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The Relationship Between North and Middle American *Stenonema* (Ephemeroptera: Heptageniidae)

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THE RELATIONSHIP BETWEEN NORTH AND MIDDLE AMERICAN *STENONEMA* (EPHEMEROPTERA: HEPTAGENIIDAE)[1]

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ABSTRACT

Stenonema integrum (McDunnough) is shown to be a junior synonym of *S. mexicanum* (Ulmer), n.syn. Subspecific status is delegated to Nearctic and Neotropical populations of this species as *S. m. integrum* and *S. m. mexicanum*, respectively. Newly studied materials from Costa Rica and Belize indicate that adults of the two subspecies may be differentiated by the presence of thoracic pleural stripes in *S. m. mexicanum*. Consistent differentiating larval characteristics are not known. A Pleistocene dispersal into Middle America and subsequent vicariance is hypothesized.

Stenonema is a strictly Western Hemispheric and essentially North American mayfly genus, with 16 currently recognized species north of Mexico (Bednarik and McCafferty 1979, McCafferty 1981). Disjunct geographic records of the genus from southern Mexico and Central America are based on specimens surrounded by some recent controversy regarding proper generic and specific identification. My current study of specimens from Costa Rica and Belize, previous comprehensive study of North American *Stenonema* (Bednarik and McCafferty 1979), and the recent study of Flowers and Peters (1981) now allow this taxonomic problem to be resolved and an explanation of historical biogeography to be hypothesized.

Edmunds et al. (1976) first reported a Neotropical distribution for *Stenonema* by simply stating that an undescribed species occurred in Central America. This report was evidently based on subimagos (Flowers and Peters 1981) that therefore could not be definitively identified to species. Allen and Cohen (1977) transferred *Heptagenia mexicana*, a species described by Ulmer (1920:70) from adults taken at Tabasco, Mexico, to *Stenonema* and assigned larvae from Guatemala (no number given) to *S. mexicana* (Ulmer) because of their distributional proximity to Ulmer's type locality.

Bednarik and McCafferty (1979) in the revision of *Stenonema* did not recognize the new combination of *S. mexicana* because Allen and Cohen had not studied the types of *H. mexicana*, and Ulmer's description was too incomplete to draw generic conclusions. Bednarik and McCafferty (1979) did study larvae they identified as *Stenonema integrum* (McDunnough) from "Guala" (possibly Guatemala) and Tamaulipos, Mexico; and they recognized Allen and Cohen's (1977) reported larvae from Guatemala as *S. integrum* because its description fit well within the larval concept of that species.

Flowers and Peters (1981) were able to study the type specimens of *H. mexicana* and confirm the new combination with *Stenonema*. Their evidence is convincing and I now concur with this nomenclatural move. (The adjectival specific epithet, however, must be changed to the neuter *mexicanum* to agree with its new genus group name. Previous authors have commonly mistaken *Stenonema* as being of feminine gender.) Flowers and Peters pointed out that the types, although in a dried state, "somewhat resemble" adults of *S. integrum*. The question at this point obviously becomes, are there one or two species of *Stenonema* represented in Middle America? Flowers and Peters apparently felt there could be two species since they attempted to provide a key to separate both adults and

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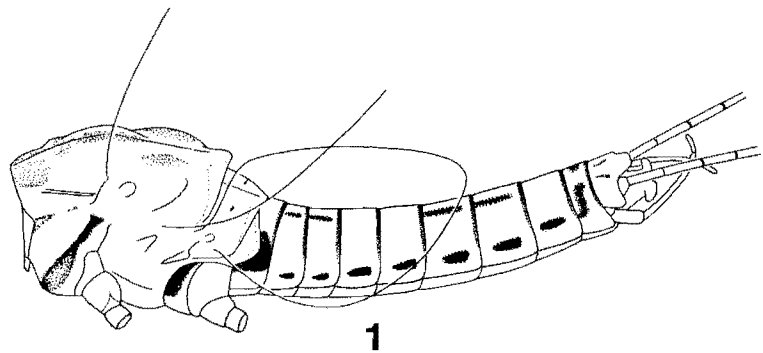
larvae of *S. integrum* and *S. mexicanum*. Their study of the larval stage included a single specimen that they reported from Panama. They indicated that *S. mexicanum* larvae would key to *S. integrum* in Bednarik and McCafferty (1979), but that lateral projections on abdominal segment 8 were subequal to projections on segment 9 in *S. mexicanum* and those on segment 8 were distinctly longer than those on 9 in *S. integrum*. Adults of *S. mexicanum* will also key to *S. integrum*, and Flowers and Peters separated them by characters of pleural maculation (round spiracular marks and diagonal thoracic streaks in *S. mexicanum* vs. diagonal spiracular marks and no thoracic streaks in *S. integrum*).

I have recently studied additional *Stenonema* from Central America as follows. Costa Rica: two male adults and four larvae, Guanacaste Province, Rio Tenorio at Finca La Pacifica, 2–11 Feb. 1969, W. P. McCafferty; Belize: one larva, Roaring Creek Riffle, 20 June 1974, V. Resh, one larva, Mopan Branch-Melchor, 27 June 1974, V. Resh. The adults from Costa Rica agree with the current concept of *S. integrum* (Bednarik and McCafferty 1979) in all respects. They also agree for the most part with the current concept of *S. mexicanum*, sensu Flowers and Peters (1981). The spiracular marks on the abdomen range from round to elongate-diagonal; however, the thorax does possess dark diagonal stripes on the pleura (Fig. 1).



