) nymphal right front leg, *P. drymo;* (25) nymph terminalia, dorsal view, *P. drymo.*

Co.; Virginia (5 88, 35 99, 1 N) Augusta Co., Giles Co., Montgomery Co., Rockingham Co., Scott Co.; West Virginia (1 8, 2 99, 1N) Greenbrier Co., Hampshire Co., Monroe Co.

Perlinella zwicki Kondratieff et al., n. sp.

- Perlinella fumipennis: Zwick, 1971: 318. (nec Walsh).
- Perlinella fumipennis: Zwick, 1973: 279 (nec Walsh); Hitchcock, 1974: 165; Stark & Gaufin, 1976: 36; Stark & Gaufin, 1979: 422.

Male. Body length 7–10 mm; forewing length 7–11 mm. General color usually dark brown to black. Head yellow except for dark pigmentation over ocellar region, 2 ocelli (Fig. 4). Prothorax without distinctive middorsal stripe (Fig. 4). Paraprocts sclerotized, with abrupt small hooklike apex (Fig. 10) curved over posterior margin of tergum 10 (Fig. 7). Aedeagus with lateral sclerites expanded in distal ¼, serrated (20–24 teeth) laterally along expanded lobe and terminating meso-apically in broad point (Fig. 13). Spinules generally distributed over membranous sac apically.

Female. Body length 8–12 mm; forewing length 8–12 mm. Color similar to that of male. Subgenital plate broadly bilobed, slightly produced with shallow notch (Fig. 16). Vagina with patches of golden brown spinulae. Spermathecum membranous, typically bearing 6 slender accessory glands apically.

Egg. Outline elongate-oval, circular in cross section. Collar stalked and umbrellalike anchor plate stalked, tubercules large, rounded (Fig. 20). Micropyles near posterior pole, above raised subequatorial ridge.

Nymph. Body length 8–10 mm. Uniformly dark brown. Head slightly wider than pronotum, with pale areas; eyes in line with lateral ocelli; anterior ocellus absent (Fig. 21). Mandibles each with 4 teeth; right mandible with teeth ¾ subparallel (as Fig. 23). Legs with a dorsal and a ventral fringe of long silky hairs (Fig. 21). Subanal lobe gills small, inconspicuous (may be broken off).

Type Material. HOLOTYPE 8, ALLOTYPE 9, South Carolina: Aiken Co., Upper Three Runs Creek, Savannah River Plant (SRP), Road C, 3 June 1984, B. C. Kondratieff. PARATYPES (all collected by B. C. Kondratieff except where indicated): Same as holotype, 1 8, 4 99. South Carolina: Aiken Co., Upper Three Runs Creek, SRP, Road C, 5 May 1984, 1 8; 27 May 1984, 3 99; 2 June 1984, 2 88, 16 99; same 5 June 1984, 2 88, 12 99; 7 July 1984, 6 99. Upper Three Runs Creek, 28 June 1977, D. Herlong and S. Prichard, 2 88, 2 99 (R.W.B.); Aiken Co., Tinker Creek, SRP Road B-1, 1 June 1977, D. Herlong and S. Prichard, 3 88, 57 99 (R.F.K.); 13 June 1977, 1 & 35 99 (R.W.B.); Barnwell Co., Four Mile Creek, SRP, Road A-7, 5 June 1985, 1 8, 1 9, Alabama: Escambia Co., Atmore, 5 June 1962, F. S. Blanton, 1 8, (R.W.B.); Perdido Creek, U.S. HWY 31, 3 June 1940, 2 99, L. Berner (I.N.H.S.). Florida: Okaloosa Co., Blackwater River, Bryant Bridge, 2.5 mi W of Holt, W. Peters et al., 1 & (R.W.B.); Shoal River, HWY 90, 26 May 1973. A. R. Gaufin (R.W.B.), 1 8, 1 9. Mississippi: Stone Co., 18-19 May 1978, 5 ôô, 3 99, P. P. Lago (U.M.).

The nymph is described from a reared male and 1 mature female nymph collected from Upper Three Runs Creek, South Carolina.

The holotype, allotype, and paratypes will be deposited in the U.S. National Museum of Natural History. Other paratypes will be deposited in the collections of the Department of Entomology, Virginia Polytechnic Institute and State University; Department of Biological Sciences, North Texas State University; Monte L. Bean Museum, Brigham Young University; R. F. Kirchner and B. P. Stark collections.

Etymology. The specific name honors Peter Zwick, who first recognized this species.

Remarks. This is the species which Zwick (1971) determined as being distinct from *P. ephyre*. Most of the specimens examined during the study were as described by Zwick (1971). However, in a series from South Carolina, there were relatively paler specimens (wings subhyaline, body color brown) whose aedeagi lacked the sharp downturned sclerotized hook; the subgenital plate was also typical of *P. zwicki* (Fig. 13 and 16). The color intensity of the body and wing pigmentation of this species varies as in all *Perlinella*.

Perlinella zwicki is a southeastern Coastal Plain stonefly, frequently inhabiting blackwater streams with shifting-sand substrata. Most of the adults were collected by light traps. Morse et al. (1980) described Upper Three Runs Creek, the type locality.

Drumming

The calls of male *P. drymo* (Fig. 26) and *P. ephyre* (Fig. 27) have identical patterns of 3 beats





Fig. 26 and 27. Male drumming calls: (26) P. drymo (after Stewart & Zeigler 1984b); (27) P. ephyre.

but different beat intervals. The second interval spacing is similar in both species $(38.0 \pm 3 \text{ msec})$ and 40.0 ± 0.1 msec, respectively), but the spacing of the first interval is substantially shorter in P. drymo (67.0 \pm 4 msec) than in P. ephyre (89.5 \pm 0.8 msec). We have also preliminary unpublished data for the related Hansonoperla appalachia, in which the male call also has 3 beats, but with the first and second intervals much longer, at about 80 and 850 msec, respectively, than in the Perlinella species. Therefore, specificity of the drumming behavior in these three species in two closely related genera lies only in the different beat intervals of male calls. Such similarity in number of beats has not been found in congeners of any other North American genus where behavior of several species is known (e.g., Taeniopteryx, Pteronarcys, Isoperla, Acroneuria). This suggests that degree of change or evolution of drumming varies among species in different genera, and that in Perlinella and Hansonoperla, change has been slower than morphological change.

It is not uncommon to collect all three species of *Perlinella* from the same stream in many areas of the southeastern United States. In these areas, *P. drymo* usually emerges from late February to early April, whereas both *P. ephyre* and *P. zwicki* usually overlap in emergence period (May to June). It will be interesting to find whether *P. zwicki*'s drumming reinforces the above hypothesis. Because *P. drymo* and *P. ephyre* have well separated emergence times, there appears to be little selective pressure for divergence of their signaling behavior.

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