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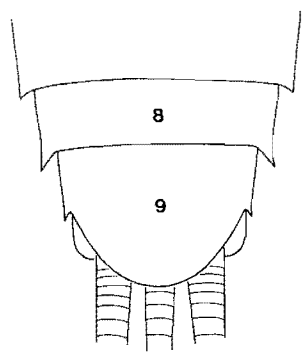

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Figs. 1–2. *Stenonema mexicanum mexicanum*. (1) Lateral body, adult male; (2) ventral posterior abdomen, larva.

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Larvae of *Stenonema* in general have provided the most reliable characters for defining species in the genus (Bednarik and McCafferty 1979). The larvae I collected in Costa Rica (almost certainly associated with the above adults from the same location) and those from Belize fit the description of *S. integrum* in North America and the description of *S. mexicanum* by Allen and Cohen (1977). In the identifying couplet provided by Flowers and Peters (1981), the larvae from Belize and three of the four Costa Rican larvae would clearly key to *S. integrum*, since projection 8 is distinctly longer than 9 (Fig. 2). The fourth larval specimen from Costa Rica is intermediate and would not clearly key to either species. Larvae of *S. integrum* from North America usually have a longer projection 8 but not always.

The above evidence indicates that the names *S. mexicanum* and *S. integrum* refer to the same species and are synonymous (*S. mexicanum* has chronological priority by four years). I have not found the thoracic pleural stripes that are present in the known Middle American adults in any North American adults. Because of this possible geographically related color variation and because of the disjunct distribution involved, it appears appropriate to assign subspecific status to the Nearctic and Neotropical populations. Thus, I designate the following nomenclatural revision: *Stenonema mexicanum* (Ulmer) = *Stenonema integrum* (McDunnough), NEW SYNONYM; composed of *Stenonema mexicanum mexicanum* (Ulmer), SENSU STRICTO (the Neotropical subspecies) and *Stenonema mexicanum integrum* (McDunnough), NEW STATUS (the Nearctic subspecies). The subspecies, besides being geographically definable, can provisionally be separated in the adult stage by the presence or absence of thoracic pleural stripes as discussed above, but morphological characteristics have not been found to consistently separate the larvae.

The designation of subspecies in *Stenonema* is not without precedent since both *S. mediopunctatum* (McDunnough) and *S. terminatum* (Walsh) have currently recognized subspecies (Bednarik and McCafferty 1979). The subspecies of *S. mexicanum* may be viewed as weakly defined in terms of subspecific criteria (Mayr 1965); however, until such time that the distribution of the species is shown to be continuous through Mexico, such a classification will remain convenient. It could further be argued that subspecies are useful descriptors of the geographic populations regardless of whether or not the thoracic character eventually proves to be variable in one or both elements.

A few comments regarding the possible origin and historical biogeography are apropos. The species is one of the three most derived members (Cluster III-B) of the genus, as evidenced by considerable relative apomorphy (Bednarik and McCafferty 1979). It is classified in the subgenus *Maccaffertium*, which evidently originated in the Appalachian area relatively recently (probably no older than early Pleistocene). An origin of early Pleistocene or more recent can be assumed for *S. mexicanum*.

Like several highly derived *Maccaffertium* species, *S. mexicanum* has become more widespread (relative to ancestral *Maccaffertium*) through the midwestern and southern United States, where warmer streams and rivers with less gradient prevail. It is most common in large, deep rivers, and is relatively pollution tolerant (Lewis 1974). (The Rio Tenorio in Costa Rica, a site of *S. m. mexicanum*, fits this general environmental description.) Among faunal categories for eastern North American Ephemeroptera species, as proposed by McCafferty and Provonsha (1978), *S. mexicanum* is a member of the second faunal category of widely adapted species ranging through most humid regions. Bednarik and McCafferty (1979) indicated that *S. m. integrum* ranges west to the hill country of central Texas, where this mountainous area may serve as a barrier to more westward dispersal. The extent of its westward limits in North America from eastern North Dakota south through Texas, however, strongly suggests that the species is limited by arid environments rather than elevational barriers. This presumed arid barrier may be generally applicable for the genus, with the exception of *S. terminatum*, which has isolated populations in the Northwest.

Given the above, particularly the relatively recent origin of *S. mexicanum*, paleoclimatic events rather than geomorphology (which has remained quite stable in the applicable areas for the past two million years) are the most essential considerations in attempting to explain the present Middle American disjunction. There are analogous

distributional patterns for other animals and plants that are explicable in terms of Pleistocene climatic events, and in many respects Middle America today has a distinct "Nearctic flavor" due to faunal and floral influxes from the north during the Pleistocene (Rich and Rich 1983).

It appears most probable that *S. mexicanum* dispersed southward along the gulf coastal region of eastern Mexico into Central America. The presence of more extensive drainages in eastern Mexico during wet, cooler periods of the Pleistocene, during the height of glaciation in North America, would have facilitated such dispersal. It was at this time also that cool periods in Middle America promoted southward dispersal of montane species into the tropics (Raven and Axelrod 1975). Later Pleistocene xeric conditions (much drier than present), especially in Mexico, would account for the recent vicariance of northern and southern *S. mexicanum*. The striped thoracic characteristic then evidently evolved or became isolated in the present Neotropical element. It would be most informative to determine the nature of the adult thoracic character in the Tamaulipos, Mexico population, which is presently known only from larvae.

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